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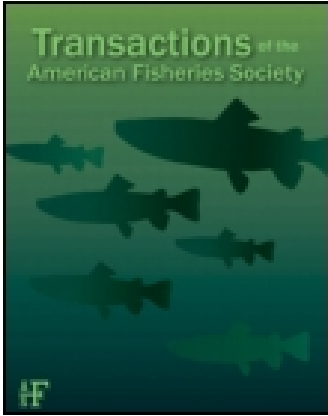
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Transactions of the American Fisheries Society

Publication details, including instructions for authors and subscription information:

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Published online: 09 Jan 2011.

To cite this article: Terry D. Beacham & Clyde B. Murray (1990) Temperature, Egg Size, and Development of Embryos and Alevins of Five Species of Pacific Salmon: A Comparative Analysis, Transactions of the American Fisheries Society, 119:6, 927-945, DOI: [10.1577/1548-8659\(1990\)119<0927:TESADO>2.3.CO;2](https://doi.org/10.1577/1548-8659(1990)119<0927:TESADO>2.3.CO;2)

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TRANSACTIONS

OF THE AMERICAN FISHERIES SOCIETY

Volume 119

November 1990

Number 6

Transactions of the American Fisheries Society 119:927-945, 1990

Temperature, Egg Size, and Development of Embryos and Alevins of Five Species of Pacific Salmon: A Comparative Analysis

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Abstract.—We examined rate of development to alevin hatching and fry emergence, embryo and alevin survival, and alevin and fry size for five Pacific salmon species. There was little difference among values for hatching and emergence time predicted by a modified thermal sums model, power law model (log-inverse Belchrádek), or quadratic model. Coho salmon *Oncorhynchus kisutch* had the fastest rates of development to hatching and emergence of the five species investigated; rankings for the other species depended upon temperature range. Coho salmon embryos had the highest survival rates at low incubation (1.5°C) temperatures. Embryos of pink salmon *O. gorbuscha* had the lowest survival at temperatures less than 4°C. For all five species, incubation temperature was the more important factor in determining alevin length, and egg size was the more important factor in determining alevin weight. Egg weight was a major determinant of fry weight at emergence. Rates of development to hatching and emergence, and alevin and fry size, differed by species in response to changes in temperature. Coho salmon alevins and fry were proportionately larger at 4°C than at 8°C or 12°C, but alevins and fry of pink salmon and chum salmon *O. keta* were largest at 8°C. Variation in development characters of Pacific salmon reflected adaptations to each species' life history pattern.

Variation in life history characters of Pacific salmon can be extensive, both among the five North American species and among spawning populations within species. Spawning time varies among and within species, and spawning times of specific populations are often related to specific water temperatures (Sheridan 1962; Brannon 1987). Embryos and alevins can be exposed to a wide temperature range during development, yet the effect of temperature regime on survival and development to fry emergence remains poorly documented, particularly at low temperatures (Alderdice and Velsen 1978; Crisp 1981, 1988). Water temperature has been the primary factor investigated in development rate studies (Emboddy 1934; Bailey and Evans 1971; Tang et al. 1987), but egg size (Rombough 1985) and genetic vari-

ation (Beacham 1988) have also been investigated.

Accurate prediction of hatching and emergence times is of practical interest in salmon culture (Rombough 1985), and some attempts have been made for some specific salmonid species (Alderdice and Velsen 1978; Crisp 1981, 1988; Jungwirth and Winkler 1984; Humpesch 1985; Tang et al. 1987; Elliott et al. 1987). Crisp (1988) indicated that the ideal approach would be to establish a set of curves relating times of hatching and emergence to temperature for each salmonid species. This has not yet been done in a systematic manner for Pacific salmon, but we have attempted this task in our study.

In our investigations of Pacific salmon development, we examined variation in a number of

developmental characters over a wide range of incubation temperatures from a number of salmon populations (Appendix Table A.1). For this study, we integrated the data from previous studies of Pacific salmon development (compiled by Velsen 1987) with more recent data to compare development in pink salmon *Oncorhynchus gorbuscha*, chum salmon *O. keta*, chinook salmon *O. tshawytscha*, sockeye salmon *O. nerka*, and coho salmon *O. kisutch*. We compared a number of models relating hatching and emergence timing to temperature for each species, and related variations in development among species to life history variations. We also evaluated the relative influences of temperature and egg weight variations on variations in alevin and fry length and weight. Finally, the size differences among species in alevin and fry were compared with differences among populations within species and among temperatures.

Methods

Hatching and emergence timing.—The data base we used was derived from Velsen (1987), and additional data on hatching and emergence times were obtained from the references in Appendix Table A.1. Ten models were fitted to the hatching and emergence times for each species. For each model, D was the observed hatching or emergence time after fertilization; T was the observed mean temperature (°C); S was the timing of spawning in the population (days after January 1); and a , b , c , and d were the constants we obtained from the fitted data. We used hatching and emergence data from both constant and variable incubation regimes. Data were transformed to natural logarithms (base e) in all models. Nonlinear models were fitted by the simplex method of parameter estimation, and the standard deviations of the parameter estimates were calculated as in Mitterreiner and Schnute (1985). The comparison of model performance required that a common data base be used for all models. Because some models (5 and 6) required knowledge of population spawning time, some data for each species were omitted if spawning time was unknown. Data for pink salmon were separated into the brood line of origin (populations spawning in either odd- or even-numbered years), because there are significant differences in developmental characters between pink salmon in the two brood lines (Beacham and Murray 1988).

The first six equations we examined were variants of a power law model (Alderdice and Velsen

1978; Murray 1980; Crisp 1981; Jungwirth and Winkler 1984; Humpesch 1985):

$$\log_e D = \log_e a - \log_e T; \quad (1)$$

$$\log_e D = \log_e a - \log_e (T - b); \quad (2)$$

$$\log_e D = \log_e a + b \log_e T; \quad (3)$$

$$\log_e D = \log_e a + b \log_e (T - c); \quad (4)$$

$$\log_e D = \log_e a + b \log_e (T - c) + d \log_e S; \quad (5)$$

$$\log_e D = \log_e a + b \log_e (T - c) + dS. \quad (6)$$

The next two models we investigated were polynomial expressions (Bottrell 1975; Tang et al. 1987):

$$\log_e D = \log_e a + b \log_e T + c(\log_e T)^2; \quad (7)$$

$$\log_e D = \log_e a + bT + cT^2. \quad (8)$$

Our final models were of the logistic or exponential type (Alderdice and Velsen 1978; Kogan 1984; Kane 1988):

$$\log_e D = \log_e a - \log_e (1 + e^b + cT); \quad (9)$$

$$\log_e D = ae^{bT}. \quad (10)$$

The goodness of fit of each model was evaluated by examining the residual sum of squares between observed and predicted values.

Variation in hatching and emergence times was also analyzed by a two-way analysis of variance (ANOVA); species, temperature, and species-temperature interaction were the sources of variation in the model. Class width for temperatures was set at 1°C intervals.

Embryo and alevin survival.—We derived embryo and alevin survival rates with respect to temperature from the data compiled by Velsen (1987), supplemented by additional sources (Appendix Table A.1). Survival rate data were used only when they were derived from constant-temperature experiments. Unweighted mean survival rates were determined for 0.5°C temperature intervals, and the results were plotted. The lower and upper temperatures at which 50% of embryos died were determined by inspection of the plotted data for each species. The upper and lower temperatures at which 50% of alevins died could not be determined for any species. This occurred because embryos were more sensitive to extreme temperatures during development than were alevins, and the death of embryos resulted in no data for alevins.

