

PREHATCH AND POSTHATCH GROWTH OF FISHES— A GENERAL MODEL

JAMES R. ZWEIFEL AND REUBEN LASKER¹

ABSTRACT

The developmental stages of fish eggs and the growth of larval fishes of several species can be represented by a Gompertz-type curve based on the observation that in widely different living systems, exponential growth tends to undergo exponential decay with time. Further, experimental studies and field observations have shown that the effect of temperature on the growth process follows the same pattern, i.e., the rate of growth declines exponentially with increasing temperature. Evidence suggests that prehatch growth rates determine ideal or optimum trajectories which are maintained after hatch in the middle temperature range but not at either extreme. Also, posthatch growth exhibits a temperature optimum which is not apparent in the incubation period. These studies have also shown that for the same spawn both the prehatch and yolk-sac growth curves reach asymptotic limits independent of temperature. Other biological events (e.g., jaw development) occur at the same size for all temperatures.

The growth of post-yolk-sac larvae follows a curve of the same type and hence the posthatch growth trajectory may be represented by a two-stage curve. For starving larvae, the second stage shows a decline in size but maintains the same form, i.e., the rate of exponential decline decreases exponentially with time.

Recent success in spawning and rearing marine fish larvae at the Southwest Fisheries Center (SWFC) (Lasker et al. 1970; May 1971; Leong 1971) has made possible a much more fundamental examination of the growth process than has heretofore been possible. Controlled laboratory experiments can now be utilized to investigate both the inherent nature of the growth process as well as the effect of some environmental factors.

Considerable care is required, however, in constructing a model² which is meaningful both mathematically and biologically. For example, almost all growth models currently in use can be derived as variations of the differential equation:

$$\frac{dW}{dt} = \eta W^m - \kappa W^n \quad (1)$$

or

$$\frac{dL}{dt} = \eta' L^{m'} - \kappa' L^{n'} \quad (1a)$$

(von Bertalanffy 1938; Beverton and Holt 1957; Richards 1959; Chapman 1961; Taylor 1962) where

¹Southwest Fisheries Center La Jolla Laboratory, National Marine Fisheries Service, NOAA, La Jolla, CA 92038.

²A model is here conceived to be a mathematical representation of change in length or weight with time under measureable environmental conditions.

W is weight, L is length, and $\eta, \kappa, m, n, m',$ and n' are arbitrary constants. These are the equations used most often to describe growth as a function of anabolic and catabolic processes of metabolism. The rate of anabolism, η , is considered to be proportional to W^m and the rate of catabolism, κ , proportional to W^n . Equation (1a) requires, in addition, the allometric relationship $W = qL^p$, where again q and p are arbitrary constants. In practice a dilemma arises from the fact that while such models yield a good empirical fit to the data, the estimates of parameters η and κ are often negative, thereby negating the assumptions on which the model is based. For $n = 1$ and $m = 0, 1, 2$, respectively, Equation (1) gives rise to the von Bertalanffy growth in length, Gompertz, and logistic growth functions. Although we have not as yet made any extensive comparisons, the fact that for $m > 1$ and $n = 1$, η and κ must be negative, suggests that in many instances the Gompertz and logistic rather than the von Bertalanffy functions may provide more appropriate models of fish growth. In particular, the simple von Bertalanffy growth model has no inflection point and hence curves such as the generalized von Bertalanffy, Gompertz, or logistic must be used when an inflection in the growth trajectory is evident.

Laird et al. (1965) have presented a Gompertz-type mathematical model of growth based on the

observation that the specific growth rate dW/Wdt of animals and their parts tends to decay exponentially with increasing age. They have shown that this relation offers a practical means of analyzing the growth of parts of embryonic and postnatal animals (Laird 1965a), the growth of tumors (Laird 1964, 1965b), whole embryos of a number of avian and mammalian species (Laird 1966a), and early stages of postnatal growth of a variety of mammalian and avian organisms (Laird 1966b). Further, Laird (1966b, 1967) has shown that postnatal growth of a variety of mammalian and avian organisms can be fitted by compounding this model with a linear growth process beginning at birth and extending on beyond the asymptotic limit of the underlying Gompertz growth process. Overall growth is assumed to be genetically determined by programming only the initial specific growth rate and the rate of exponential decay, these governing growth processes then act on a genetically determined original mass to produce the observed course of growth to a final limiting size characteristic of the species and individual.

Mathematically, these assumptions are described by the two equations:

$$\frac{dW(t)}{dt} = \gamma(t)W(t)$$

$$\text{and}^3 \quad \frac{d\gamma(t)}{dt} = -\alpha\gamma(t)$$

which have the solution

$$W(t) = W_0 e^{\frac{A_0}{\alpha}(1 - e^{-\alpha t})}, \quad (2)$$

where W_0 is weight at $t = 0$, A_0 is the specific growth rate at $t = 0$, α is the rate of exponential decay and the specific growth rate at time t , $A_t = A_0 e^{-\alpha t}$.

Laird et al. (1965) indicated that an additional growth component not included in the Gompertz equation may be due to the accumulation of products that are not self-reproducing or to renewal systems that are not in exact physiological equilibrium and suggested the compound growth curve:

$$W = W_G + \beta \int_0^t \frac{W_G}{M} dt \quad (3)$$

where W_G is the mass due to the Gompertz growth process, β is the rate of linear growth, and M is the asymptotic limit of the growth process. She also suggests that this linear process starts in the early embryonic period, if not at conception. For the age interval covered in this paper, however, the linear growth component ($W - W_G$) was not found to be important.

Several characteristics of the curve are worthy of mention:

1. The asymptotic limit M is $W_0 \text{Exp}(A_0/\alpha)$.
2. The point of inflection (t_i, W_i) = $\left[\frac{1}{\alpha} \ln(A_0/\alpha), W_0 \text{Exp}\left(\frac{A_0}{\alpha} - 1\right) \right]$.
3. The zero point on the time scale may be shifted to any point t_Δ without changing the form of the equation with new parameters $W_\Delta = W(\Delta)$, $A_\Delta = A_0 e^{-\alpha \Delta}$ where α remains unaltered.

