

SELECTIVE MORTALITY OF JUVENILE SOCKEYE  
(Oncorhynchus nerka) IN BABINE LAKE DETERMINED  
FROM BODY-OTOLITH RELATIONSHIPS

by

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## ABSTRACT

The presence of differential growth and mortality was investigated among juvenile sockeye (Oncorhynchus nerka) in Babine Lake. Emergent fry were collected from the rivers and artificial spawning channels of the Fulton River and Pinkut Creek systems in May and early June of 1979. Juvenile samples were tow-netted from Babine Lake in July, August and September, and smolt samples were collected in May and June of the following year at the outlet of the Babine-Nilkitkwa lake system.

Fork lengths and the dimensions of sagitta otoliths were measured. Orthogonal polynomials fitted to Ln fork length versus Ln otolith size between the stages of fry emergence and smolt migration were sigmoid with  $r^2$  values of 0.97 to 0.98.

Significant stock differences were found among linear regressions of Ln fork length versus Ln total otolith length of emergent fry from Fulton River, Pinkut Creek and the three artificial spawning channels. Grouping of Fulton versus Pinkut or of river versus channel sources was not obvious. An average regression was calculated for general use with emergent fry from the main lake population.

Instantaneous growth rate of fry in early July was positively correlated with fork length. The distributions of emergent fork length back-calculated from juvenile and smolt samples indicated higher mortality rates among fry with smaller fork lengths at emergence. The timing of the selective mortality was between mid-August and smolt migration in the following spring.

The association of smaller initial body size with increased probability of parasitization by the cestode Eubothrium salvelini, subsequent slower growth and the effect on the size distribution of the year class is discussed.

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## INTRODUCTION

The purpose of this study was to ascertain, by means of back-calculation methods using periodic growth rings of sagitta otoliths, the effect of emergent body size on the subsequent survival of sockeye (Oncorhynchus nerka) fry in Babine Lake (fig.1).

Size selective mortality has been investigated in the early life history of several species of juvenile salmonids. Parker (1971) suggested that early marine mortality of juvenile pink (Oncorhynchus gorbuscha) and chum (Oncorhynchus keta) salmon due to predation by juvenile coho (Oncorhynchus kisutch) was biased towards the smaller individuals of the prey population. Healey (1982) has also demonstrated size selective mortality during the early marine life of juvenile chum salmon and considered predation a likely cause of mortality. Bilton et al. (1982) have found an optimum window for time and size of release for survival of coho smolts released from hatcheries and suspect food supply and predation to be major factors operating on juvenile survival. Releases of chinook (Oncorhynchus tshawytscha) and coho juveniles from hatcheries have also indicated that larger individuals survive at higher rates.

The early life history of juvenile sockeye salmon has been studied intensively, particularly in Cultus and Babine Lake,

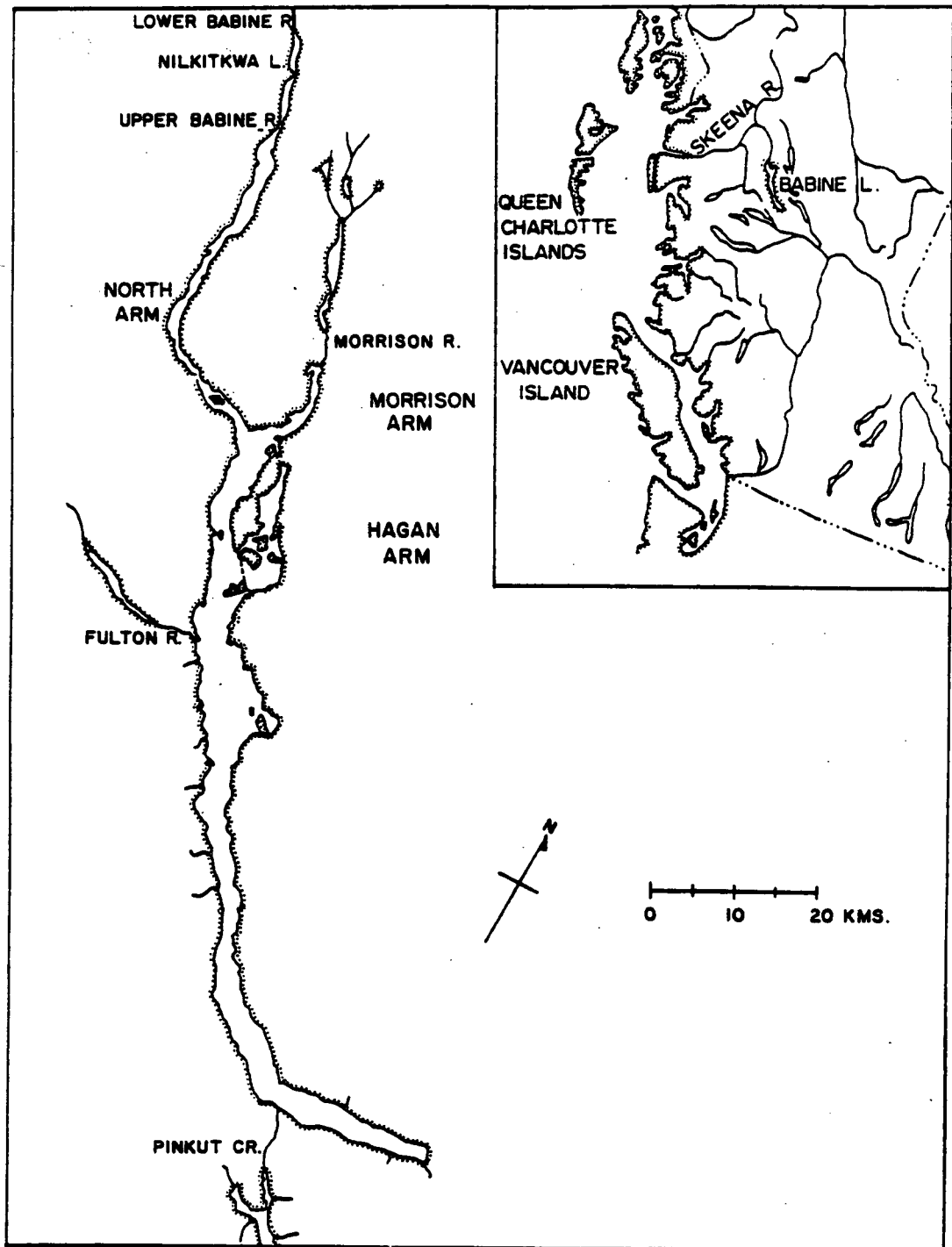


Figure 1 Map of Babine Lake and geographic location in British Columbia.

but most studies have provided only incidental information on size selective mortality. Releases of marked juveniles in Cultus Lake (Foerster, 1938) did not indicate any difference in survival between the wild population and the larger individuals of the reared marked groups. Evidence suggests however, that increased survival of the reared population to the migrant stage may have been offset by an increase in the incidence of residualism; individuals who remain in the lake and mature. Predation on juvenile sockeye has also been investigated in Cultus Lake (Ricker, 1941; Foerster and Ricker, 1941) but the studies did not investigate differential mortality within year classes, although increased predation on individuals because of their smaller size is hypothesized.

Boyce (unpublished) attempted to study the relationship between the initial size of fry at lake entry and subsequent survival in Babine lake by marking artificially reared sockeye fry but complications due to disease outbreaks are thought to have caused severe mortality among the test groups. The dependence of juvenile sockeye survival on the available food supply in Babine Lake is mentioned by Rankin (1977) but the mechanism of mortality was not investigated.

A fin-clipping study by McDonald (1969) on the 1965 brood at Babine Lake is perhaps the best source of information on differential mortality among juvenile sockeye.

Emergent fry from Fulton River and Fulton spawning channel no.1 were fin-clipped and recovered throughout their one year lake rearing period and as smolt when they migrated from Babine Lake. Although initial size differences between the two groups persisted to the smolt stage, survival rates of the two groups were similar.

Figure 2 shows that fry-to-smolt survival in Babine Lake is highly variable. It also suggests that at medium levels of fry production similar to that of the 1978 brood, additional fry production above the pre-Babine Development levels does not lead to increased smolt outputs. This type of response to increased fry numbers, a switching-over response by predators from

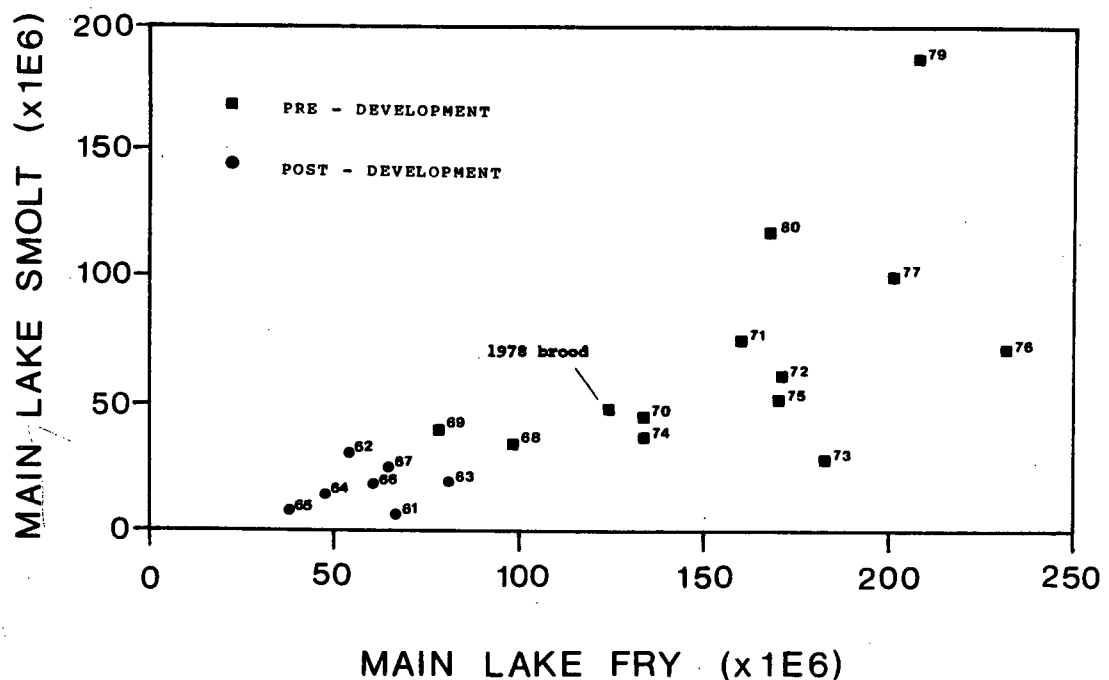


Figure 2 Sockeye smolt versus fry production in the Main Basin of Babine Lake (1961 to 1980 brood years).

alternate prey sources to increased numbers of sockeye fry has been discussed by Ricker (1941). Increased survival rates at higher fry production levels may also represent a swamping of the lake's predator population. The presence of depensatory mortality at medium levels of fry production.

In light of the investigations on other species, the presence of depensatory predation may suggest that differential mortality does occur on sockeye in Babine Lake at medium levels of fry production. The absence of size-dependent mortality among the 1965 brood, the lowest fry production year recorded, is not inconsistent with Ricker's theory of predators switching to alternate sources in the absence of adequate fry numbers.

The initial distributions of body size of the juvenile and smolt populations in this study were back-calculated from body-otolith relationships determined for the 1978 sockeye brood in Babine Lake. Back-calculation of body size from periodic rings in the hard parts of fish has been documented by several authors. Reviews of various back-calculation techniques are given by Hile (1970), Bagenal and Tesch (1978) and Carlander (1981). The use of daily growth rings in the sagitta otoliths of fish has become an established technique for size determination (Jonsson and Stenseth, 1977; Marshall and Parker, 1982; Neilson and Geen, 1982; Struhsaker and Uchiyama, 1979; Wild and Foreman, 1980; Wilson, 1981; Wilson and Larkin, 1982).



Babine Lake was selected as the study area for an investigation of differential mortality among juvenile sockeye. Babine is the largest lake of the Skeena River system which, as a whole, ranks second in British Columbia as a producer of sockeye salmon. Due to the importance of the Babine system (Shepard and Withler, 1958; Larkin and McDonald, 1968), enumeration facilities exist to provide accurate estimates of adult and smolt populations for management of the Babine stocks. It is also the site of the Babine Lake Development Project (Anon, 1965; Heskin, 1967; Ginetz, 1977; West, 1978) which produces most of the fry to the Babine system. Fry enumeration and quality monitoring programs carried out at the development project provided the opportunity to estimate the size distribution of the initial fry population in Babine Lake.

## GENERAL METHODS

### Fish Collection and Preservation

Samples were collected in the main basin and spawning tributaries of the Babine Lake system. For this study, the main basin region is considered to be the Babine Lake system minus the North Arm and Nilkitkwa Lake region. The 1978 brood was sampled in the spring of 1979 at emergence, during the summer lake residency period and the following spring at migration from the lake as one-year old (sub 2) smolts.

Stratified sampling of emergent fry was carried out at five fry sources; the Fulton River, Fulton spawning channel no.1, Fulton spawning channel no.2, Pinkut Creek and the Pinkut spawning channel. Fifty fry were taken randomly from each source near the peak of the nightly migration three times weekly, throughout the period of migration (May - early June). After length and weight measurements were taken, the fry were preserved in 70% ethanol for subsequent sampling of otoliths.

Estimates of the number of fry migrating nightly from each source were provided by the fry enumeration programs of the Department of Fisheries and Oceans. The nightly migration estimates were used to calculate weighted distributions from the stratified fry samples.

