Evidence for Size-Selective Mortality of Juvenile Sockeye Salmon (*Oncorhynchus nerka*) in Babine Lake, British Columbia

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Otolith – body length relations and back-calculation procedures were used to test the hypothesis that mortality of juvenile sockeye salmon (*Oncorhynchus nerka*) in Babine Lake, British Columbia, is size selective. Samples of the 1978 brood of sockeye were collected as fry from spawning tributaries as juveniles in the main basin, and as smolts at the outlet. Total otolith length was chosen as the most useful otolith dimension for back-calculation of fork length at emergence. Sockeye from the various tributaries show different fork length – otolith length relationships necessitating a weighting procedure for comparisons involving samples of mixed stocks from the lake. Instantaneous daily growth rate and ln fork length during the early lake-rearing period were significantly correlated. Smaller juveniles grew more slowly than larger individuals in mid-July, and a hierarchy of sizes was maintained. The distributions of total otolith length at emergence for fry, surviving juveniles, and smolts indicate selective mortality of fish with smaller otoliths, hence of small size at emergence. Survivals from the lower and upper halves of the initial total otolith length distribution were 8.9 and 63.6%, respectively. Comparable estimates for back-calculated fork lengths at emergence were 27.2 and 43.4%. Size-selective mortality is most intense in the late summer and early autumn, and may be associated with predation and parasitism.

Les auteurs ont utilisé les relations de longueur entre les otolithes et le corps de même que des procédures de calcul à rebours pour tester l'hypothèse voulant que la mortalité des saumons nerka (*Oncorhynchus nerka*) juvéniles du lac Babine (Colombie-Britannique) soit sélective quant à la taille. Des saumons nerka de la classe annuelle de 1978 ont été prélevés sous forme d'alevins dans les tributaires de frai, de juvéniles dans le bassin principal et de smolts dans l'embouchure du cours d'eau. La longueur totale des otolithes a été choisie comme dimension la plus utile au calcul à rebours de la longueur à la fourche à l'émergence. Les saumons provenant de tributaires différents présentaient des relations longueur à la fourche – longueur des otolithes variables, ce qui a nécessité de peser les poissons afin de permettre la comparaison d'échantillons de stocks mixtes prélevés dans le lac. Le taux de croissance quotidien instantané et le logarithme de la longueur à la fourche présentaient une corrélation significative au début de la période de croissance en lac. Le taux de croissance des plus petits juvéniles était inférieur à celui des indidivus plus gros à la mi-juillet et une hiérarchie des tailles a été maintenue. Les distributions des longueurs totales des otolithes des alevins à l'émergence, des juvéniles ayant survécu et des smolts indiquaient l'existence d'une mortalité touchant sélectivement les poissons possédant les plus petits otolithes, donc les plus petits poissons à l'émergence. Les taux de survie des poissons correspondant aux demies inférieure et supérieure de la distribution des longueurs totales des otolithes de départ étaient, respectivement, de 8,9 et de 63,6 %. Des estimations comparables, calculées à rebours, des longueurs à la fourche à l'émergence donnaient des valeurs respectives de 27,2 et de 43,4 %. La mortalité sélective quant à la taille est plus intense à la fin de l'été et au début de l'automne et pourrait être liée à la prédation et au parasitisme.

The purpose of this study was to ascertain the effect of body size at emergence on the subsequent survival of sockeye salmon (*Oncorhynchus nerka*) fry in Babine Lake, British Columbia. The early life history of juvenile sockeye has been studied intensively but most studies have provided only incidental information on size-selective mortality. Releases of marked juveniles in Cultus Lake (Foerster 1938) did not indicate a difference in the percentage return as adults from the sea of wild fish and the larger of reared individuals. Increased survival of the reared fish to the migrant smolt stage may have been offset by increased residualism. Predation on juvenile sockeye was also investigated in Cultus Lake (Ricker 1941; Foerster and Ricker 1941), and although increased predation on smaller individuals was hypothesized, differential mortality within year classes remained untested.

Boyce (1982) pursued a relationship between initial size of fry at lake entry and susceptibility to parasitic infection (Boyce 1974), but disease caused severe mortalities and vitiated comparison among the test groups. Dependence of juvenile sockeye survival on available food supply in Babine Lake was

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considered by Rankin (1977) but the mechanism of mortality was not investigated.

A mark—release study by McDonald (1969) on the 1965 brood at Babine Lake revealed that although initial size differences between Fulton River and Fulton spawning channel fry persisted to the smolt stage, survival rates of the two groups were similar.

Thus, while size-dependent survival of juvenile sockeye has been considered for several stocks and associated with predation and parasitism, the mortality or its possible mechanisms have not been demonstrated.

The use of daily growth rings in sagitta otoliths for size determination has been well documented (e.g. Jonsson and Stenseth 1977; Marshall and Parker 1982; Neilson and Geen 1982; Struhsaker and Uchiyama 1976; Wild and Foreman 1980; Wilson and Larkin 1982). Otolith growth rings which correspond statistically to daily growth increments in juvenile sockeye (Wilson and Larkin 1982) provide a useful tool to reexamine the hypothesis: Do slow-growing individuals have a lower survival rate?

In this study, we have tested for size-selective mortality by examining differences between the length frequency distribution of the fry population which entered Babine Lake and that at emergence back-calculated from juveniles and smolts of the same brood captured at later dates.

