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TEMPERATURE SPECIFIC EQUATIONS FOR GROWTH AND DEVELOPMENT OF THE ANCHOVY, ENGRAULIS MORDAX, DURING EMBRYONIC AND LARVAL STAGES

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ABSTRACT

The relationship between temperature and the time required for anchovy eggs or larvae to reach any developmental stage or length from fertilization to metamorphosis (app. 35 mm) is described using an application of the Gompertz equation. It was found that, when the growth curves of yolk-sac larvae at different temperatures are back extrapolated to the period before hatching, then the median time to reach a particular stage of egg development corresponds to the attainment of the same length at all temperatures. Thus embryonic development and growth may be viewed as a single process when development-equivalent lengths are assigned to each egg stage. For feeding larvae, the increase in temperature specific growth rate relative to a standard temperature was the same as in the embryonic period. Size or age specific daily growth rates calculated from a two-cycle growth equation agree with growth of laboratory reared and sea-caught larvae. Variability in size within a cohort of known age larvae is explained by differences in intrinsic growth parameters measurable at hatching.

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Investigations of environmental effects on the early growth of fishes (embryonic and larval) are an essential element in understanding the dynamics of fish populations. Growth models are needed which take into account the major controlling variables of temperature, life stage and food. During the embryonic period, defined as that from fertilization to the onset of feeding, temperature imposes an almost deterministic growth trajectory but thereafter growth is directly controlled by the availability of food and modulated or regulated indirectly by temperature through the rate of digestion and metabolism.

Zweifel and Lasker (1976) showed that for any temperature T, change in length with age of yolk-sac larvae could be represented by the Gompertz equation

$$L_t = L_o \exp\left\{A_{o,T}/\alpha_T \,[1-\exp(-\alpha_T(t-t_o))]\right\} \qquad (1)$$

where L_t = length at time t, L_o and $A_{o,T}$ are initial conditions at T and $t=t_o$ and α_T depends on T. They also showed evidence that events such as hatching, functional jaw development, etc. occurred at the same size at all temperatures. Zweifel (this issue) states that given these two conditions, the temperature specific time t_T to any event is also an equation of the Gompertz form, i.e.

$$t_T = t_{To}\exp\left\{A_0/\alpha[1-\exp(-\alpha(T-T_0))]\right\}.$$

Thus the coefficient α_T in equation (1) is, apart from a constant α_0, the reciprocal of the event time t_T i.e.,

$$\alpha_T = \alpha_0\exp\left\{-A_0/\alpha[1-\exp(-\alpha(T-T_0))]\right\} \qquad (1a)$$

Zweifel (this issue) demonstrates that complex growth relationships may sometimes be resolved as replications or cycles of a simple growth equation. In this paper, we use the growth equation (1) and the temperature relationship (1a) to develop a two cycle temperature dependent growth model from fertilization through metamorphosis.

We apply the Gompertz model to laboratory data on the growth of anchovy larvae, *Engraulis mordax* and calculate the parameters required for the estimation of age and daily growth rate at any temperature and life stage. Diet was not included in the model because growth was measured only at densities of cultured foods such that food was known not to be limiting.

In the first section of this paper we show evidence that the parameters of (1) and (1a) remain constant throughout embryological development. In the second section we show that the temperature dependent growth of anchovy larvae reared through metamorphosis is the laboratory may be described by a two cycle temperature dependent Gompertz equation in which two of the temperature dependent parameters remain constant throughout. In a final section we show that our results are consistent with other published records of growth on northern anchovy larvae and evaluate some of the implications of the model equations.

The solutions for all equations and models requiring iterative solutions are obtained by the procedure of Conway _et al_ (1970), a least squares technique which requires the definition of the functional relationship, its first derivatives with respect to each parameter and reasonable initial parameter values. The definitions of all models are given in the Mathematical Appendix and the relevant number N is indicated in the text as [N].

Initial parameter estimates required for the solution of the non-linear equations used in this paper may be obtained by a variety of methods. We present here examples for two procedures (Methods 1 and 2) based on linear regression techniques. The techniques will be of interest to those attempting to use a Gompertz equation or model for their own data. Those interested only in results may skip to the final paragraph of this section without fear of missing or ignoring elements critical to the paper.

Method 1

The first method, more applicable when observations are not made at equal intervals, is based upon the linearizing transformation

$$\ln\ [\pm \ln(Y_X/Y_\infty)] = a + b\ (X-X_0) \qquad (2)$$

where $k = A_0/\alpha$, $Y_\infty = Y_0\exp(k)$ is the limiting or asymptotic size and the size is positive or negative as the relationship is decreasing or increasing. Estimates of $a = \ln(k=A_0/\alpha)$ and $b = \alpha$ are obtained by fitting equation (2) for a range of Y_∞ (the asymptotic minimum or maximum) values. The parameters of choice are those which maximize the linear correlation coefficient. This method is generally useful only with calculators or computers which permit storage of the input data. As an example, we use the times to hatch for combined anchovy and sardine data as shown in Table 1, where $Y = t_T$, $X = T$ and $X_0 = T_0 = 10.2$. Parameter estimates near the maximum linear correlation coefficient are shown below .

Y_∞	R^2	Y_0	A_0	α
10.70	0.986765	156.21	-0.1984	0.0740
10.80	0.986766	156.36	-0.1989	0.0744
10.90	0.986767	156.51	-0.1999	0.0748
11.00	0.986766	156.66	-0.1998	0.0752
11.10	0.986763	156.81	-0.2003	0.0756

"Best" estimates by this method are $A_0 = 0.1994$, $= 0.0748$, $Y_\infty = 10.90$ and $Y_0 = Y_\infty\exp(A_0/\alpha) = 156.51$.[2]

Method 2

The second method is based upon the theoretical relationship of observations at successive time, age, or temperature in the Gompertz equation, i.e.

$$\ln Y_{X+1} = a + b \ln Y_X \tag{3}$$

where $b = \exp(-\alpha)$ and $a = Y_\infty(1-b)$. Ordinary linear regression may be used to obtain estimates of

$$\hat{\alpha} = -\ln(b) \tag{3a}$$

$$\hat{Y}_\infty = \exp(\hat{a}/1-\hat{b}) \tag{3b}$$

and an estimate of the parameter $\hat{A}_0 = \hat{\alpha}\hat{k}$ can be obtained from the equation

$$\hat{k} = \frac{1}{n} \Sigma \ln(\hat{Y}_\infty/Y_X) \exp[\hat{\alpha}(X-X_0)] \tag{3c}$$.

As an example we use only the sardine hatching data (Table 1) because it was recorded in equal intervals of temperature. For this data we have

$X=T$	$X-X_0$	Y_x	Y_{x+1}
11	0	140.0	115.0
12	1	115.0	93.0
13	2	93.0	78.5
14	3	78.5	68.1
15	4	68.1	60.2
16	5	60.2	53.7
17	6	53.7	48.4
18	7	48.4	43.2
19	8	43.2	39.3
20	9	39.3	34.0

$\hat{b} = 0.9210$

$\hat{a} = 0.1916$

$\hat{Y}_\infty = 11.3275$

$\hat{\alpha} = 0.0822$

$\hat{k} = -2.5296$

$\hat{A}_0 = 0.2080$

$\hat{Y}_o = 142.16$

As shown by Zweifel (this issue) these estimates are origin and scale dependent. The conversions required for $X_o = T_o = 10$ used in Method 1 are $\alpha' = \alpha = .0822$, $\hat{k}' = -2.5296 \exp(.0822) = -2.7464$ and $t_o = 11.3275 \exp(2.7464) = 176.56$.