The fundamental concept of the Laird-Gompertz model is one of change in weight or mass with time, being due primarily to the self-multiplication of cells and genetically determined limitations on the growth parameters. The use of length as the measured variable is thus a matter of convenience due to the fact that weight measurements are much more time consuming, especially in early larval growth, but also in juvenile and adult fishes. As indicated in Equation (1a), if a true allometric relationship existed, the choice would be unimportant. However, all experimental evidence indicates that both length and weight can be described by a Gompertz-type curve. Hence, it can be shown that 1) the growth rate for both changes continually with time and 2) the form of the length-weight relationship will change continually except for two special instances. Laird et al. (1968) has shown that this occurs only when the rates of exponential decay are the same and either the two measured variables begin growth at different times at the same initial rate or at different rates at the same time. In all other cases the allometric plot will be nonlinear. For

$$L = L_0 e^{K_L(1 - e^{-\beta t})}$$

$$\text{and} \quad W = W_0 e^{K_W(1 - e^{-\alpha t})}$$

³In the usual Gompertz representation the rate of exponential growth is assumed to decline logarithmically as W approaches the asymptote $M = W_0 e^{\frac{A_0}{\alpha}}$, i.e., $\frac{dW}{dt} = \alpha W \ln(M/W)$.

the length-weight relationship is

$$\ln W = \ln W_0 + K_W \left[1 - \left(\frac{K_L - \ln(L/L_0)}{K_L} \right)^{\alpha/\beta} \right]. \quad (4)$$

Only when $\alpha = \beta$ does the relationship reduce to the linear form

$$\ln W = \ln W_0 + \frac{K_W}{K_L} \ln(L/L_0).$$

As shown in Figure 1, departure from linearity will not always be great, but for extrapolation the effect of overestimation at larger sizes may become serious.

Throughout this paper, growth will, by necessity, be measured in terms of length rather than weight even though the model equation is developed from the opposite point of view. It should be remembered, however, that no allometric relationship is assumed, i.e., no relationships among the two sets of parameters are assumed except as they are jointly a function of age.

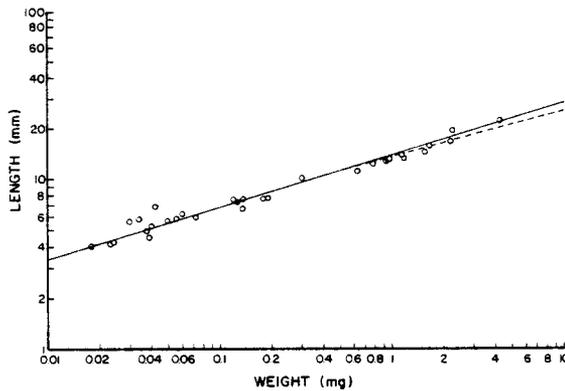


FIGURE 1.—Length-weight relationship in larval anchovies: Solid line fitted from $\log W = a + b \log L$; dashed line fitted from Equation (4); estimates are coincident up to 10 mm.

INITIAL ESTIMATES

Equation (2) may be rewritten as follows:

Let $K = A_0/\alpha$

and $M = W_0 e^K,$

then $W(t) = M e^{-K e^{-\alpha t}},$

or $\ln[-\ln(W(t)/M)] = \ln K - \alpha t,$

and hence the logarithm of the logarithm of the ratio of size to the asymptotic limit M with the sign changed will be linearly related to time t with parameters $\ln K$ and $-\alpha$. W_0 may be obtained from the relationship $\ln M = \ln W_0 + K$. Note: For decreasing curves, use the reciprocal of the observed values.

VARIABILITY, ESTIMATION, AND TRANSFORMATION BIAS

It is an unfortunate circumstance that the determination of the "best" estimation procedure can rarely be separated from the determination of the "best" mathematical model, i.e., there is no recognized best estimation procedure except in some specialized instances. This is brought about by the fact that almost all parametric estimation procedures assume some information concerning the form and stability of the "error" distribution. This requires, at the very least, the knowledge that the variance is constant and, at the most, the exact form of the error distribution. Since the term "error" in the biological sciences takes a meaning quite different from that in the physical and mathematical sciences in that it represents, in the main, natural variability rather than measurement or experimental error and since natural variability is large (especially so in cold-blooded organisms), few a priori assumptions can be made.

Since most estimation procedures assume a normal distribution of errors at each point along the curve with equal variance (homoscedasticity), the obvious approach, when no more plausible alternative is available, is to fit the situation to this mold.

Some general recommendations are helpful. "Although no clear rule may be safely offered for the taking of logarithms to reduce data to manageable configurations, nevertheless, this transformation (logs) is probably the most common of all. Almost all data that arise from growth phenomenon, where the change in a datum is likely to be proportional to its size and hence errors are similarly afflicted, are improved by transforms to their logarithms" (Acton 1959: 223). Specifically, it can be shown that the logarithmic transformation will induce homoscedasticity in those instances

where the standard deviation is proportional to the population mean, i.e., $\sigma = \beta\mu$ or $\log \sigma = \log \beta + \log \mu$. Hence, a plot of $\log \sigma$ on $\log \mu$ will have a slope of unity and the antilog of the intercept will define the proportionality constant. Plots of $\log \sigma$ on $\log \mu$ were made for several experiments where data were available for extended periods of time. None of the regression coefficients was significantly different from unity. These experiments cover a variety of life stages and environmental situations from controlled laboratory experiments on larval anchovies (Lasker et al. 1970) to large tank feeding of anchovies captured from the wild at 75 mm (Paloma, SWFC, unpubl. data) to samples of adult sardines obtained from bait boats (Lasker 1970). Growth for the 75-mm anchovies was slow and much more uniform than for the other experiments as indicated by the mean square errors in Table 1. The analysis of covariance (Table 1) shows no difference in slope for either length or weight from larval, juvenile, and adult fishes. The average slopes are 0.9981 for larvae and adults and 1.1061 for juveniles. With a slope of unity, the proportionality constant can be estimated by $\text{Exp}(\ln \bar{\sigma} - \bar{\ln} \mu)$. The results from the several experiments are shown below:

	σ/μ	
	Length	Weight
Lasker et al. (1970):		
Experiment 1	0.12	0.39
Experiment 2	0.12	0.33
Paloma ⁴	0.06	0.20
Lasker (1970)	0.04	0.13

Not unexpectedly, variation in weight exceeds that of length and both decrease with increasing age.

The question of normality and its relationship to homoscedasticity is more tenuous, but again some help is available. In practical work, it is generally assumed that both x and $\log x$ can be regarded as normally distributed as long as the coefficient of variation $C = \sigma/\mu < 1/3$ or $\sigma_{\log x} < 0.14$ (Hald 1952: 164). This allows transformation for one desideratum without noticeably affecting another.