Methods

Fish Collection and Preservation

Samples of the 1978 brood were collected as fry in the spring of 1979 in the spawning tributaries of the Babine Lake system, as juveniles in the summer of 1979 in the main basin of Babine Lake, and as smolts in the spring of 1980 at the time of seaward migration. Three times weekly at the peak time of the nightly migration from early May to mid-June, 50 fry samples were taken at each of five locations: Fulton River, Fulton spawning Channels 1 and 2, Pinkut Creek, and Pinkut spawning channel. After length and weight measurements of anaesthetized fry were taken, the fry were preserved in 70% ethanol (Brothers et al. 1983) for subsequent extraction of otoliths: No difficulties were encountered with the effect of 70% ethanol on otoliths, those of sockeye being less susceptible than those of larval cod (Gadus morhua), as reported by Radtke and Waiwood (1980). Estimates of the number of fry migrating nightly from each location were provided from the fry enumeration programs of the Department of Fisheries and Oceans. Nightly migration estimates were used to weight length frequency distributions by location from the fry samples.

Juveniles were captured with a 2 × 2 m midwater trawl (Gjernes 1979), towed by a single boat from a distance of 60 m, and fished at a depth of 2 m. A Furuno echo sounder aided selection of likely capture sites. During July 11–13, August 22–24, and September 19–21, trawling was conducted throughout the main basin, individual sampling locations collectively reflecting the seasonal distribution pattern of juveniles as previously reported by McDonald (1969).

Smolt samples were collected throughout the period of migration in late May and early June 1979 at the outlet of the Babine–Nilkitkwa Lake system where a smolt sampling program is carried out annually by the Department of Fisheries and Oceans. Fifty smolts taken randomly from every second
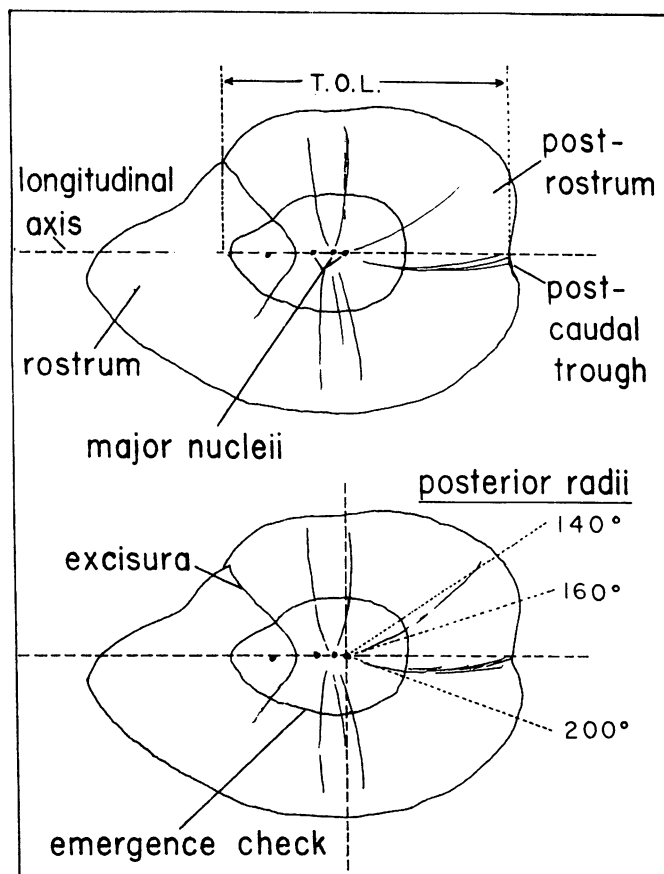

Fig. 1. Two diagrams of the sagitta of juvenile sockeye viewed from the distal side indicating various features used in orientation for measurement. T.O.L. = total otolith length.

night's catch were preserved in 70% ethanol. As with fry sampling, nightly estimates from the smolt enumeration program were used to weight the samples to calculate population length frequency distributions.

Otolith Preparation and Measurement

Fish <40 mm were held in an inverted position, the opercular plates removed exposing the gill structures, and the otoliths then teased from the sacculus on the tip of a probe. For larger fish (40–90 mm) the head was split along the longitudinal axis exposing on either side the sagittae which could be removed with forceps. Otoliths were cleaned of membranes and stored in MicroTest 3034 tissue culture plates. Left or right otoliths were randomly selected for observation and measurement. Otoliths were either attached with an acrylic adhesive to microscope slides, sulcal surface upwards, and ground against sintered glass plate using carborundum No. 50 aluminum oxide powder mixed with water, or for larger fish, prepared by the method of Neilson and Geen (1982).

Prior to photographing, mounted otoliths were cleared in glycerol. The time required for rings to become and remain visible is related to otolith size. Fry otoliths exhibit maximum ring counts after approximately 6 h of clearing and begin to overclarify after another 6 h. The clearing process can be reversed by soaking in ethanol. Smolt otoliths require several days to clear, but remain readable for a much longer period. As a standard procedure before photographing, fry otoliths were cleared for 4–6 h, juvenile samples for 24 h, and smolt otoliths