Juveniles were tow-netted from Babine Lake in mid-July, August and September of 1979. The net was a 2-meter square mouth mid-water trawl, designed by the Lake Fertilization Division of the Salmonid Enhancement Program (Gjernes, 1978). The net was towed in an S-pattern by a single boat from a distance of 60 meters and fished at a depth of 2 meters. A Furuno echo sounder was used as an aid to detect fish and select likely tow-netting sites.

At each juvenile sampling period, tow-netting was carried out throughout the main basin. Previous studies by McDonald (1969) had determined that fry initially migrate southward in the main basin, then distribute themselves randomly by mid-Summer; by fall they are concentrated in the north end of the basin. The tow-netting samples reflected this migration pattern but were inadequate to attempt to make inferences as to the population density except for the most general of areas. The period immediately after dusk was usually the most productive but tow-netting was often carried out from dusk to dawn. Catches were immediately placed in 70% ethanol for examination at a later date and the time and location noted. The representativeness of the tow samples is questionable. Even though samples were taken throughout the lake, the relatively small sampling effort involved may have been concentrated on the head or tail ends of migrating schools of juveniles and hence may be biased to smaller or larger individuals.

Smolt samples were collected throughout the smolt migration from the Babine system in late May and early June of 1980. Samples were taken at the Babine Lake smolt trap, located at the outlet of the Babine - Nilkitkwa Lake system where a smolt enumeration and sampling program is carried out annually by the Department of Fisheries and Oceans. Fifty smolts taken randomly from every second night's catch were preserved in 70% ethanol for examination at a later date. As with the fry sampling, nightly migration estimates from the smolt enumeration program were used to weight the samples to calculate the length distributions of the main lake smolt population.

#### Otolith Removal and Storage

Fork lengths were measured to the nearest 0.5 mm and both sagitta otoliths were removed from each sample. Two dissection methods were used to remove the otoliths, depending on the size of the fish. For those less than approximately 40 mm, the ventral dissection method described by Wilson (1981) was most suitable. The fish was held in an inverted position and the opercular plates removed, exposing the gill structures. The otoliths were then teased from the sacculus on the tip of a probe. For larger fish (40-90 mm) dissecting scissors were used to split the head along the longitudinal axis exposing on either side the sagittae which could be removed with forceps. This method was fast and very few otoliths were damaged. Otoliths

were cleaned of membranes and stored in the wells of MicroTest 3034 tissue culture plates. The Microtest plate conveniently holds 60 numbered wells which can be sealed by placing a square of 1/16 inch plexiglass over the wells and holding it in place with a piece of sponge between the plexiglass and the cover lid.

Elastic bands about the containers prevented accidental opening. Wet storage in 70% ethanol was used initially but later abandoned when it was realized that exposure to air was not destructive and did not involve periodic refilling to replace evaporative loss.

#### Otolith Preparation and Photographing

Left or right otoliths were randomly selected for observation and measurement. Two methods were used to prepare otoliths for photographing.

Fry otoliths were attached to microscope slides, sulcal surface upwards, with an acrylic adhesive (Crazy Glue) for convenience of handling and to maintain an even plane when grinding. When required, mounted otoliths could be removed by soaking in acetone which lifted the glue from the slide surface. For all but the emergent fry otoliths, removal of overburden was required and was done by hand, using a sintered glass plate and carborundum No. 50 aluminum oxide powder mixed with water as

a lapping compound. These methods were adequate but care and attention was needed to keep the grinding plane even.

A second and superior method developed by Neilson and Geen (1981) was used for the larger underyearling tow and smolt samples. Heat sensitive glue which could be removed by the application of small amounts of heat was used to mount the otoliths on glass slides. The slides were held in a jig supported on three legs which could be moved over the grinding surface. This maintained an even grinding plane and constant pressure on the grinding surface. Mylar grinding sheets of 25 and 0.5 micron grit were used in place of the carborundum powder.

Prior to photographing, mounted otoliths were cleared in glycerol. The time required for the appearance of rings and the period for which they are visible is related to otolith size. The small otoliths of fry produced maximum ring counts after approximately six hours of clearing, and would begin to over-clarify in another six. The clearing process could be reversed by soaking the mount in ethanol. The large smolt otoliths required several days to clear, but remained readable for a much longer period. Because of this variability, standard periods for clearing were used for optimum display of rings before photographing. Fry otoliths were cleared for 4 to 6 hours, juvenile samples cleared for 24 hours and smolt otoliths from 2 to 3 days.

Two camera-microscope systems were used. The majority of otoliths were photographed through an Olympus trinocular compound microscope with a Wild 35 mm automatic camera, using transmitted light and Kodak Panatomic-X ASA 32 film.

Approximately 20% of the fry samples were photographed with a Zeiss Ikon camera on a Zeiss compound microscope. Magnifications of 50x and 200x were used on the Olympus system and 64x and 160x were used on the Zeiss system. Negatives were mounted in 35 mm slide holders and projected with an Opus photographic enlarger (x10) or a 35 mm slide projector (x13.2).

#### Otolith Measurements

The sagitta otoliths of sockeye fry are species distinctive but their shape varies between individual fish, and the sagitta otoliths in a single fish may have different shapes. To standardize measurements between samples, a generalized otolith was used to define common reference points when measuring otolith dimensions. The terminology is that used by Pannella (1981).

The typical sagitta of a juvenile sockeye is laterally compressed and elliptical from the distal side (fig.3). The long axis is oriented along that of the fish with the rostrum anterior and postrostrum posterior. The convex proximal side is divided by the sulcus acusticus, a sulcal groove containing

nerve attachments. On the distal face the sulcal groove is seen terminating as inflections along the sagitta margin, antero-dorsally as the excisura and posteriorly as the postcaudal trough. Along the longitudinal axis of the otolith proper are three major nuclei referred to by some authors (Neilson and Geen, 1982) as primordia. Additional minor nuclei (2-5) may be found nearby, anteriorly along the longitudinal axis.

Radial bands caused by the intersection of domes of concentric growth are usually present. They provide cues to the position of the major nuclei and orientation of the vertical and horizontal axes. The bands, sometimes curved, are perpendicular to the rings of growth and converge toward their respective nuclei. The antero-dorsal band which intersects the excisura is particularly useful. It indicates the position of the excisura on sagittae displaying no inflection or double inflections on the margin.

For purposes of reference, the angle of radial measurement was defined in compass degrees as indicated in figure 3.

Various otolith measurements are described in the literature. Comparisons between studies are often difficult however, because relationships are species and age specific, and different otolith dimensions are used.



Jonsson and Stenseth (1979) compared three posterior radii of the sagitta otoliths of Brown Trout (Salmo trutta L.) with fish length. Selecting the radii which gave the best correlation, six regression models were examined including a fourth order polynomial equation. Campana (pers. comm.) has related the length of starry flounders (Platichthys stellatus) to three linear measurements of the otolith: total length, central nucleus to posterior edge and peripheral nucleus to posterior edge. Wild and Foreman (1980) considered three locations of otoliths of adult yellowfin tuna (Thunnus

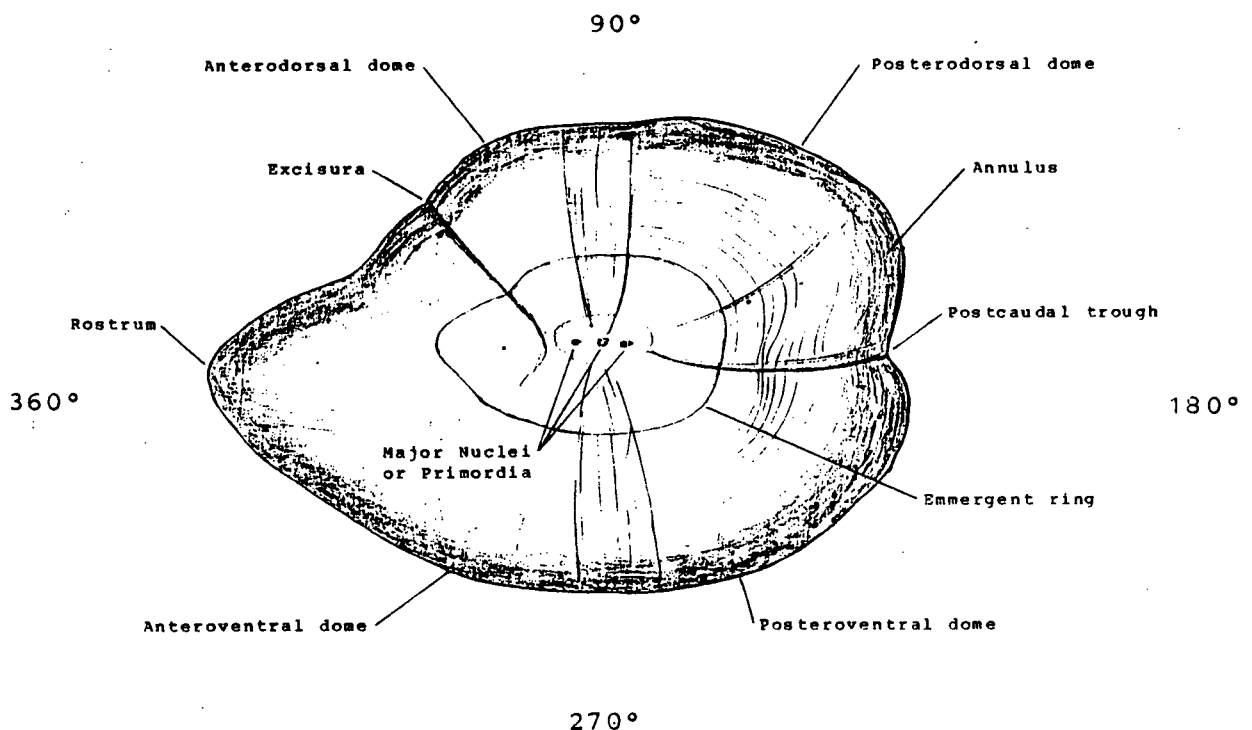


Figure 3 Distal face of a generalized sockeye smolt sagitta.

albacares) and skipjack tuna (Katsuwonus pelamis): the ventral edge below the primordium, the postrostrum and the rostrum. Neilson and Geen (1982) working on chinook (Oncorhynchus tshawytscha) juveniles have used the total length of the otolith minus the length of the rostrum. Wilson and Larkin (1982) working with sockeye (Oncorhynchus nerka) fry measured a dorsal posterior radius at  $40^\circ$  from the longitudinal axis. The axis was defined as the line passing from the tip of the rostrum through the posterior nucleus. Hence, a standard and widely accepted otolith measurement is not apparent.

In this study, five otolith dimensions were investigated. Radii were measured from the posterior major nucleus at  $140^\circ$ ,  $160^\circ$  and  $200^\circ$  (fig.4). The fourth dimension was total length, defined as the distance along the longitudinal axis, from the point perpendicular to the rostral inflection to the intersection of the axis and the posterior edge (fig.5). The intersection was used regardless of the presence of posterior lobes extending past the intersection, or whether the postcaudal trough was not centered on the axis. The fifth measurement was a simple estimate of cross sectional area. Sixteen radii at  $22.5^\circ$  intervals were measured from the center nucleus and the areas of the enclosed triangles summed. This measurement could be more easily made by planimetry or by digitizing on a computer graphics tablet. For the number of samples involved in this study however, the above method was adequate.

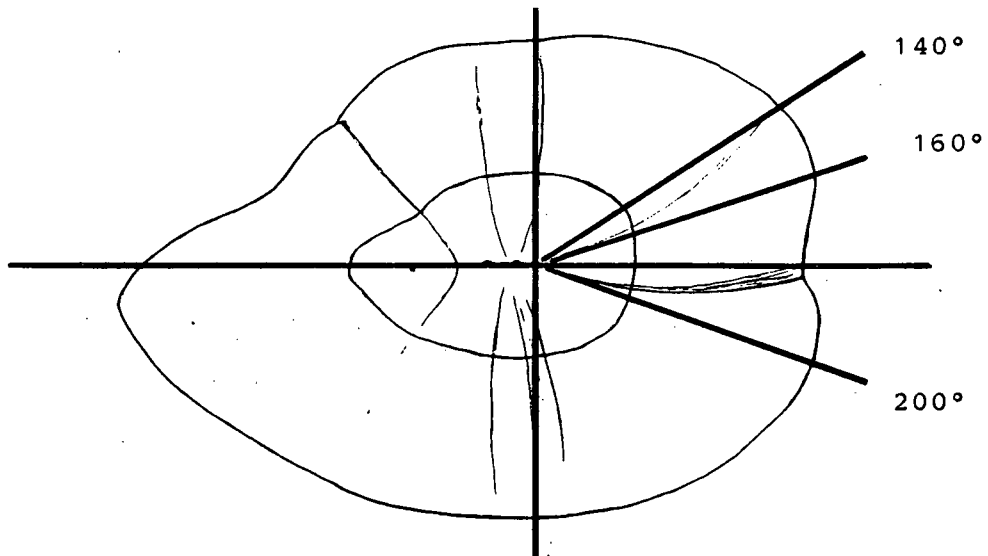


Figure 4 Posterior radii at 140°, 160° and 200° from an emigrating sockeye smolt.