Paloma (see footnote 4) collected one or two samples per month of laboratory-reared anchovies for a period of nearly 2 yr. Approximately 25 fish were taken for each sample. We examined normality in terms of skewness (G_1) and kurtosis (mean absolute deviation A). Although sample

TABLE 1.—The relationship of mean and standard deviation for both length and weight measurements in fishes.

	$\log \sigma = \alpha + \beta \log \mu$		Analysis of covariance deviations from regression		
	α	β	df	s.s.	m.s.
	Larvae and adults:				
Length ¹ exp. 1	-1.5568	1.6979	6	0.3308	0.0551
exp. 2	-0.8003	0.8281	8	0.7167	0.0896
Weight ¹ exp. 1	-0.4192	1.0373	6	0.1572	0.0262
exp. 2	-0.4852	1.0077	8	0.4241	0.0530
Length ²	-1.8093	1.0848	60	2.2933	0.0382
Weight ²	-0.4748	0.7906	60	2.5913	0.0432
		Within	148	6.5134	0.0440
		Between	5	0.1425	0.0285
		Common	153	6.6559	
$F = 0.0285/0.0440 = 0.65$					
Juveniles:					
Length ³	-1.3975	1.1644	31	0.3658	0.0118
Weight ³	-0.8000	1.1029	31	0.1511	0.0048
		Within	62	0.5169	0.0083
		Between	1	0.0002	0.0002
		Common	63	0.5171	
$F = 0.0002/0.0083 = 0.02$					

¹Lasker et al. (1970), larval anchovies.
²Lasker (1970), adult sardines.
³Paloma: unpublished data available at SWFC, juvenile anchovies.

sizes are small, in terms of positive (>mean) and negative (< mean) coefficients, the transformation was effective in normalizing both fish weight and length as shown below:

		L	log L	W	log W
$G_1(\mu_{G_1} = 0)$	>	19	17	24	16
	≤	14	16	19	17
$A(\mu_A = 0.7979)$	>	18	17	17	17
	≤	15	16	16	16

For these same samples, length and weight were assumed bivariate-log normal and confidence regions were calculated for each sample. On the average, 96% of the observations fell within the 95% confidence ellipse.

In summary, there is strong evidence that the logarithmic transformation will be required to stabilize the variability in all phases of fish growth and that such a transformation will support the assumption of a normal distribution at least in the intermediate size range (75-100 mm) and most likely at other sizes as well.

Seemingly then, the conditions have been met for implementation of either the maximum likelihood or least squares estimation process. However, two problems remain, neither of which has an entirely satisfactory solution. The first, the absence of an explicit solution of the normal equations, arises because the parameters enter the model in a nonlinear manner and, as is usual in

⁴ Paloma, P. Unpublished data available at SWFC.

situations of this kind, an iterative procedure is required. The one employed for this paper is Marquardt's algorithm (Conway et al. 1970). Procedures such as this are usually justified on the basis that for large samples and independent observations the estimates obtained are "very close" to those which would be obtained by plotting the likelihood function itself (Box and Jenkins 1970: 213). In truth, the small sample bias and variability of such estimates remains unknown. In growth data the second problem is that sequential observations are not likely to arise from entirely independent processes. This fact is usually manifested as a series of runs above and below a fitted curve rather than random variation. One simple explanation is that growth is in reality a series of asymptotic curves and that oscillations around a fitted curve indicate more than one growth cycle. In this case, the basic assumption of the estimation procedure and the likelihood function itself will not be met. No satisfactory solution to this problem has been proposed and none is proffered here. However, since the same larvae were not measured at different ages and since correlated observations usually have little effect on the estimates of mean values, such estimates will likely not be seriously biased. Using these estimates, "goodness of fit" is examined through the magnitude of the residual mean square and the pattern of residuals along the growth curve, rather than using significance tests or confidence intervals.

One further point often considered but left unsaid is the effect of transformations on the estimated means. Such changes of scale can lead to serious biases and errors in interpretation, especially when the coefficient of variation is large. When the exact form of the error distribution is known the bias can usually be determined mathematically. For the log normal, for example, it is necessary to add one-half of the error mean square before calculating the antilog mean. Unfortunately, in practical work, it is generally impossible without very large samples, to determine the distributional form. As stated above, for many situations, x and $\log x$ can both be considered to be normally distributed. In these intermediate cases, however, the bias correction for $\log x$ will be small so, that as a general rule, one can state that whenever a transformation is made, the correction for transformation bias should be used.

RESULTS

Growth Cycles

Previous work on the growth of larval anchovies (Kramer and Zweifel 1970) suggested that the Laird form of the Gompertz equation might provide a useful model of larval growth. Figure 2 reveals several phenomena found to be almost universal in larval growth: 1) there is a moderate increase in length during the interval following hatch that is followed by 2) a period of minimal growth accompanied by nearly uniform variability, and 3) at the onset of feeding, the mean size increases rapidly with variability proportional to the square of the mean size.

Farris (1959) noted the rapid leveling off in growth following hatch for the Pacific sardine and three other species and approximated the growth rate by two discontinuous curves and indicated that "a more detailed study would probably reveal a nonlogarithmic continuous growth function."

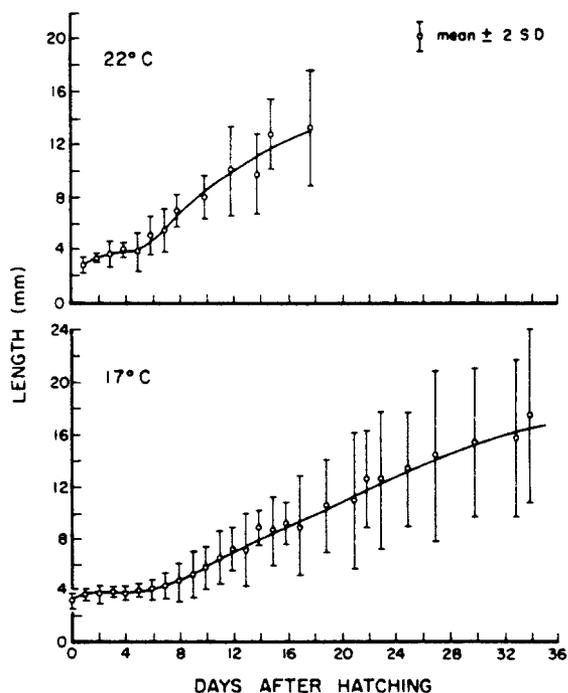


FIGURE 2.—Change in length of yolk-sac and feeding larval anchovies at two temperatures, 17° and 22°C from Kramer and Zweifel (1970); curves are two-cycle Laird-Gompertz.