Alevin and fry size.—Data for predictions of alevin and fry size, given egg size and developmental temperature, were derived from studies conducted in our laboratory (Appendix Table A.1), in which a constant temperature regime was main-

tained during development. When the preserved samples of alevins and fry were measured and weighed, fork length was recorded in our laboratory to the nearest 0.1 mm, total weight was recorded to the nearest milligram, the yolk was separated from the rest of the body and weighed (mg), and tissue weight was determined by subtraction (total weight - yolk weight). Usually 30 alevins and 30 fry were sampled from each female at each constant temperature, and the means of each character examined were used in subsequent analyses.

Because the original data were obtained from samples that had been preserved in 10% formalin, they were transformed to fresh sample length and weights by multiplying preserved, water-hardened egg weight by 0.86, alevin length by 1.03, alevin weight by 0.91, fry length by 1.05, and fry weight by 0.88 (Murray 1980). Four models were fitted to the alevin and fry length data. In all models, L was fork length (mm); T was temperature during development ($^{\circ}\text{C}$); W was fresh, water-hardened egg weight (mg); and a , b , c , and d were fitted constants. Temperatures included in the analysis were 1.5 $^{\circ}\text{C}$ (coho salmon only); 2 $^{\circ}\text{C}$ (coho and sockeye salmon); 4 $^{\circ}\text{C}$, 8 $^{\circ}\text{C}$, and 12 $^{\circ}\text{C}$ (all species); and 15 $^{\circ}\text{C}$ (all species except coho salmon). Data points were lengths and weights of alevins or fry by female at each temperature. The models were

$$\log_e L = \log_e a + b \log_e W + c \log_e T + d (\log_e T)^2; \quad (11)$$

$$\log_e L = \log_e a + b \log_e W + c \log_e T; \quad (12)$$

$$L = a + bW + cT + dT^2; \quad (13)$$

$$L = a + bW + cT. \quad (14)$$

The fit of each model to the observed data was evaluated by examining the proportion of total variation accounted for (R^2). We examined prediction of alevin and fry weight by models (13) and (14), with weight as the dependent variable.

The relative effects of temperature and egg weight variation on subsequent alevin and fry size were investigated with the ANOVA model

$$Y_{ijk} = \mu + T_i + W_j + TW_{ij} + e_{ijk}; \quad (15)$$

Y_{ijk} = the observed alevin or fry size; μ = overall mean size; T_i = effect of temperature; W_j = effect of egg weight-class; TW_{ij} = interaction between temperature and egg weight; and e_{ijk} = effect of the k th observation in subgroup ij . Temperatures for each species analysis have been previously outlined. Five egg weight-classes (mg) were used for each species (Table 1). We determined the proportion of total observed variation in alevin and

TABLE 1.—Egg weight-classes used in ANOVA to examine relative effects of temperature and egg weight on alevin and fry size for five species of Pacific salmon.

Salmon species	Class boundaries (mg)
Pink	≤ 135 , 136–160, 161–190, 191–220, ≥ 221
Chum	≤ 190 , 191–235, 236–280, 281–325, ≥ 326
Chinook	≤ 315 , 316–355, 356–395, 396–435, ≥ 436
Coho	≤ 165 , 166–230, 231–295, 296–360, ≥ 361
Sockeye	≤ 90 , 91–110, 111–130, 131–150, ≥ 151

fry length and weight accounted for by temperature and egg weight by estimating variance components for each of the effects in the analysis and dividing by the total observed variation. Each species was examined separately.

We examined variation in alevin and fry lengths and weights within and among species with the ANOVA model

$$Y_{ijk} = \mu + S_i + P_{ij} + T_k + ST_{ik} + PT_{ijk} + e_{ijk}; \quad (16)$$

Y_{ijk} = observed mean character size; μ = overall mean size; S_i = effect of species; P_{ij} = effect of population within species; T_k = effect of temperature during development; ST_{ik} = interaction between species and temperature; PT_{ijk} = interaction between populations within species and temperature; and e_{ijk} = effect of the l th observation in subgroup ijk . Temperatures included in the analysis were 2, 4, 8, 12, and 15 $^{\circ}\text{C}$. Variance components were determined for each effect in the analysis. Satterthwaite's (1946) approximation was necessary for an appropriate test of the effect of species.

Results

Hatching Time

Accuracy of estimation of hatching time varied among the models investigated; more accurate models had lower residual sums of squares (Table 2). Model (1), the thermal sums model, assumes that hatching requires a constant number of degree-days or accumulated thermal units (days \times temperature) above 0 $^{\circ}\text{C}$. It generally provided the poorest description of hatching time, and its residual sum of squares was generally the highest of all the models. Model (2), a variant of the thermal sums model, assumes that hatching requires a constant number of degree-days above a threshold temperature that is estimated separately for each species. This temperature correction to model (1) improved predictions of hatching times signifi-

TABLE 2.—Residual sums of squares between observed and predicted values for hatching and emergence times for 10 models and five Pacific salmon species. TSS is total observed sum of squares; *N* is the number of data points used in each analysis.

Model or statistic	Pink salmon		Chum salmon	Chinook salmon	Coho salmon	Sockeye salmon
	Odd year	Even year				
Hatching time						
1	2.492	3.150	2.172	0.097	3.687	5.248
2	0.587	0.241	0.543	0.093	1.019	0.378
3	0.738	0.270	0.733	0.097	1.549	0.915
4	0.559	0.237	0.491	0.059	0.743	0.276
5	0.468	0.224	0.426	0.057	0.741	0.246
6	0.539	0.224	0.506	0.057	0.741	0.330
7	0.556	0.242	0.489	0.058	0.745	0.269
8	0.512	0.195	0.559	0.079	0.764	0.267
9	0.755	0.599	1.725	0.364	1.754	0.555
10	0.646	0.465	1.115	0.213	1.149	0.393
TSS	10.821	13.081	36.271	10.160	42.171	18.087
<i>N</i>	80	85	160	48	120	64
Emergence time						
1	1.069	3.197	1.757	0.419	4.900	6.780
2	0.102	0.040	0.699	0.395	0.579	0.827
3	0.072	0.074	0.454	0.416	0.777	2.923
4	0.072	0.040	0.326	0.263	0.575	0.807
5	0.060	0.037	0.271	0.259	0.571	0.724
6	0.074	0.038	0.620	0.261	0.581	0.727
7	0.072	0.040	0.329	0.264	0.572	0.797
8	0.077	0.042	0.360	0.273	0.612	0.798
9	0.377	0.122	1.214	0.398	1.567	1.751
10	0.295	0.093	1.662	0.300	1.151	1.390
TSS	6.079	6.511	26.274	8.858	26.773	25.697
<i>N</i>	58	54	112	53	92	106

cantly. Model (3), a basic parabolic curve, provided a less accurate description of hatching time than did model (2). When a temperature correction was incorporated in the basic parabolic curve (model 4, the log-inverse Belehrádek model), it produced a more accurate fit for all species, as did a spawning time correction incorporated into the log-inverse Belehrádek model (5). However, comparison of models (5) and (6) indicated that spawning time should be incorporated in the logarithmic form. The quadratic model (7) provided a reasonably accurate description of hatching time, as did a semilogarithmic form of the quadratic model (8). Although a logistic model (9) and exponential model (10) described hatching time more accurately than model (1) and generally accounted for at least 95% of the observed variation in hatching time, models (2)–(8) provided greater accuracy in data description.

