Does mortality select size or growth potential in young sockeye salmon (*Oncorhynchus nerka*)? A simulation based on otolith – fish size relationships[1]

M.G. Meekan, D.A.J. Ryan, J.J. Dodson, and S.P. Good

Abstract: There is conflicting evidence on the role of size-selective mortality in the demography of populations of young sockeye salmon (*Oncorhynchus nerka*). A previous field study suggested that increases in mean fork length and otolith size at emergence observed in a cohort of salmon between fry and smolt stages were due to size-selective mortality, such that fry with small fork lengths underwent higher mortality than larger individuals. However, a subsequent study used a simulation to show that such increases could not have been achieved by size-selective mortality without levels of survivorship of the cohort far lower than those that had been observed in the field. To account for field observations, the simulation study proposed that individuals with high metabolic rates had better survivorship, a process that was termed "selection for growth potential." Here, we use a simulation approach to show that size-selective mortality may result in shifts in mean fork length and otolith size at emergence comparable with those observed in the field at total mortalities within the range of estimates of natural values. The contrasting outcomes of earlier simulation work and the present study are probably due to the assumption by the former that otolith and fish size in young salmon were weakly correlated and the use of an inappropriate model of size-selective mortality. We conclude that size-selective mortality can explain the results of previous field studies and that little empirical evidence exists to support the hypothesis of selection for growth potential in cohorts of young salmon.

Résumé : Les données concernant le rôle de la mortalité sélective en fonction de la taille dans la démographie du jeune saumon rouge (*Oncorhynchus nerka*) sont contradictoires. Dans une étude sur le terrain effectuée antérieurement, on avait avancé une hypothèse selon laquelle l'accroissement de la longueur moyenne à la fourche et de la taille des otolithes à l'émergence observé dans une cohorte de saumons suivie depuis le stade de l'émergence des alevins jusqu'au stade du smolt était dû à la mortalité sélective en fonction de la taille, la mortalité étant plus lourde chez les alevins de faible longueur à la fourche que chez les sujets de plus grande taille. Or, dans une étude réalisée par la suite, on s'est servi d'un modèle de simulation pour montrer que l'accroissement des paramètres de longueur à la fourche et de taille d'otolithes ne pouvait pas s'expliquer par un phénomène de mortalité liée à la taille si les taux de survie de la cohorte n'étaient pas de beaucoup inférieurs à ceux mesurés sur le terrain. Dans cette étude en simulation, on expliquait les valeurs mesurées sur le terrain par une hypothèse selon laquelle le taux de survie est meilleur chez les saumons à métabolisme élevé en raison d'un phénomène de « sélection du potentiel de croissance ». Nous avons aussi eu recours à un modèle de simulation pour montrer que la mortalité liée à la taille peut causer des changements de longueur moyenne à la fourche et de taille des otolithes à l'émergence comparable à ceux observés sur le terrain lorsque la mortalité totale se trouve entre les valeurs estimatives limites de la mortalité naturelle. Si nos résultats diffèrent beaucoup de ceux obtenus dans l'étude antérieure, c'est probablement parce que dans cette dernière on a supposé une faible corrélation entre la taille des otolithes et la longueur à la fourche du jeune saumon, et l'on n'a pas utilisé le modèle approprié pour représenter la mortalité sélective par taille. Nous sommes parvenus à la conclusion que la mortalité sélective par taille peut expliquer les résultats des études antérieures faites sur le terrain, et qu'il n'y a guère de données empiriques pour étayer l'hypothèse d'une sélectivité favorisant le potentiel de croissance dans des cohortes de jeunes saumons.

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M.G. Meekan[2] and D.A.J. Ryan. The Australian Institute of Marine Science, PMB 3, Townsville M.C., Qld 4810, Australia.
J.J. Dodson and S.P. Good.[3] Département de biologie, Université Laval, Ste-Foy, QC G1K 7P4, Canada.

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[2] Author to whom all correspondence should be addressed. e-mail: m.meekan@aims.gov.au
[3] Current address: Agency of Natural Resources, Vermont Department of Fish and Wildlife, R.R. 2, Box 2161, Pittsford, VT 05763, U.S.A.