Although the single stage model used by Kramer and Zweifel (1970) provides an adequate growth curve, two growth cycles are evident: one extending from hatching to the depletion of the yolk sac and the other a more rapid growth at the onset of feeding. Thus, a two-stage model was used to obtain the curves in Figure 2. The fitting procedure is outlined in the Appendix.

It is evident that early larval growth of this species can be represented by a two-stage Laird growth curve. The characteristics of the growth curves of feeding larvae, i.e., the second cycle, may be related to several environmental factors of which the two most important are probably food ration and temperature. However, an examination of data available on nonfeeding larvae (Figure 3) indicated that even in food-limited situations, change in size may be represented by the two-stage Laird curve.

Growth From Hatch to Depletion of Yolk Sac

The characteristics of the early posthatch growth of larval fishes is more completely described by Lasker (1964). In this series of experiments, growth in length of the Pacific sardine, *Sardinops sagax*, was measured for up to 10 days following hatching at 12 temperatures in the range 11°-21.3°C. The parameters of a single stage Laird curve (Equation 2) were estimated for each of these experiments. Data only up to the day preceding the first decrease in size were used in the calculations.

Even though for such short time series, the parameters are highly correlated due to near-redundancy of one of the parameters, two observations were striking; there was a nearly constant estimated hatching length of about 3.75 mm and a nearly constant estimated maximum length of about 6.1 mm. Accordingly, those experiments with hatching lengths near 3.75 mm and a measured increase in size of at least 3 days were fitted to the reparameterized model:

$$L(t)_T = L_0 e^{K(1 - e^{-\alpha_T t})}$$

where $K = A_{0_T} / \alpha_T$

and the T subscript indicates temperature in °C. A plot of α_T on temperature revealed another Laird-Gompertz curve approaching an asymptote at higher temperatures.

A five parameter model:

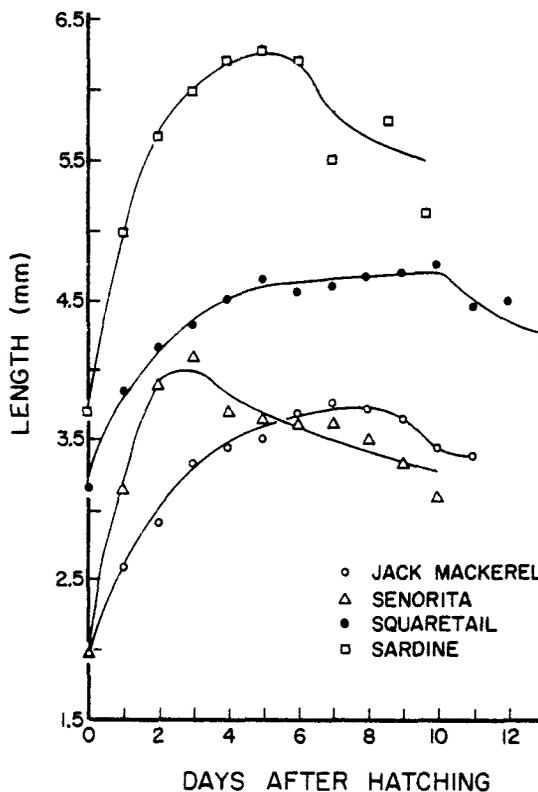


FIGURE 3.—Change in length of yolk-sac and starving larvae; curves are two-cycle Laird-Gompertz.

$$L(t)_T = L_0 e^{K(1 - e^{-\alpha_T t})} \tag{5}$$

where $\alpha_T = \alpha_0 e^{m(1 - e^{-\beta T})}$ (5a)

was used to fit the growth data from all experiments and provided an excellent fit except at the highest temperature where growth was always overestimated. This suggested a temperature optimum with growth rates decreasing as the absolute difference $|T - T_{opt}|$ increases. Following Stinner et al. (1974), who used a different temperature function, we assumed symmetry around the optimum.

Using Equation (5a), the origin of the temperature scale may easily be shifted to the optimum T_{opt} by the relationships:

$$\alpha_{opt} = \alpha_0 e^{m(1 - e^{-\beta T_{opt}})}$$

and $m_{opt} = m e^{-\beta T_{opt}}$

and letting $\Delta = |T - T_{\text{opt}}|$

we have the symmetric relationship

$$\alpha_T = \alpha_{\text{opt}} e^{m_{\text{opt}}(1 - e^{-\beta\Delta})} \quad (5b)$$

Substituting Equation (5b) for Equation (5a) and treating T_{opt} as an unknown parameter, a six parameter model was fitted to the growth data with the results shown in Table 2.

TABLE 2.—Growth in length of yolk-sac larvae of the Pacific sardine at several temperatures.

Length		SE	Age (days)	Temperature (°C)	N
Observed ¹	Estimated ²				
3.76	3.72	0.15	0.00	11.00	7
4.30	4.27	0.27	1.00		4
4.78	4.71	0.50	2.00		4
4.97	5.06	0.25	3.00		2
3.77	3.72	0.20	0.00	12.00	9
4.50	4.40	0.24	1.00		11
4.71	4.91	0.29	2.00		8
5.04	5.28	0.44	3.00		6
5.50	5.54	0.36	4.00		3
3.73	3.72	0.16	0.00	13.00	8
4.50	4.55	0.23	1.00		17
4.97	5.12	0.41	2.00		11
5.46	5.49	0.45	3.00		9
4.80	4.72	0.20	1.00	14.00	22
5.39	5.33	0.27	2.00		19
5.65	5.67	0.36	3.00		9
3.93	4.08	0.13	0.30	14.20	11
4.08	4.09	0.13	0.30	14.30	5
5.14	4.89	0.44	1.00	15.00	17
5.59	5.51	0.35	2.00		20
5.96	5.81	0.32	3.00		10
3.71	3.72	0.25	0.00	16.00	21
5.01	5.07	0.25	1.00		19
5.68	5.67	0.26	2.00		23
5.99	5.91	0.15	3.00		11
6.23	6.00	0.11	4.00		9
3.74	3.72	0.22	0.00	16.80	14
5.20	5.21	0.16	1.00		16
5.77	5.78	0.20	2.00		22
6.14	5.97	0.20	3.00		13
3.69	3.97	0.10	0.10	17.80	5
5.27	5.38	0.19	1.00		16
5.86	5.88	0.23	2.00		22
6.06	6.01	0.22	3.00		19
3.71	3.72	0.21	0.00	18.80	4
5.46	5.53	0.18	1.00		18
5.98	5.95	0.21	2.00		25
6.09	6.04	0.15	3.00		18
3.73	3.72	0.10	0.00	19.60	4
5.36	5.58	0.19	1.00		18
5.73	5.97	0.17	2.00		15
5.93	6.04	0.25	3.00		16
5.10	4.83	0.12	0.50	20.50	12
5.46	5.45	0.16	1.00		12
5.43	5.32	0.03	1.00	21.30	3
5.90	6.00	0.13	3.00		5

¹From Lasker (1964).