Finally, the word parameter continues to hold different interpretations for mathematicians and biologists. For the former it is simply a variable in the mathematical equation; for the latter it often represents measureable components of the biological system such as temperature or food. In this paper, the mathematical interpretation prevails.

Effects of Temperature on Embryonic Development of Fishes

Egg Development

Quantification of growth on a continuous basis during embryological stages is difficult because egg development is monitored by the appearance of more or less easily recognizable events (see Ahlstrom, 1943) while larval growth is measured as change in length or weight. Since development, like growth, is a continuous process, these stages are no more discrete measurements than length or weight. Zweifel and Lasker (1976) showed that development equivalent lengths could be assigned to egg stages so that the same form of mathematical equation could be used to represent temperature dependent development as was used to measure change of length or weight with age. They used separate equations for egg development and growth in the yolk-sac stage. The primary objective of this section is to show, based on examination of a more extensive data set than was available to them, that not only the form but also the parameters of equations (1) and (1a) remain constant throughout the embryonic period.

Zweifel (this issue) shows: a) that the Gompertz equation is preferable to other methods (e.g. ln-linear regression or the Arrhenius equation) for expressing the relationship between temperature and time to reach a particular stage of embryonic development; and b) that two of the Gompertz model parameters (A_0,α) expressing the relationship of time to stage are the same for all stages of development. Thus, individual curves expressing the relation between the appearance of a stage and temperature differ only in an origin parameter $Y_0(S)$. Model [2] provides the solution for several Gompertz growth equations with a common A_0 and α.

The results presented in Zweifel and Lasker (1976) indicated that the temperature vs. development curves for the northern anchovy, *E. mordax* and the Pacific sardine, *S. sagax*, were indistinguishable. Thus in order to obtain more precise estimates of the parameters of the temperature relationship in the embryonic stage, we used the data from both species as shown in Table 1. Only the time to hatch (hours) was used to obtain initial values of A_0 and α because data on other stages of development did not span a sufficiently large temperature range. Using Method 1, estimates were $A_0 = .1944$ and $\alpha = .0748$.

To obtain initial values $Y_0(S)$ of the time to stages at $T = T_0 = 10°$ C for [2], the time to hatch $Y_0(H)$ was multiplied by the ratio (observed time to stage S)/(observed time to hatch) for the midrange temperature 16.0° C. The final parameter estimates and the estimated times to stage using the combined data (Table 1) are essentially the same as when a separate model [2] is used for each species (see Zweifel and Lasker 1976).

The evidence presented above demonstrates that the relation between temperature and the time to reach a given stage of egg development can be represented by a series of Gompertz equations in which the parameters A_0 and α remain constant. For purposes of modeling and interpolation for missing stages, it is often convenient to express the relationship between the intercepts of the separate curves and the stage in mathematical form. The estimated intercepts for the combined anchovy and sardine data showed a nearly perfect linear relationship between stage and time (Figure 1). This relationship provides a simple method of writing a general equation for developmental stage, developmental time and temperature. Since there is no a priori reason to suppose that the developmental indexes (stages) fall on any natural measurement scale, points falling off the line may be assigned new staging numbers which represent their true position on the grading scale. Then the coefficients of the relationship $Y_0(S,T_0) = f(a,b,S)$ may be inserted in the equation for the time $t_{S,T}$ to stage S at temperature T; e.g., in the linear case,

$$t_{S,T} = (a+bS)\exp -A_0/\alpha[1-\exp-\alpha(T-T_0)] \qquad (4)$$

Similarily for the developmental rate $D_{S,T} = 1/t_{S,T}$ we have in logarithmic form

$$-\ln D_{S,T} = \ln(a+bS)-A_0/\alpha\ [1-\exp(-\alpha(T-T_0))]. \qquad (4a)$$

For the anchovy-sardine data A_0 = .2156, = .0786, a = -10.65 and b = 15,84 so that, $t_{s,T}$ = (-10.65 + 15.84S) exp -2.7430 [1-exp(-0.0786 (T-10))] where hatch is assigned a stage of 11.3.[3]

Growth in Yolk-Sac Stage

Growth in the yolk-sac stage is a short but critical link between the almost deterministic growth of the embryo within the egg and the stochastic growth processes of the feeding larvae. Quantification of this period requires careful consideration for several reasons: 1) in this period of rapidly changing morphology, weight rather than length would be the preferred parameter but only length is usually measured, 2) it is difficult to measure accurately the average length at time of 50% hatch, and 3) the depletion of the yolk-sac and the onset of feeding overlap so that two mechanisms of growth curve simultaneously. In this section we show that the five parameter model [3] described by Zweifel and Lasker (1976) can be used to express the relationship of time and size of yolk-sac larvae at any temperature when the parameters A_0 and α of equation (1a) are determined from [2] using only information on egg development.

Kramer (unpublished data, SWFC, La Jolla, California) measured the standard length and the depth of the yolk sac of anchovy larvae at 14, 17 and 20° C through the onset of feeding. He also determined the percent P of larvae with food in the gut in the 17 and 20° C experiments. Standard lengths for pre-feeding and feeding larvae are shown in Table 2 together with the percent of larvae with detectable food in the gut.

The average length of larvae when most were feeding was about 4.1 mm and was just slightly larger than the maximum length (4.05) reached by non-feeding larvae at 14°.

The five parameter model [3] relating time and size at several temperatures is defined by the two equations

$$L_t = L_o \exp\left\{k\ [1-\exp(-\alpha_T t)]\right\} \tag{5}$$

and

$$\alpha_T = \alpha_o \exp\left\{m[1-\exp(-\beta(T-T_o))]\right\} \tag{6}$$

Initial values of the parameters $m = 2.7430$ and $\beta = .0786$ are obtained from the staging or incubation curve (i.e. $m = A_o/\alpha$ and $\beta = \alpha$). Initial estimates for the other parameters are easily obtained using Method 2, equation 6 and interpolated lengths[4] at intervals of .5 mm.

For the 20° experiment, we have

Age	Interpolated Length
2.0	3.00
2.5	3.80
3.0	4.00
3.5	3.96
4.0	4.05
4.5	4.20
5.0	

$\hat{b} = .3661$

$\hat{a} = .8963$

$\hat{L}_\infty = 4.1128$

$\hat{k}^5 = .2201$

$\hat{\alpha}_T = 1.0048$

From equation (6) we obtain $\hat{\alpha}_0 = .2257$. The parameter estimates converted to a zero origin and unity scale and used as first estimates for the iterative solution of [3] were

$$\hat{k} = 0.2201\exp(2/.5) = 12.2500$$

$$\hat{L}_0 = 4.1128\exp(-12.25) = 1.9680*10^{-5}$$

$$\hat{\alpha}_0 = .2257/.5 = 0.4514$$

$$\hat{m} = 2.7430$$

and $$\hat{\beta} = 0.0786$$

Final parameter estimates were $L_0 = 2.1371\times10^{-5}$, $k = 12.1628$, $\alpha_0 = 0.4654$, $m = 2.744$ and $\beta = 0.0786$.[6] The estimated asymptotic size $L_0\exp(k)$ is 4.093 mm. The estimated size at hatch obtained by calculating size for the incubation time at any temperature from Table 1 is 2.56 mm.

The estimated size at age for yolk sac larvae at the three temperatures is shown together with the observed means in Table 2. Agreement is generally good throughout.