Our choice of which model to use was based on model performance, particularly accuracy in describing hatching time at low incubation temperatures. We chose models (2), (4), (5), and (7) for further consideration because of their low residual sums of squares. Model (2) was generally the least

accurate and model (5) the most accurate in describing data over the observed temperature range for each species, as indicated by the proportion of variance (r^2) explained by each model (Appendix Table A.2). Differences among the models were minor, usually less than 1% of the total observed variation. Performances of models (2), (4), and (7) at low incubation temperatures were similar (Figure 1). Model (5) could not be compared graphically with the other models because it contained two independent variables.

Hatching time data were available for mean incubation temperatures between 2 and 3°C for odd- and even-year pink salmon and for chum and chinook salmon, and between 1 and 2°C for coho and sockeye salmon. Predictions of hatching time at 1°C were made with models (2), (4), and (7), but the predictions were extrapolations because a mean incubation temperature of 1°C until hatching was outside of the range of temperatures investigated. Predicted hatching times at 1°C were generally higher for model (2) than for models (4) and (7) (Table 3). All three models may have overestimated hatching time for chinook salmon at 1°C. Models (2), (4), and (7) all provided good descrip-

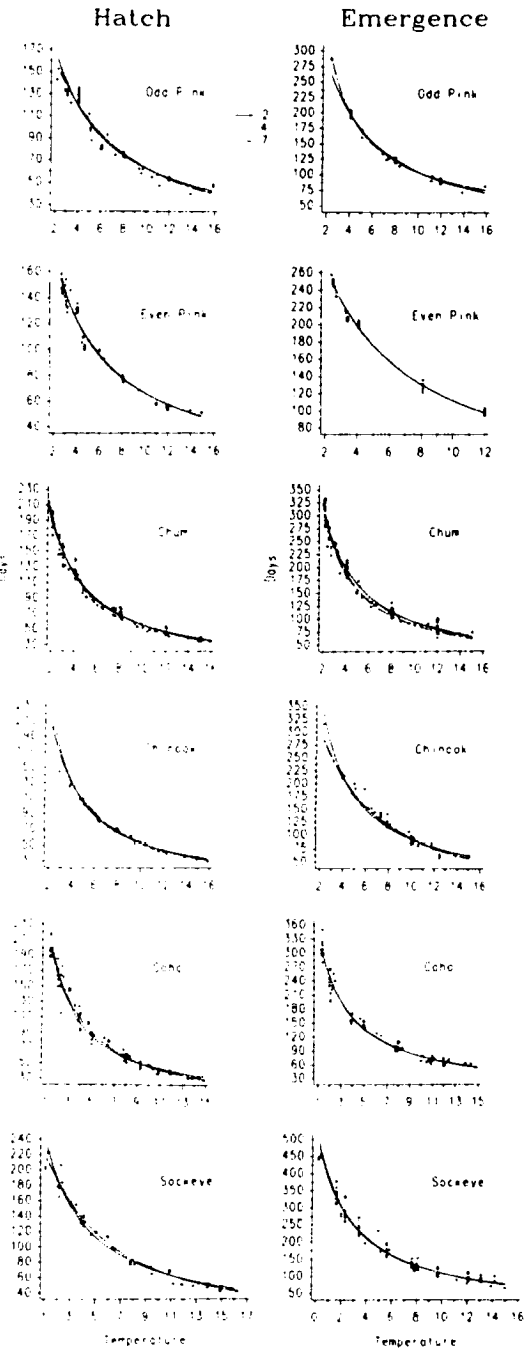


FIGURE 1.—Observed and predicted times (d) of alevin hatching and fry emergence in relation to temperature (°C) for five species of Pacific salmon, including pink salmon spawned in odd or even years. Data points were derived from Velsen (1987) and references in Appendix Table A.1; predictions are from models (2), (4), and (7).

TABLE 3.—Hatching and emergence times at 1°C for Pacific salmon, predicted by three different models.

Salmon species	Model		
	2	4	7
Hatching time			
Pink (odd year)	220	197	173
Pink (even year)	218	232	246
Chum	293	262	270
Chinook	476	314	340
Coho	250	219	217
Sockeye	246	225	217
Emergence time			
Pink (odd year)	362	568	564
Pink (even year)	323	326	329
Chum	440	532	567
Chinook	724	409	365
Coho	344	338	344
Sockeye	386	379	392

tions of the available data, but models (4) and (7) may have provided more reliable extrapolations at very low temperatures.

Significant effects of population spawning time on subsequent hatching time were observed for odd-year pink salmon, chum salmon, and sockeye salmon, and the *d* constant in model (5) was significantly different from zero for these species (Appendix Table A.2). In these species, alevin hatching occurred later in early spawning populations compared with late-spawning populations when the same incubation temperature was examined.

Development rates to hatching time clearly differed among the species investigated ($F = 4.56$; $df = 60, 477$; $P < 0.01$). Although each species showed a general decrease in hatching time with increasing incubation temperature, coho salmon generally had the fastest rate of development at all observed temperatures (Figure 2), whereas sockeye and pink salmon had the slowest rate of development at temperatures above 5°C. Hatching time of even-year pink salmon alevins was later than that of odd-year alevins for all temperatures investigated, but the differences were greater at the higher incubation temperatures (Figure 2). At about 5°C, hatching time of pink, chum, and chinook salmon alevins was similar. Below 5°C, development rate of chinook salmon alevins slowed considerably relative to the other species, and below 3°C, they required the longest time to hatch.

Emergence Time

As they were for hatching time, models (1), (9), and (10) were less accurate in predicting emergence time than the other seven models (Table 2),

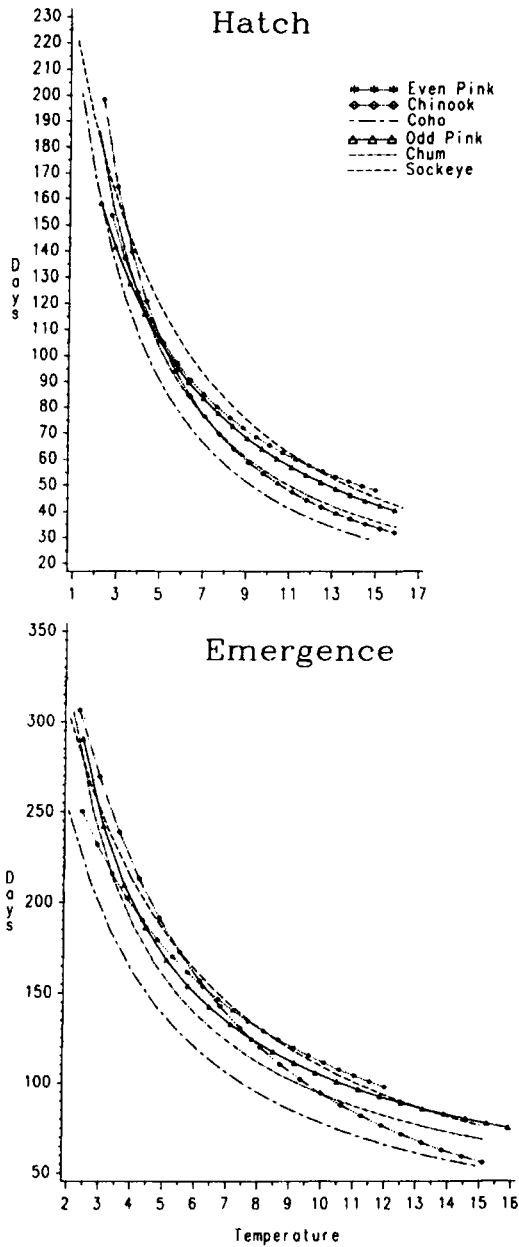


FIGURE 2.—Comparison of predicted (model 4) hatching and emergence times (d) in relation to temperature ($^{\circ}\text{C}$) for five species of Pacific salmon, including pink salmon spawned in odd or even years.

although models (9) and (10) accounted for about 95% of the observed variation in emergence time. Model (5) consistently provided the most accurate description of the emergence data for the five species examined, but the remaining models were almost as accurate (Table 2).