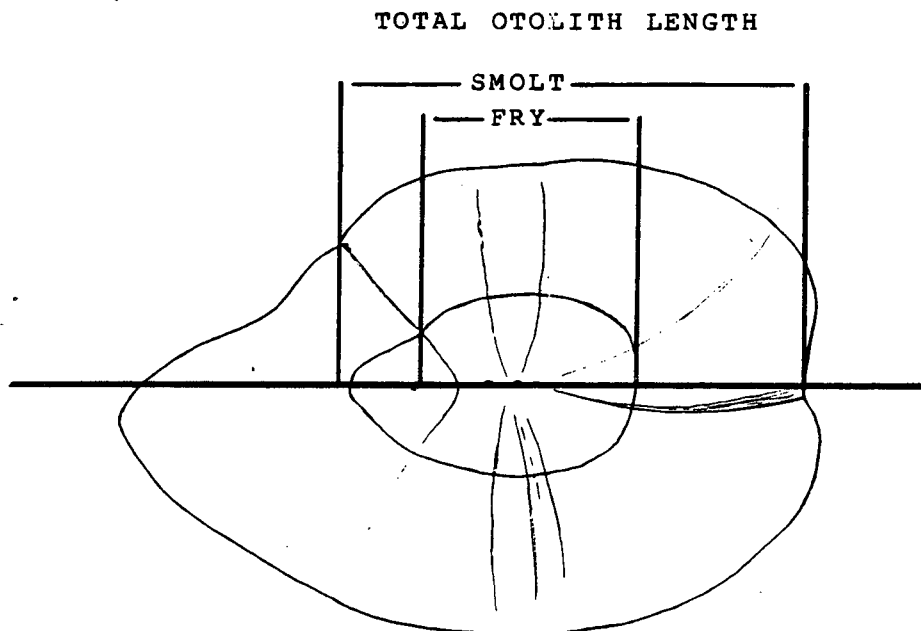


Figure 5 Total otolith length of sagitta from sockeye at emigrating smolt and emergent fry stages.

The fourth measurement is that described by Neilson and Geen (1981) as "total otolith length minus the rostrum". The radial measurement at 140° is similar to that used by Wilson and Larkin (1982), but the longitudinal axis from which it is measured is slightly different, being defined by the positions of the center nuclei and not the tip of the rostrum.

Dimensions of the enlarged images were measured to the nearest millimeter, giving an average precision of about 0.7 per cent. The second measurement error was in determining the exact position of the nuclei. Using a rigorous measurement procedure, the smallest radii could be estimated with 95 per cent confidence limits of 1 to 2 per cent, equivalent to about 2 to 3 microns, from three independent measurements.

The following procedure was used to define the position of nuclei and the sagitta axes prior to measuring total length and radii :

- A template with vertical and horizontal axes plus the three radii was positioned under the projected image with the vertical axis of the template passing through the center nucleus and aligned with the vertical axis of the otolith. Radial bands were useful in defining the exact position of the nucleus and the vertical axis.

- The template was then moved vertically to position its horizontal axis through the center nucleus, defining the longitudinal axis of the otolith.

- To measure posterior radii, the template was then moved laterally, positioning its origin at the posterior nucleus. In some otoliths this nucleus was not clearly defined. Posterior radial bands, converging towards the nucleus would then be used to estimate the exact location of the nucleus. Radial measurements were then read directly from scaled radii on the template.

- Total otolith length measurements were made by moving the template laterally, positioning the vertical axis through the rostral inflection and measuring from the template origin to the intersection of the longitudinal axis and the edge of the postrostrum. For otoliths displaying multiple or no rostral inflections, an equivalent point was estimated by the intersection of the dorso-anterior radial band and the otolith edge.

## FORK LENGTH VERSUS OTOLITH SIZE RELATIONSHIPS

Relationships from Fry Emergence to Smolt Migration

General polynomials were derived to describe the dependence of fork length on otolith size for sockeye between the stages of fry and smolt. Over the one year interval from fry to smolt, the form of the fork length versus otolith radii or total otolith length relationship is sigmoid. The data were transformed by natural logarithms and fitted with stepwise orthogonal polynomials, with rejection of successive powers set at a probability of 0.01. This resulted in 8th to 12th order equations with some coefficients approaching magnitudes of 10 to the fourteenth power. The regressions which were highly significant with  $R^2$  values ranging from 0.97 to 0.98 but were unwieldy because of the number of terms and rounding errors.

The high order of the polynomials was caused by the complexity of the relationships and the large sample sizes. Each relationship between fork length and otolith radius contained a total of 480 fry, juvenile and smolt samples. The total otolith length regression, including data from the investigation of stock specific relationships at emergence, used approximately 1200 samples. When the potential order or number of variables is large ( $K > 10$ ) and the number of data points is much larger (5K to 10K) then "overfitting" may occur (Draper and Smith, 1966).

Provided that all important terms have been included and the above conditions are met, additional terms will continue to be added as the residual mean square stabilizes around the true population variance.

Third order orthogonal polynomials fitted to the transformed data sets were significant with  $R^2$  values of approximately 0.94. They were discarded however, as plots of the residuals against otolith size showed periodic biases.

Sixth order orthogonal polynomials are presented as a compromise of manageable coefficients with suitably distributed residuals for predictive inference (table 1). The relationships are significant ( $p < .01$ ) with  $R^2$  values ranging from 0.97 to 0.98. The polynomials are shown fitted to the data in figure 6. The residuals plotted against radii and total length are shown in figure 7. The residuals are evidently normally distributed around the axis and show no marked non-random trends.

The complexity implied by these relationships may be a consequence of the range of life history phases that are included. Morphological changes are easily seen as newly emerged fry absorb the last of their yolk and begin active feeding in the lake. Marked changes in the body length to weight relationship take place between the times of lake entry and emigration.

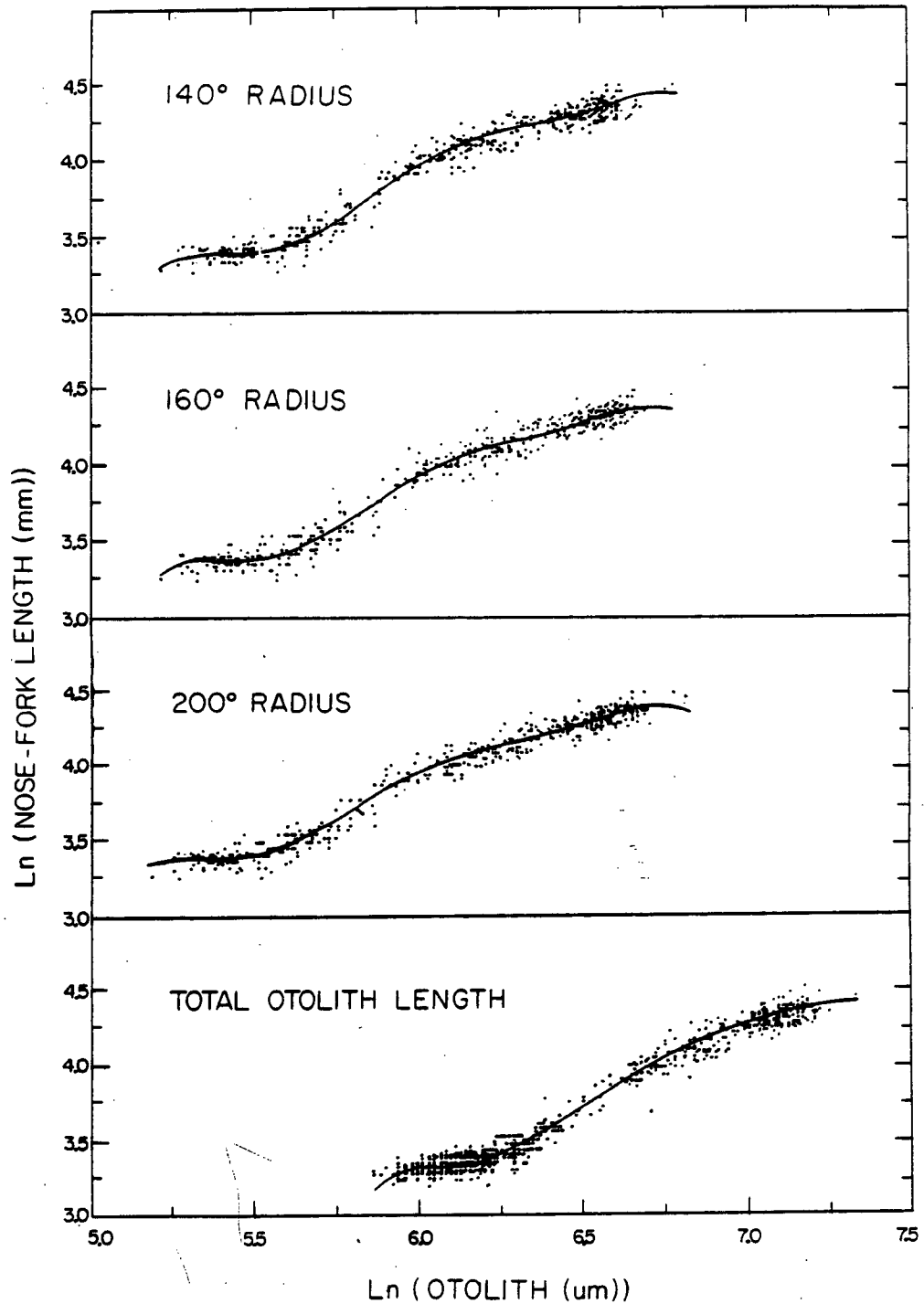


Figure 6 Relationships between  $\ln$  fork length versus  $\ln$  otolith radius at 140°, 160° and 200°, and  $\ln$  total otolith length for 1978 brood sockeye between the stages of emergent fry and emigrating smolts from the Babine Lake system, B.C.



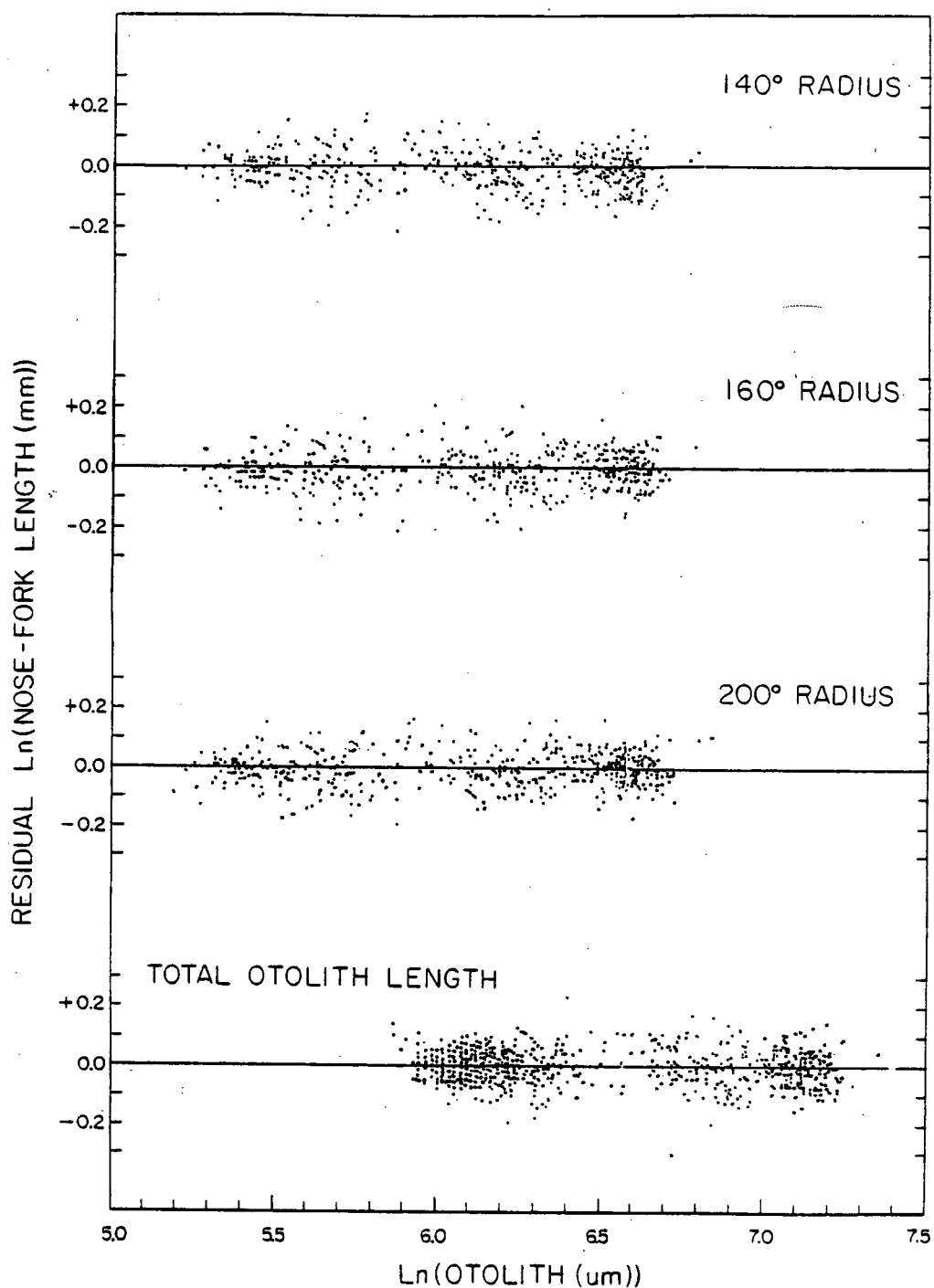


Figure 7 Residuals from 6th order orthogonal polynomial regressions of Ln nose-fork length on Ln otolith radius at 140°, 160° and 200°, and Ln total otolith length.

Allometric growth of the otolith also occurs as the posterior lobes extend. Asynchronous growth between the axial body length and otolith radius was not investigated but is another possible cause of the complexity of the body-otolith relationship.

Stock specific relationships may also have caused irregularities in the relationship. Juveniles were sampled throughout the main basin of the lake but the tow-netting

Table 1 Orthogonal polynomial coefficients for the relationships between Ln fork length (mm) versus Ln otolith radius (microns) at 140°, 160° and 200°, and Ln total otolith length (microns) for sockeye between the stages of emergent fry and emigrating sub-2 smolt from the 1978 brood, Babine Lake, BC.