The relationship

$$L_t = 2.1372 * 10^{-5} \exp \left\{12.1628 \left[1-\exp(-\alpha_T t)\right]\right\} \text{ with}$$

$$\alpha_T = .4654 \exp \left\{2.7440 \left[1-\exp(-.0786(T-10))\right]\right\}$$

is shown in Figure 2 for the three experimental temperatures. The growth process described in this analysis is dynamic rather than static. In Figure 3, the instantaneous growth rates

$$\frac{d\ln L_t}{dt} = k\alpha_T \exp(-\alpha_T t)$$

are shown to decrease dramatically and continuously with age. Thus, the description of growth is a series of age specific growth rates, i.e., a growth process. In this sense, the yolk-sac growth curves appear as a simple extension of the pre-hatch growth trajectories.

The procedure outlined in this section is based on the assumption of a single temperature function throughout the embryonic period. The practical importance is that careful staging of eggs at a single temperature (preferably in the mid-range of the survival temperatures) together with the temperature function at one or two selected stages will provide the complete temperature-development-growth relationship in the embryonic period. As evidence we use data for the growth of yolk-sac larvae of the Pacific sardine, *S. sagax* at 7 temperatures (13-18.8° C) reported by Lasker (1964). Since we have shown that the temperature-developmental relationship is similar for the anchovy and sardine it should be possible to predict the growth of yolk-sac larvae from observations at only one or two temperatures.

Using Method 2 and equation (6) and data for a mid-range temperature (16° C), we obtained parameter estimates as shown below:

$$\begin{array}{lll}
\hat{b} = .4522 & \hat{L}_0 = \hat{L}_\infty \exp(-\hat{k}) = 3.75 & \hat{a} = 1.0116 \\
\hat{m} = 2.7430 & \hat{\alpha}_T = -\ln(\hat{b}) = .7936 & \hat{L}_\infty = 6.3392 \\
\hat{\beta} = .0786 & \hat{\alpha}_0 = .2829 & \hat{k} = .5250
\end{array}$$

The observed and estimated sizes at age for several temperatures in the range 13-19° C are shown in Table 3. The largest discrepancy is approximately 5% of the observed size.

The similarity of the parameter estimates for the temperature functions in sardine, anchovy and herring (reported by Zweifel this issue) may be of general biological interest. In fact, if T_0 is set to 11 (the lowest temperature with significant survival) rather than 10° for the anchovy and sardine, the estimates are nearly identical (.2374, .0782, .2332, .0786). *This suggests that only staging at a single temperature and the minimum survival temperature may be required to determine the effect of temperature on the development of fish eggs.*

A Two Cycle Temperature Dependent Growth Model of Anchovy Larvae from Fertilization through Metamorphosis

In this section we develop a two cycle temperature dependent growth model for anchovy for the period from fertilization through metamorphosis at high densities of cultured foods. The data used to describe growth in anchovy from fertilization to the onset of feeding was presented in the preceeding section. Data used for growth of larval anchovy after the onset of feeding was obtained from laboratory rearing experiments using cultured foods, (*Gymnodinium splendens*, *Brachionus plicatilus*, *Tisbe furcata*, and *Artemia salina nauplii*). Culture techniques, food densities, egg stocking densities and containers were the same as those described by Hunter (1976, Group 5). Usually samples of 15 or more larvae were removed and measured every other day. One group was reared to 35 mm at 16.2 ± .95° C (presented by Hunter, 1976); another to 16 mm at 12.7 ± .23° C and a third to 12 mm at 18.8 ± 26° C. Owing to the large number of individual observations (1774) iterative solutions using individual larval lengths were impractical and consequently, we used the mean length for each age.

A direct estimate of the temperature function for growth of feeding larvae could not be made because we have data for only three temperatures. The uniformity of the temperature function throughout the embryonic stage suggested that the temperature dependent growth model for that period could be generalized for use in larvae after the onset of feeding. To examine this possibility, a temperature dependent model [3] and a two cycle model [4] were combined to provide [5], a two cycle temperature dependent growth model:

$$L_t = L_0 \exp\left\{k_1 \ [1-\exp(-\alpha_{1,T}(t-t_0))]\right\} \tag{7}$$

$$\alpha_{1,T} = \alpha_{1,0} \exp\left\{m \ [1-\exp(-\beta(T-T_0))]\right\} \qquad L \leq L^* \tag{7a}$$

$$L_t = L^* \exp\left\{k_2 \ [1-\exp(-\alpha_{2,T}(t-t^*))]\right\} \qquad L > L^* \tag{7b}$$

$$\alpha_{2,T} = \alpha_{2,0} \exp\left\{m \ [1-\exp(-\beta(T-T_0))]\right\} \tag{7c}$$

where the relationship between the time to onset of feeding t* and size at first feeding L* at temperature T is

$$t^* = \ln\left[\frac{k_1}{k_1-\ln(L^*/L_0)}\right] \Big/ \alpha_{1,T} \tag{7d}$$

Initial estimates k_2 and $\alpha_{2,0}$ required for growth of feeding larvae were obtained from the 16.2° experimental data shown in Table 4 again using Method 2 and equation 6 where $\hat{b} = 0.9380$, $\hat{a} = 0.2394$ and $\hat{k}_2 = 2.408$. The asymptotic size is 47.5688 mm and $\alpha_{2,0} = 0.0640$. These parameters are converted to those appropriate to the origin of first feeding (approximately 4.09 mm) and a scale of 1 day intervals. 4.09 occurs at approximately -0.25 on the original scale or at about .5 days. Thus the necessary conversions are $\hat{k}_2 = 2.4080\exp(0.0640 * 0.25) = 2.4468$ and $\alpha_{2,0} = 0.0111$.

The final parameter estimates were $L_o = 2.137*10^{-5}$, $k_1 = 12.1628$, $\alpha_{1,o} = .4494$, $m = 2.7440$, $\beta = .0786$, $k_2 = 2.3237$, $\alpha_{2,o} = .0134$ and $L* = 4.090$ mm, where $t_o = 0$ and $T_o = 10$. The estimated maximum size attained in the second growth cycle is 41.77 mm.

The fit, as shown in Table 4, is generally good throughout for the three laboratory rearing experiments. In nearly all instances, departures from the observed growth trajectories represent a temperature change of ± .5° C which was the usual variation in temperature within rearing containers. In table 5, the growth trajectories from stage I eggs to 40 mm larvae are calculated for a temperature range of 12 to 22° C.

The period over which feeding begins is of critical consideration both from the ecological standpoint of survival (May, 1974) and from the analytical standpoint of growth analysis. During this stage larvae use endogenous as well as exogenous sources of energy. Larvae may remain in the size range associated with the onset of feeding (4-4.5 mm) for extended periods depending on the availability and type of foods present. Anchovy larvae fed only the small prey Gymnodinium splendens, remained within this size range for 12 days although survival remained high (45%) (Hunter, unpublished data) and incidental capture of larger prey can enhance survival without measureable growth (Lasker and Zweifel, 1978). Further, the threshold for the onset of feeding is food density dependent (Lasker, 1975). Thus larvae may use endogenous sources of energy for variable periods depending on food availability, posing analytical problems in determining when the second or food dependent growth cycle begins.

Further, anchovy egg size varies seasonally and large and small eggs from the same spawning batch show statistically different ($p \leq .01$) larval hatching lengths as shown in table 6. Thus, egg size effects the duration larvae spend in the critical size range at the onset of feeding.