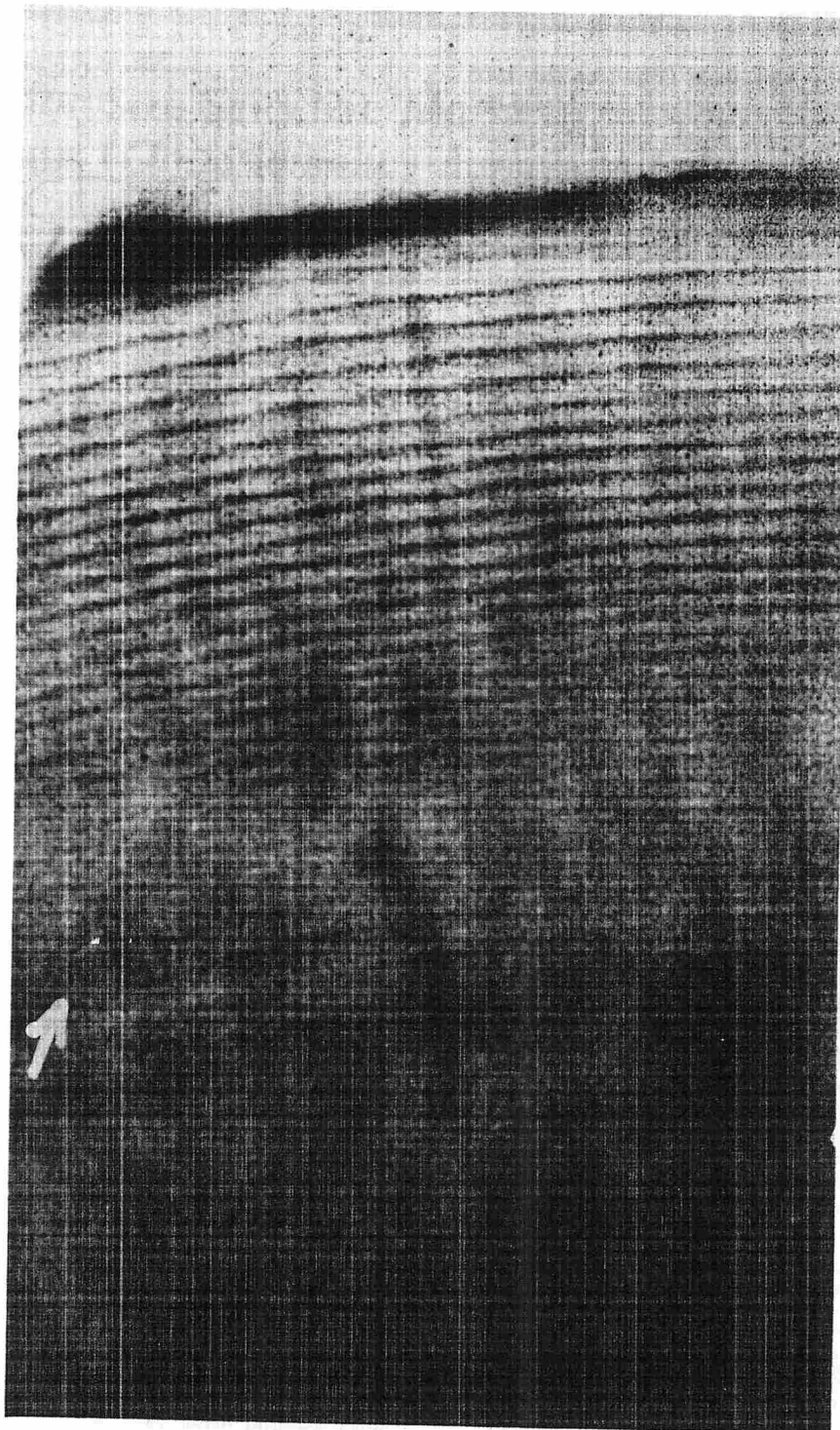Can. J. Fish. Aquat. Sci., Vol. 44, 1987

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FIG. 2. Portion of sagitta of juvenile sockeye indicating the light zone bordered by a distinct dark band which indicates emergence and the transition to active foraging.

from 2 to 3 d.

The sagitta otoliths of sockeye fry are distinctive but their shape varies among individual fish, and those of 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 of Pannella (1980).

The typical sagitta of a juvenile sockeye is laterally compressed and elliptical viewed from the distal side (Fig. 1). The long axis is oriented with the rostrum anterior and postrostrum posterior. The convex proximal side is divided by the grooved sulcus acusticus. On the distal face the sulcal groove terminates anterodorsally as the excisura and posteriorly as the postcaudal trough. On the longitudinal axis of the otolith there are three major nuclei referred to as primordia (Neilson and Geen 1982). Additional minor nuclei (two to five) may be found anteriorly along the longitudinal axis.

The convergence of radial bands at the intersection of domes

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of concentric growth usually provides cues to the position of the major nuclei and orientation of the vertical and horizontal axes. The anterodorsal band which intersects the excisura is particularly useful, indicating the position of the excisura on sagittae displaying no inflection or double inflections on the margin.

Various otolith measurements have been related to body size. Jonsson and Stenseth (1977) compared the relationship of length to three posterior radii of the sagitta otoliths of brown trout (*Salmo trutta*). Selecting the radii which gave the best correlation, six regression models were examined including a fourth-order polynomial equation. S. Campana (DFO, Bedford Institute of Oceanography, Dartmouth, N.S., 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. For chinook salmon (*O. tshawytscha*) juveniles, Neilson and Geen (1982) used the total length of the otolith minus the length of the rostrum. Wilson and Larkin (1982) measured a dorsal posterior radius at 40° from the longitudinal axis for sockeye fry, the axis defined as the line from the tip of the rostrum through the posterior nucleus.

The emergence of fry from the gravel of the spawning stream may occur after the deposition of a variable number of "daily rings" (Wilson and Larkin 1982) and is marked on the otolith by a narrow zone of discontinuity which may extend around the whole of the otolith or be exhibited in only portions of the periphery. It appears as a light zone, bordered by a distinct dark band (Fig. 2), and is referred to in this text as the emergence check. Marshall and Parker (1982) named it the "first-feeding check." In either case, it is usually distinguishable and is assumed to be coincident with emergence and the transition from yolk absorption to active foraging in the lake.

In the present study, five otolith dimensions were measured, the first three the radii emanating from the posterior major nucleus at 140, 160, and 200° from the longitudinal axis on which lie the three major nuclei (Fig. 1). The fourth dimension was total otolith length, the distance along the longitudinal axis from a point perpendicular to the rostral inflection to the intersection of the axis and the posterior edge (Neilson and Geen 1982). The intersection was used regardless of the presence of lobes extending posterior to the intersection, or whether the postcaudal trough was not centered on the axis. The fifth dimension was a crude estimate of the saggital sectional area based on measuring 16 radii at 22.5° intervals and summing the areas of the enclosed triangles. Greater precision could have been obtained by planimetry (Habib 1976) or by digitizing on a computer graphics tablet. For the limited number of samples involved in this study, the method used was considered adequate.