Again, further examination of models (2), (4), and (7) revealed that, as for hatching time, differences among the models were minor (usually $< 1\%$ of the observed variation). The accuracy of each model in describing emergence time at low incubation temperature was similar (Figure 1). Model (4) may have provided a better description at very low incubation temperatures, as illustrated for sockeye salmon at 0.25°C (Figure 1).

Population spawning time had a significant effect on timing of fry emergence for pink, chum, and sockeye salmon, and the effect was most marked in chum salmon (Appendix Table A.3). Fry emergence occurred later in early spawning populations compared with late-spawning populations at the same incubation temperature.

Development rates to fry emergence varied significantly ($F = 5.63$; $df = 46, 398$; $P < 0.01$) among the species compared, and coho salmon fry took the shortest time to emerge at any temperature examined (Figure 2). At temperatures above 4°C , odd-year pink salmon fry emerged earlier than even-year fry, but the reverse was true below 4°C ; thus, there was a differential effect of temperature on developmental rate of pink salmon with respect to brood line. Sockeye and pink salmon fry took the longest time to emerge at incubation temperatures above 8°C , but at temperatures below 4°C , chinook salmon fry took the longest time to emerge.

Embryo and Alevin Survival

The lower temperature at which 50% of embryos died was 3.5°C for even-year pink salmon, 4.5°C for odd-year pink salmon, 2.5°C for chum salmon, 3.0°C for chinook salmon, and 1°C for both sockeye and coho salmon (Figure 3). In general, sockeye and coho salmon were better adapted than pink and chum salmon to withstand very low water temperature during development, and chinook salmon had an intermediate tolerance. The upper temperature at which 50% of embryos died was above 15°C for even-year pink salmon, about 15.5°C for odd-year pink salmon, above 16°C for chum salmon, 16°C for chinook salmon, 15.5°C for sockeye salmon, and 13.5°C for coho salmon (Figure 3). Thus, sockeye and coho salmon embryos were the best adapted to survive at low incubation temperatures, but among the poorest adapted to survive at high incubation temperatures.

Alevin survival rates were greater than 90% at about 2°C for all species except pink salmon; for that species, complete embryo mortality at 2°C

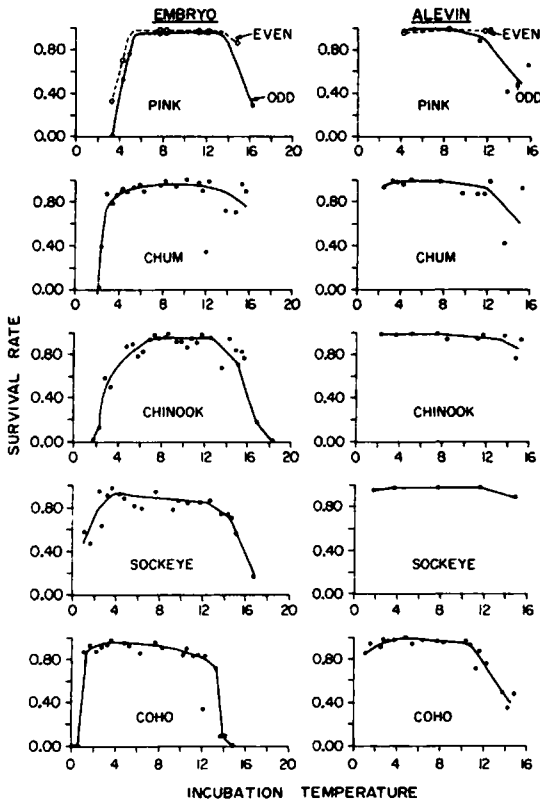


FIGURE 3.—Observed survival rates of embryos and alevins during development under constant temperature (°C) regimes for five species of Pacific salmon, including pink salmon spawned in odd or even years.

precluded information on alevin survival rates. The upper temperature of 50% alevin mortality was uncertain for all species except coho salmon; incubation temperatures in excess of 14°C caused mortality above 50% for these fish (Figure 3). As for embryos, coho salmon alevins appeared to be less well adapted to high water temperatures than the other species.

Alevin and Fry Size

Of four polynomial expression models we compared that incorporated egg weight and temperature, alevin length was generally predicted most accurately from model (11) (Table 4). Because length-weight relationships are usually expressed as a power law model, it might be expected that the logarithmic form of the polynomial model would be a substantially better description of length variation than a nonlogarithmic form. However, only a marginal improvement in the fit of the model to the observed data was obtained. Of non-

TABLE 4.—Proportion of total observed variation (R^2) accounted for by models (11–14) for alevin and fry length and weight for five species of Pacific salmon. N is the number of data points used in each analysis.

Salmon species	Length, by model				Weight, by model		N
	11	12	13	14	13	14	
Alevin							
Pink	0.34	0.12	0.31	0.12	0.70	0.68	342
Chum	0.32	0.16	0.29	0.13	0.80	0.78	282
Chinook	0.76	0.56	0.74	0.65	0.88	0.88	87
Coho	0.82	0.67	0.86	0.74	0.97	0.94	175
Sockeye	0.83	0.40	0.80	0.53	0.93	0.91	99
Fry							
Pink	0.27	0.22	0.27	0.23	0.45	0.42	341
Chum	0.53	0.46	0.52	0.46	0.71	0.66	282
Chinook	0.72	0.51	0.72	0.60	0.84	0.82	87
Coho	0.87	0.74	0.80	0.66	0.90	0.74	175
Sockeye	0.79	0.54	0.83	0.69	0.89	0.81	99

logarithmic forms of the polynomial model, model (13) always provided a better description of the data than model (14) (Table 4).

Initial egg size and water temperatures during development both contributed significantly to describing variation in alevin and fry size (Appendix Table A.4). Temperature variation was the more important factor in determining alevin length, and egg size the more important factor for alevin weight (Table 5). However, egg weight variation still accounted for about 10–30% of the observed variation in alevin length. Temperature had relatively less influence on fry length than on alevin length for pink, chum, and coho salmon (Table 5). How-

TABLE 5.—Percentage of total observed variation for alevin and fry length and total weight (model 15) caused by variance among incubation temperatures (V_t) and among egg weight-classes (V_w) for five species of Pacific salmon.