All of the above factors can alter size and age relationships. In order to facilitate the comparison of individual experiments, size and temperature specific daily growth rates were calculated from the growth equations. For prefeeding larvae the age specific daily growth rate dL/dt is

$$L_t k_{1,T} \exp(-\alpha_{1,T})$$

and for feeding larvae, the corresponding equation is

$$L_t k_2 \alpha_{2,T} \exp[-\alpha_{2,T}(t-t^*)]$$

where $L_t, \alpha_{1,T}$, $\alpha_{2,T}$ and t^* are defined by equations (7a-d). The calculations for a range of temperatures 12-22 are given in Table 7.

Comparisons of the Model to Growth of Larvae in the Sea and to Other Laboratory Studies

In order to compare other growth data to our results, we use the laboratory growth equivalent temperature (LGET) calculated for any length L and age from hatch A. The LGET is derived as follows:

For feeding larvae, the equation analogous to (7d) is

$$t = \ln\left[\frac{k_2}{k_2-\ln(L/4.090)}\right]\Big/\alpha_{2,T} \qquad (11)$$

where t is time from first feeding and $\alpha_{2,T}$ is defined in (7c). The origin is set to time of hatch by substituting the size at hatch (L_H=2.56 mm) for L in equation (11), solving for t at any temperature and estimating $k'_1 = k_1\exp(-t\alpha_{2,T})$. For 16° C, we have $t = -4.91$ and $\alpha_{2,T} = .0374$ so that

$$A = \ln\left[\frac{2.7918}{2.7918-\ln(L/L_H)}\right]\Big/\alpha_{2,T}$$

Solving this equation for temperature T we obtained the rather formidable but useful equation

$$\text{LGET} = T_o - \frac{1}{\beta}\ln\left\{1-\frac{1}{m}\ln\left[\frac{\ln\left(\frac{k_2}{k_2-\ln(L/L_H)}\right)}{\alpha_{2,o}}\right]\right\} \qquad (12)$$

where $k_2 = 2.7918$, $L_H = 2.56$, $\alpha_{2,o} = .01335$, $\beta = .0786$, $m = 2.7440$ and $T_o = 10°$.

Growth of field caught larvae estimated from daily increments on otoliths was compared to that predicted from the equations (7a) and (7c). Methot and Kramer (1979) found that the average daily growth rates of 4-20 mm sea caught larvae did not differ from that predicted by the model for an average surface temperature. However, some of the growth rates from single stations correspond to model estimates as much as ± 3° C from the local surface temperature. A variety of causes may be reasonable; the most obvious possibilities are an unrepresentative temperature, net selection, size specific mortality and the quantity of esculent particles within the larval ambit.

To examine the possible effects of differential mortality or sampling selection and to evaluate the stability of the form of the growth relationship, the 15 larvae in each sample for the 16° C experiment were stratified by size into 5 groups (i.e. 3 larvae per group). In table 7 the observed means for these five groups which represent the 10, 30, 50, 70 and 90th percentiles are shown for ages 4-74 days. Table 8 shows that differences in egg size or length at hatch (5-10%) cannot account for the persistent differences throughout the experiment. If however, larvae differ in initial rates of growth and maintain their relative rates over considerable periods of time, then variation in genetically determined initial rates of growth would result in grwoth curves (each percentile) of the same form and the growth curves could be predicted from the variability of the initial growth rates.

Assuming that the logarithms of the initial growth rates are normally distributed, i.e. $Z_p = \ln(A_p/\mu/\sigma)$, $\mu = A_o$, $\sigma = \text{var} \ln A_o$ and

$f(Z)=N(\mu,\sigma)$, the estimated growth curves at each percentile (Z_p 1.29, -.525, 0.0, .525, 1.29) were calculated and are shown in table 7 with = .0455, an average standard deviation of the logarithms of the observed lengths on the first day of feeding. The close agreement of the observed and predicted growth curves supports the assumption of intrinsic differential rates of growth.

The laboratory growth equivalent temperature determined at A=50 for each percentile is given in table 8. The upper 99 and lower 1 percentiles ($Z=\pm 2.33$) were determined for the same population in order to examine the effect of extreme mortality or selection. The slowest growing larvae (1%) represent a LGET decrease of only 2° C while the fastest (99%) maintain a growth rate equivalent to a 3.5° increase in LGET. Thus, the dynamic range of growth in the laboratory is asymmetrical with a greater range above the average growth rate. This suggests that if mortality is higher for small larvae, apparent growth rates considerably above the estimated curve would result, and the net capture of slower swimming larvae in field samples would result in a smaller negative bias.

Sakagawa and Kimura (1976) presented one of the earliest attempts to maintain anchovy larvae for an extended period of time. Unfortunately, few details of the experiment were available although it was known that temperature was not controlled and was probably near ambient air temperature. Hiatuses occur in both the sampling interval and in the rates of growth indicating modifications of the environmental regime. The LGET's increase continuously from 14.8° at 8 days to 19.4° at 44 days. The average daily growth rate from 8 to 26 days was (17.2-4.81)/18=.69 mm/day which corresponds to the average (.56 + .82)/2=.69 mm/day for a

19° C growth curve over the same size interval. Similarly, the period from 26 to 44 days corresponds to the rates for a 22° curve from 17 to 33 mm. A rapid slowing of the growth occurs beyond 35 mm.

Kramer and Zweifel (1970) reported the results of three rearing experiments for anchovy, two at 17° C and one conducted at room temperature presumed to be about 22° C. Larvae in these experiments reached feeding size (i.e. 4.09 mm) later than predicted from our model (equation 10d). The delay was approximately one day for the combined 17° experiments and approximately 2 days for the 22° experiment with these corrections, the LGETs were 16.7 and 21.2° C respectively.

Thus, the model shows general agreement to all published data on laboratory growth rates of northern anchovy where food was considered adequate (Kramer and Zweifel, 1970; Sakagawa and Kimura, 1976) and to those of sea caught larvae determined from daily rings on the otoliths (Methot and Kramer, 1979). The two cycle Gompertz model adequately describes the appearance of developmental events and growth from fertilization through metamorphosis as a function of temperature. We do not assign any special significance to this particular mathematical relationship except to note its conceptual simplicity and wide applicability (see, Zweifel, this issue). The evidence presented for the persistence of differential intrinsic rates of growth predictable from the variation in size of newly hatched larvae suggests that the Gompertz equation may be a useful stochastic modeling tool.

MATHEMATICAL APPENDIX

> I do not say: science is useful because it allows us to construct machines; I do say: machines are useful, for by working for us they permit us more time to study science.
>
> --Jules Henri Poincare (1854-1912)

The formulae presented in this section are all extensions or generalizations of the simple Gompertz equation (model (1).

An abundance of fitting procedures are now available for estimating the parameters of non-linear models (see, e.g., Chambers, 1973). We used the technique of Conway *et al*. (1970), a least squares procedure which requires the definition of the functional relationship and the first derivatives with respect to each parameter.

The terminology for such fitting procedures has become more or less standardized. Using the Fortran conventions, the functional relationship F(I) is defined in terms of parameters P(J), and the independent variables X(I,K) where I=1,N; J=1, NP and K=1, NX. The observed independent variable is Y(I) and the derivatives are defined as PP(I,J). For measurements of growth of larval fish, the standard deviation is generally proportional to the mean (see table 4) so that usually the logarithmic transformation is required for homogeneity. Thus for the equations below F(I) corresponds to the logarithm of the measured length. For the independent variables, X(I, 1) = age, X(I,2) = temperature and X(I,3) identifies a grouping such as stage of egg development.