Order	Radius 140°	Radius 160°	Radius 200°	Total Otolith length
constant	-193382.89	-210289.34	-129298.33	-311595.70
1	193507.04	210537.62	130508.35	280521.51
2	-80506.644	-87647.458	-54758.770	-105070.85
3	17825.906	19421.103	12225.728	20958.907
4	-2215.6265	-2415.8643	-1531.9535	-2348.3730
5	146.57611	159.96699	102.15684	140.14400
6	-4.0324030	-4.4051223	-2.8324161	-3.4801885
$R^2$	0.9740	0.9726	0.9751	0.9823
Sy*x	0.2496	0.2527	0.2466	0.2256

surveys were not extensive. Changes in tow-netting efficiency and non-random distributions of stocks within the lake could have biased the representation of individual stocks. Stock specific relationships were tested among the five sources of emergent fry (next section).

#### Relationships for Emergent Fry

The 6th order polynomials derived previously are suitable for use with juvenile sockeye in Babine Lake but for emergent fry and smolts, near the ends of the observed size ranges, they are not sufficiently descriptive of the variability. At emergence the body-otolith relationships are near linear. For this reason, simple linear regressions were investigated for emergent fry.

Sub-samples of 71 fry were selected randomly from the Fulton River and Pinkut Creek fry samples. Total otolith lengths, cross sectional area and posterior radii at 140°, 160° and 200° were transformed with natural logarithms and fitted by least squares predictive and geometric mean functional regressions (Ricker, 1973) shown in table 2.

All five otolith dimensions were significantly correlated with fork length but there were differences in the ease of measurement and the goodness of fit. Cross sectional area is

the best estimator of fork length for emergent sockeye fry ( $p < .001$ ) with an  $R^2$  value of 0.5190. However, it is the most tedious measurement to make and not all otoliths display the (required) continuous emergence check.

The posterior radii regressions were significant ( $p < .01$ ) but  $R^2$  values were only in the range of 0.11 to 0.14. For investigations such as growth rates over short periods, they are

Table 2 Predictive (P) and Functional (F) regressions of nose-fork length (mm) on five otolith dimensions (um); Cross Sectional Area (A); Total Otolith Length (T); and, Posterior Radii (R) at 140°, 160° and 200° for emergent sockeye fry from the Fulton River and Pinkut Creek systems.

Otolith Dimension	Regression			$R^2$	n
C.S. Area	$\text{Ln}(L) = 0.3220 + 0.2514 * \text{Ln}(A)$	(P)		0.5219*	71
C.S. Area	$\text{Ln}(L) = -0.8510 + 0.3480 * \text{Ln}(A)$	(F)			
Total Length	$\text{Ln}(L) = 1.6447 + 0.2842 * \text{Ln}(T)$	(P)		0.2501*	71
Total Length	$\text{Ln}(L) = -0.1001 + 0.5683 * \text{Ln}(T)$	(F)			
Radius 140°	$\text{Ln}(L) = 2.3081 + 0.1992 * \text{Ln}(R)$	(P)		0.1427*	71
Radius 140°	$\text{Ln}(L) = 0.5269 + 0.5274 * \text{Ln}(R)$	(F)			
Radius 160°	$\text{Ln}(L) = 2.4879 + 0.1659 * \text{Ln}(R)$	(P)		0.1140*	71
Radius 160°	$\text{Ln}(L) = 0.7194 + 0.4914 * \text{Ln}(R)$	(F)			
Radius 200°	$\text{Ln}(L) = 2.3730 + 0.1878 * \text{Ln}(R)$	(P)		0.1271*	69
Radius 200°	$\text{Ln}(L) = 0.5406 + 0.5267 * \text{Ln}(R)$	(F)			

\*  $P < .01$

practical relationships to use because specific growth rings need not be traced around the otolith.

Total otolith length was selected as the most suitable dimension for back-calculating size at emergence. The  $r^2$  value is only 0.2501 but it is useful for estimating the mean Ln fork length of distributions of samples. It is also an easy measurement to make as the emergence check is readable at the excisura and post-caudal groove on most otoliths.

#### Stock Differences at Emergence

Stock differences in the body-otolith relationships at emergence were tested using total otolith length at emergence. Approximately 25 fry were taken from each source, three times weekly, over the period of fry migration. Total otolith lengths of those samples not photographed were measured directly under a compound microscope with an ocular micrometer. Fork length and total otolith length data from each fry source were transformed with natural logarithms and fitted by least squares predictive regressions (fig.8).

Analysis of covariance revealed significant differences among the body-otolith relationships of the various fry sources. Scheffé's multiple range test indicated two homogeneous subsets among the covariate slopes and 4 subsets among the mean fork

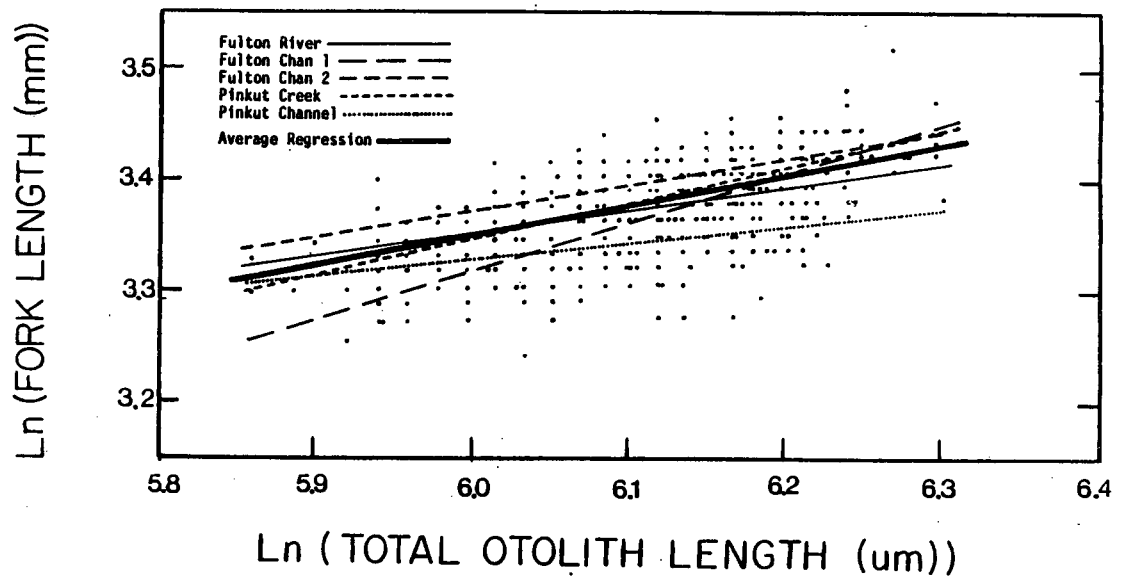


Figure 8 Predictive regressions of Ln fork length versus Ln total otolith length of emergent sockeye fry from the Fulton River and Pinkut Creek systems.

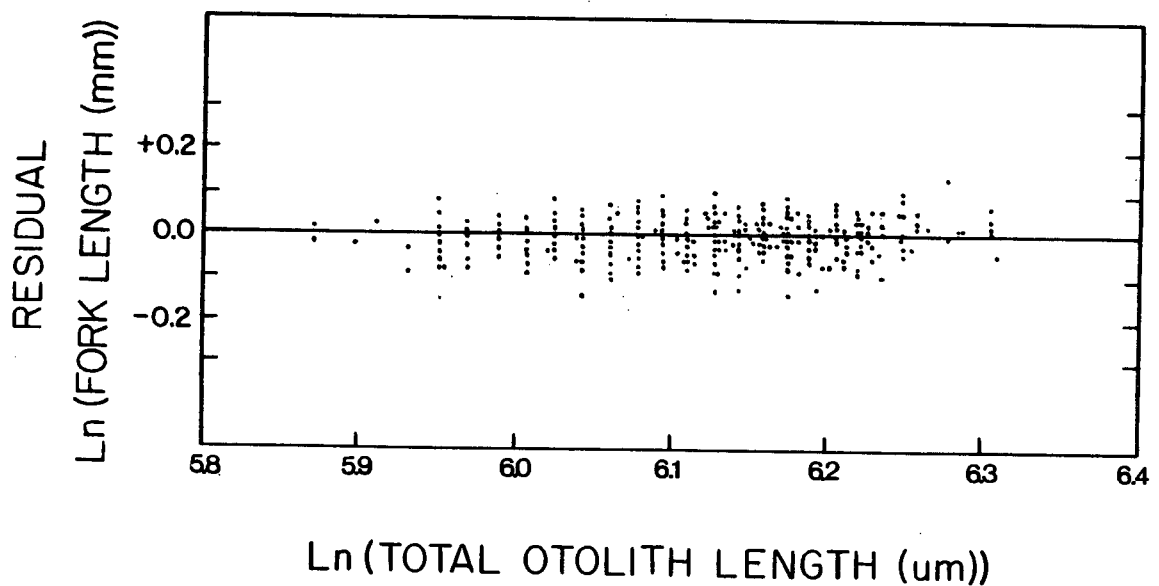


Figure 9 Residuals from the average predictive linear regression of Ln fork length versus Ln total otolith length, for emergent sockeye fry from the Fulton River and Pinkut Creek systems.

lengths (table 3). Grouping of channel versus river or Fulton versus Pinkut stocks was not obvious.

Stock differences among the body-otolith relationships at emergence exist. However, the means to identify juvenile and smolt samples by stock does not exist for this study, precluding the use of stock specific relationships. Therefore, an average regression was calculated for the total population of main basin fry.

Mean fork length and total otolith length at emergence of the main lake fry population were estimated by summing the means for each fry source, weighted by the relative 1978 brood fry production (eq.1). Fry production by those main lake stream spawners not studied was assumed to be equal to 233 fry per spawner and their body-otolith relationships assumed to be similar to those from Pinkut Creek (McDonald, pers. comm.).

The combined regression coefficient was a weighted mean of the different sources (eq.2). The combined intercept was calculated using weighted mean fork and total otolith lengths from each source (eq.3).

The resulting average regression was highly significant ( $p < .001$ , table 3). Residuals from the average regression, (fig.9) appeared to be homogeneous and normally distributed

Table 3 Predictive regressions for the relationship between Ln fork length and Ln total otolith length at five fry sources on the Babine Lake system. Slopes and means that are underlined are not significantly different from each other (Scheffes multiple range test,  $p=.05$ ). Average main lake regression is calculated from the combined fry sources, weighted by relative fry production.

Source	Pinkut Channel	Fulton River	Fulton Chan. 2	Pinkut Creek	Fulton Chan. 1	Main Lake
intercept	2.38017	1.86284	1.96408	1.26758	0.87015	1.52293
slope (b)	0.15850	0.24940	0.23500	0.34607	0.40849	0.30493
Sy*x	0.03523	0.03096	0.03152	0.03716	0.04537	0.03717
R <sup>2</sup>	0.0856	0.2265	0.1572	0.2633	0.3577	0.2152
t(b)	3.18	6.67	6.39	7.86	9.35	14.97
p(b=0)	<.01	<.001	<.001	<.001	<.001	<.001
n	110	154	221	175	159	819
Source	Pinkut Channel	Fulton Chan. 1	Pinkut Creek	Fulton River	Fulton Chan. 2	Main Lake
mean y	3.34716	3.37263	3.38095	3.39146	3.40723	3.38786
Sy	0.03667	0.05643	0.04318	0.03509	0.03426	0.04603



around the x-axis. Loss of precision by use of the average regression was not great: the mean increase in standard deviation from regression, weighted by relative fry production, was less than 2 per cent for each stock.

Back-calculation errors due to stock differences can be estimated from figure 8. The average regression under-estimates length at emergence in stocks for which the relationship lies above the average regression and over-estimates lengths for those below, by an amount equal to the difference between the

$$\bar{F}_c = \sum_k P_k * \bar{F}_k \quad \bar{T}_c = \sum_k P_k * \bar{T}_k \quad (\text{eq.1})$$

$$b_c = \frac{\sum_k \frac{P_k}{S_k} \sum_i (\bar{F}_{ik} - \bar{F}_c) (\bar{T}_{ik} - \bar{T}_c)}{\sum_k \frac{P_k}{S_k} \sum_i (\bar{T}_{ik} - \bar{T}_c)^2} \quad (\text{eq.2})$$

$$a_c = \bar{F}_c - b_c * \bar{T}_c \quad (\text{eq.3})$$

where  $P_k = N_k / \sum_k N_k$   
 $S_k = n_k / \sum_k n_k$   
 $N_k =$  Fry production at source k  
 $n_k =$  Fry samples at source k  
 $F_{ik} =$  Emergent fork length i at source k  
 $T_{ik} =$  Emergent total otolith length i at source k

predicted values at any given total otolith length. The largest errors are associated with the Pinkut spawning channel stock, which has the relationship most different from the average regression. However, the bias (overestimated fork lengths) is not critical when working with large random samples from the juvenile and smolt populations, because the channel produced only 7.5 per cent of the main lake fry population in 1979.

## GROWTH RATE IN BABINE LAKE

Fork lengths of the main lake fry population for the 1965 (McDonald, 1969) and the 1978 broods are plotted from emergence to smolt migration in figure 10. The growth pattern of the two broods is similar. In each, the range of fork lengths increased dramatically during the early lake rearing period, indicating a large variation among the growth rates of individual fry. Some of the July fry displayed high growth rates while others showed little increases over May sizes.