Fig. 1. Relative frequencies of (A) total otolith length and (B) predicted fork length at emergence for fry, juveniles in mid-July, mid-August, and mid-September, and 1+ smolts for the 1978 brood of sockeye salmon in Babine Lake, British Columbia. Data redrawn from figs. 6 and 7 in West and Larkin (1987). The regression equations used to generate predicted fork lengths are given in table 4 in West and Larkin (1987).
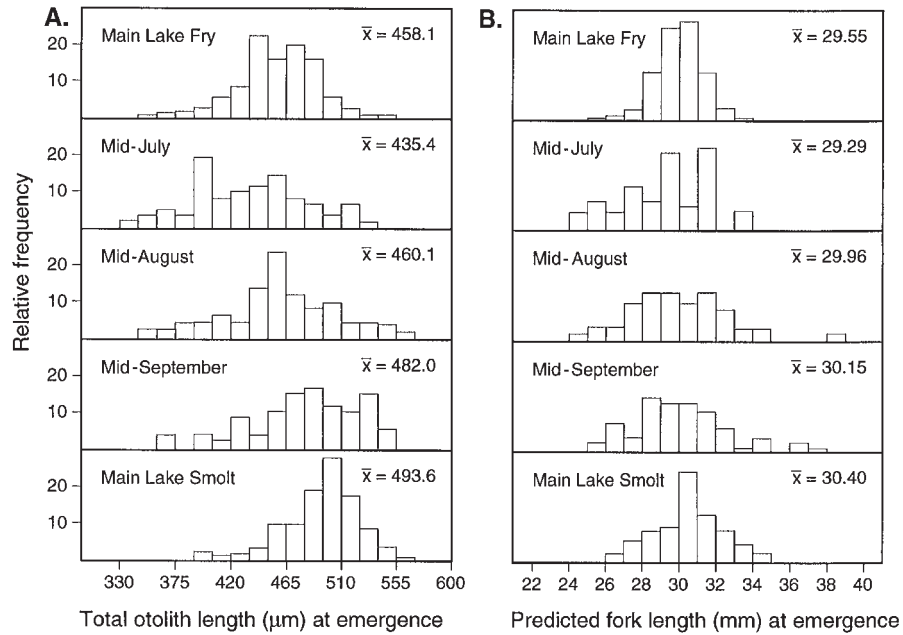
Introduction

Size- and (or) growth-selective mortality appears to have an important influence on the demography of fish populations (Bailey and Houde 1989). The analysis of age and growth information contained in otoliths can provide a convenient means of assessing the timing and extent of these processes, particularly when selection begins early in the life history of young fish (Campana 1996; Meekan and Fortier 1996).

West and Larkin (1987) used otolith analysis to examine the size-selective mortality of sockeye salmon (*Oncorhynchus nerka*) following emergence of fry from the redd in Babine Lake, British Columbia. They compared backcalculated distributions of otolith size at emergence from a cohort of fry that was sampled at emergence in the spring, at monthly intervals during the summer, and then again in the following spring, 1 year after emergence when the fry had become smolts. Comparison of these distributions showed a strong shift in mean otolith size at emergence with time (Fig. 1A, redrawn from West and Larkin 1987). Mean otolith length at emergence in the first spring sample was 458.1 μm. While there was little change in distributions of otolith size at the next sampling occasion in mid-July, there was a marked shift of distributions towards those individuals that had large otoliths at emergence by the end of the summer. This shift had become even more pronounced when the cohort was resampled as smolts, 1 year after emergence. At this time, the mean backcalculated otolith length at emergence of the cohort was 493.6 μm.

These measurements of otolith size were used by West and Larkin (1987) to reconstruct distributions of fork lengths at emergence (Fig. 1B). Backcalculations of fork length were made using linear (ln–ln) regressions between otolith size and fork length from fry collected at emergence and from fry collected on each sampling occasion. Comparison of distributions

of fork length of the cohort displayed a shift towards larger sizes at emergence with time. In the initial spring sample, the mean fork length at emergence of the cohort was 29.55 mm, while 1 year later, the mean fork length at emergence of the cohort had increased to 30.40 mm.

West and Larkin (1987) attributed the change in mean otolith size and fork length at emergence in the cohort of young salmon to size-selective mortality. They argued that fry with smaller fork lengths at emergence underwent higher mortality than those with larger fork lengths, resulting in a shift of distributions of both fork and otolith lengths. Calculations of relative mortality rates provided some evidence to support this conclusion. Survival from the fry to smolt stages of salmon with otoliths below the mean length of 458.1 μm at emergence was 8.9%, while survival of salmon with otoliths above this mean value was estimated to be 63.6%. Although mortality estimated from the backcalculated fork lengths showed a similar pattern, survival of fish below and above the mean fork length of 29.55 mm was 27.2 and 43.3%, respectively. West and Larkin (1987) suggested that the difference between these estimates of relative mortality may have been due, at least in part, to errors introduced by the backcalculation procedure.