Model	Definition	Fortran Expression
[1]	F(I)	ln P(1) +P(2)*(1-exp(-P(3)*X(I,1)))/P(3)
	PP(I,1)	1/P(1)
	PP(I,2)	(F(I) -lnP(1))/P(2)
	PP(I,3)	P(2)*((X(I,1)*P(3) +1)*exp(-P(3)*X(I,1))-1)/P(3)**2
[2]	ID	X(I,3)
	F(I)	lnP(ID) + P(NP-1)*(1-exp(-P(NP)*X(I,2)))/P(NP)
	P(I,ID)	1/P(ID)
	P(NP-1)	(F(I)-lnP(ID))/P(NP-1)
	P(I,NP)	P(NP-1)*((X(I,2)*P(NP)+1)*exp(-P(NP)*X(I,2))-1)/P(NP)**2
[3]	AT	P(3)*exp(P(4)*(1-exp(P(5)*X(I,2))))
	F(I)	ln P(1) + P(2)*(1-exp(-AT*X(I,1)))
	DP	P(2)*X(I,1)*exp(-AT*X(I,1))
	PP(I,1)	1/P(1)
	PP(I,2)	(F(I)-lnP(1))/P(2)
	PP(I,3)	DP*AT/P(3)
	PP(1,4)	DP*AT*(1-exp(-P(5)*X(I,2)))
	PP(I,5)	DP*AT*P(4)*X(1,2)*exp(-P(5)*X(I,2))

Model	Definition	Fortran Expression
[4]	D1	MIN(X(I,1),P(6))
	D2	Max(X(I,1)-P(6),0)
	D3	0 IF X(I,1)<P(6), otherwise 1
	F(I)	ln P(1) + P(2)*(1-exp(-P(3)*D1))/P(3) +P(4)*(1-exp(-P(5)*D2))/P(5)
	PP(I,1)	1/P(1)
	PP(I,2)	(1-exp(-P(3)*D1))/P(3)
	PP(I,3)	P(2)*((P(3)*D1+1)*exp(-P(3)*D2)-1)/P(3)**2
	PP(I,4)	(1-exp(-P(5)*D2))/P(5)
	PP(I,5)	P(4)*((P(5)*D2+1)*exp(-P(5)*D2)-1/P(5)**2
	PP(I,6)	D3*(P(2)*exp(-P(3)*D1)-P(4)*exp(-P(5)*D2))
[5]	AT	P(4)*exp(P(5)*(1-exp(P(6)*X(I,2))))
	BT	P(7)*AT/P(4)
	CT	ln(P(2)/(P(2)-ln(P(8)/P(1)))/AT
	D1	MIN(X(I,1),CT)
	D2	MAX(X(I,1)-CT,o)
	D3	0 IF X(I,1) < CT, otherwise 1

Definition	Fortran Expression
DT	D2*(AT*P(2)*exp(-AT*D1)-BT*P(3)*exp(-BT*D2)
DP1	D3*P(2)*exp(-AT*D1)-DTxcT/AT
DP2	D2*D3P(3)*exp(-BT*D2)
F(I)	lnP(1) +P(2)*(1-exp(-AT*D1))+P(3)*(1-exp(-BT*D2))
PP(I,1)	1/P(1)
PP(I,2)	1-exp(-AT*D1)
PP(I,3)	1-exp(-BT*D2)
PP(I,4)	DP1*AT/P(4)
PP(I,5)	(DP1*AT+DP2*BT)*(1-exp(-P(6)*X(I,2)))
PP(I,6)	(DP1*AT+DP2*BT)*P(5)*X(I,2)*exp(-P(6)*X(I,2))
PP(I,7)	DP2*BT/P(7)
PP(I,8)	DT

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FOOTNOTES

[1] Zweifel and Lasker (1976) set T_0 to 0 but we prefer to use an origin close to the minimum survival temperature for ease of estimation and understanding.

[2] Fortran and Algol versions of this program are available at the SWFC.

[3] On the other hand, Zweifel (this issue) shows that for the herring data of Colby and Brooks (1973), the relationship $f(a,b,S)$ is log-linear. The parameters ar $A_0 = .2374$, $\alpha = .0782$, $a = 2.8910$ and $b = .1164$, i.e., $t_{S,T} = \exp 2.8910 + .1164S - 3.0358 \;\; 1-\exp - .0782(T-0.5)$.

[4] No estimates were made for the 14° data because no food was available in that experiment.

[5] Using (3d), k may be estimated from any or all data points. In this instance we consider the early observations more reliable. These estimates are obtained from the first observation only i.e. $\ln(Y_\infty/Y_0)$.

[6] Because the estimates m and β obtained from egg development were believed to be the best available, these two parameters were held constant.

FIGURES

Figure 1. Time to stage 0 (Y_0) of anchovy eggs.

Figure 2. Length at age of anchovy larvae from fertilization to onset of feeding.

Figure 3. Estimated instantaneous growth rates in mm/day of anchovy larvae during the embryonic period.