To define the position of the axes prior to measurement, a template was positioned under the projected image so that the intersection of horizontal and vertical axes passed through the central nucleus and the vertical axis aligned with the vertical axis of the otolith. To measure posterior radii, the template was positioned with its origin at the posterior nucleus. Total otolith length measurements were made positioning the vertical axis of the template 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 dorsoanterior radial band and the otolith edge (Fig. 1).
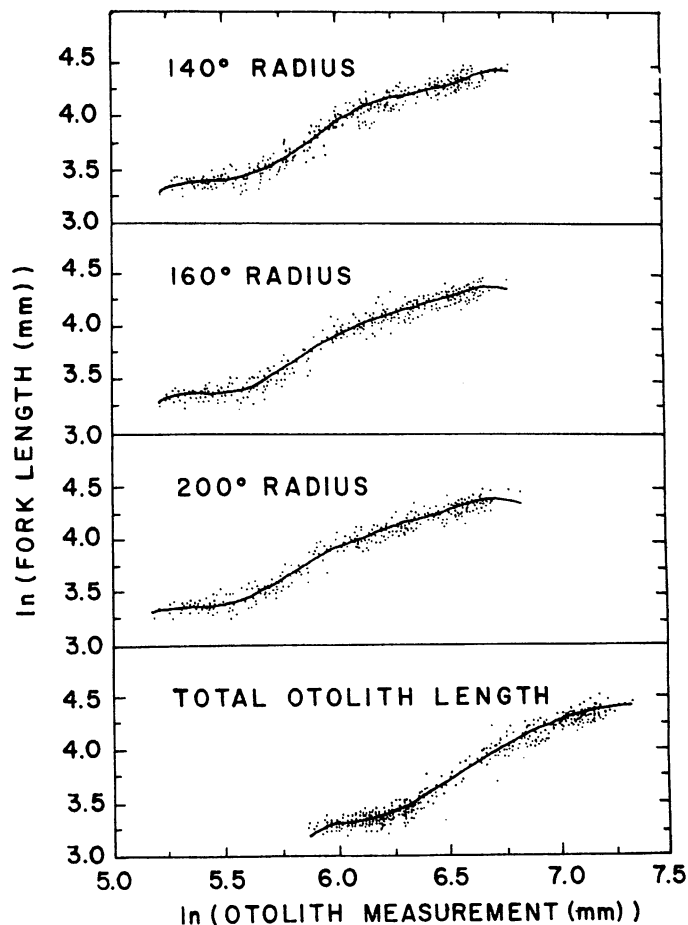
FIG. 3. Relationships between ln fork length and ln otolith measurement for 1978 brood juvenile sockeye from Babine Lake, B.C.

TABLE 1. Orthogonal polynomial coefficients for the relationships between ln fork length (mm) and ln otolith radius (μm) at 140, 160, and 200° and ln total otolith length (μm) for juvenile sockeye from the 1978 brood, Babine Lake, B.C.

Order of polynomial	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
S_{yx}	0.2496	0.2527	0.2466	0.2256

Dimensions of the enlarged images of the otoliths were measured to the nearest millimetre, giving an average precision of 0.7%. A second measurement error was associated with determining the exact position of the nuclei, but repeated tests using three independent measurements of the same otolith indicated that the smallest radii could be measured to within 1–2%, equivalent to about 2–3 μm.

Fork Length − Otolith Size Relationships

Over the 1-yr interval from fry to smolt, the form of the

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Table 2. Predictive (P) and functional (F) regressions (Ricker 1973) of ln fork length (mm) on five otolith dimensions (μm) (cross-sectional area (A), total otolith length (T), and posterior radii (R)) at 140, 160, and 200° for a representative sample of emergent sockeye fry from the Fulton River and Pinkut Creek systems. All regressions are significant at $p \leqslant 0.01$.

Otolith dimension		Regression				r^2	n
Cross-sectional area	ln (L) =	0.3220	+ 0.2514 ln (A)	(P)		0.5219	71
Cross-sectional area	ln (L) =	−0.8510	+ 0.3480 ln (A)	(F)			
Total length	ln (L) =	1.6447	+ 0.2842 ln (T)	(P)		0.2501	71
Total length	ln (L) =	−0.1001	+ 0.5683 ln (T)	(F)			
Radius 140°	ln (L) =	2.3081	+ 0.1992 ln (R)	(P)		0.1427	71
Radius 140°	ln (L) =	0.5269	+ 0.5274 ln (R)	(F)			
Radius 160°	ln (L) =	2.4879	+ 0.1659 ln (R)	(P)		0.1140	71
Radius 160°	ln (L) =	0.7194	+ 0.4914 ln (R)	(F)			
Radius 200°	ln (L) =	2.3730	+ 0.1878 ln (R)	(P)		0.1271	69
Radius 200°	ln (L) =	0.5406	+ 0.5267 ln (R)	(F)			

Table 3. Predictive regressions for the relationship between ln fork length at emergence (x) and ln total otolith length (y) at five fry sources on the Babine Lake system. Slopes that are underlined are not significantly different from each other (Scheffés multiple range test, $p = 0.05$). The main lake regression was calculated from the combined fry sources, weighted by relative fry production.