Mosegaard (1990) reanalysed the results of West and Larkin (1987) to examine the suggestion that size-selective mortality of fry could account for shifts in mean otolith length at emergence. Mosegaard simulated distributions of fork length at emergence from distributions of otolith length (Fig. 1A, top panel) using the regression between fork and otolith length at emergence shown in table 3 in West and Larkin (1987). Distributions of fork lengths at emergence were then subjected to differing degrees of selective mortality. Initially, a random sample of fry consisting of 10% of individuals below and 64% above the mean fork length of 29.74 mm was taken, which approximately corresponded to the survivorship

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pattern found in distributions of otolith length by West and Larkin (1987). This selection shifted mean fork length at emergence to 30.42 mm; however, mean otolith length only shifted to 467 μm. To determine what levels of mortality were required to obtain the much larger shift in mean otolith length (to 493.6 μm) that had been recorded by West and Larkin (1987), this simulation was then repeated with all individuals below a mean fork length undergoing mortality and all those above the mean surviving. Eight mean fork lengths were chosen, ranging from 30 to 33.5 mm. These simulations showed that to obtain a mean otolith length at emergence of 493.6 μm at the smolt stage, the cohort of young salmon had to undergo levels of total mortality that were up to an order of magnitude higher than those that had been recorded in the field. Thus, Mosegaard (1990) concluded that selective mortality based on fork length alone could not account for the shift in otolith length at emergence found by West and Larkin (1987).

As otolith growth may be strongly influenced by metabolic rate during the early life history of salmon (Mosegaard and Titus 1987; Mosegaard et al. 1988), Mosegaard (1990) proposed that shifts in otolith size may be largely due to a selection for metabolic rate. He argued that larger otolith size at emergence may reflect higher metabolic rates, rather than larger body size (fork length). High metabolic rate was thought to lead to higher growth rate, better competitive ability, higher survivorship, and ultimately larger body size at later life history stages. This process was later termed "selection for growth potential" by Titus and Mosegaard (1991).

To generate distributions of fork length, Mosegaard (1990) utilized a linear regression analysis that had been calculated between otolith and fork lengths at emergence by West and Larkin (1987). The relationship between these variables was weak (r^2 0.255). In a recent study, Meekan et al. (1998) demonstrated that when linear regression is used to compare otolith and body size in larval fish, the strength of the correlation between these variables is highly dependent on the choice of measures used to estimate size and on the age and size range of fish used in the analysis. This can be illustrated by comparing regression analyses calculated by West and Larkin (1987) for a sample of emergent fry. When area of the otolith was used as a measure of size rather than total length or radius of the otolith, there was up to a fivefold increase in strength of the correlation between otolith and fish size (see table 2 in West and Larkin 1987). Similarly, there was a large change in the strength of correlations that was dependent on the age of fry used in the regression analyses. At emergence, when the range of sizes in the cohort of fry was narrow, the correlation between somatic and otolith growth was poor (r^2 0.255). When the cohort was resampled at older ages and growth had propagated differences in size among individuals, correlations between otolith and fish size increased (r^2 0.31 to 0.64, table 4 in West and Larkin 1987).

These results have important implications for Mosegaard's simulation study. If otolith and fish size are strongly correlated, selection of individuals with large body sizes will result in an increase in mean body and otolith size at emergence in the cohort, since the surviving fish will tend to have large otoliths. When there is a poor correlation between these variables, selection will result in an increase in mean body size; however, the change in mean otolith size will be less marked, as the large, surviving fish may not necessarily have large

otoliths. Under such conditions, a very high intensity of selection for larger body sizes will be required to produce shifts in mean otolith length of the cohort. Thus, the extreme levels of mortality that were required by Mosegaard's simulation to reproduce the results of West and Larkin (1987) may have been strongly influenced by the use of a regression relationship where otolith and fish size were weakly correlated.

A second potential problem with Mosegaard's simulations involved the means by which mortality was imposed. To produce shifts in mean otolith length at emergence, a step-function was imposed where all individuals smaller than mean values of fork length underwent a consistently high level of mortality, while all those individuals larger than mean fork length underwent a consistently low level of mortality. In contrast, natural mortality is more likely to operate as a smooth curve, with each size-class of fry within the cohort having differing levels of survivorship. Mortality, if size selective, will remove progressively fewer individuals as the size of fry increases. Evidence for variation in mortality rates among members of the cohort can be shown by comparing the distributions of otolith length in Fig. 1A. After 1 year, those individuals that had very small otoliths at emergence had disappeared, while some individuals were present in the final sample of the cohort that had larger otoliths at emergence than any that were found in the initial sample. One possible explanation for the sudden appearance of these fry with large otoliths is that at emergence, they were a very rare component of the cohort and unlikely to be sampled. Between fry and smolt stages, these fish underwent extremely low levels of mortality so that they became relatively more abundant and were thus included in samples at the smolt stage. This implies that survivorship of fry in the cohort varied from negligible to very high levels.