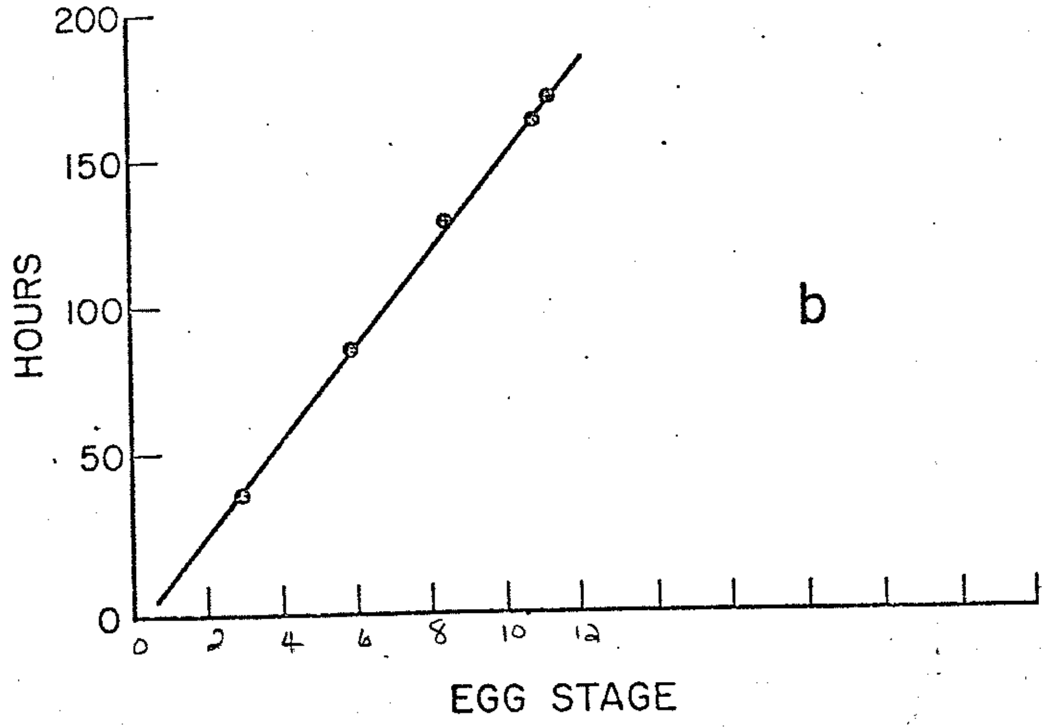

Figure 1

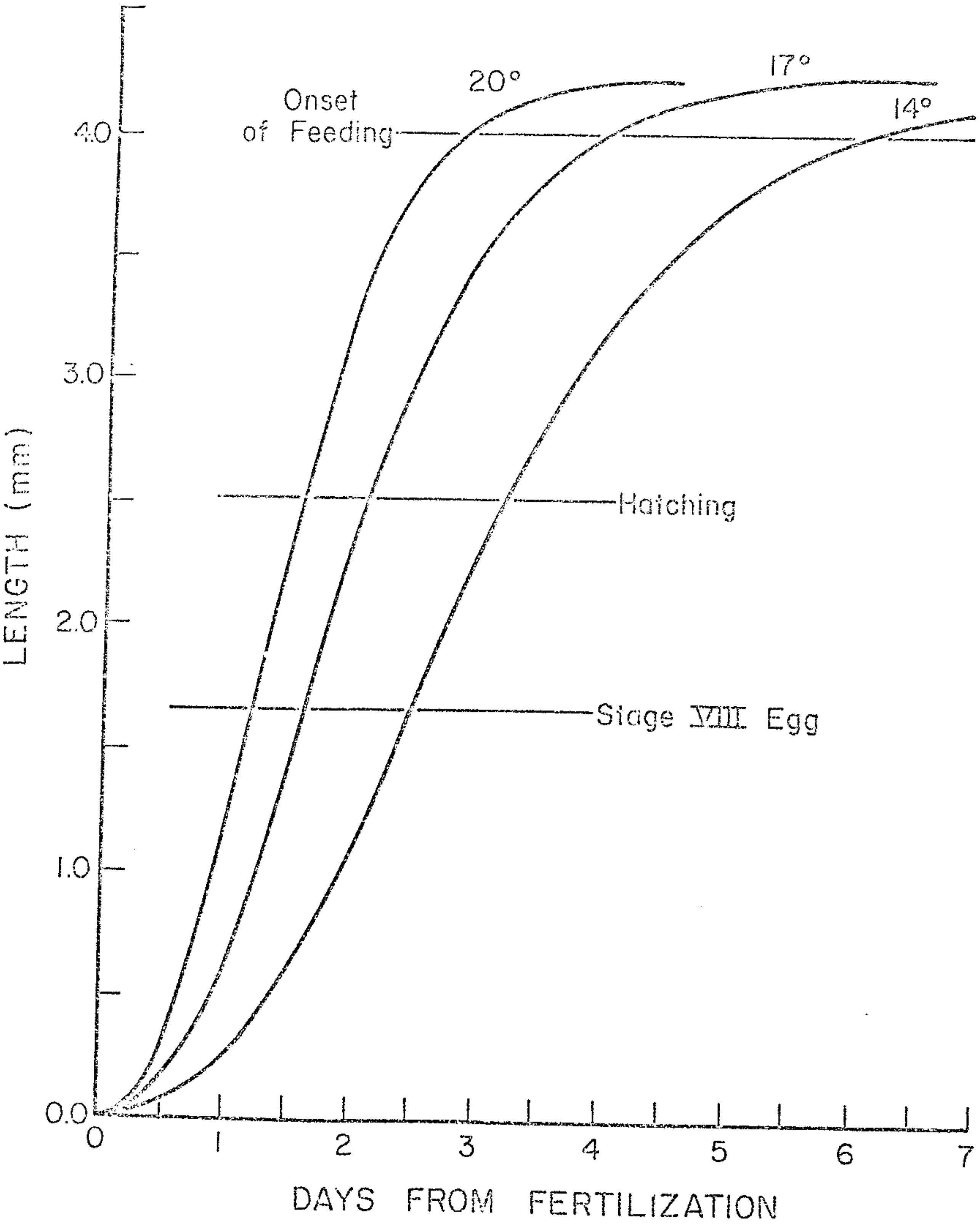
LENGTH (mm)
0.0
1.0
2.0
3.0
4.0
0
1
2
3
4
5
6
7
DAYS FROM FERTILIZATION
20°
17°
14°
Onset of Feeding
Hatching
Stage VIII Egg

Figure 2

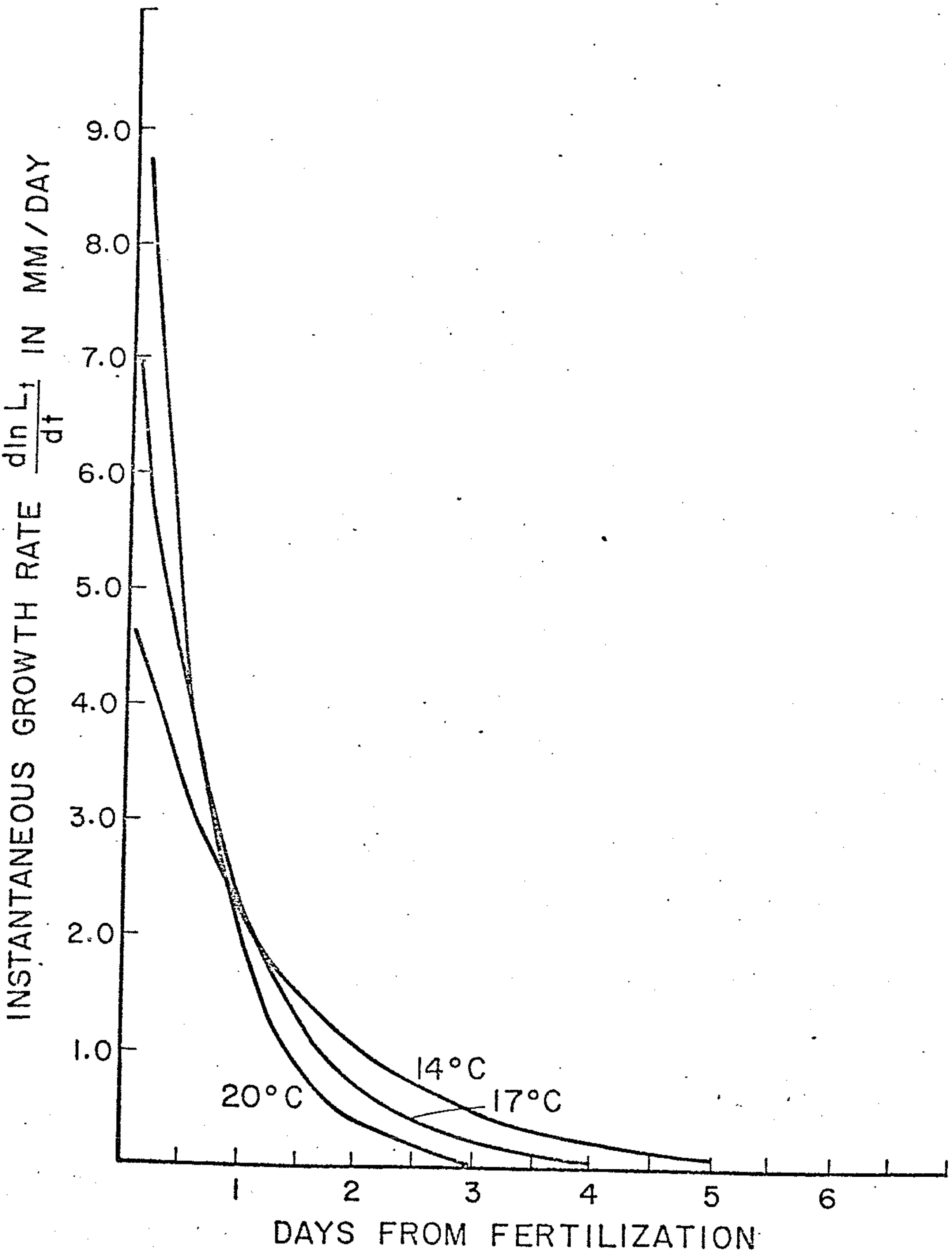
INSTANTANEOUS GROWTH RATE $\frac{d\ln L_t}{dt}$ IN MM / DAY
9.0
8.0
7.0
6.0
5.0
4.0
3.0
2.0
1.0
14°C
17°C
20°C
1
2
3
4
5
6
DAYS FROM FERTILIZATION