²Calculated from Equations (5) and (5b) with parameters $L_{\infty} = 3.716$, $K = 0.4872$, $\alpha_{\text{opt}} = 1.8523$, $m = 3.3878$, $\beta = 0.0490$, and $T_{\text{opt}} = 19.38$.

Growth From Fertilization to Hatch

Coincident to the investigation of early larval

growth, a study of the incubation times for the sardine showed that they also could be characterized by a Laird-Gompertz curve. The fitting of Equation (5a) with α_T being incubation time showed no bias at any point along the curve (Figure 4). Unlike the posthatch growth curves, however, no evidence of a temperature optimum was found, i.e., incubation time did not increase at high temperatures. One possible explanation is that larvae which expire cannot be included and hence mortality introduces a negative bias in the estimate of average or median incubation time.

The question arises whether changes in growth rates occur at hatching, i.e., is there a single curve from fertilization to onset of feeding? It can be shown that under the Laird-Gompertz model where growth is approaching a common asymptote from a common origin, i.e. fertilization, the incubation time I_T is simple multiple of the decay rate α_T . From Equation (5) we may solve for the time to hatch I_T at size L_h to obtain:

$$I_T = \ln \left(\frac{K}{K - \ln(L_h / L_0)} \right) / \alpha_T$$

Since incubation times were not available for all temperatures used in the growth experiment, the sardine curve from Figure 4 was used to convert all data taken at temperatures less than optimum to time from fertilization and fitted to Equation (5).

The results for sardines indicated an increasing size at hatch with increasing temperature which was not evidenced by the observed data and an overestimate of size at temperatures less than 14°C. It was thus concluded that a change in growth rate occurs at hatch, the more noticeably at extreme temperatures and that the prehatch curve must be estimated separately.

The parameters of the prehatch growth curves were obtained by fitting the equation

$$L_h = L_0 e^{K(1 - e^{-\alpha T})} \quad (6)$$

to only data obtained less than 12 h following hatch. The average estimated hatching size was 3.73 mm and the asymptotic limit was 6.13 mm. The plot for several selected temperatures is shown in Figure 5. Laird (1965a) has shown that the length scale may be standardized and logically simplified by expressing size relative to the asymptotic limit. Biological events such as

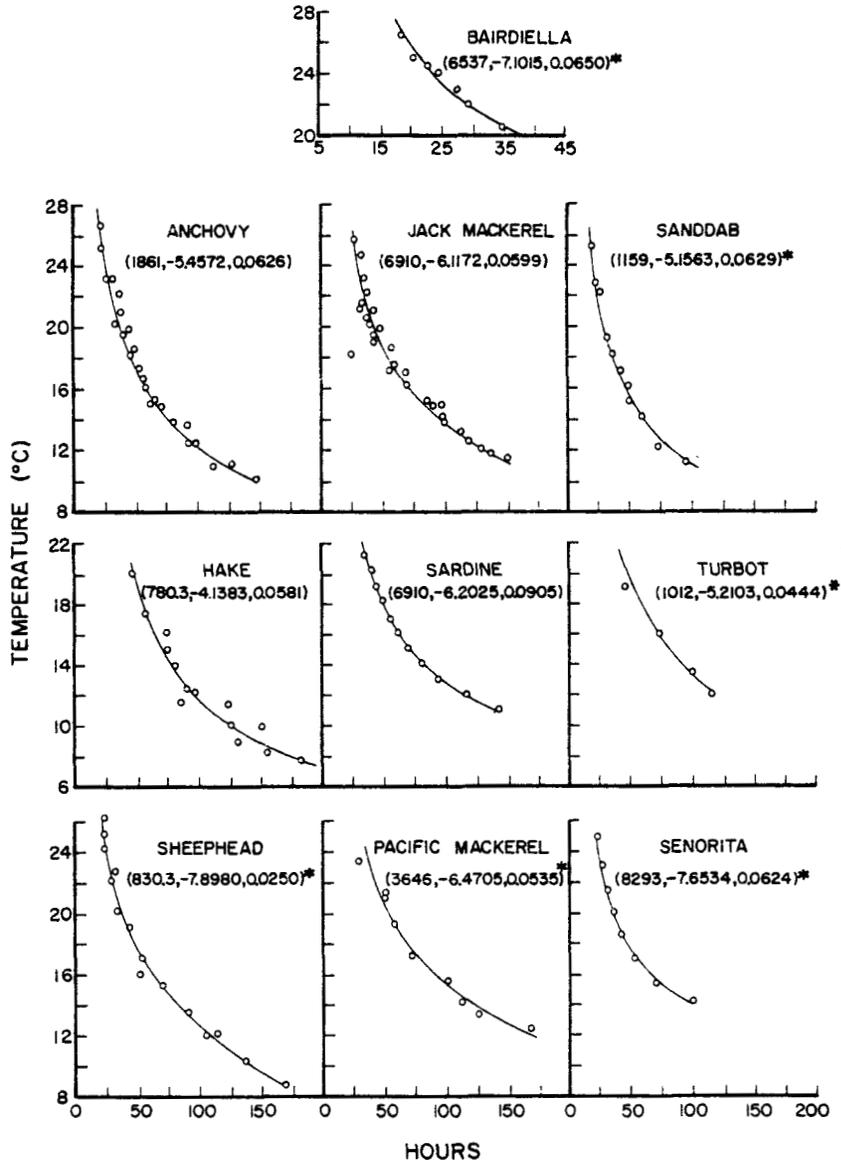


FIGURE 4.—Observed (o) and estimated (curve) (parameters in parentheses are I_0 , m , and β for the equation $I_T = I_0 e^{-m(1 - e^{-\beta T})}$ and * indicates time from stage III eggs) incubation times for anchovy, *Engraulis mordax* [combined data from Lasker (1964) and Kramer (unpubl. data) available at SWFC]; hake, *Merluccius productus*; sheephead, *Pimelometopon pulchrum*; bairdiella, *Bairdiella icistia*; jack mackerel, *Trachurus symmetricus*; sardine, *Sardinops sagax*; Pacific mackerel, *Scomber japonicus* (Watanabe 1970); sanddab, *Citharichthys stigmaeus*; turbot, *Pleuronichthys decurrens*; señorita, *Oxyjulis californica*.