While Mosegaard (1990) conceded that a uniform level of survivorship among members of the cohort of differing fork lengths was unlikely to be realistic, he considered that his approach was conservative and that even more extreme levels of mortality would be required to produce shifts in mean otolith length if rates of survivorship differed among size-classes. However, this is not necessarily the case. A simulation where the same high level of mortality is applied to all individuals smaller than the mean size while all individuals larger than the mean undergo the same low level of mortality will result in the inclusion of small fry from the lower end of the distribution of fork lengths in calculations of means that may not have, under natural conditions, survived. Similarly, at the upper end of the distribution, large fry will undergo mortality where, in reality, survivorship may have been close to 100%. This source of error will not only apply to those fry that occur at the ends of the distribution of fork lengths and are a relatively rare component of the cohort, but also to those near mean values. At the center of the distribution, small changes in survivorship among size-classes of fork length will have a major effect on mean values, since the majority of individuals lie within this part of the distribution.

Here, we simulate size-selective mortality in a cohort of young sockeye salmon fry using field data published by West and Larkin (1987). The outcomes of these simulations are compared with those of Mosegaard (1990). We did this by firstly repeating the approach of Mosegaard (1990) where high and low levels of mortality were applied consistently to all

Fig. 2. Frequency distributions of total otolith length at emergence for fry (hatched bars) and 1+ smolts (shaded bars) from the 1978 brood of sockeye salmon in Babine Lake, British Columbia. Data redrawn from Fig. 1A (bottom panel, 1+ smolts) and table 1 in Mosegaard (1990). The survivorship curve is calculated by comparing frequency distributions using nonlinear regression (see Methods for details) is shown.
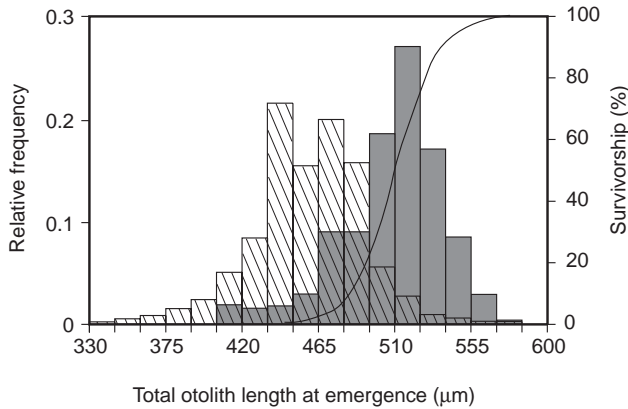
individuals below and above mean values of fork length in a cohort that had been generated using a regression between otolith and fork lengths calculated by West and Larkin (1987). The error used to generate distributions of fork lengths was altered in successive runs of the simulation so that the otolith – fish size relationship varied from weak (r^2 0.255) to strong (r^2 0.95).

Next, we estimated a survival curve from the distributions of otolith length at emergence that were obtained from successive samples by West and Larkin (1987) (Fig. 2). This survivorship curve was applied to distributions of fork lengths at emergence that had been generated using the regression between otolith and fork lengths calculated by West and Larkin (1987). The size of the error term in this regression was then reduced and the simulation repeated. These simulations allowed us to examine the effect of a survival curve (rather than a step-function where all individuals below mean fork lengths undergo the same high level of mortality, while those above the mean undergo the same low level of mortality) and variability in the strength of the otolith – fish size relationship on the amount of mortality required to produce shifts in mean fork and otolith lengths at emergence with time.

Methods

Generation of random observations of fork length from distributions of otolith length

We generated 1000 data sets of 400 otolith lengths from the frequency distribution of otolith lengths shown in Fig.1A (top panel) using the inverse transformation method (Naylor et al. 1966) (PROC RANUNI, SAS V6). The regression equation (table 3 in West and Larkin 1987)

$$\text{Fork length (fl)} = e^{1.52293 + 0.30493 \ln(x) + error}$$

where the error term was assumed to be a random normal variate with mean 0 and standard deviation (SD) 0.037 was then used to transform the simulated otolith lengths into fork lengths for all data sets. This resulted in 1000 data sets each with 400 simulated otolith and fork length measurements. The error of 0.037 was chosen to correspond to the SD used in simulations by Mosegaard (1990). This error was then

progressively reduced to 0.02, 0.015, 0.005, and 0 and a further 1000 data sets generated for each level of error. These SDs corresponded to (ln–ln) regression equations between otolith and fork length where the average $r^2 = 0.54$, 0.68, 0.95, and 1, respectively.