Source	Pinkut Channel	Fulton River	Fulton Channel 2	Pinkut Creek	Fulton Channel 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
S_{yx}	0.03523	0.03096	0.03152	0.03716	0.04537	0.03717
R^2	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
$p(b = 0)$	<0.01	<0.001	<0.001	<0.001	<0.001	<0.001
n	110	154	221	175	159	819
$\bar{y}$	3.34716	3.39146	3.40723	3.38095	3.37263	3.38786
S_y	0.03667	0.05643	0.04318	0.03509	0.03426	0.04603

various fork length versus otolith measurement relationships was moderately sinuous (Fig. 3). During the juvenile period the otolith grows at a more rapid rate than fork length, a positive allometry that would give way to a negative allometry at later stages in the life history (E. B. Brothers, 3 Sunset West, Ithaca, NY 14850, pers. comm.). The data transformed by natural logarithms to make variances homogeneous and fitted with stepwise orthogonal polynomials resulted in 8th- and 12th-order equations with some coefficients approaching magnitudes of 10^{14}. Although the regressions were highly significant with R^2 values ranging from 0.96 to 0.98, they were to some extent an artifact of the sample size (Draper and Smith 1966). Third-order polynomials were significant with R^2 values of approximately 0.94, but the residuals were not normally distributed. Sixth-order orthogonal polynomials were a useful compromise, being significant ($p < 0.01$) for all otolith measurements with R^2 values ranging from 0.97 to 0.98 (Table 1). Although the polynomial expressions were used for back-calculation over short intervals in the midrange of the fry to smolt period, there were substantial errors when the back-calculation extended to the ends of the range of observations.

For estimating fork length at emergence, it was found to be preferable to use the relationship between fork length and otolith size of emergent fry coupled with that for fish of the time period from which length at emergence was to be back-

calculated. For back-calculation of fork length, the 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 (Carlander 1981).

A subsample of 71 emergent fry from the Fulton River and Pinkut Creek systems indicated significant predictive and functional linear correlations (Ricker 1973) between fork lengths and the five otolith measurements (Table 2). Sagittal section area was the best estimator of fork length, perhaps reflecting that daily growth increments are not always distributed in the same way around the periphery of the sagittal plane, where their width is greatest (Dunkelberger et al. 1980), and that an integration of the increments along all radii is accordingly more representative of the daily growth of the otolith. For the three posterior radius regressions the correlations were poor ($r^2 = 0.11$–0.14). Total otolith length ($r^2 = 0.25$) was a better estimator of fork length. There is evidently considerable variability in fork length for a given otolith size. However, total otolith length is measured more easily and with greater precision than sagittal section area, and the emergence check is discernible at the excisura and postcaudal groove of most otoliths.

Stock differences in the body length − otolith dimension relationships at emergence were examined with samples com-

TABLE 4. Predictive linear regressions of ln fork length at capture (Fc) on ln total otolith length at capture (Tc) for 1978 brood sockeye in 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	r^2
mid-July	ln (Fc) = −4.08384 + 1.19502 ln (Tc)	0.6422
mid-August	ln (Fc) = −2.43577 + 0.95689 ln (Tc)	0.6295
mid-September	ln (Fc) = −1.14453 + 0.76759 ln (Tc)	0.4510
Smolt	ln (Fc) = 0.77640 + 0.49969 ln (Tc)	0.3136
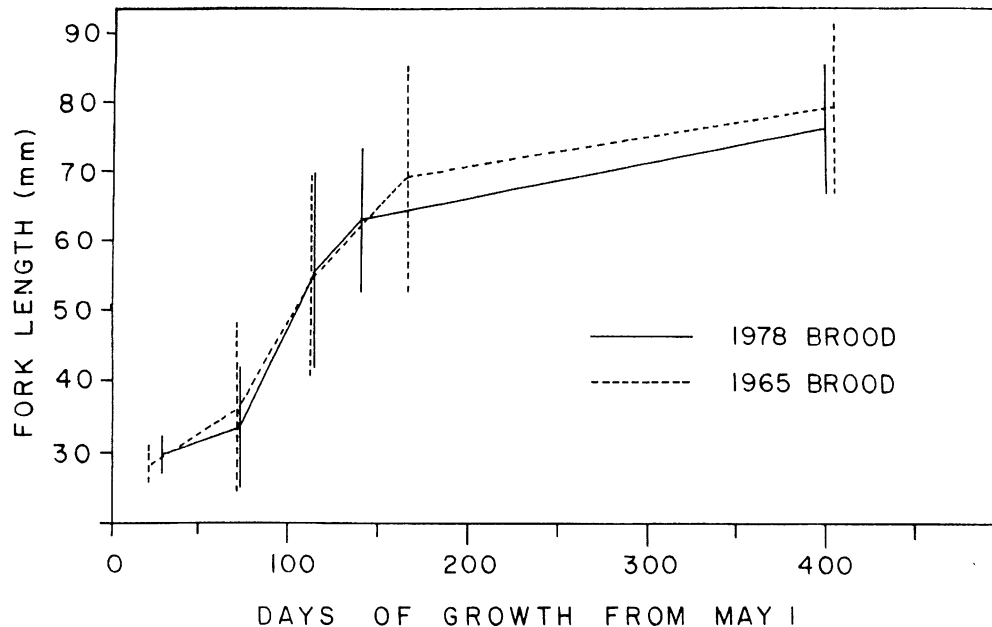
FIG. 4. Mean fork length of 1978 and 1965 brook sockeye (McDonald 1969) from fry emergence to smolt emigration from Babine Lake, B.C. Vertical bars represent two standard deviations on either side of the mean.

prising subsamples of approximately 25 fry from each source, taken three times weekly, over the period of fry migration. The regressions were significant for all stocks, but for Pinkut Channel and Fulton Channel 2, the relationship was highly variable (r^2 = 0.0856 and 0.1572, respectively). Scheffés multiple range test indicated two homogeneous subsets with respect to slope (Table 3). Within the larger subset there were three subsets with respect to adjusted ln mean fork length: the Fulton River and Pinkut Creek samples forming one subset, the other two, Pinkut Channel and Fulton Channel 2, each comprising separate subsets. Within the second subset the two subsamples, Pinkut Creek and Fulton Channel 1, were significantly different with respect to adjusted ln mean fork length. Thus, there is no obvious grouping of channel fry as opposed to river fry or of Fulton fry as opposed to Pinkut fry.