Salmon species	Length		Weight	
	V_t	V_w	V_t	V_w
Alevin				
Pink	29	12	4	50
Chum	11	9	2	53
Chinook	59	13	1	68
Coho	37	32	6	55
Sockeye	54	25	4	67
Fry				
Pink	4	20	2	37
Chum	4	33	5	44
Chinook	48	18	16	53
Coho	4	54	9	53
Sockeye	59	20	7	80

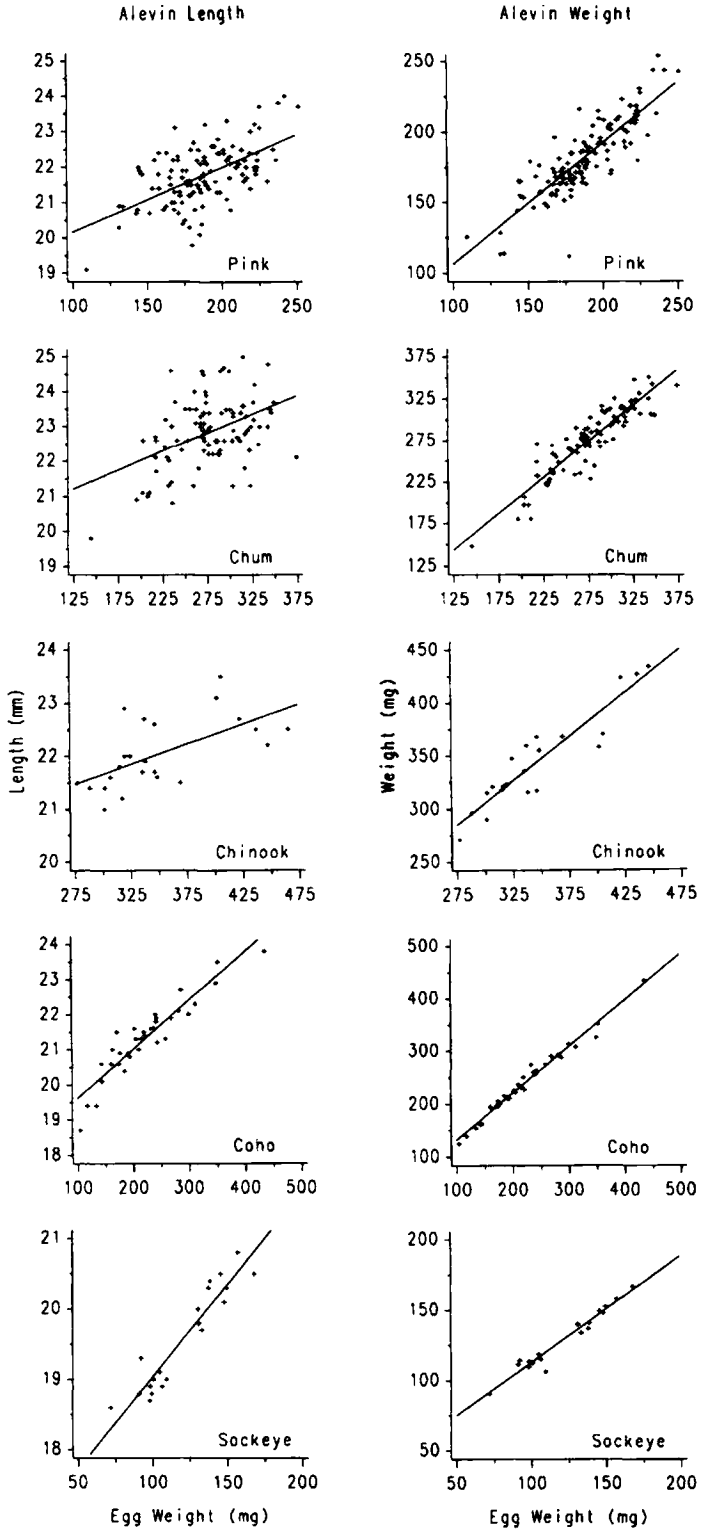


FIGURE 4.—Comparison of egg weight to length (mm) and weight (mg) of alevins at hatching under a constant temperature regime of 8°C during development for five species of Pacific salmon. Data for both brood lines of pink salmon are combined.

ever, for chinook and sockeye salmon, temperature variation still had an effect on fry length. Egg weight of all species was a major component of subsequent fry weight at emergence (Table 5).

At 8°C, variation in egg weight accounted for more variation in alevin weight at hatching than alevin length (Figure 4). If temperature is constant during development, alevin length and weight can be predicted from egg size (Figure 4), as can fry length and weight (Figure 5). Heavier eggs produce larger alevins and fry.

Significant differences ($P < 0.01$) among species were found for all alevin and size characters examined. The species variance component usually accounted for over 60% of total observed variation (Table 6). Significant differences ($P < 0.01$) were also found among populations within species; population variation was the next most significant variance component after species variance. Species and population differences largely reflected egg size differences both among and within species. Temperature variation had the greatest effect on alevin length and the least effect on yolk weights at hatching and emergence.

Different trends were observed in the response of species to changes in temperature during development for all characters examined (all differences were significant at $P < 0.05$), indicating that the species were adapted to different thermal regimes during development. For example, coho salmon alevins and fry were larger at a development temperature of 4°C and smaller at 12°C, whereas pink and chum salmon alevins and fry were largest at 8°C (Figure 6). Pink and chum salmon appear to be better adapted for development at warmer water temperatures than are chinook, sockeye, and coho salmon.

Discussion

We found little difference among values predicted by a modified thermal sums model, a power law (log-inverse Belehrádek) model, or a quadratic model over the observed temperature range. The models only differed significantly for low-temperature extrapolations. Additional data on hatching and emergence time at very low incubation temperatures are necessary in order to evaluate the different models (Alderdice and Velsen 1978; Crisp 1981). We obtained data on hatching and emergence times for mean temperatures below 3°C for all five salmon species examined. The choice of which model to use in describing hatching and emergence times is largely empirical in nature, in that the model that ac-

counts for the highest proportion of observed variation or that provides the most realistic extrapolations is generally favored by an individual investigator. If additional data become available on hatching and emergence timing at very low incubation temperatures, we expect that there will be little difference in values among the three models, provided the models are modified to take account of any new data.

Hatching of alevins is a distinctive event and can be determined objectively. Although temperature variation during development is a major source of variation in hatching time, additive genetic variation (McIntyre and Blanc 1973; Sato 1980; Beacham 1988), changes in temperature (Heggberget and Wallace 1984), oxygen concentrations (Silver et al. 1963; Garside 1966), and light intensity (Kwain 1975) can also influence hatching time. The timing of fry emergence or swim-up is more difficult to determine consistently among studies. When fry leave the gravel redd in the natural environment, they generally become neutrally buoyant and positively phototactic. These criteria have been used in laboratory studies to define the point at which fry emergence occurs (Mason 1976; Godin 1980; Beacham and Murray 1985). Alevins reared without gravel during development in the laboratory may swim up before alevins reared under an identical temperature regime in the natural environment, presumably because the latter are hampered by the physical difficulty of emerging from the gravel (Crisp 1988). In some cases, laboratory estimates of timing of emergence may underestimate such timing in the natural environment.