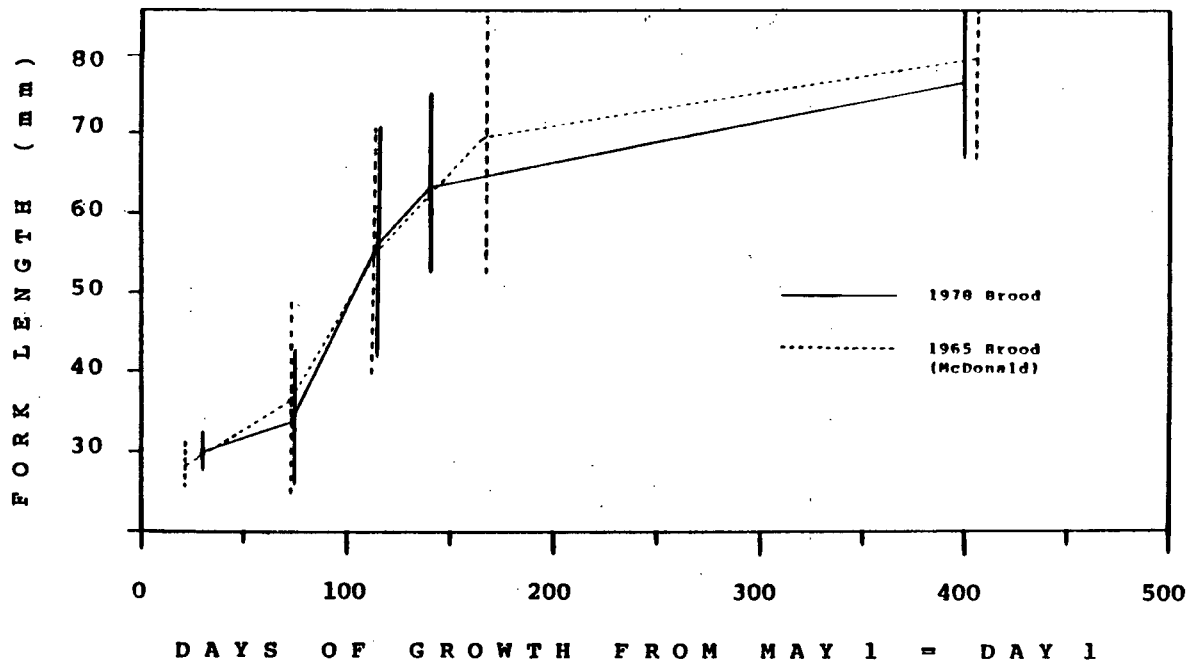


Figure 10 Mean fork lengths of 1978 and 1965 brood sockeye from fry emergence to smolt emigration from Babine Lake. Vertical bars represent two standard deviations on either side of the mean.

The mean fork length during the spring did not increase by comparison with the subsequent growth over the summer months. The range of fork lengths did not change greatly over the summer or winter periods.

McDonald found higher growth rates during the early lake rearing period among the larger Fulton river fry than among the smaller channel fry. The dependence of growth rate on fish size in early July was investigated for the 1978 brood. The daily growth rings in the otoliths of the July tow samples were measured over the 20 days prior to capture. Fork lengths were then back-calculated using the 6th order polynomial derived previously for 140° radii (eq.4). Deviations from the predictive function at the time of capture were assumed to be constant over the back-calculated period and estimated as  $\ln$  fork length at capture minus the predicted  $\ln$  fork length at capture.

$$\ln F_t = f(T_t) + \ln F_c - f(T_c) \quad (\text{eq.4})$$

where  $f(x)$  = 6th order polynomial of  $\ln$  fork length  
versus  $\ln$  total otolith length

$F_t$  = Fork length  $t$  days before capture

$F_c$  = Fork length at capture

$T_t$  = Total otolith length  $t$  days before capture

$T_c$  = Total otolith length at capture

A plot of the individual growth curves is confusing, therefore the samples were then grouped into 1 mm intervals of fork length at capture and the average back-calculated fork lengths plotted over time (fig.11).

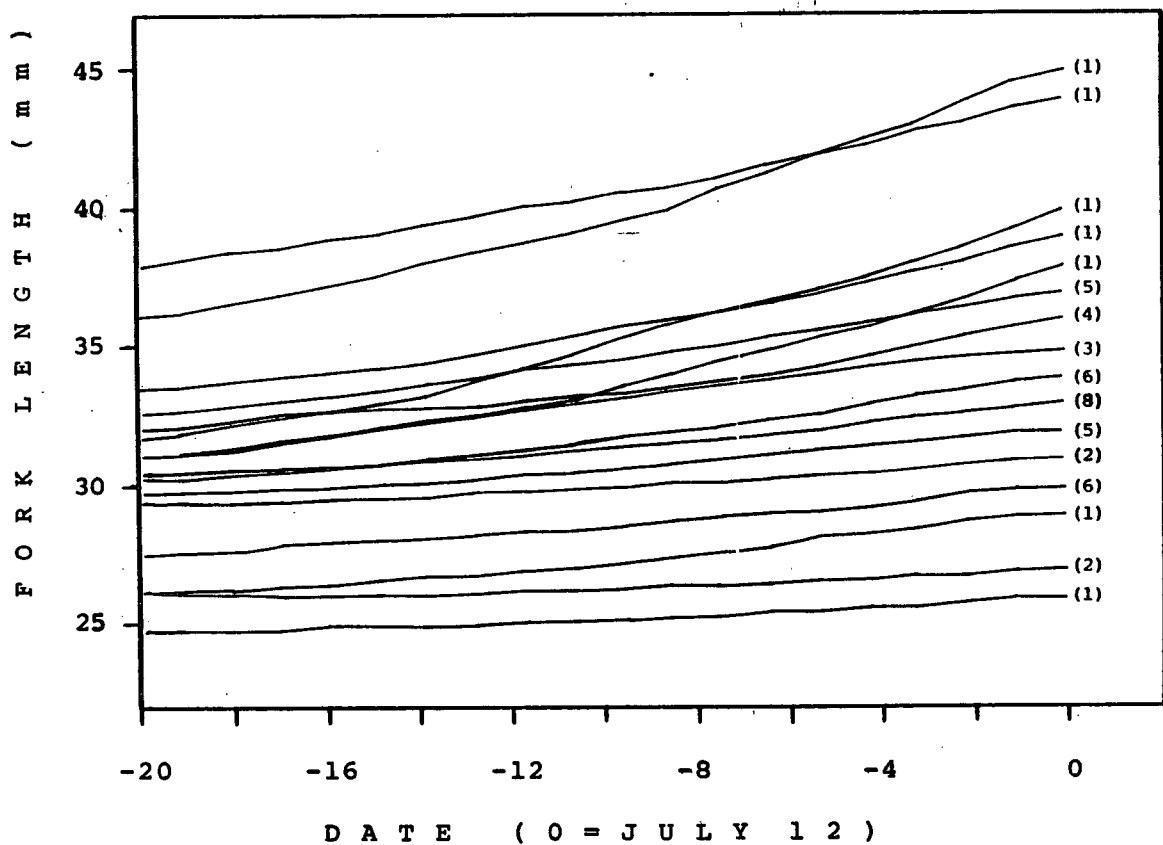


Figure 11 Mean fork lengths of the 1978 brood sockeye fry over the 20 day period prior to capture in July (central capture data = July 12). Numbers in brackets indicate sample size.

The orderly divergence of the growth curves and the low incidence of crossing-over suggests that a relationship exists between instantaneous growth rate and Ln fork length, and accordingly a maintenance of a hierarchy of lengths within the fry population. The correlation of instantaneous daily growth rates and Ln fork length in figure 12 was significant ( $r^2 = 0.6142$ ).

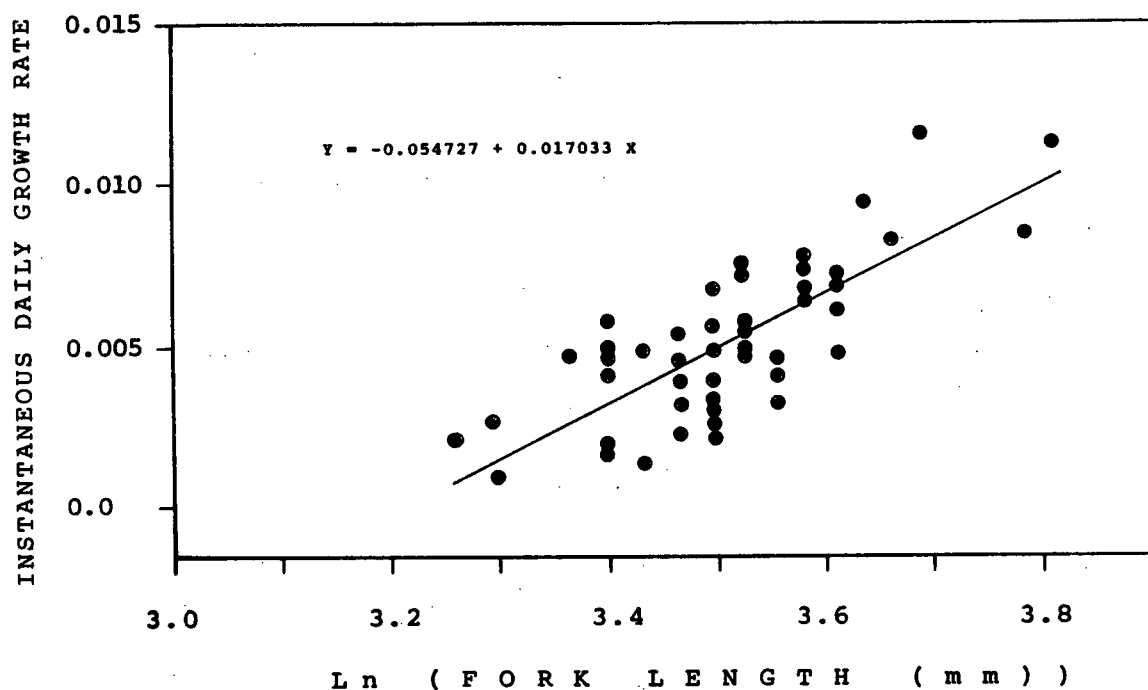


Figure 12 Instantaneous daily growth rates in relation to Ln fork length over the 20 days prior to capture (central capture date = July 12) of the 1978 brood sockeye in Babine Lake.

## SELECTIVE MORTALITY IN BABINE LAKE

Total Otolith Length at Emergence

Total otolith length at emergence ( $T_e$ ) was compared among the fry, juvenile and smolt populations. The distributions of total otolith length at emergence of the daily fry samples were weighted by the number of migrating fry (eq.5). The resulting distributions of each fry source were then summed to estimate the distribution of total otolith length at emergence of the main lake fry population (eq.6).

$$P(f)_{ijk} * N(f)_{jk} = T(f)_{ik} \quad (\text{eq.5})$$

where  $P(f)_{ijk}$  = Fraction of fry with  $T_i$  on day  $j$  at source  $k$

$N(f)_{jk}$  = Number of fry on day  $j$  at source  $k$

$T(f)_{ik}$  = Number of fry with  $T_i$  at source  $k$

$$\text{and } \sum_{ij} P(f)_{ijk} = 1$$

$T$  = Total otolith length at emergence

$$T(f)_i = \sum_k (T(f)_{ik} * W_k) \quad (\text{eq.6})$$

where  $T(f)_i$  = Number of fry with  $T_i$  in the lake

The daily smolt distributions of total otolith length at emergence were weighted by the daily migration numbers and summed to estimate the distribution of total otolith lengths at emergence of the main basin smolt population (eq.7). The observed distributions of the tow samples were not modified.

$$P(s)_{ij} * N(s)_j = T(s)_i \quad (\text{eq.7})$$

where  $P(s)_{ij}$  = Fraction of smolt with  $T_i$  on day  $j$

$N(s)_j$  = Number of smolts on day  $j$

$T(s)_i$  = Number of smolts with  $T_i$

and  $\sum_{ij} P(s)_{ij} = 1$

$T$  = Total otolith length at emergence

The resulting total otolith length distributions are given in table 4. An abundance of small otoliths observed in July did not appear in the estimated main lake fry population, and this was part of a trend for small otoliths to disappear between the fry and smolt stages (fig.13). Between the fry and smolt stages the relative frequency of otoliths with emergent total otolith lengths smaller than the mean of the fry population decreased from 47.5 to 11.3 per cent at the smolt stage (table 5).



Table 4 Distributions of total otolith length at emergence (Te) for weighted emergent fry samples, tow samples in July, August and September, and weighted smolt samples from the Babine smolt trap. All samples from the 1978 brood of the Babine Lake main basin sockeye.