The combined regression for the main lake was obtained by weighting the samples from each source by the relative 1978 brood fry production. Fry production from the small streams which were not studied was assumed to be equal to 233 fry per spawner (McDonald and Hume 1984) and fork length − otolith relationships assumed to be most similar to those from Pinkut Creek (Table 3).

The combined average regression was highly significant (p < 0.001, Table 3). Residuals from the average regression were homogeneous and normally distributed. Use of the average regression gave minor loss of precision: the mean increase

in standard deviation from regression, weighted by relative fry production, was less than 2% for each stock. In back-calculations, the average regression underestimated length at emergence in stocks for which the relationship was above the average regression and overestimated lengths for those below. The largest errors were associated with the Pinkut spawning channel stock, which has the relationship most different from the average regression. However, the bias (overestimated fork lengths) is small because the channel produced only 7.5% of the main lake fry population in 1979.

The combined average regression was used as the predictive function for back-calculation of ln total fork length at emergence. Regressions for each of the other life history stages (Table 4) were used as the functions for evaluating the deviation of the observed length at capture from the expected length at capture. This procedure assumes that deviations from the predictive relationships were constant over the range of ln total otolith length. That is, for fish of any given length, those with relatively large otoliths at emergence were assumed to have equally relatively large otoliths at subsequent stages in the life history. While this may not be true for individuals and might not be a valid procedure for back-calculating individual growth histories, it is satisfactory for describing the statistical characteristics of growth in the population.

To obtain for the main lake the distribution of total otolith length at emergence from the samples of emerging fry, the
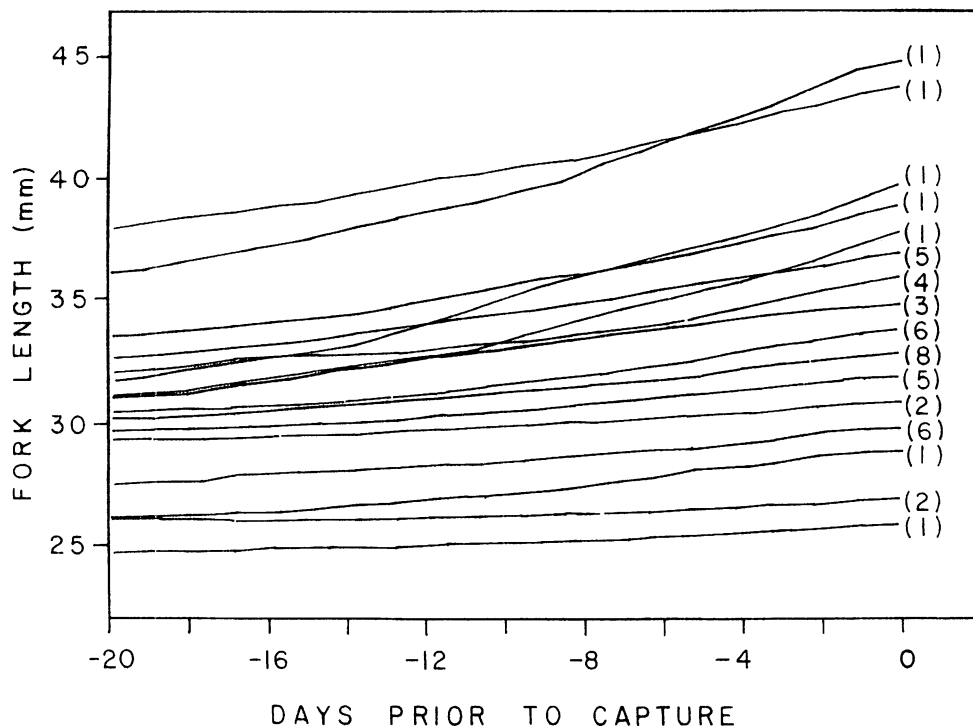
FIG. 5. For groups of individuals assembled at 1-mm intervals of fork length at capture, estimated mean fork lengths over the 20-d period prior to capture in July, the central capture date being July 12. Numbers in parentheses indicate sample size.

daily distribution of total otolith length was weighted by the daily count of fry for each source of fry. The daily distributions from all sources were then summed. A similar procedure was used to obtain the distribution of total otolith length at emergence from the daily samples of smolts at their single point of collection at the outlet of Babine Lake.

Results

Growth Rate in the Lake

The growth rate of the 1978 brood as indicated by the mean fork length at capture of main lake fry was similar to that for the 1965 brood (McDonald 1969) (Fig. 4). The range of fork lengths increased rapidly during the early lake-rearing period, indicating a large variation in growth rates of individual fry.

The relationship of growth rate to fish length in late June and early July was assessed by measuring the growth for the 20 d prior to capture in the otoliths of the July 12 tow samples and back-calculating fork lengths using the sixth-order polynomial for the relationship between fork length and the 140° radius measurement of the otolith. Mean growth increments over the 20-d period for groups of individuals at 1-mm intervals of fork length at capture show an orderly divergence (Fig. 5), implying a relationship between growth rate and fork length that would lead to maintenance of a hierarchy of lengths. The correlation of instantaneous daily growth rates and ln fork length was significant ($r^2 = 0.6142$).