Simulation of size-selective mortality using a step-function

Comparisons of distributions of otolith and fork lengths of fry collected at emergence and at smolt stages were used by West and Larkin (1987) to calculate relative survivorships of fry above and below mean values of fork length. These estimates were then used by Mosegaard (1990) to simulate size-selective mortality in a cohort of fry. In his study, constant proportions of individuals above and below mean values were removed from distributions of fork lengths. We repeated his simulation protocol by randomly removing fish from the data sets in the following manner. Each of the simulated pairs of data was randomly assigned a number between 0 and 1 using the RANUNI procedure in SAS V6. In the first run of the simulation, fish that had fork lengths smaller than the mean had a survivorship of 27%, while those above the mean had a survivorship of 43%. Consequently, all data pairs that had been assigned a number larger than 0.27 and had fork lengths smaller than the mean value were removed, resulting in 27% survivorship for this part of the cohort. All data pairs that had been assigned a value larger than 0.43 and had fork lengths greater than the mean were also removed, resulting in 43% survivorship for this upper part of the cohort. Mean otolith and fork lengths of the survivors were then obtained for each data set. These values were averaged among the 1000 data sets and SDs of the means were calculated. The simulation was then repeated for the fork length data sets that had been generated with differing levels of error.

The entire process was then repeated using survivorships of 10 and 64% below and above mean fork lengths, respectively. These levels of survivorship corresponded to the estimates calculated by West and Larkin (1987) and used in simulations of size-selective mortality by Mosegaard (1990).

Estimation of the survival curve

It was assumed that survival due to size-selective mortality could be approximated by a monotonic increasing, S-shaped curve described by

$$s(x) = e^a/(1 + e^a)$$

where $s(x)$ is the probability that a fry with an otolith length of x will survive to the smolt stage and $a = \beta_0 + \beta_1 x$ where β_0 and β_1 represent the location and slope of the curve, respectively. Using PROC NLIN (SAS V6), the following relationship was used to estimate $s(x)$:

$$g_i(x) = (s(x)f_i(x))/c_i$$

where c_i is the sum of $s(x)f_i(x)$ over all otolith size-classes in the distribution, $g_i(x)$ is the observed percentage of fry surviving to the smolt stage for size-class i (Fig. 2), and $f_i(x)$ is the observed percentage of fry at emergence for size-class i (Fig. 2). The parameter estimates for β_0 and β_1 calculated by the nonlinear regression were –41.907 58 and 0.081 90, respectively, and the midpoint of the curve lay at 511.69 μm.

Application of the survivorship curve to distributions of fork lengths

The nonlinear regression resulted in the parameter estimates for the curve being expressed in terms of otolith radius. To apply the curve to distributions of fork length, these values were transformed to fork lengths using the regression equation (table 3 in West and Larkin 1987) without an error term, resulting in the following survivorship curve:

$$s(y) = e^a/(1 + e^a)$$

where $s(y)$ is the probability that a fry with a fork length of y will survive to the smolt stage and $a = -41.90758 + 0.00056y^{3.28}$. In

Table 1. Mean otolith and fork lengths at emergence of a cohort of sockeye salmon after constant survivorships were applied to distributions of fork length below and above mean values.

	27% below, 43% above mean				10% below, 64% above mean			
	Mean	SD	Min.	Max.	Mean	SD	Min.	Max.
Error = 0.005, $r^2 = 0.95$								
Otolith length (μm)	464.31	2.64	455.74	472.31	476.58	2.14	470.15	484.61
Fork length (mm)	29.81	0.05	29.62	29.98	30.07	0.04	29.95	30.24
Survivorship (%)	34.84	2.32	27.00	42.50	36.81	2.46	28.00	43.75
Error = 0.015, $r^2 = 0.68$								
Otolith length (μm)	463.32	2.75	454.63	471.27	473.58	2.26	466.45	479.81
Fork length (mm)	29.84	0.06	29.63	30.04	30.15	0.05	30.01	30.32
Survivorship (%)	34.83	2.42	27.50	42.50	36.55	2.41	29.5	44.25
Error = 0.02, $r^2 = 0.54$								
Otolith length (μm)	462.82	2.58	455.33	471.62	471.92	2.30	465.41	479.07
Fork length (mm)	29.86	0.07	29.63	30.09	30.2	0.05	30.03	30.37
Survivorship (%)	34.84	2.30	27.75	42.25	36.47	2.43	29.50	43.50
Error = 0.037, $r^2 = 0.26$								
Otolith length (μm)	461.48	2.71	451.36	470.14	467.94	2.48	460.24	476.03
Fork length (mm)	29.95	0.10	29.61	30.28	30.47	0.08	30.19	30.77
Survivorship (%)	34.84	2.45	28.00	43.75	36.36	2.44	29.50	44.00

Note: Survivorships used in the simulations are shown in the column headings. Distributions of fork lengths were generated using a linear (ln–ln) regression between otolith and fork lengths calculated by West and Larkin (1987). The error levels used in successive simulations are shown. Means and SDs were derived from 1000 distributions of 400 individuals.

addition to $s(y)$, a random uniform variate (l_i) was generated using RANUNI (SAS V6) and individual fish were categorized as survivors if l_i was less than $s(y)$; otherwise the fish was removed from the data set. Mean otolith and fork lengths of the survivors were obtained and these values were averaged among the 1000 data sets and SDs of the means calculated. The simulation was then repeated for the fork length data sets that had been generated with differing levels of error.