Total Otolith Length at Emergence	Weighted Fry Samples		Observed Tows			Weighted Smolt Samples	
	no.	%	July	Aug	Sept	no.	%
330 - 345			1				
345 - 360	2	0.299	2	1			
360 - 375	3	0.398	3	1	2		
375 - 390	8	0.996	2	2	0		
390 - 405	19	2.291	12	2	2	2.6	1.532
405 - 420	41	4.980	5	3	1	1.4	0.817
420 - 435	68	8.366	6	2	5	2.3	1.328
435 - 450	178	21.912	7	7	2	4.6	2.656
450 - 465	126	15.538	9	12	6	15.8	9.193
465 - 480	159	19.622	5	6	9	15.8	9.193
480 - 495	130	16.036	4	4	10	32.2	18.692
495 - 510	46	5.677	2	5	7	46.9	27.273
510 - 525	22	2.689	4	2	6	29.7	17.262
525 - 540	6	0.697	1	2	9	14.4	8.376
540 - 555	4	0.498		2	3	5.3	3.064
555 - 570				1		1.0	0.613
mean	458.1		435.4	460.1	482.0	493.6	
variance	182.5		2130.8	1971.4	1772.4	904.8	
n	812		63	52	62	172	

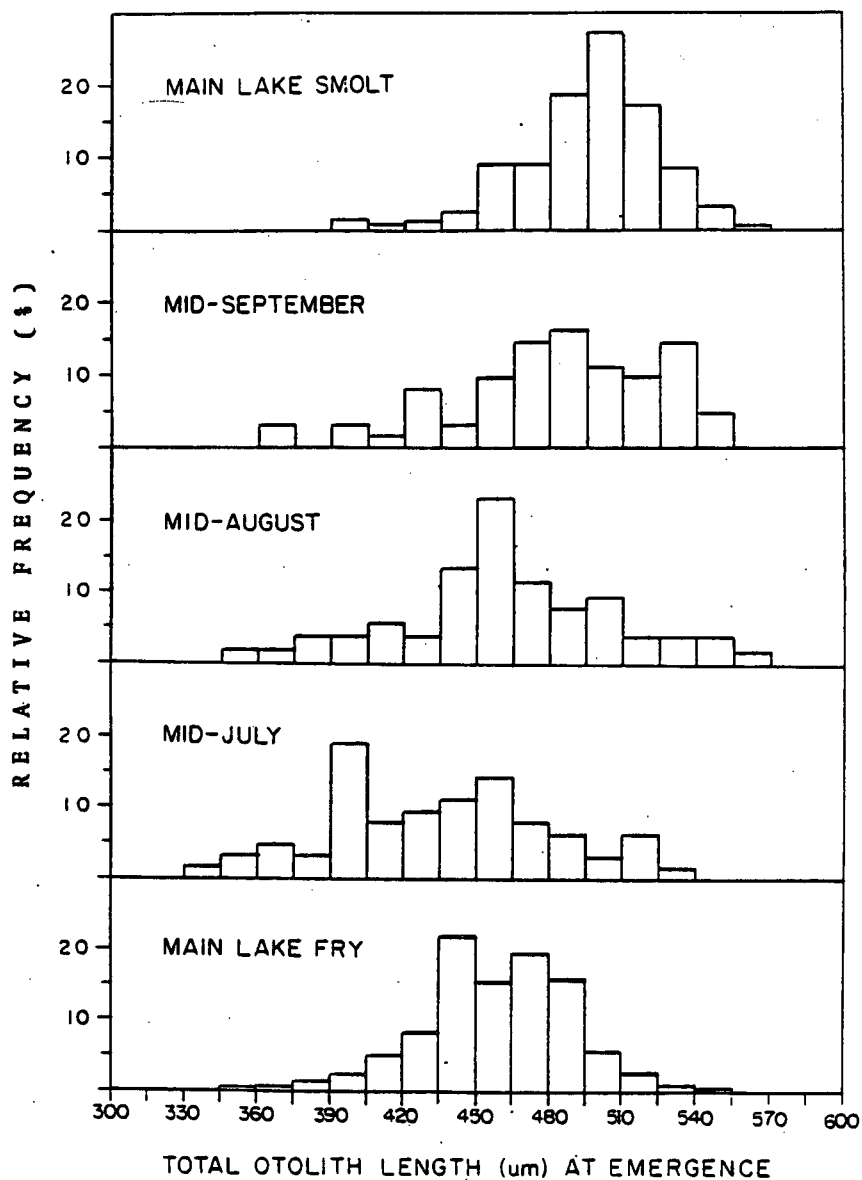


Figure 13 Histograms of the relative frequencies of total otolith length (um) at emergence during: fry emergence, mid-July, mid-August, mid-September and at the sub-2 smolt emigration, for the 1978 brood sockeye from the main basin of Babine Lake, B.C.

Fry survivals from the two halves of the emergent total otolith length distribution were 8.9 per cent and 63.6 per cent. The resulting shift in the mean total otolith length from 458.1 to 493.6 microns (fry to smolt) was highly significant ( $p < .001$ ).

Table 5 Fry to smolt survival (s) and instantaneous mortality rate (z) of sockeye fry with total otolith lengths at emergence above and below the mean of the 1978 brood.

Total Otolith Length at Emergence	Fry		Smolt		Surv. rate (s)	Instant. mortality rate (z)
	%	millions	%	millions		
< mean	47.5	59.4	11.3	5.3	0.089	2.4166
> mean	52.5	65.6	88.7	41.7	0.636	0.4531
total	100.0	125.0	100.0	47.0		

Ricker (1969) provides an index of the intensity of selection (r) which compares instantaneous mortality rates of the parts of a population within one probable error (0.6745s) on either side of the mean (eq.8). This is equivalent to the difference in average instantaneous mortality rates between the two halves of the distribution if the instantaneous mortality rate is a linear function of the independent variable. The calculated r of the total otolith length at emergence from fry to smolt stage is :

$$\begin{aligned}
 r &= 1.349 \, d / s && \text{(eq.8)} \\
 &= 1.349 * (458.1 - 493.6) / 13.51 \\
 &= -3.55 \quad \text{(index of relative selectivity)}
 \end{aligned}$$

The difference in the observed instantaneous mortality rates for the two halves of the distribution in table 5 was  $(0.4531 - 2.4166) = -1.9635$  which is different from the calculated value of  $-3.55$ . This discrepancy is due to the failure of the data to meet the underlying assumption of the index - a linear change in the instantaneous mortality rate ( $z$ ) over the range of the independent variable. The intensity of negative selection against the smaller otoliths is constant and intense up to 485 microns, slightly beyond the mean total otolith length (fig.14).

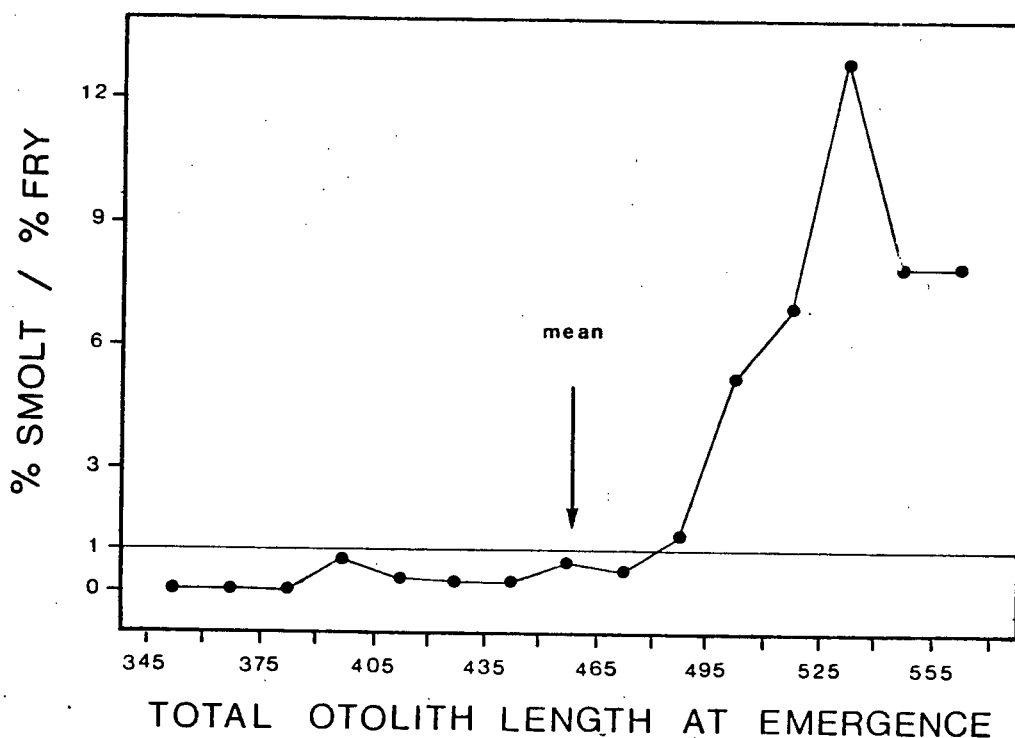


Figure 14 Selectivity of total otolith length at emergence ( $T_e$ ) between the fry and smolt stages (relative frequency of smolt  $T_e$  / relative frequency of fry  $T_e$ ).

### Fork Length at Emergence

Ln fork length at emergence (Fe) was back-calculated from Ln total otolith length. To prevent divergence near the ends of the observed range of Ln total otolith length, the 6th order polynomial was replaced with predictive linear regressions calculated from the data of each sampling period (table 6). Since the form of the relationship is linear at each sampling period, and the data are normally distributed around the regression lines, their use is valid for back-calculation purposes. The average regression calculated previously for the main lake fry population was used as the predictive function for Ln total otolith length at emergence and the appropriate regression for each life history stage (table 6) was used for the function of Ln fork length versus Ln total otolith length at capture.

Table 6 Predictive linear regressions of Ln fork length at capture (Fc) versus Ln total otolith length at capture (Tc) for the 1978 brood sockeye at: fry emergence, mid-July, mid-August, mid-September and at the sub-2 smolt emigration from the main basin of Babine Lake.

Life History Stage	Predictive Regression			
Fry Emergence	Ln(Fe)	=	1.39577 + 0.32543 *	Ln(Te)
mid-July	Ln(Fc)	=	-4.08384 + 1.19502 *	Ln(Tc)
mid-Aug	Ln(Fc)	=	-2.43577 + 0.95689 *	Ln(Tc)
mid-Sept	Ln(Fc)	=	-1.14453 + 0.76759 *	Ln(Tc)
Smolt	Ln(Fc)	=	0.77640 + 0.49969 *	Ln(Tc)

note : Fe = Fc and Te = Tc for emergent fry

Ln fork length at emergence (Fe) of the juvenile and smolt samples was back-calculated from Ln emergent total otolith length (eq.9). Deviations of each sample from the predictive regression at the time of capture were assumed to be constant over the range of Ln total otolith length, as in equation 4. A correction (C) was included to remove bias caused by selective mortality. Selection on smaller emergent fry causes the distribution of survivors and the resulting predictive regression to shift upwards, biasing the deviation of observed fork lengths from the predicted fork length downwards. Hence, the effect is similar to Lee's phenomena but in the opposite direction. Based on the assumption that deviations from the predictive relationship are constant for each sample, C can be estimated by the mean emergent fork length of the juvenile or

$$\text{Ln Fe} = f(\text{Te}) + \text{Ln Fc} - f(\text{Tc}) + C \quad (\text{eq.9})$$

where  $f(\text{Te})$  = Predicted Ln Fe from regression of  
Ln Fe versus Ln Te

$f(\text{Tc})$  = Predicted Ln Fc from regression of  
Ln Fc versus Ln Tc

Te = Total otolith length at emergence

Tc = Total otolith length at capture

Fe = Fork length at emergence

Fc = Fork length at capture

C = Mean Ln Fe of the fry population minus  
the mean Ln Fe of surviving population

smolt distribution minus the mean fork length of the initial fry population.

The distribution of emergent fork lengths for the main lake fry population was calculated from the stratified fry samples using the same procedure as for the distribution of total otolith lengths at emergence (eq.5 & 6). The stratified samples of smolts were pooled and grouped into 0.5 mm intervals of fork length at capture. The distribution of emergent fork lengths within each interval was then weighted by the distribution of fork lengths of the main lake smolts (eq.10). Back-calculated distributions of emergent fork length for the tow samples were not modified. The resulting distributions of fork length at emergence are given in table 7.

$$P(s)_{ij} * N(s)_j = Fe(s)_i \quad (\text{eq.10})$$

where  $P(s)_{ij}$  = Fraction of smolts with  $Fe_i$  and  $Fc_j$

$N(s)_j$  = Number of smolts with  $Fc_j$

$Fe(s)_i$  = Number of smolts with  $Fe_i$

$Fe$  = Fork length at emergence

$Fc$  = Fork length at capture

$$\text{and } \sum_{ij} P(s)_{ij} = 1$$

Table 7 Distributions of fork length (mm) at emergence for weighted emergent fry samples, observed tow samples in July, August and September, and weighted smolt samples from the Babine smolt trap. All samples are from the 1978 brood of the Babine Lake main basin sockeye. See text for weighting procedures.

Fork Length at Emergence (mm)	Weighted Fry		Observed Tows			Weighted smolts	
	no.	%	July	Aug	Sept	no.	%
23 - 24			1				
24 - 25			4	1			
25 - 26	2.4	0.3	2	2	1		
26 - 27	6.5	0.8	7	2	4	1.3	0.7
27 - 28	27.6	3.4	6	6	4	1.8	1.1
28 - 29	122.6	15.1	8	8	8	8.9	5.2
29 - 30	241.2	29.7	11	8	9	16.2	9.4
30 - 31	261.5	32.2	12	6	11	23.5	13.7
31 - 32	121.0	14.9	7	6	10	39.6	23.0
32 - 33	28.4	3.5	2	6	6	40.6	23.6
33 - 34	0.8	0.1	1	3	2	18.1	10.5
34 - 35				2	2	11.6	6.7
35 - 36				0	2	6.1	3.6
36 - 37				0	1	1.6	1.0
37 - 38				0	2		
38 - 39				1			
mean	29.55		28.84	30.00	30.62	31.08	
variance	1.352		5.025	6.586	7.013	3.841	
n	812		61	51	62	172	



Histograms of the relative frequencies of emergent fork lengths at each sampling period (fig.15) indicate selection against fry with small emergent fork lengths. The increase in mean fork length from 29.55 to 31.08 mm between the fry and smolt stages was significant ( $p < .001$ ). Fry to smolt survivals of the two halves of the distribution above and below the mean emergent fork length of the fry are 51.5 per cent and 12.7 per cent respectively (table 8).

Table 8 Fry to smolt survival (s) and instantaneous mortality rate (z) of sockeye fry with emergent fork lengths above and below the mean of the 1978 brood.