Selective Mortality in the Lake

The distributions of total otolith length at emergence for the main lake fry, tow-netted juveniles, and smolts exhibit a trend for fish with small otoliths at emergence to disappear between the fry and smolt stages (Fig. 6). The mean total otolith length at emergence for emerging fry was 458.1 μm, and 47.5% were smaller than the mean. For the smolts, only 11.3% had otoliths less than 458.1 μm in total length at emergence. Fry to smolt survivals of those below and above the mean of total otolith length at emergence were 8.9 and 63.6%, respectively, and correspond to instantaneous mortality rates of 2.42 and 0.45. The resulting shift in the mean total otolith length at emergence from 458.1 to 493.6 μm was highly significant (ANOVA, $p < 0.001$). The shift was most pronounced in the latter part of the summer and the early autumn.

The relative frequencies of back-calculated fork lengths at emergence (Fig. 7) indicate selection against fry of small fork lengths. The increase in mean fork length at emergence from 29.55 to 30.40 mm (difference 0.85 mm, $s^2 = 1.352$) between the fry and smolt stages was statistically significant (ANOVA, $p < 0.001$), and most of the change occurred in the late summer and early autumn. Fry to smolt survivals of those above and below the mean of the distribution of mean fork length at emergence were 27.2 and 43.4%, respectively, corresponding to instantaneous mortality rates of 1.31 and 0.83.

The greater degree of selection against fish with relatively small otoliths than of fish of lesser fork length may reflect the lack of precision and perhaps a bias in the back-calculation procedure, but another possible explanation is that otolith length may be better correlated with weight than length of the fish. Thus, relatively short but heavy fish would have large otoliths and would have lower mortality rates than implied by their length. Further, the greatest mortality would be among the relatively shorter and lighter fish.

Discussion

It is well known that growth rate varies within populations

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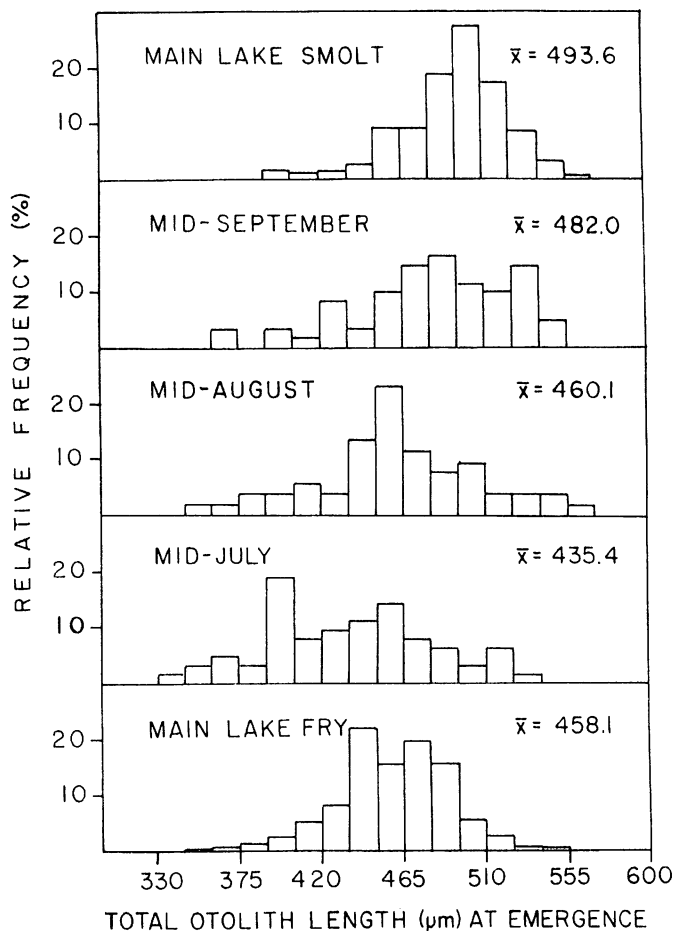
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Fig. 6. Histograms of total otolith length at emergence for fry, for juveniles in mid-July, mid-August, and mid-September, and for sub-2 smolts for the 1978 brood sockeye from the main basin of Babine Lake, B.C.
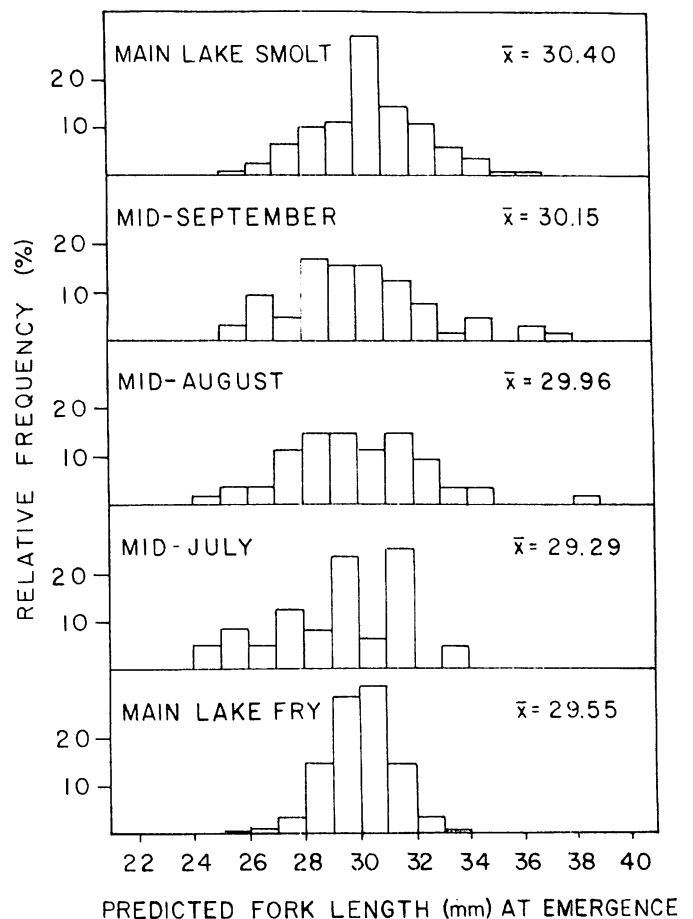