The nonlinear regression outlined above resulted in fish with fork lengths of 30.72 mm lying at the midpoint of the survivorship curve. These individuals had a 50% chance of being removed from the data sets during the simulation. Fish with fork lengths larger than this value had a greater chance of survivorship, while fish with lengths smaller than this value had a lower chance of survivorship. However, since this survivorship curve was calculated from single samples of the population, it represented only one possible estimate of the actual pattern of survivorship of the cohort from fry to smolt stages. Consequently, we altered slopes and intercepts to generate three new curves, each of which lay further to the left of the original survivorship curve on the *x*-axis (see Fig. 2) with midpoints at 30.5, 29.5, and 28.5 mm, respectively. These new curves were then applied to the data sets of fork length that had been generated with the differing errors shown above. This allowed us to examine the effect of differences in the position of the survivorship curve on shifts in otolith size at emergence between fry and smolt stages.

Results

Simulated data sets of otolith and fork lengths at emergence had mean values of 458.65 μm (± 1.55 SD) and 29.70 mm (± 0.04 SD), respectively. Changes in mean otolith and fork lengths at emergence in simulations where constant proportions of individuals below and above mean values of fork length underwent mortality are shown in Table 1. These survivorships (27 and 43%, 10 and 64% of fry below and above mean fork lengths) corresponded to those calculated by West and Larkin (1987) and used in simulations by Mosegaard

(1990). When they were applied to distributions of fork length generated with the same large error (0.037) used by Mosegaard (1990), the results were identical to those calculated by his simulation (Table 1, bottom block of data). For example, at survivorships of 27 and 43% below and above mean values of fork length, Mosegaard (1990) calculated that mean otolith length shifted to 461 μm, while mean fork length shifted to 29.97 mm. Using the same levels of error (0.037) and survivorship, our simulation produced shifts in mean otolith and fork length to 461.48 μm and 29.95 mm, respectively. At levels of survivorship of 10 and 64% above and below mean values, Mosegaard's simulation resulted in shifts of mean otolith length to 467 μm and a shift in fork length to 30.42 mm, while our simulation produced shifts in mean otolith and fork lengths to 467.94 μm and 30.47 mm, respectively.

When our simulation applied mortality as a step-function to data sets of fork length that had been generated using smaller errors, so that fish and otolith size were more closely correlated, the resulting shifts in mean otolith and fish size were still smaller than those found by West and Larkin (1987). The application of uniform survivorships of 10 and 64% below and above mean fork length to data sets where otolith and fish size were tightly coupled (error = 0.005, equivalent to $r^2 = 0.95$) shifted mean otolith length to only 476.6 μm (± 2.14 SD, Table 1), a value well below the shift to 493 μm that was recorded by West and Larkin (1987).

Shifts in mean otolith and fork length after the survivorship curve (Fig. 2) was applied to the distributions of fork lengths at emergence are shown in Table 2. When the curve was imposed on the fork length data set that had been generated without error, mean otolith size shifted to 504.81 μm (± 4.48 SD). When applied to distributions of fork length that were generated using a relatively large error (0.037), there was a shift in mean fork length to 31.34 mm (± 0.07 SD) and a

Table 2. Mean otolith and fork lengths at emergence of a cohort of sockeye salmon after application of a survivorship curve to distributions of fork lengths that were generated using a linear (ln–ln) regression between otolith and fork lengths calculated by West and Larkin (1987).

	Mean	SD	Min.	Max.
Error = 0, $r^2 = 1$				
Otolith length (µm)	504.81	4.48	491.47	523.05
Fork length (mm)	30.58	0.08	30.32	30.94
Survivorship (%)	7.76	1.27	3.75	11.5
Error = 0.005, $r^2 = 0.95$				
Otolith length (µm)	503.21	4.24	490.80	519.44
Fork length (mm)	30.61	0.08	30.38	30.93
Survivorship (%)	8.24	1.31	4.50	12.25
Error = 0.015, $r^2 = 0.68$				
Otolith length (µm)	494.22	3.58	483.14	509.92
Fork length (mm)	30.80	0.07	30.59	31.02
Survivorship (%)	11.72	1.62	7.25	17.25
Error = 0.02, $r^2 = 0.54$				
Otolith length (µm)	489.37	3.35	478.62	501.52
Fork length (mm)	30.92	0.07	30.71	31.14
Survivorship (%)	14.24	1.80	9.25	20.50
Error = 0.037, $r^2 = 0.26$				
Otolith length (µm)	477.59	2.87	467.14	487.18
Fork length (mm)	31.34	0.07	31.07	31.59
Survivorship (%)	22.57	2.20	15.7	31.75

Note: Distributions were generated using errors of 0, 0.005, 0.015, 0.02, and 0.37. Means and SDs were derived from 1000 distributions of 400 individuals. The equation for the survivorship curve is given in the Methods section.

corresponding shift in otolith length to 477.59 µm (± 2.87 SD). Application of the survival curve to distributions of fork length that had been generated using a small error (0.005) resulted in a smaller shift in mean fork length to 30.61 mm (± 0.08 SD) but a much greater shift in mean otolith length to 503.21 µm (± 4.24 SD).