Fork Length at Emergence	Fry		Smolt		Surv. rate (s)	Instant. mortality rate (z)
	%	millions	%	millions		
< mean	35.9	44.8	12.2	5.7	0.127	2.0617
> mean	64.1	80.2	87.8	41.3	0.515	0.6637
total	100.0	125.0	100.0	47.0		

The observed difference between the instantaneous mortality rates of the two halves of the fork length distribution is  $(0.6637 - 2.0617) = -1.398$ . Ricker's calculated index between the two halves is -1.775. The agreement between the calculated and observed indices of selection on fork length is closer than for total otolith length. The lower observed index however, indicates that selection against fork length does not change linearly over the range of fork lengths and that the intensity

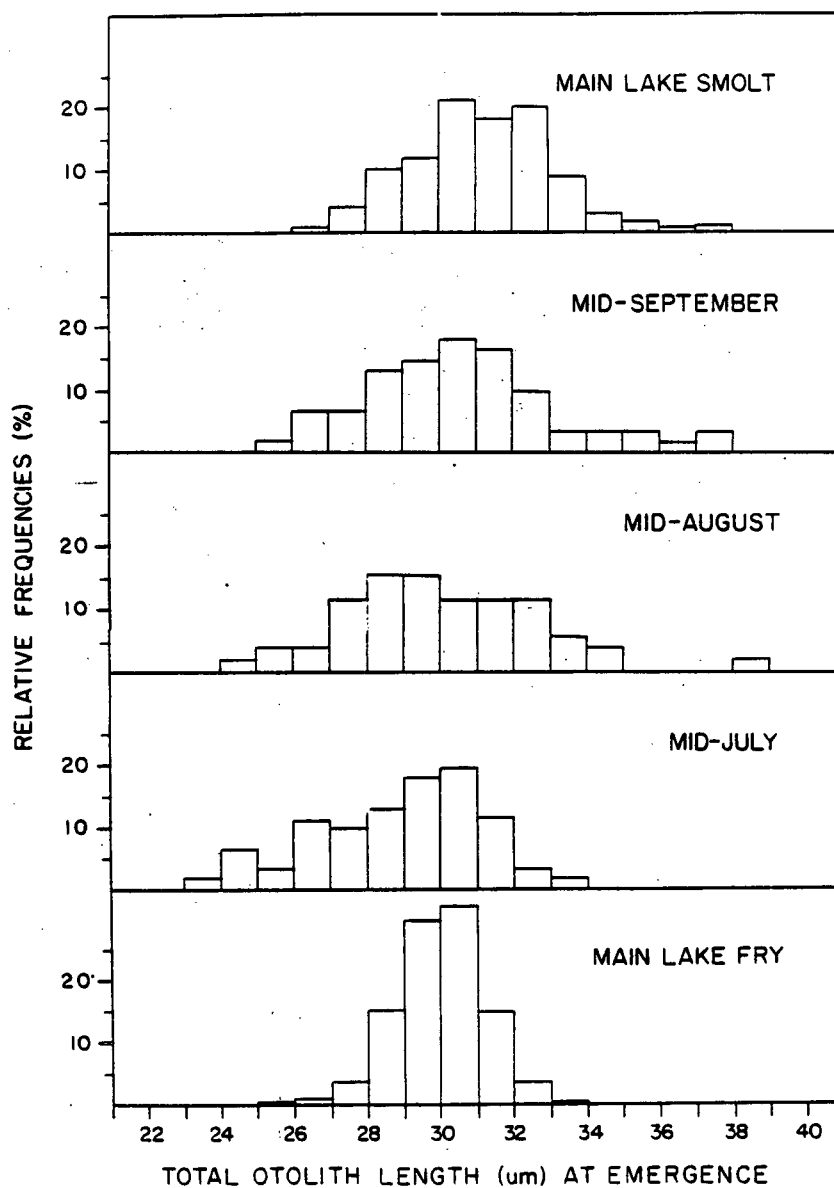


Figure 15 Histograms of the relative frequencies of fork lengths (mm) at emergence during: fry emergence, mid-July, mid-August, mid-September and at the sub-2 smolt emigration for the 1978 brood sockeye from the main basin of Babine Lake, B.C.

of selection remains high over the range of the smaller fork lengths.

Plotting an estimate of selectivity, the ratio of relative frequency of smolt to that of the fry population, over intervals of emergent total otolith length indicates that mortality is intense up to about 31 mm emergent fork length (fig.16).

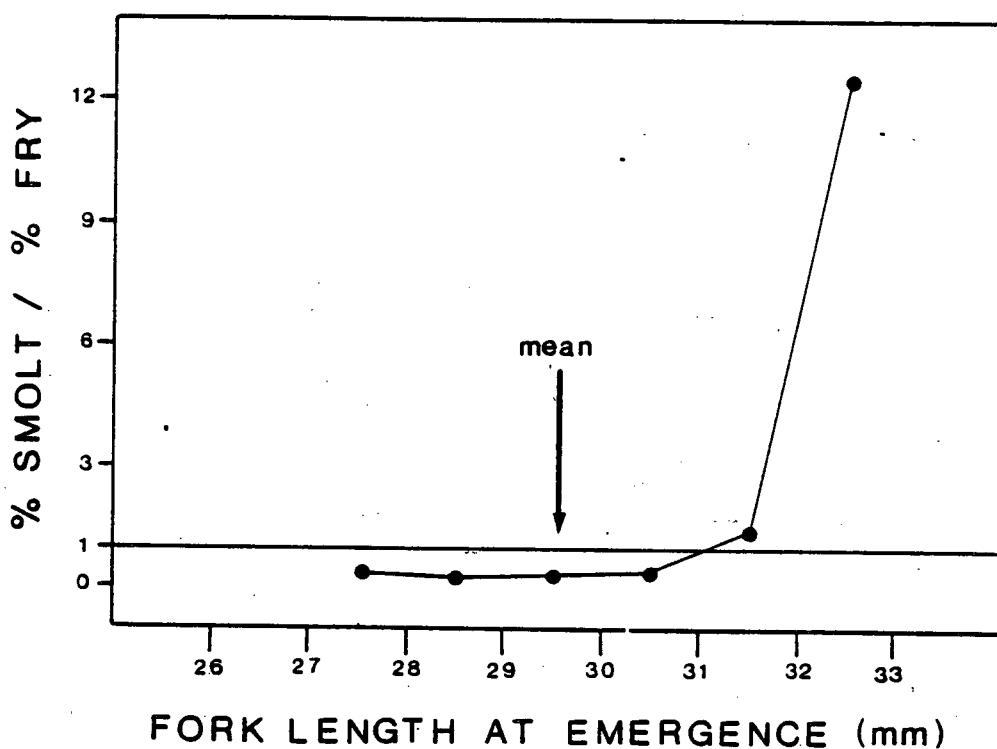


Figure 16 Selectivity of fork length at emergence (Fe) between the fry and smolt stages (Relative frequency of smolt Fe / relative frequency of fry Fe).

### Fork Length Versus Total Otolith Length

Distributions of Ln fork length at emergence versus Ln total otolith length at emergence are shown for each sampling period in figure 17. The trend of removal of fry with small total otolith lengths and small fork lengths at emergence is obvious. However, the correlation between body and otolith size raises the question : Is selection against the two parameters independent or does selection against one parameter cause an apparent selection against the other?

A simple exercise was carried out to test the independence of selection on each characteristic. Records of fry with total otolith lengths less than 480 microns were selectively removed. The mean total otolith length and fork length of the remaining samples were then weighted by the relative production of their respective fry sources. The mean total otolith length at emergence of the adjusted main lake fry population was similar to that of the smolt population, but only 48 per cent of the shift in mean fork length between the fry and smolt stages was accounted for (table 9). Performing the converse operation by removing all records of fry with fork lengths less than 30.5 mm shifted the mean fork length close to that of the smolts but caused only 43 per cent of the observed shift in total otolith length. Thus, it cannot be shown that selective mortality operates only on emergent fork length or on emergent total

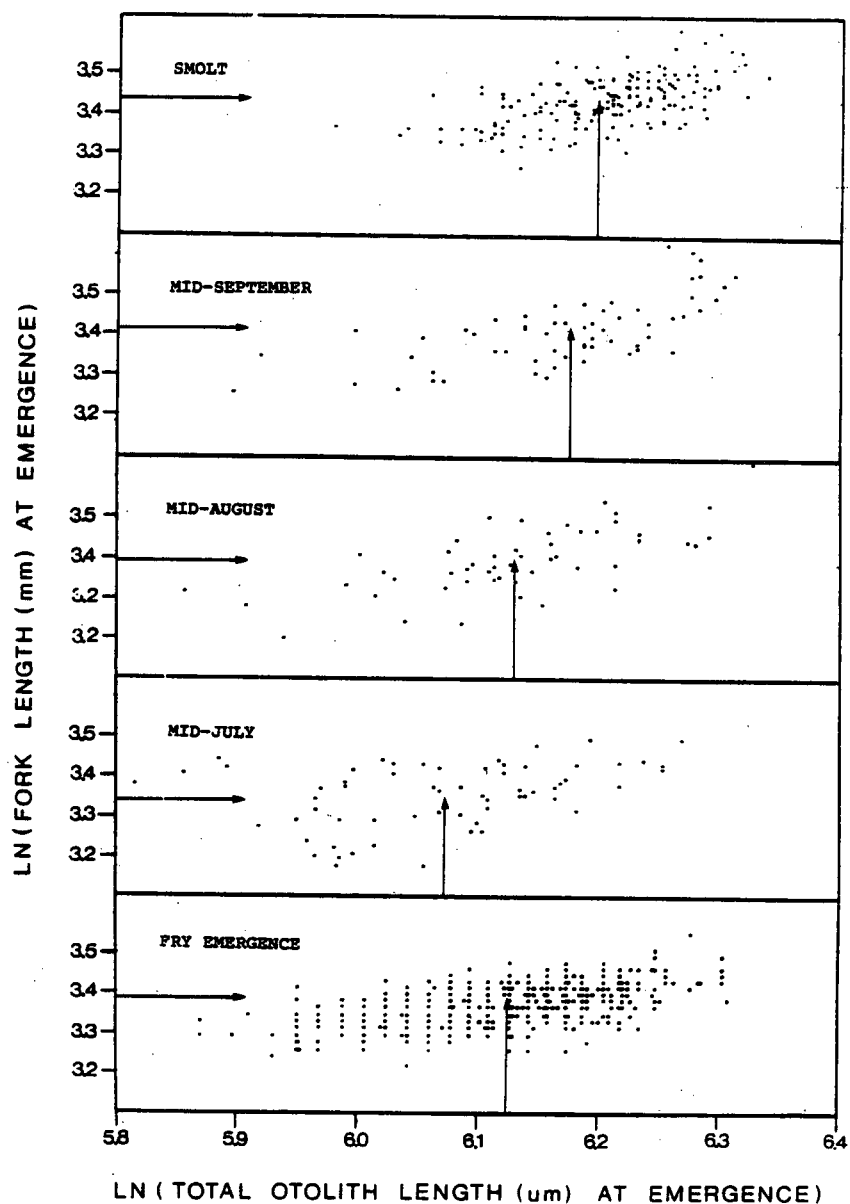


Figure 17 Ln fork length (mm) at emergence and Ln total otolith length ( $\mu\text{m}$ ) at emergence for sockeye at fry emergence, mid-July, mid-August, mid-September and at the sub-2 smolt emigration from the main basin of Babine Lake, B.C. Arrows indicate means.

otolith length.

Table 9 Mean fork length at emergence (Fe) and mean total otolith length at emergence (Te) of the fry and smolt populations, and of the fry population when samples with fork lengths less than 30.5 mm are removed and when samples with total otolith length less than 480 microns (um) are removed.

<u>Main Lake Population</u>	<u>Mean Te</u>	<u>Mean Fe</u>
Fry	29.55	458.1
Smolt	31.08	493.6
Fry with Te > 30.5 mm	30.92	473.4
Fry with Fe > 480 um	30.28	493.1

The bivariate means of the distributions are plotted in figure 18. The 95 per cent confidence ellipses have been calculated from principal components analysis (Sokal and Rohlf, 1969). Before examining the confidence regions, bias of the tow-net samples in mid-July, mid-August and mid-September should be considered. The position of the mid-July mean below that of the emergent fry population is questionable. Even if the size of the fry from the unstudied streams was overestimated by assuming that they were similar to those from Pinkut Creek, they are too few in numbers to cause the observed shift in mean size. Biased tow-net sampling is a more probable explanation of the

small size of the fry in the mid-July sample.

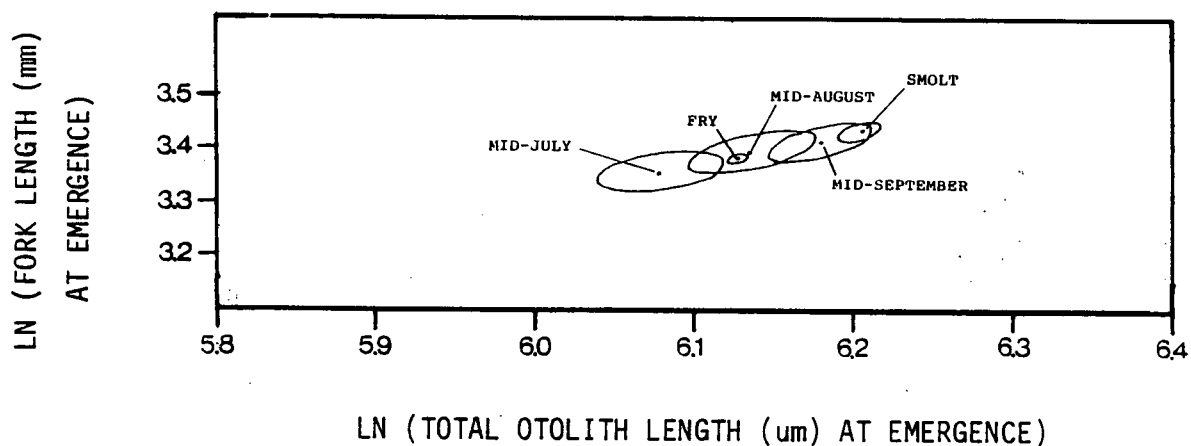


Figure 18 Bivariate means and 95 per cent confidence ellipses of the Ln fork length (mm) versus Ln total otolith length distributions at emergence.