Rather than basing estimates of timing of emergence on neutral buoyancy or phototaxes, some investigators have used alevin weight criteria to define the timing. The most commonly used criterion is maximum alevin wet weight (Heming 1982; Rombough 1985), and a close correspondence between timing of emergence and achievement of maximum alevin wet weight has been reported (Heming 1982). Estimates of timing of complete yolk absorption by alevins have also been reported (Tang et al. 1987), as well as the timing of potential first feeding, defined as the point at which yolk weight is reduced to 5% of total weight (Kane 1988). In our study, data derived from different methods of estimating timing of emergence have been used, and we have assumed that estimates derived from the different methods are equivalent.

Holtby et al. (1989) fit semilogarithmic models

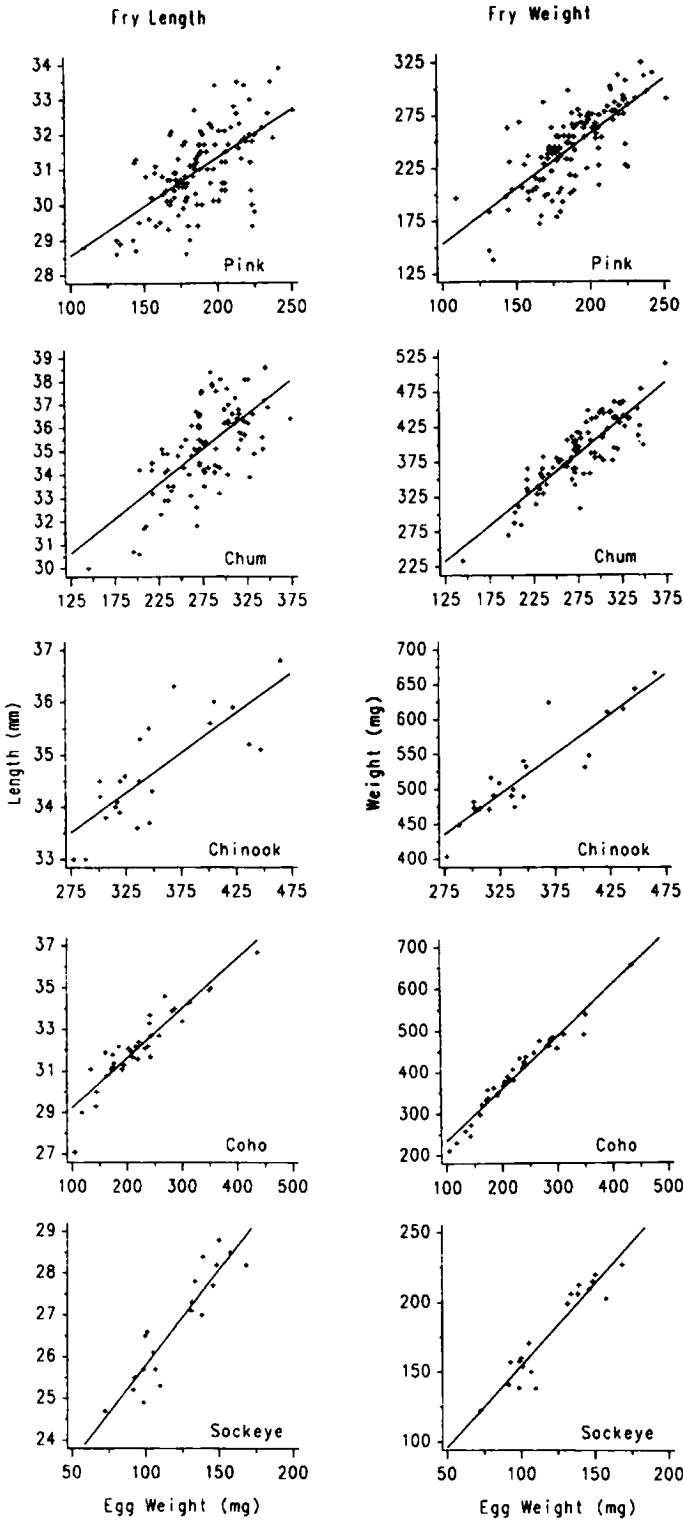


FIGURE 5.—Comparison of egg weight to length (mm) and weight (mg) of fry at emergence under a constant temperature regime of 8°C during development for five species of Pacific salmon. Data for both brood lines of pink salmon are combined.

TABLE 6.—Percentage of total observed variation (model 16) for alevin and fry developmental characters caused by variance among species (V_s), among populations within species (V_p), among temperatures (V_t), among species-temperature interactions (V_{st}), and among population-temperature interactions (V_{pt}), as well as by residual variance (V_e).

Character	V_s	V_p	V_t	V_{st}	V_{pt}	V_e
Alevin						
Length	47.7	15.7	10.8	8.9	5.5	11.4
Total weight	79.5	12.4	0.7	0.1	0.0	7.3
Yolk weight	79.0	11.9	0.5	0.3	0.0	8.3
Tissue weight	62.9	14.1	4.5	5.2	4.5	8.8
Fry						
Length	73.2	10.7	4.0	0.2	2.3	9.6
Total weight	82.5	9.1	1.6	0.5	0.4	5.9
Yolk weight	63.3	12.6	0.3	1.6	3.7	18.5
Tissue weight	80.6	8.7	2.7	0.7	1.5	5.8

to describe timing of emergence of chum and coho salmon fry in the natural environment. Although their models provided less accurate predictions than ours of the data that were used (chum salmon $r^2 = 0.88$; coho salmon $r^2 = 0.67$), and Holtby et al. were not certain of the timing of adult spawning in their study stream, their predicted times of emergence of chum salmon fry at 4°C (192 d versus 189 d from our model 4) and coho salmon fry (176 d versus 163 d from our model 4) were similar to our own. These agreements suggest that although we used data from laboratory studies our models may provide reasonable predictions of timing of fry emergence in the natural environment.

Species of Pacific salmon (pink, chum, chinook, coho, sockeye) generally spawn in the autumn, and water temperatures after egg fertilization decline during development. Compensation in development rate can be observed in all species in response to this decline. If the rate is measured in thermal units (degree-days), then more thermal units are required for hatching at high incubation temperatures than at low temperatures. This compensation minimizes the effect of abnormal temperature variations (Brannon 1987). Without such compensation, if water temperatures were unusually warm during development over the winter, fry emergence in the spring would occur earlier than normal, and fry survival would probably be reduced. However, the increased thermal unit requirement for development at higher temperatures would tend to minimize the effect of unusually warm water, and fry emergence would occur at a time more appropriate for survival.

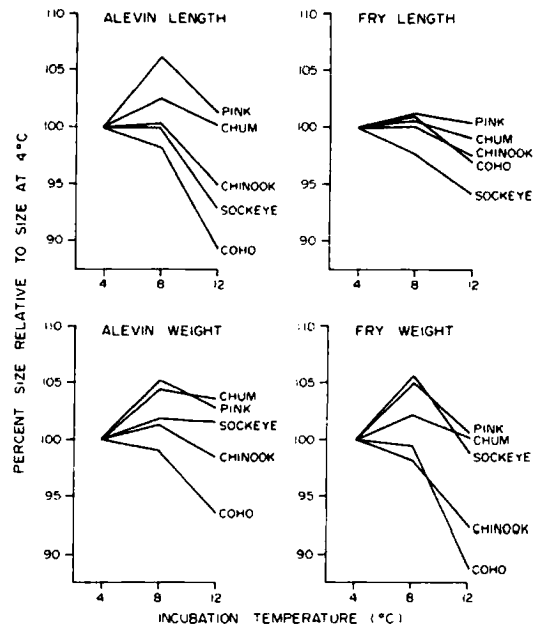


FIGURE 6.—Length and weight of Pacific salmon alevins and fry at incubation temperatures of 8 and 12°C relative to size at 4°C; size at 4°C is defined as 100%. Data for both brood lines of pink salmon are combined.