The imposition of the survivorship curve on distributions of fork lengths that had been generated without an error component gave a total survivorship of the cohort from fry to smolt stages of 7.8%. When the survivorship curve was applied to the distributions of fork lengths that had been generated with error components, survivorship increased (Table 2). Distributions that were generated using a medium amount of error (0.015), corresponding to a relationship between otolith and fork length where $r^2 = 0.68$, showed a shift in mean otolith length equivalent to that found by West and Larkin (1987). This shift was achieved with a survivorship of 11.72% (± 1.62 SD). Where a greater level of error (0.02, corresponding to an r^2 of 0.54) was introduced into the generation of fork length distributions, application of the survivorship curve resulted in a shift in mean otolith length that was slightly smaller than the value recorded by West and Larkin (1987), but still within 1.5 SD of their estimate. This shift was obtained with a total survivorship of 14.24% (± 1.80 SD).

By altering the slope and intercept of the survivorship curve derived from the comparison of otolith size distributions, three new curves were produced that allowed progressively greater survivorship of the cohort between fry and smolt stages. Application of these new curves to distributions of fork length generated using the differing levels of error usually resulted in smaller shifts in mean otolith size at emergence than the shift found when the original curve was used in the simulation (Table 3). When the first of these curves was applied to data sets of fork length generated with a level of error of 0.005, the resultant shifts in mean otolith and fork lengths were indistinguishable from those recorded by West and Larkin (1987). These were achieved with a survivorship of 15.11% (± 1.87 SD). When this curve was applied to fork lengths generated with an error of 0.02, fork length shifted to 30.74 mm (± 0.05 SD) and otolith length to 484.90 µm (± 2.77 SD). In this case, about 20% of the cohort survived to the smolt stage. Application of the remaining survivorship curves resulted in shifts of mean otolith length to values that were considerably smaller than that recorded by West and Larkin (1987), irrespective of the amount of error used in the generation of distributions of fork length.

Discussion

Varying the strength of the regression relationship between otolith and fish size and the imposition of a survivorship curve on distributions of fork length had major effects on the amount of size-selective mortality required to produce shifts in mean otolith length at emergence in a cohort of young sockeye salmon. We were able to reproduce the results of Mosegaard's (1990) study by repeating his simulation protocol, where mortality was applied as a step-function to distributions of fork length that had been generated using a large amount of error (0.037). When the strength of the correlation between otolith and fish size was increased and mortality again applied as a step-function to fork lengths, our simulation achieved shifts in mean otolith length at emergence that were greater than those found in Mosegaard's (1990) study, but were still considerably smaller than the shift recorded by West and Larkin (1987). However, the use of a survivorship curve, rather than removal of constant fractions of the cohort above and below mean values of fork length, resulted in shifts in mean otolith length that were often greater than the value recorded in the Babine Lake system.

The survivorship curve enabled us to create shifts in mean otolith length comparable with those described by West and Larkin (1987) at survivorships ranging from 7.6 to 20% of the cohort between fry and smolt stages. Prior to the study of West and Larkin (1987), McDonald and Hume (1984) monitored survival of sockeye salmon in Babine Lake over a 16-year period. Based on estimates of numbers of fry entering and smolts exiting the lake, they calculated that survival rates between these stages ranged from 7.5 to 49.9% (mean 30.44, SD 10.82). Thus, our shifts in mean otolith length at emergence were achieved at survivorships within the range of values that have been observed under natural conditions. In contrast, simulations of size-selective mortality by Mosegaard (1990) were unable to replicate the change in mean otolith length found by West and Larkin (1987) without the imposition of mortalities that were up to an order of magnitude greater than those recorded by McDonald and Hume (1984). Our simulations show that this result was probably due to the assumption by Mosegaard (1990) that mortality would remove constant

Table 3. Mean otolith and fork lengths at emergence of a cohort of sockeye salmon after application of three survivorship curves to distributions of fork lengths that were generated using a linear (ln–ln) regression between otolith and fork lengths calculated by West and Larkin (1987).