The September mean is mid-way between the August and smolt samples, suggesting that the process of selective mortality is beginning by mid-August and is half completed by mid-September. However, considering the possible sampling bias of the tow samples, the only significant statement to be made is that the mid-August mean is similar to that of the fry sample and different from the smolt. The mid-September mean may be similar to the mean in August or at the smolt stage.

## GENERAL DISCUSSION

Differential growth and large increases in the variation of fish size were found in the early rearing period of juvenile sockeye in Babine Lake. Several authors have investigated growth in the first year of rearing and the effects of growth and competition on the eventual size of fish within a year class.

Discussions of growth disparity begin with an explanation of the variation in spawning time, genetic determination, egg size and environmental conditions and other such things which affect the initial variation in body size. The effects of cannibalism and predation on subsequent growth and variation are then mentioned and most involve ration and the relative ability of members within a year class to obtain prey. DeAngelis and Coutant (1979) found that under conditions of surplus ration, the average growth rate of smallmouth bass populations was constant with time and that the growth rate of individuals was independent of fish size and normally distributed. Under competitive conditions however, the advantage of large body size and the decreasing availability of ration to the smaller members of a population has been found to increase the variability of body size and to cause bimodal size distributions among largemouth bass (Shelton et. al., 1979; Timmons and Shelton, 1980; DeAngelis and Coutant, 1982).



In early July, the linear dependance of growth rate on fork length and the sudden increase in variability of fork length suggest that competition for rations may be taking place. Under these conditions growth depensation can occur, that is; larger individuals will grow faster than the smaller individuals, maintaining the relative heirarchy of sizes and increasing the variability of the length distribution.

The effect of ration on the body-otolith relationship may be a source of error in the study of early growth rates. Marshall and Parker (1982) found significant differences between the slopes of the relationships of starved and fed groups of juvenile sockeye of similar size. When starved for two to three weeks, the relationship of fork length to otolith diameter developed a lower slope. This was believed to be a short term reponse to starvation but the effect of ration on the relationship might affect results. Hence, if the correlation of July growth rate and fork length was brought about by competition for food and starved fish developed a body-otolith relationship with a lower slope, then the use of an average relationship would underestimate the growth of the fast growing fish and overestimate that of the small slow growing fish. This bias would only have made the disparity of the estimated growth rates conservative.

The effect of predation and starvation could bias the

estimate of fork lengths at emergence upwards. Constant removal of small individuals from the population by selective predation would cause the next individuals in turn to become "small" in relation to the population. Starvation via competition for a diminishing food supply would then result in smaller fish being associated with larger otoliths and causing subsequent over-estimation of emergent fork lengths of small fry in the back-calculation process.

Selective mortality was found to act against fry with small fork lengths and small total otolith lengths at Emergence. Selection based on otolith size is unlikely but the emergence checks were measured directly and distributions of emergent fork length from the smolt samples are unlikely to be biased unless the weighting process of the nightly samples was in error. Selection against otolith size is more likely related to some other body characteristic associated with otolith size such as endomorphy, the ratio of skeletal structure to body size. Fork length and otolith size are correlated but selection cannot be shown to act independently on one characteristic alone.

The timing of selective mortality of fry with small otoliths and of lesser length appears to be between mid-August and the following spring. One hypothesis of delayed mortality related to emergence characteristics and the early rearing period involves parasitization by the cestode *Eubothrium salvelini*.

The parasite is ingested along with copepods which are an intermediate host of the parasite and a major food item of juvenile sockeye. The parasite is then released into the intestine of the juvenile sockeye which is the terminal host, and lodges itself in the pyloric caeca, absorbing nutrients from food passing through the intestine of the sockeye and reducing the growth rate of the fish.

Boyce (1974) found that the Eubothrium infection rate declined sharply as the fork length of sockeye increased above the 36 to 45 mm range. Presumably, either the intestinal tract and pyloric caeca were by then too large to allow the parasite to wedge itself into the end of the pyloric caeca or the fry may have developed by then immune systems to cope with the parasite.

Boyce (1977) discusses how parasitization generally reduces the ability of infected juveniles to withstand stress but infected juveniles may survive to the smolt stage. Bilton and Robbins (1971) found that juvenile sockeye in November could withstand up to twenty weeks of starvation without undue mortality. However, parasitization could cause mortality among the infected juveniles by reducing the growth rate and allowing selective predation to remove the infected fish.

The implication for survival is that faster growing fry and fry which are initially larger would successfully compete for

rations, growing more quickly and spending less time in the size range susceptible to parasitization. Continued higher growth rates would then lead to increased survival through avoidance of predation mortality.

## SUMMARY

1. The relationship between fork length and otolith size, and differential growth and mortality based on emergent characteristics was investigated for the 1978 brood sockeye from the main basin of Babine Lake.
2. The body-otolith relationship of sockeye between the stages of fry emergence and smolt migration is a complex curve for which 6th order orthogonal polynomials were derived for back-calculating fork lengths from total otolith length and three otolith radii.
3. Linear regressions of fork length on five otolith dimensions were derived for emergent fry. In order of decreasing significance the otolith dimensions are: 1) cross sectional area; 2) total otolith length; 3) 140° radius; 4) 200° radius; and, 5) 160° radius.
4. Significant differences were found among the fork length versus total otolith length relationships of emergent fry from different sources. No grouping of Fulton versus Pinkut or river versus channel sources was obvious. A combined predictive regression was derived for use with the total main basin fry population.

5. The mean growth rate of the juvenile population is lower in the spring than in the summer. Individual July growth rates are positively correlated with fork length. This may be due to competition for prey and could cause growth depensation, explaining the increased variance of length in the early spring.
6. Selective mortality was found to operate against juveniles with small fork lengths as emergent fry and against juveniles with small emergent total otolith lengths or some characteristic associated with small otoliths.
7. The timing of selective mortality based on emergent characteristics appears to occur between mid-August and the next spring. A hypothesis of delayed mortality involving parasitization by the cestode Eubothrium salvelini and subsequent predation mortality of juvenile sockeye is discussed.

## LITERATURE CITED

- Anon. 1965. Proposed sockeye salmon development program for Babine Lake. Canada. Dept. of Fisheries. Pacific area and Fisheries Research Board. report 1965-9. 53 pp.
- Bagenal, T.B. and F.W. Tesch. 1978. Age and Growth, in: IBP Handbook no. 3, 3rd ed., Methods for assessment of fish production in fresh waters. T.B. Bagenal (ed.). pp. 101 - 136. Blackwell scientific publications, Oxford.
- Bilton, H.T. and G.L. Robbins. 1971. Response of young sockeye salmon (Oncorhynchus nerka) to prolonged periods of starvation. J. Fish. Res. Bd. Can. 28: 1757-1761.
- Boyce, N.P.J. 1974. Biology of Eubothrium salvelini (Cestoda: Pseudophyllidea) a parasite of juvenile sockeye salmon (Oncorhynchus nerka) of Babine Lake, British Columbia. J. Fish. Res. Board Can. 31: 1735-1742.
- Boyce, N.P.J. 1977. Effects of a parasite, Eubothrium salvelini (Cestoda: Pseudophyllidea), on the resistance of juvenile sockeye salmon (Oncorhynchus nerka), to zinc. J. Fish. Res. Board Can. 34: 706-709.
- Carlander, K.D. 1981. Caution on the use of the regression method of back-calculating lengths from scale measurements. Fisheries, 6: 2-4.
- DeAngelis, D.L. and C.C. Coutant. 1979. Growth rates and size distributions of first-year smallmouth bass populations: Some conclusions from experiments and a model. Trans. Am. Fish. Soc. 108: 137-141.
- DeAngelis, D.L. and C.C. Coutant. 1982. Genesis of bimodal size distributions in species cohorts. Trans. Am. Fish. Soc. 111: 384-388.
- Draper, N.R. and H. Smith. 1966. Applied Regression analysis. John Wiley & Son, Ltd., New York, N.Y.
- Foerster, R.E. 1938. Mortality trend among young sockeye salmon (Oncorhynchus nerka) during various stages of lake residence. J. Fish. Res. Board Can. 4: 184-191.
- Foerster, R.E. and W.E. Ricker. 1941. The effect of reduction of predaceous fish on survival of young sockeye salmon at Cultus Lake. J. Fish. Res. Board Can. 5: 315-336

- Ginetz, R.M.J. 1977. A review of the Babine Lake Development Project, 1961-1977. Canada Dept. of Fisheries. Technical Report Series No. t-77-6.
- Gjernes, T. 1979. A portable midwater trawling system for use in remote lakes. Can. Fish. Mar. Serv. Tech. rep. No. 888. 13 pp.
- Healey, M.C. 1982. Timing and relative intensity of size-selective mortality of juvenile chum salmon (Oncorhynchus keta) during early sea life. Can. J. Fish. Aquat. Sci. 39: 952-957.
- Heskin, B.A. 1967. The Babine Lake Development Program for sockeye salmon. Canada Dept. of Fisheries Rept. 3, 15pp.
- Hile, R. 1970. Body-scale relation and calculation of growth in fishes. Trans. Am. Fish. Soc. 99: 468-474.
- Jonsson, B. and N.C. Stenseth. 1977. A method for estimating fish length from otolith size. Drottningholm: Inst. of Freshwater Research, Report No.56, pp: 81-86.
- Larkin, P.A. and J.G. McDonald. 1968. Factors in the population biology of the sockeye salmon of the Skeena River. J. Anim. Ecol. 37:229-258.
- Marshall, S.L. and S.S. Parker. 1982. Pattern identification in the microstructure of sockeye salmon (Oncorhynchus nerka) otoliths. Can. J. Fish. Aquat. Sci. 39: 542-547.
- McDonald, J.G. 1969. Distribution, growth, and survival of sockeye fry (Oncorhynchus nerka) produced in natural and artificial stream environments. J. Fish. Res. Board Can. 26: 229-267.
- Neilson, J.D. and G.H. Geen. 1982. Otoliths of chinook salmon (Oncorhynchus tshawytscha): Daily growth increments and factors influencing their production. Can. J. Fish. Aquat. Sci. 39: 1340-1347.
- Pannella, G. 1980. Growth patterns in fish sagittae, p.519-560. in (D.C. Rhoads and R.A. Lutz eds.) Skeletal growth of aquatic organisms: biological records of environmental change. Plenum Press, New York, NY.
- Parker, R.R. 1971. Size selective predation among juvenile salmonid fishes in a British Columbia inlet. J. Fish. Res. Board Can. 28: 1503-1510.



- Rankin, D.P. 1977. Increased predation by juvenile sockeye salmon (Oncorhynchus nerka Walbaum) relative to changes in macrozooplankton abundance in Babine Lake, British Columbia. MSc. Thesis. Dept. of Zoology. Univ. of B.C. 101 pp.
- Ricker, W.E. 1941. The consumption of young sockeye salmon by predaceous fish. J. Fish. Res. Board Can. 5: 293-313.
- Ricker, W.E. 1969. Effects of size-selective mortality and sampling bias on estimates of growth, mortality, production, and yield. J. Fish. Res. Board Can. 26: 479-541.
- Ricker, W.E. 1973. Linear regressions in fishery research. J. Fish. Res. Board Can. 30: 409-434.
- Shelton, W.L., W.D. Davies, T.A. King and T.J. Timmons. 1979. Variation in the growth of the initial year class of largemouth bass in West Point reservoir, Alabama and Georgia. Trans. Am. Fish. Soc. 108: 142-149.
- Shepard, M.P. and F.C. Withler. 1958. Spawning stock size and resultant production for Skeena sockeye. J. Fish. Res. Board Can. 15: 1007-1025
- Sokal, R.R. and F.J. Rohlf. 1969. Biometry. The principles and practice of statistics in biological research. W.H. Freeman and Company. San Fransico.
- Struhsaker, P. and J.H. Uchiyama. 1979. Age and growth of the neh, Stolephorus purpureus (Pisces: Engraulidae), from the Hawaiian Islands as indicated by daily growth increments of sagittae. Fish. Bull., U.S. 74: 9-17.
- Timmons, T.T. and W.L. Shelton. 1980. Differential growth of largemouth bass in West Point Reservoir, Alabama-Georgia. Trans. Am. fish. Soc. 109: 176-186.
- West, C.J. 1978. A review of the Babine Lake Development Project 1961 - 1977. Canada Dept. of Fisheries, Technical Report series No. 812.
- Wild, A. and T.J. Foreman. 1980. The relationship between otolith increments and time for yellowfin and skipjack tuna marked with tetracycline (in English and Spanish). Inter-Amer. Trop. Tuna Comm., Bull., 17: 509-557.
- Wilson, K.H. 1981. Daily rings in otoliths of sockeye salmon (Oncorhynchus nerka) and their relationship to growth. MSc. Thesis. Univ. of B.C. Dept. of Zoology. 53 pp.

Wilson, K.H., and P.A. Larkin. 1982. Daily growth rings in the otoliths of juvenile sockeye salmon (Oncorhynchus nerka). Can. J. Fish. Aquat. Sci. 37: 1495-1498.