Water temperatures after egg fertilization increase in spring-spawning species. In contrast to autumn-spawning Pacific salmonids, spring-spawning species (rainbow trout *O. mykiss*, grayling *Thymallus thymallus*) require fewer thermal units at high incubation temperatures than at low temperatures (Jungwirth and Winkler 1984). As development occurs under a warming temperature regime, increased water temperatures would probably indicate more favorable conditions for enhanced survival, and fry emergence would occur earlier. The differential responses of autumn and spring spawners to changes in water temperature during development likely reflect adaptations to the environmental conditions they encounter during development.

Variation among Pacific salmon species was observed in development rate, embryo and alevin survival, and alevin and fry size when the same temperatures occurred during development. Coho salmon had the fastest development rate to hatching and emergence, the highest embryo survival at low temperatures during development, and the largest alevins and fry at 4°C, compared with warmer developmental temperatures. Coho salmon are also among the latest spawning of the species examined, and their apparent adaptation to

low water temperatures during development suggests that the species is adapted to spawning during late autumn and early winter. Pink salmon had relatively slow development rates, the poorest embryo survival at low water temperatures, and small alevins and fry at 4°C, compared with those that developed at 8°C. Pink salmon spawn early in autumn, and again the variation in characters associated with development suggest that the variation reflects adaptation to the species life history pattern. In British Columbia, development to fry emergence generally occurs at mean temperatures of 6°C or less in the natural environment. Coho and chum salmon are the latest-spawning species, and they generally had the fastest rates of development to fry emergence under temperature conditions likely encountered in the natural environment.

Because the species showed different trends in emergence timing with respect to changes in development temperature, it seems reasonable to infer that these different trends reflect adaptive variation in the species' response to environmental temperature during development. Population-specific differences in development can also exist (Beacham and Murray 1987b; Tang et al. 1987), and populations that spawn in extreme environments can probably be expected to have different rates of development and survival than populations in more moderate environments. For example, chum salmon that spawn in the Yukon River have faster rates of development than comparable populations in British Columbia (Beacham et al. 1988).

The development time to hatching has been reported to increase progressively for coho, chum, chinook, pink, and sockeye salmon (Ievleva 1951; Withler and Morley 1970; Smirnov 1975; Murray and McPhail 1988). Our study showed that this is true for incubation temperatures above 5°C. At lower temperatures, the relative ranking of the species changes, and development time to hatching is slowest for chinook salmon at temperatures below 3°C. The relative development rates among Pacific salmon species depend upon the temperature during development.

Size of alevins and fry was clearly influenced by both the temperature experienced during development and the size of eggs from which they originated. We found that egg weight was usually the more important determinant of fry length and certainly of fry weight. Larger alevins and fry are generally derived from larger eggs (Smirnov 1975; Kazakov 1981; Wallace and Aasjord 1984). Size

of salmon alevins and fry may be important in determining subsequent growth and survival (Bams 1969; Fowler 1972), and if there is a fry size at emergence for optimal survival, then the appropriate initial egg weight can be selected and water temperature possibly controlled during development in order to produce fry of the optimum size.

A substantial global warming is expected to occur in the next 50–100 years as a result of increased atmospheric levels of carbon dioxide and the subsequent climate change (Wigley et al. 1980; Pittock and Salinger 1982). Coho salmon appear to be the species that would be most significantly affected by such warming. They appear to be adapted for low water temperatures during development, and a trend of increasing temperatures during development would likely influence survival dramatically. Climate change may also reduce summer precipitation in the Pacific northwest portion of North America, and again this could have serious implications for survival of age-0 coho salmon. It might also be expected that the distributions of all species will shift northward.

Acknowledgments

We are indebted to Frank Velsen for his careful compilation of hatching time and embryo survival data (Velsen 1987), which provided the starting point for our analysis. Wally Barner supervised our previous laboratory analysis of variation in developmental characters of Pacific salmon, and also provided substantial support for the current analysis. The manuscript was substantially improved by the comments of referees and editors.

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Received September 6, 1989

Accepted April 17, 1990

Appendixes follow

Appendix: Data Sources and Parameter Estimates

TABLE A.1.—Sources of data in addition to Velsen's (1987) that were used to analyze embryo survival rates, hatching times, alevin survival rates, and emergence times for five species of Pacific salmon.

Data present				Reference
Embryo survival	Hatching time	Alevin survival	Emergence time	
Pink salmon				
X	X	X	X	Beacham and Murray (1986a)
X	X	X	X	Murray and Beacham (1986a)
X	X	X	X	Beacham and Murray (1987a)
X	X	X	X	Beacham and Murray (1988)
X	X	X	X	Beacham (1988)
X	X	X	X	Murray and McPhail (1988)
X				Brannon (1987)
Chum salmon				
X	X	X	X	Beacham et al. (1985)
X	X	X	X	Beacham and Murray (1985)
X	X	X	X	Beacham and Murray (1986b)
X	X	X	X	Murray and Beacham (1986b)
X	X	X	X	Beacham and Murray (1987a)
X	X	X	X	Murray and Beacham (1987)
X	X	X	X	Beacham and Murray (1987b)
X	X	X	X	Beacham et al. (1988)
X	X	X	X	Murray and McPhail (1988)
	X			Disler (1953)
	X			Soin (1954)
	X			Kubo et al. (1955)
Chinook salmon				
X	X	X	X	Murray and Beacham (1987)
X	X	X	X	Beacham and Murray (1989)
X	X	X	X	Murray and McPhail (1988)
			X	Rombough (1985)
			X	Heming (1982)
Sockeye salmon				
X	X	X	X	Beacham and Murray (1989)
			X	Brannon (1987)
X		X	X	Mead and Woodall (1968)
X	X	X	X	Murray and McPhail (1988)
	X			Hanamura (1966)
Coho salmon				
X	X	X	X	Murray and McPhail (1988)
X	X	X	X	Murray et al. (1990)
X	X	X	X	Tang et al. (1987)
	X			Shapovalov and Berrian (1940)
	X			Shaw and Magh (1943)
	X			Gribanov (1948)
	X			Ievleva (1951)
	X			Shapovalov and Taft (1954)
	X			Allen (1957)
	X			Smirnov (1960)
X	X	X	X	Murray (1980)
	X			Smirnov (1975)

TABLE A.2.—Parameter estimates for models (2), (4), (5), and (7) when used to predict hatching times for Pacific salmon. Standard deviations are in parentheses. The values $\log_e a$, b , c , and d are fitted constants in the models. Proportions of total variation accounted for (r^2) are also listed.