	Curve 1		Curve 2		Curve 3	
	Mean	SD	Mean	SD	Mean	SD
Error = 0, $r^2 = 1$						
Otolith length (µm)	495.71	3.06	472.91	1.71	463.81	1.52
Fork length (mm)	30.41	0.06	29.98	0.03	29.80	0.03
Survivorship (%)	14.42	1.76	58.01	2.42	84.90	1.78
Error = 0.005, $r^2 = 0.95$						
Otolith length (µm)	494.66	3.13	472.80	1.71	463.80	1.52
Fork length (mm)	30.44	0.05	29.99	0.03	29.80	0.03
Survivorship (%)	15.11	1.87	57.89	2.45	84.74	1.79
Error = 0.015, $r^2 = 0.68$						
Otolith length (µm)	488.50	2.90	471.80	1.72	463.85	1.53
Fork length (mm)	30.62	0.06	30.09	0.04	29.85	0.03
Survivorship (%)	18.44	1.96	57.05	2.45	83.35	1.88
Error = 0.02, $r^2 = 0.54$						
Otolith length (µm)	484.90	2.77	471.14	1.78	463.86	1.60
Fork length (mm)	30.74	0.05	30.17	0.04	29.88	0.04
Survivorship (%)	20.72	1.95	56.50	2.49	82.26	1.90
Error = 0.037, $r^2 = 0.26$						
Otolith length (µm)	475.87	2.61	468.67	1.94	463.73	1.65
Fork length (mm)	31.17	0.07	30.52	0.06	30.10	0.06
Survivorship (%)	27.99	2.28	54.89	2.51	77.46	2.06

Note: Distributions were generated using errors of 0, 0.005, 0.015, 0.02, and 0.37. Means and SDs were derived from 1000 distributions of 400 individuals. Each curve lay to the left on the *x*-axis of the original survivorship curve shown in Fig. 2. Midpoints for curves 1–3 were 30.5, 29.5, and 28.5 mm, respectively.

proportions of the cohort above and below mean values of fork length and that otolith and fish size were weakly correlated (r^2 0.255).

When survivorship curves were imposed on distributions of fork lengths, it was not necessary to assume that fish and otolith size were strongly correlated ($r^2 > 0.80$) to achieve a shift in mean otolith length that was comparable with that recorded in the field by West and Larkin (1987). Application of the size-selective survivorship curve to fork length distributions that were generated using an error of 0.02, equivalent to a regression relationship where otolith and fish size were moderately correlated (r^2 0.54), resulted in a shift in mean otolith length at emergence to 489 µm and a survivorship of 14% of the cohort from fry to smolt stages. Regression analyses calculated by West and Larkin (1987) between otolith size and fork length of fry at emergence show that a correlation of this strength could be obtained by using area of the otolith as a measure of size, rather than total length. Such changes in the strength of regression relationships probably reflect the relative amounts of measurement error that are associated with differing estimates of otolith size (Meekan et al. 1998).

Our results show that it is not necessary to invoke mortality based on selection for any trait of individuals other than body size (fork length) to account for the results of West and Larkin (1987). Differences in size among individuals are known to have an important influence on dominance hierarchies and life history patterns at older ages in salmonids (Fausch 1984; Metcalfe et al. 1992). West and Larkin (1987) suggested that size

differences among members of a cohort of young salmon are established at the time of emergence and are then propagated by growth. Meekan et al. (1998) have shown that such variation may in turn be generated from differences among individuals that are present at hatching. This implies that the traits upon which selective mortality will act may be established at hatching.

There is little direct evidence of selective mortality of salmon fry as a function of variability in metabolic rates among individuals rather than body size (selection for growth potential). With the exception of the simulation study of Mosegaard (1990), the only other published evidence that this process might occur has been the work of Titus and Mosegaard (1991). In their study, brown trout (*Salmo trutta*) fry that were raised in tanks underwent selective mortality so that the surviving individuals were those that had large otoliths at emergence. From a simulation based on growth and starvation rates, they concluded that this mortality was unlikely to be size selective. As in Mosegaard's (1990) study, a weak relationship (r^2 0.06) between otolith and fish size was a central assumption of their simulation. However, the strength of correlations between these variables recorded by Titus and Mosegaard (1991) may have been influenced by the use of dry weights as a measure of fish size. At emergence, it is likely that traits of fry other than body size such as gut contents, condition, and the amount of yolk sac absorption contribute to measures of dry weight. Furthermore, the weight of remaining yolk at emergence should be negatively correlated with fish size. Due to such

confounding influences, weak correlations between otolith and fish size might be expected when dry weight is used as a body size measure at emergence. The present study demonstrates that this will have an important influence on the amount of size-selective mortality that is required to produce shifts in mean otolith size in a cohort of young fish. Despite these caveats, it is still possible that metabolic rates may contribute to the process of selective mortality that occurs during the early life history of salmonid fishes, since growth and metabolic rates will be strongly correlated.

Acknowledgments

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