Fig. 7. Histograms of predicted fork length at emergence for fry, for juveniles in mid-July, mid-August, and mid-September, and for sub-2 smolts for the 1978 brood sockeye from the main basin of Babine Lake, B.C.

of juvenile salmon. Differences in egg size, emergence timing, together with spatial and temporal variation in environmental conditions, contribute to differences in size within cohorts. Competition may exaggerate variability in size and growth rate. DeAngelis and Coutant (1979) found that growth rate of juvenile smallmouth bass (*Micropterus dolomieu*) on surplus ration was independent of size, which was normally distributed. With competition for food, growth rates are more variable and size distributions may become bimodal (Shelton et al. 1979; Timmons and Shelton 1980; DeAngelis and Coutant 1982). Mason (1969) found that initial differences, compounded by competition through territoriality, were instrumental in determining social status, growth, and emigration rate in juvenile coho (*O. kisutch*).

Initial size differences of <1 mm fork length may thus have profound implications for growth and mortality of individuals within cohorts of juvenile sockeye. The linear dependence of growth rate on fork length of juvenile sockeye during July is not surprising and presumably reflects a competition for food resources. The disparity in estimated growth rates of Babine sockeye juveniles is considered to be conservative. Starved fish develop a body length – otolith relationship of lower slope than fed fish (Marshall and Parker 1982); hence, our use of an average slope underestimates the growth of faster growing fish and overestimates that of slower growing fish, biases which would reduce disparity among estimated growth rates. The

relationships between body weight and otolith dimensions may be more precise for describing growth.

From observations on five broods of sockeye, McDonald (1969) and McDonald and Hume (1984) concluded that there was no size-selective mortality between pairs of stocks from the Fulton and Pinkut systems despite initial differences in mean size, which is seemingly contradictory to the present results. However, the mean may not necessarily reflect the history of individuals within the population.

Ricker (1969) showed that the change in instantaneous mortality rate resulting from linear change in selective pressure may be calculated as the ratio of the shift in mean length and its variance. The observed shift in mean length at emergence observed in this study was 0.85 mm with variance 1.352, implying a change in instantaneous mortality rate of 0.63/mm. Multiplying this estimate by the difference in fork length in any pair of observations enables an estimate of the survival rate of one of the pair from that of the other. Table 5 provides estimates of the increased survival rate for the five pairs reported by McDonald and Hume (1984). While it is inherent in the calculation that the change will always be in the right direction, there is nevertheless a fair measure of agreement between the observed and predicted survival rates, especially bearing in mind that the change in selection pressure may not be a linear function of the shift in mean length. Hence, while there may be significant selective mortality against small indi-

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Brood year	Group	Emergent length (mm)	Fry to smolt survival (%)	Predicted survival rate (%)
1965	Fulton River	29.3	12.7	
	Fulton Channel 1	29.1	14.3	16.4
1966	Fulton River	29.4	25.8	25.4
	Fulton Channel 1	29.0	19.9	
1967	Fulton River	29.3	29.3	
	Fulton Channel 1	29.8	33.2	40.2
1970	Fulton Channel 2	30.3	25.0	25.4
	Pinkut Channel	30.2	23.9	
1971	Fulton Channel 2	30.0	37.2	33.0
	Pinkut Channel	29.6	25.6	

viduals within a population, selection might not be obvious from comparison of two populations undergoing a common selection.

Parallel changes in rates of growth and survival are often postulated (for example, Isaacs 1964) but there is little direct evidence of their occurrence. Methot and Kramer (1979) examined the possible effect of selective mortality on estimates of growth rate of northern anchovy (*Engraulis mordax*) larvae based on relating standard length to the number of daily otolith increments, concluding that the effects were not sufficient to introduce a substantial bias. It was also suggested that back-calculation of growth histories of individuals from daily growth rings could be used to provide information on differential mortality. Healey (1982) demonstrated size-selective mortality in chum salmon (*O. keta*), and Parker (1971) suggested that early marine mortality of juvenile chum and pink salmon (*O. gorbuscha*) from predation by juvenile coho was biased toward smaller individuals. The present findings were unequivocal: there is a selective mortality of fish that were relatively small at the time of emergence as fry. Those that start small tend to stay in the lower end of the size distribution and become progressively smaller compared with larger individuals at the other end of the size distribution. Differential mortality is apparently most intense in the latter part of the summer and in early autumn.

The proximate causes of mortality are presumably size related, such as predation, or condition related, such as disease and parasitism. The likelihood of death literally from starvation appears unlikely. Sockeye juveniles reared in laboratory conditions until November withstood 20 wk of starvation without significant mortalities (Bilton and Robins 1971), and although the fish were larger than juveniles in Babine Lake and were being held at a later season, their durability was impressive.

Size-related mortality in Babine juvenile sockeye may be induced by parasitism of the cestode *Eubothrium salvelini*. The susceptibility of fry to infection by the parasite declines sharply as fork length of sockeye juveniles increases above the range of 35–45 mm (Boyce 1974). Larger and faster growing fry move quickly through this size range, and hence may be less prone to debilitating effects of the parasite. Although infected juveniles may survive to the smolt stage, in laboratory conditions they are less able to cope with stress and exhibit reduced growth, swimming performance, and survival (Boyce and Behrens Yamada 1977; Boyce 1979, 1982; Boyce and

Clarke 1983). Smith (1973) suggested that such indirect effects on juvenile quality could cause mortality from other sources. Higher predation rates on the smaller and less vigorous parasitized fish in the lake are an additional possibility.

Acknowledgments

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