Model	$\log_e a$	b	c	d	r^2
Odd-year pink salmon					
2	6.663 (0.03)	-2.557 (0.24)			0.946
4	7.962 (0.98)	-1.382 (0.28)	-5.942 (2.53)		0.948
5	10.746 (1.17)	-1.409 (0.27)	-6.070 (2.50)	-0.483 (0.13)	0.957
7	5.153 (0.13)	0.006 (0.14)	-0.194 (0.04)		0.949
Even-year pink salmon					
2	6.749 (0.02)	-2.910 (0.14)			0.982
4	6.375 (0.26)	-0.885 (0.08)	-1.850 (0.74)		0.982
5	5.037 (0.68)	-0.837 (0.07)	-1.444 (0.62)	0.215 (0.14)	0.983
7	5.507 (0.08)	-0.397 (0.09)	-0.076 (0.02)		0.982
Chum salmon					
2	6.413 (0.01)	-1.079 (0.06)			0.985
4	7.049 (0.20)	-1.209 (0.06)	-2.407 (0.42)		0.987
5	7.978 (0.28)	-1.272 (0.07)	-2.898 (0.46)	-0.127 (0.03)	0.988
7	5.600 (0.04)	-0.404 (0.05)	-0.125 (0.01)		0.987
Chinook salmon					
2	6.283 (0.01)	-0.125 (0.09)			0.991
4	7.192 (0.25)	-1.292 (0.08)	-2.056 (0.55)		0.994
5	7.726 (0.54)	-1.320 (0.08)	-2.252 (0.60)	-0.078 (0.07)	0.994
7	5.829 (0.08)	-0.536 (0.09)	-0.116 (0.02)		0.994
Coho salmon					
2	6.240 (0.02)	-1.045 (0.13)			0.976
4	7.889 (0.41)	-1.536 (0.12)	-4.085 (0.76)		0.982
5	7.427 (0.80)	-1.533 (0.12)	-4.062 (0.75)	0.078 (0.12)	0.982
7	5.378 (0.04)	-0.250 (0.05)	-0.184 (0.02)		0.982
Sockeye salmon					
2	6.727 (0.01)	-2.394 (0.10)			0.979
4	8.734 (0.73)	-1.589 (0.20)	-7.067 (1.68)		0.985
5	9.848 (0.78)	-1.583 (0.18)	-6.834 (1.50)	-0.208 (0.08)	0.986
7	5.379 (0.04)	-0.076 (0.05)	-0.185 (0.02)		0.985

TABLE A.3.—Parameter estimates for models (2), (4), (5), and (7) when used to predict fry emergence times for Pacific salmon. Standard deviations are in parentheses. The values $\log_e a$, b , c , and d are fitted constants in the models. Proportions of total variation accounted for (r^2) are also listed.

Model	$\log_e a$	b	c	d	r^2
Odd-year pink salmon					
2	7.190 (0.02)	-2.663 (0.13)			0.983
4	6.233 (0.12)	-0.693 (0.04)	0.153 (0.37)		0.988
5	7.243 (0.34)	-0.682 (0.04)	0.239 (0.32)	-0.186 (0.06)	0.990
7	6.335 (0.09)	-0.768 (0.09)	0.015 (0.02)		0.988
Even-year pink salmon					
2	7.339 (0.01)	-3.755 (0.09)			0.994
4	7.231 (0.32)	-0.967 (0.10)	-3.446 (0.92)		0.994
5	8.074 (0.50)	-0.979 (0.10)	-3.580 (0.92)	-0.145 (0.06)	0.994
7	5.795 (0.04)	-0.212 (0.06)	-0.111 (0.02)		0.994
Chum salmon					
2	6.982 (0.02)	-1.447 (0.10)			0.973
4	6.307 (0.20)	-0.764 (0.07)	-0.039 (0.43)		0.988
5	8.377 (0.22)	-0.851 (0.04)	-0.657 (0.29)	-0.318 (0.03)	0.990
7	6.341 (0.06)	-0.793 (0.08)	0.007 (0.02)		0.988
Chinook salmon					
2	6.872 (0.01)	-0.332 (0.20)			0.955
4	10.404 (1.60)	-2.043 (0.43)	-7.575 (3.20)		0.970
5	10.319 (1.56)	-1.994 (0.40)	-7.195 (3.01)	-0.003 (0.00)	0.971
7	5.901 (0.17)	-0.016 (0.18)	-0.249 (0.05)		0.970
Coho salmon					
2	6.812 (0.01)	-1.643 (0.10)			0.978
4	7.018 (0.28)	-1.069 (0.09)	-2.062 (0.58)		0.979
5	7.599 (0.80)	-1.073 (0.10)	-2.092 (0.60)	-0.098 (0.13)	0.979
7	5.842 (0.04)	-0.394 (0.06)	-0.109 (0.02)		0.979
Sockeye salmon					
2	7.227 (0.01)	-2.560 (0.16)			0.968
4	7.647 (0.31)	-1.134 (0.10)	-3.514 (0.72)		0.969
5	9.404 (0.65)	-1.169 (0.11)	-3.833 (0.82)	-0.289 (0.09)	0.972
7	5.970 (0.02)	-0.276 (0.02)	-0.121 (0.01)		0.969

TABLE A.4.—Parameter estimates for model (11) for prediction of length and for model (13) for prediction of weight for alevins and fry of Pacific salmon that were maintained at different constant temperatures during development. Standard errors are in parentheses. The values $\log_e a$, b , c , and d are fitted constants for model (11), and a , b , c , and d are fitted constants for model (13).

Salmon species	$\log_e a$ or a	b	c	d
Alevin length				
Pink	1.74 (0.11)	0.13 (0.02)	0.68 (0.06)	-0.17 (0.02)
Chum	2.17 (0.09)	0.11 (0.01)	0.39 (0.05)	-0.10 (0.01)
Chinook	1.95 (0.13)	0.13 (0.02)	0.46 (0.07)	-0.13 (0.02)
Coho	2.18 (0.04)	0.17 (0.01)	0.08 (0.01)	-0.04 (0.00)
Sockeye	2.09 (0.06)	0.14 (0.01)	0.31 (0.02)	-0.10 (0.01)
Alevin weight				
Pink	5.01 (6.31)	0.82 (0.03)	5.60 (1.03)	-0.33 (0.06)
Chum	12.41 (7.88)	0.82 (0.03)	9.58 (1.44)	-0.53 (0.09)
Chinook	21.38 (15.30)	0.93 (0.04)	2.42 (2.49)	-0.16 (0.13)
Coho	5.63 (3.12)	0.89 (0.01)	11.92 (0.84)	-0.77 (0.06)
Sockeye	12.19 (2.96)	0.82 (0.02)	3.88 (0.53)	-0.19 (0.03)
Fry length				
Pink	2.52 (0.08)	0.14 (0.01)	0.23 (0.05)	-0.06 (0.01)
Chum	2.13 (0.09)	0.22 (0.01)	0.29 (0.05)	-0.08 (0.01)
Chinook	2.43 (0.12)	0.14 (0.02)	0.41 (0.06)	-0.11 (0.01)
Coho	2.46 (0.03)	0.18 (0.01)	0.12 (0.01)	-0.04 (0.00)
Sockeye	2.57 (0.07)	0.13 (0.01)	0.22 (0.03)	-0.08 (0.01)
Fry weight				
Pink	29.03 (14.32)	1.08 (0.07)	9.34 (2.33)	-0.55 (0.13)
Chum	65.11 (14.47)	1.13 (0.05)	14.82 (2.64)	-1.02 (0.16)
Chinook	152.26 (1.21)	1.21 (0.07)	5.47 (4.35)	-0.64 (0.22)
Coho	-23.10 (9.46)	1.31 (0.04)	48.28 (2.54)	-3.21 (0.19)
Sockeye	9.86 (6.58)	1.31 (0.05)	8.29 (1.18)	-0.55 (0.07)