Figure 3

larvae at three temperatures, Kramer (unpublished data).

mperature	Incumbation Time (days)	Days from Hatch	Age (days)	Observed Length	Estimated Length	Percent Feeding
14	3.34	.88	4.22	3.12	3.36	--
		1.12	4.46	3.13	3.50	--
		1.38	4.72	3.40	3.63	--
		1.67	5.01	3.64	3.74	--
		1.92	5.26	3.69	3.81	--
		2.42	5.76	3.79	3.92	--
		2.92	6.26	3.95	3.99	--
		3.42	6.76	3.80	--	00
		3.92	7.26	3.97	--	00
		4.42	7.76	3.79	--	00
		4.92	8.26	4.05	--	00
		5.42	8.76	3.93	--	00
		5.92	9.26	3.81	--	00
		6.42	9.76	3.87	--	00
17	2.19	.04	2.23	2.67	2.63	--
		.20	2.39	2.79	2.89	--
		.37	2.56	3.22	3.12	--
		.54	2.73	3.29	3.32	--
		.79	2.98	3.72	3.54	--
		1.04	3.23	3.87	3.70	--
		1.29	3.48	3.98	3.82	--
		1.54	3.73	4.02	3.90	00
		1.83	4.02	4.02	3.97	60
		2.12	4.32	3.94	4.02	50
		2.42	4.61	4.21	4.04	89
		2.71	4.90	4.10	4.06	33
		3.00	5.19	4.23	4.07	No. obs.
		3.29	5.48	4.04	4.08	No. obs.
20	1.57	.00	1.57	2.64	2.56	--
		.12	1.69	2.91	2.84	--
		.25	1.82	3.16	3.10	--
		.38	1.95	3.34	3.31	--
		.50	2.07	3.56	3.47	--
		.71	2.28	3.74	3.68	--
		1.00	2.57	3.83	3.86	--
		1.17	2.74	3.83	3.93	--
		1.42	2.99	4.00	4.00	00
		1.62	3.19	4.08	4.03	00
		1.83	3.40	3.98	4.05	88
		2.04	3.61	3.96	4.07	100
		2.29	3.86	4.02	4.08	80
		2.50	4.07	4.09	4.09	67
		2.71	4.28	4.30	4.09	89
		2.92	4.49	4.20	4.09	90

---

[1] Length = $2.13675 \times 10^{-5} \exp(12.1631(1-\exp(-\alpha_T AGE)))$; $\alpha_T = .4652 \exp(2.7440(1-\exp(-.0786(T-10))))$.

Table 1. Observed (OBS) and estimated (EST)[1] time in hours to developmental egg stages[2] and hatch for the Pacific sardine(s) and northern anchovy(a).

	Stage									Hatching		
	3		6		8-9		11					
TEMP	OBS(36.36)EST		OBS(84.49)EST		OBS(125.40)EST		OBS(162.57)EST			TEMP	OBS(168.06)EST	
13.5 s	20.4	18.8	41.8	43.7	62.5	64.8	82.6	84.0		11.0 s	140.0	136.6
13.8 a	20.0	17.9	42.0	41.6	58.0	61.8	78.0	80.1		11.1 a	113.0	133.9
14.0 s	18.9	17.3	39.1	40.3	58.3	59.8	77.2	77.6		12.0 s	115.0	112.8
14.5 s	17.4	16.1	36.6	37.3	59.4	55.4	72.2	71.8		12.5 a	98.0	103.0
15.0 s	16.2	14.9	34.3	34.6	50.7	51.4	67.5	66.7		13.0 s	93.0	94.5
15.2 a	15.0	14.5	35.0	33.7	50.0	50.0	65.0	64.8		13.8 a	80.0	82.8
15.5 s	14.9	13.9	32.1	32.3	47.2	47.9	63.1	62.1		14.0 s	78.5	80.2
16.0 s	13.8	13.0	30.0	30.1	44.0	44.7	59.0	58.0		15.0 s	68.1	68.9
16.5 s	0.0	12.1	28.1	28.2	41.1	41.9	51.0	54.3		15.2 a	63.0	67.0
16.6 a	10.0	12.0	26.0	27.8	39.0	41.3	55.1	53.6		16.0 s	60.2	59.9
17.0 s	0.0	11.4	26.3	26.5	0.0	39.3	51.5	50.9		16.6 a	55.0	55.4
18.0 a	9.0	10.1	24.0	23.5	35.0	34.9	44.0	45.2		17.0 s	53.7	52.6
19.4 a	8.0	8.7	21.0	20.2	33.0	29.9	39.0	38.8		18.0 a	49.0	46.7
20.8 a	6.0	7.6	19.0	17.6	28.0	26.1	35.0	33.8		18.0 s	48.4	46.7
										19.0 s	43.2	41.8
										19.4 a	40.0	40.1
										20.0 s	39.3	37.8
										20.8 a	36.0	35.0
										21.0 s	34.0	34.4

[1] Estimates obtained from the equation $t_{S,T} = Y_0(S) \exp\left\{-\frac{.2157}{.0786}\left[1-\exp\left(-.0786(T-10)\right)\right]\right\}$ where the intercept $Y_0(s)$ is identified in parentheses.

[2] Egg stages are defined by Ahlstrom (1943).

13.8
15.2
16.6

Table 2. Observed and estimated[1] size at age for yolk sac anchovy larvae at three temperatures, Kramer (unpublished data).

Temperature	Incumbation Time (days)	Days from Hatch	Age (days)	Observed Length	Estimated Length	Percent Feeding
14	3.34	.88	4.22	3.12	3.36	--
		1.12	4.46	3.13	3.50	--
		1.38	4.72	3.40	3.63	--
		1.67	5.01	3.64	3.74	--
		1.92	5.26	3.69	3.81	--
		2.42	5.76	3.79	3.92	--
		2.92	6.26	3.95	3.99	--
		3.42	6.76	3.80	--	00
		3.92	7.26	3.97	--	00
		4.42	7.76	3.79	--	00
		4.92	8.26	4.05	--	00
		5.42	8.76	3.93	--	00
		5.92	9.26	3.81	--	00
		6.42	9.76	3.87	--	00
17	2.19	.04	2.23	2.67	2.63	--
		.20	2.39	2.79	2.89	--
		.37	2.56	3.22	3.12	--
		.54	2.73	3.29	3.32	--
		.79	2.98	3.72	3.54	--
		1.04	3.23	3.87	3.70	--
		1.29	3.48	3.98	3.82	--
		1.54	3.73	4.02	3.90	00
		1.83	4.02	4.02	3.97	60
		2.12	4.32	3.94	4.02	50
		2.42	4.61	4.21	4.04	89
		2.71	4.90	4.10	4.06	33
		3.00	5.19	4.23	4.07	No. obs.
		3.29	5.48	4.04	4.08	No. obs.
20	1.57	.00	1.57	2.64	2.56	--
		.12	1.69	2.91	2.84	--
		.25	1.82	3.16	3.10	--
		.38	1.95	3.34	3.31	--
		.50	2.07	3.56	3.47	--
		.71	2.28	3.74	3.68	--
		1.00	2.57	3.83	3.86	--
		1.17	2.74	3.83	3.93	--
		1.42	2.99	4.00	4.00	00
		1.62	3.19	4.08	4.03	00
		1.83	3.40	3.98	4.05	88
		2.04	3.61	3.96	4.07	100
		2.29	3.86	4.02	4.08	80
		2.50	4.07	4.09	4.09	67
		2.71	4.28	4.30	4.09	89
		2.92	4.49	4.20	4.09	90

---

[1] Length = $2.13675*10^{-5}$ exp $(12.1631(1-\exp(-\alpha_T AGE)))$; $\alpha_T = .4652 \exp(2.7440(1-\exp(-.0786(T-10))))$.