developmental egg stages, hatching, and development of the functional jaw occur at fixed points along the curves. Ahlstrom (1943) reported time to several developmental egg stages at different

temperatures from field observations. In addition, Lasker (1964) showed incubation times and time to the development of the functional jaw for a wider range of temperatures. Each of these events can

be identified as a fixed percentage point in Figure 5 or the estimated value

$$t_{LT} = \ln \left(\frac{K}{K - \ln(L_T/L_0)} \right) / \alpha_T \quad (7)$$

as shown in Table 3.

Lasker (1964) found that the functional jaw did not develop at the lowest two temperatures in agreement with the result that the critical size would not be reached until well after yolk absorption.

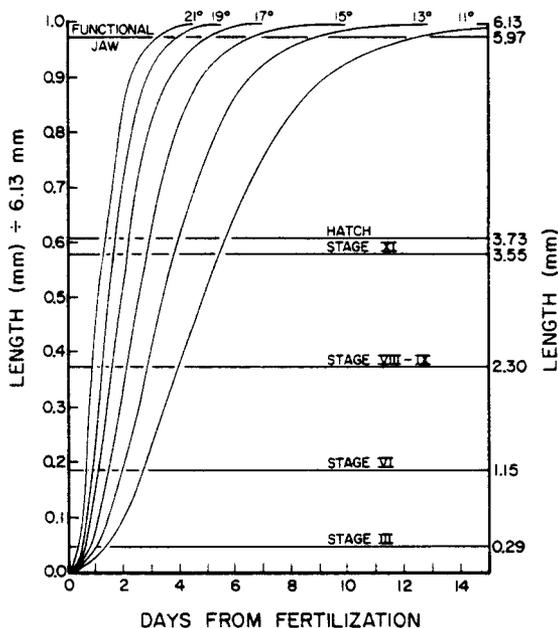


FIGURE 5.—Prehatch growth curves estimated from Equations (5) and (5a) for the Pacific sardine.

Incubation Times

Incubation times were available for several other species. The fitting of Equation (5a) for each species showed no clear bias at any point along the curve (Figure 4). As for the sardine, no evidence of a temperature optimum appeared for any of the species in the temperature ranges used in the experiments. However, it was observed that the decay parameter was relatively constant varying from 0.03 to 0.09 with a mean value of 0.05. When Equation (5a) was fitted with the temperature decay parameter, β , the same for all species, incubation times were closely approximated by Equation (5a) with parameters as shown in Table 4.

The incubation curves used here differ significantly from those calculated from the classical Arrhenius equation: $\log(\text{incubation time}) = a + b/\text{absolute temperature}$. Using this method, nearly all species showed a characteristic underestimate at the temperature extremes and overestimates in the middle range as shown for the northern anchovy, *Engraulis mordax* (Figure 6).

Prehatch Growth Curves for Other Species

In addition to incubation times for the northern anchovy, Kramer⁵ recorded time to several developmental egg stages. Also, Lasker (1964) provided time to hatch from stage IV⁶ (Table 5). Further, Hunter (pers. commun.) indicates that

⁵Unpublished data available at SWFC.

⁶Stages of embryological development are those described by Ahlstrom (1943).

TABLE 3.—Observed (Obs.) and estimated (Est.)¹ time in hours to developmental egg stages², hatch, and appearance of the functional jaw of the Pacific sardine.

Temp. (°C)	Ahlstrom (1943)								Lasker (1964)				
	Stage III		Stage VI		Stages VIII-IX		Stage XI		Temp. (°C)	Incubation time		Functional jaw	
	Obs.	Est.	Obs.	Est.	Obs.	Est.	Obs.	Est.		Obs.	Est.		
13.5	20.4	20.1	41.8	42.9	62.5	63.2	82.6	85.4	11	140	135	—	—
14.0	18.9	18.6	39.1	39.7	58.3	58.5	77.2	79.0	12	115	114	—	—
14.5	17.4	17.3	36.6	36.8	59.4	54.3	72.2	73.3	13	93	96	213	216
15.0	16.2	16.1	34.3	34.2	50.7	50.4	67.5	68.1	14	78.5	82.4	179	185
15.5	14.9	15.0	32.1	31.9	47.2	46.9	63.1	63.4	15	68.1	71.0	156	160
16.0	13.8	14.0	30.0	29.7	44.0	43.7	59.0	59.1	16	60.2	61.6	136	138
16.5	—	—	28.1	27.7	41.1	40.8	55.1	55.2	17	53.7	53.8	119	121
17.0	—	—	26.3	26.0	—	—	51.5	51.6	18	48.4	47.3	105	106
									19	43.2	41.8	94	94
									20	39.3	39.2	85	84
									21	34.0	33.2	77	75

¹ $L_0 = 0.0341$, $K = 5.20$, $\alpha_0 = 0.0317$, $m = 6.19$, and $\beta = 0.0489$.

²Egg stages are defined in Ahlstrom (1943).

TABLE 4.—Parameters for estimating incubation time I at centigrade temperature T from the relationship $I_T = I_0 e^{m(1 - e^{-\beta T})}$ for several fishes where β is the same for all species.

Species	I_0	m	β
Sefiorita			
<i>Oxyjulis californicus</i>	16,103	-7.9531	0.0527
Bairdiella			
<i>Bairdiella icistia</i>	13,170	-6.8216	0.0527
Pacific mackerel			
<i>Scomber japonicus</i>	3,580	-6.4896	0.0527
Jack mackerel			
<i>Trachurus symmetricus</i>	1,854	-6.2486	0.0527
Pacific sardine			
<i>Sardinops sagax</i>	2,121	-6.2322	0.0527
Northern anchovy			
<i>Engraulis mordax</i>	1,389	-5.5218	0.0527
Speckled sanddab			
<i>Citharichthys stigmæus</i>	984.6	-5.4258	0.0527
California sheephead			
<i>Pimelometopon pulchrum</i>	11,316	-5.4194	0.0527
Turbot			
<i>Pleuronichthys decurrens</i>	11,065	-4.7059	0.0527
Pacific hake			
<i>Merluccius productus</i>	699.2	-4.1772	0.0527

¹Time from stage III eggs.

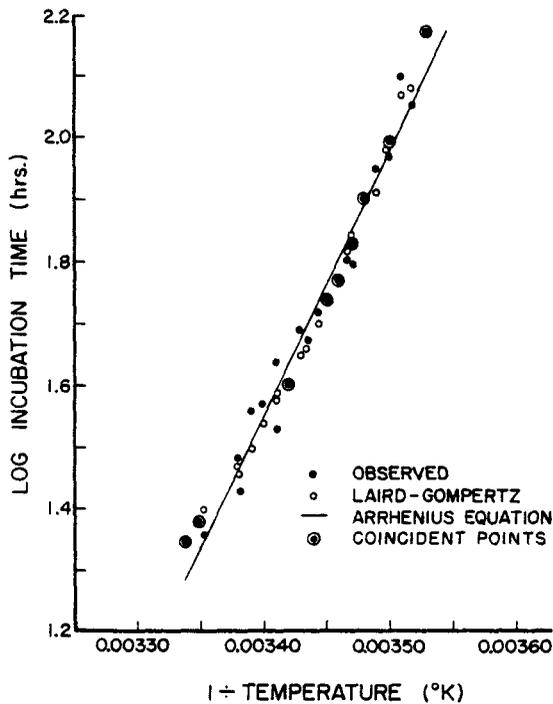


FIGURE 6.—A comparison of two methods of fitting the temperature-incubation time relationship in the northern anchovy.

larval anchovy, on the average, hatch at about 2.9 mm.

Prehatch growth curves were obtained by fitting Equation (6) to hatch sizes of 2.85 at all observed temperatures as shown in Figure 7.

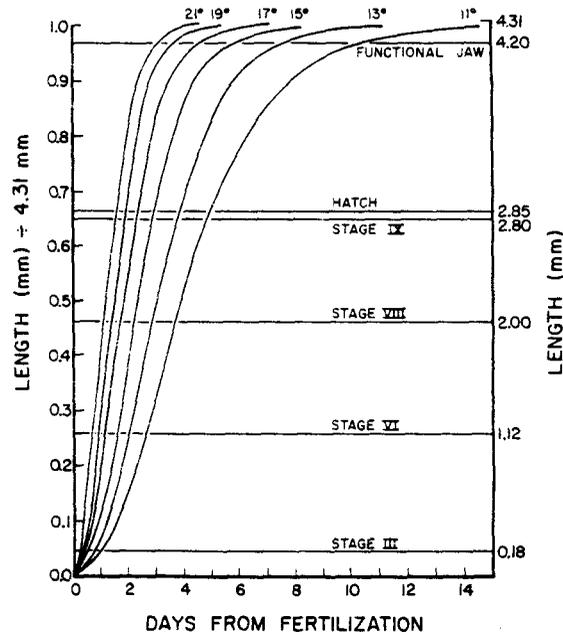


FIGURE 7.—Prehatch growth curves estimated from Equations (5) and (5a) for the northern anchovy.

Comparison with the sardine curves indicate that similar events (i.e., stages of development) occur relatively later for the anchovy. Observed and estimated event times are shown in Table 5.

Except for size at hatch, development data for the prehatch stage was not available for any other species. The curves may, if desired, be easily constructed from the parameters as shown in Table 6.

DISCUSSION

Nothing seems more true than the statement of Thompson (1942:158), "Every growth-problem becomes at last a specific one, running its own course for its own reasons. Our curves of growth are all alike—but no two are ever the same. Growth keeps calling our attention to its own complexity. . . . not least in those composite populations whose own parts aid or hamper one another, in any form or aspect of the struggle for existence."

The truth of this statement has been realized in the disappointing search for growth models derived from physiochemical processes. While it is true that the mathematical form of some equations arrived at from metabolic considerations are the same as those derived in other ways, more

TABLE 5.—Observed (Obs.) and estimated (Est.)¹ time in hours to developmental egg stages², hatch, and appearance of the functional jaw of the northern anchovy.

Temp. (°C)	Kramer (unpubl. data)								Lasker (1984)					
	Stage III		Stage VI		Stage VIII		Stage XI		Incubation time		Temp. (°C)	Stage IV to hatch		
	Ops.	Est.	Obs.	Est.	Obs.	Est.	Obs.	Est.	Obs.	Est.		Obs.	Est.	
11.1	—	—	—	—	—	—	—	—	—	113	118.8	11	81	83
12.5	—	—	—	—	—	—	—	—	—	98	95.1	12	65	71
13.8	20	15.2	42	41.8	58	59.4	78	77.1	80	78.2	13	58	61	
15.2	15	12.6	35	34.6	50	49.1	65	63.7	63	64.7	16.8	38	37	
16.6	10	10.6	26	29.0	39	41.2	51	53.4	55	54.2	17.8	34	33	
18.0	9	9.0	24	24.6	35	35.0	44	45.4	49	46.0	18.8	31	29	
19.4	8	7.7	21	21.1	33	30.0	39	39.0	40	39.5	19.6	28	26	
20.8	6	6.7	19	18.4	28	26.1	35	33.8	36	34.3	20.5	25	24	

¹Estimates obtained from Equation (7) with parameters as shown in Table 6.²Egg stages are defined by Ahlstrom (1943).

TABLE 6.—Mathematical parameters for prehatch growth curves of six fishes. See text for notation.

Species	L_0	K	α_0	m	β	Average size at hatching
<i>Trachurus symmetricus</i>	0.0005	9.0986	0.0226	5.8338	0.0588	1.95
<i>Sardinops sagax</i>	0.0341	5.1918	0.0317	6.1876	0.0490	3.74
<i>Engraulis mordax</i>	0.0250	5.1493	0.0412	5.5338	0.0546	2.86
<i>Citharichthys stigmæus</i>	0.1814	5.0600	0.0270	6.2898	0.0319	1.97
<i>Oxyjulis californicus</i>	0.0425	4.7164	0.0572	7.2126	0.0260	1.89
<i>Pleuronichthys decurrens</i>	0.1843	3.2915	0.0480	4.5184	0.0528	3.00

often than not no meaningful biological interpretation of the metabolic parameters can be made. The essence of the growth equation used here is genetically programmed processes of exponential growth and of exponential decay of the specific growth rate. The most probable source of exponential growth is, of course, self-multiplication of cells, the causes of decay are many but not well understood. Laird (1964, 1965a, b, 1966a, b, 1967) has shown that this kind of relationship offers a practical means of analyzing growth of all tumors, as well as embryonic and postnatal growth of a number of avian and mammalian species. We have shown that at least the early stages of the growth of fishes follows a similar pattern.

As with other organisms, several growth cycles exist in fishes. The number of such cycles which will be recognized is determined by the time scale of measurements. We have used three cycles: 1) from fertilization to hatching, 2) from hatch to onset of feeding, and 3) feeding larvae.

In addition, we have observed that the temperature specific growth follows a similar pattern, i.e., exponential increase with an exponential decay of the temperature specific growth rate. In some instances a temperature optimum exists beyond which the specific growth rate begins to decline, although this may be related to food requirements at onset of feeding. Further, we have observed

that for the same spawn 1) the asymptotic limit of each growth cycle is independent of temperature and 2) the biological events such as developmental egg stages, hatching, functional jaw development, etc., occur at the same size at all temperatures.

Figure 8 shows posthatch growth curves of the sardine as 1) extrapolated from the prehatch curves and 2) obtained from posthatch data. Although the curves are quite similar at higher temperatures, differences in the lower temperature range are large. Nevertheless, the time to development of the functional jaw is much more accurately determined from the extrapolated curve, indicating an intrinsic process independent

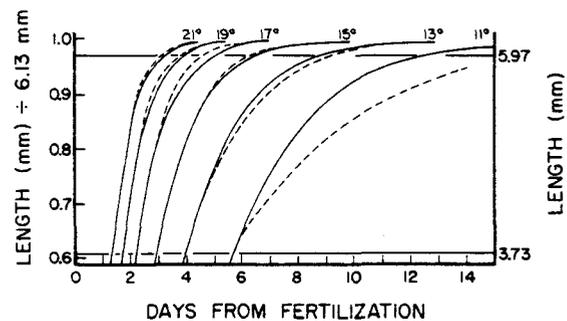


FIGURE 8.—Posthatch growth curves of the northern anchovy. Solid lines are extrapolated from prehatch curve. Broken lines are fitted to actual growth data.

of actual realized size. Comparison of the extrapolated curves for the sardine and anchovy, Figures 5 and 7, shows that for the same temperature and relative to the asymptotic size, hatching occurs later for the anchovy, but jaw development and first feeding occur at about the same time.

In summary, each growth cycle may be represented by an equation of the form

$$L = L_0 e^{K(1 - e^{-\alpha_T t})}$$

with $\alpha_T = \alpha_0 e^{-m(1 - e^{-\beta T})}$

or $\alpha_T = \alpha_{opt} e^{m_{opt}(1 - e^{-\beta \Delta})}$

with $\Delta = |T - T_{opt}|$

when a temperature optimum exists. The time required to attain a given size S is

$$t_S = \ln \left[\frac{K}{K - \ln(S/L_0)} \right] / \alpha_T$$

which has the same form as the original equation.

Most of the data available were from studies of two species, *Sardinops sagax* and *Engraulis mordax*, so that generalizations must be made with caution. Nevertheless, incubation times for several other species fit the model well.

Finally, it seems worthwhile to repeat that every growth problem becomes at last a specific one depending on many factors known or unknown, measureable or not. For example, time of fertilization will often not be known and age determinations will be inexact. Further, Hunter and Lenarz⁷ have shown that egg size is a measurable and probably important factor in growth and survival of anchovy larvae. For feeding larvae, the quantity and quality of food is critical. Egg size appears to affect growth by a simple scale factor, all events being shifted up or down in proportion to the egg size. Variation in food may result in many "artificial" cycles when nutritional and caloric requirements are not met. Nevertheless, it seems clear that at least the early growth of many fishes may be described in terms of genetically determined but dynamically changing growth rates as defined by the Laird-Gompertz growth function.

⁷Hunter, J., and W. Lenarz. 1974. A discussion on the adaptive values of variation of fish egg sizes. Unpubl. manuscr., 7 p. Southwest Fisheries Center, Tiburon Laboratory, National Marine Fisheries Service, NOAA, Tiburon, CA 94920.

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APPENDIX

The estimation procedure of Conway et al. (1970) is a least squares procedure which requires only the definition of the functional relationship and the first derivative with respect to each parameter. Although not stated explicitly, constant variance is assumed and, hence, the logarithmic form will be used throughout. For a single-cycle Laird-Gompertz curve the equations are as follows:

$$\ln F = \ln F_0 + A[1 - \text{Exp}(-\alpha t)]/\alpha$$

$$\frac{\partial \ln F}{\partial F_0} = 1/F_0$$

$$\frac{\partial \ln F}{\partial A} = [1 - \text{Exp}(-\alpha t)]/\alpha$$

$$\frac{\partial \ln F}{\partial \alpha} = A[(\alpha t + 1) \text{Exp}(-\alpha t) - 1]/\alpha^2$$

For a two-cycle curve with the second cycle beginning at $t = t^*$ the equations are:

$$\ln F = \ln F_0 + A[1 - \text{Exp}(\alpha \Delta_1)]/\alpha + B[1 - \text{Exp}(-\beta \Delta_2)]/\beta$$

$$\frac{\partial \ln F}{\partial F_0} = 1/F_0$$

$$\frac{\partial \ln F}{\partial A_0} = [1 - \text{Exp}(-\alpha \Delta_1)]/\alpha$$

$$\frac{\partial \ln F}{\partial \alpha} = A[(\alpha \Delta_1 + 1) \text{Exp}(-\alpha \Delta_1) - 1]/\alpha^2$$

$$\frac{\partial \ln F}{\partial \beta} = [1 - \text{Exp}(-\beta \Delta_2)]/\beta$$

$$\frac{\partial \ln F}{\partial \beta} = \beta[(\beta \Delta_2 + 1) \text{Exp}(-\beta \Delta_2) - 1]/\beta^2$$

$$\frac{\partial \ln F}{\partial t^*} = [A \text{Exp}(-\alpha \Delta_1) - B \text{Exp}(-\beta \Delta_2)]$$

where $\Delta_1 = \text{MIN}(t, t^*)$
 $\Delta_2 = \text{MAX}(t - t^*, 0)$.

FORTTRAN programs are available for fitting single-cycle, temperature-dependent and multi-cycle, temperature-dependent curves at SWFC.