Table 3. Observed and estimated length at age of sardine larvae during the yolk-sac stage.

	Days from Hatching											
	0		1		2		3		4		5	
Temp	0	E	0	E	0	E	0	E	0	E	0	E
13°	3.73	3.75	4.50	4.61	4.97	5.23	5.46	5.64	5.74	5.90	--	--
14°	3.98	3.75	4.80	4.74	5.39	5.40	5.65	5.80	5.91	6.04	--	--
15	--	--	5.14	4.87	5.59	5.55	5.96	5.93	6.11	6.13	--	--
16	3.75	3.75	5.01	5.00	5.68	5.69	5.99	6.04	6.22	6.20	6.29	6.28
16.8°	3.74	3.75	5.20	5.10	5.78	5.79	6.14	6.11	6.25	6.24	6.26	6.30
17.8	3.69	3.75	5.27	5.22	5.86	5.90	6.06	6.17	6.18	6.28	--	--
18.8	--	--	5.46	5.33	5.98	5.99	6.09	6.22	--	--	--	--

hatching through metamorphosis at several temperatures.

Source*	Observed Mean	S.D.	N	Estimated	Age from Fertilization	Temp.
H	4.16	.17	14	4.05	9.14	12.7
	4.16	.15	11	4.09	11.14	
	4.72	.31	14	4.87	16.14	
	5.05	.53	10	5.35	18.14	
	5.73	.71	13	6.12	21.14	
	5.93	.70	11	6.67	23.14	
	8.41	1.18	11	8.71	30.14	
	10.49	1.59	10	10.96	37.14	
	12.74	1.56	10	13.32	44.14	
	14.17	1.72	10	15.75	51.14	
	16.33	2.26	41	18.16	58.14	
K	3.12	.18	10	3.17	4.09	14.0
	3.13	.19	10	3.34	4.34	
	3.40	.19	10	3.51	4.64	
	3.64	.14	9	3.65	4.94	
	3.69	.24	10	3.72	5.14	
	3.79	.18	10	3.86	5.64	
	3.95	.12	10	3.95	6.14	
J	3.80	.18	50	3.87	4.87	15.0
H	4.03	.05	15	4.09	6.43	16.2
	4.26	.10	15	4.45	8.43	
	5.44	.14	15	5.26	10.43	
	6.12	.23	15	6.13	12.43	
	7.31	.20	15	7.07	14.43	
	9.19	.23	15	8.07	16.43	
	10.56	.17	15	9.11	18.43	
	11.34	.37	15	10.20	20.43	
	11.96	.28	15	11.32	22.43	
	14.02	.31	15	12.98	24.43	
	14.48	.52	15	13.64	26.43	
	15.20	.49	18	14.82	28.43	
	18.26	.42	15	16.01	30.43	
	18.66	.40	26	17.19	32.43	
	17.97	.53	15	18.36	34.43	
	19.69	.37	15	19.51	36.43	
	20.24	.86	15	20.65	38.43	
	21.67	.61	16	21.76	40.43	
	23.32	.53	15	22.83	42.43	
	25.12	.42	15	23.88	44.43	
	24.46	.49	15	24.89	46.43	
	23.67	1.10	15	25.87	48.43	
	26.39	.60	15	26.80	50.43	
	28.26	.71	15	27.70	52.43	
	27.15	1.01	15	28.56	54.43	
	29.27	.35	15	29.38	56.43	
	31.51	.58	16	30.16	58.43	
	31.79	1.19	15	30.90	60.43	
	31.29	1.02	15	31.60	62.43	
	33.62	.77	16	32.26	64.43	
	34.09	.92	20	32.89	66.43	
	32.09	1.12	15	33.48	68.43	
	32.93	1.22	15	34.04	70.43	
	35.54	1.31	18	35.05	74.43	

Table 4. Observed and estimated time to size for anchovy larvae from hatching through metamorphosis at several temperatures.

Source*	Observed Mean	S.D.	N	Estimated	Age from Fertilization	Temp.
H	4.16	.17	14	4.05	9.14	12.7
	4.16	.15	11	4.09	11.14	
	4.72	.31	14	4.87	16.14	
	5.05	.53	10	5.35	18.14	
	5.73	.71	13	6.12	21.14	
	5.93	.70	11	6.67	23.14	
	8.41	1.18	11	8.71	30.14	
	10.49	1.59	10	10.96	37.14	
	12.74	1.56	10	13.32	44.14	
	14.17	1.72	10	15.75	51.14	
	16.33	2.26	41	18.16	58.14	
K	3.12	.18	10	3.17	4.09	14.0
	3.13	.19	10	3.34	4.34	
	3.40	.19	10	3.51	4.64	
	3.64	.14	9	3.65	4.94	
	3.69	.24	10	3.72	5.14	
	3.79	.18	10	3.86	5.64	
	3.95	.12	10	3.95	6.14	
J	3.80	.18	50	3.87	4.87	15.0
H	4.03	.05	15	4.09	6.43	16.2
	4.26	.10	15	4.45	8.43	
	5.44	.14	15	5.26	10.43	
	6.12	.23	15	6.13	12.43	
	7.31	.20	15	7.07	14.43	
	9.19	.23	15	8.07	16.43	
	10.56	.17	15	9.11	18.43	
	11.34	.37	15	10.20	20.43	
	11.96	.28	15	11.32	22.43	
	14.02	.31	15	12.98	24.43	
	14.48	.52	15	13.64	26.43	
	15.20	.49	18	14.82	28.43	
	18.26	.42	15	16.01	30.43	
	18.66	.40	26	17.19	32.43	
	17.97	.53	15	18.36	34.43	
	19.69	.37	15	19.51	36.43	
	20.24	.86	15	20.65	38.43	
	21.67	.61	16	21.76	40.43	
	23.32	.53	15	22.83	42.43	
	25.12	.42	15	23.88	44.43	
	24.46	.49	15	24.89	46.43	
	23.67	1.10	15	25.87	48.43	
	26.39	.60	15	26.80	50.43	
	28.26	.71	15	27.70	52.43	
	27.15	1.01	15	28.56	54.43	
	29.27	.35	15	29.38	56.43	
	31.51	.58	16	30.16	58.43	
	31.79	1.19	15	30.90	60.43	
	31.29	1.02	15	31.60	62.43	
	33.62	.77	16	32.26	64.43	
	34.09	.92	20	32.89	66.43	
	32.09	1.12	15	33.48	68.43	
	32.93	1.22	15	34.04	70.43	
	35.54	1.31	18	35.05	74.43	
	35.26	1.35	17	[illegible]	[illegible]	

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ESTIMATED DAYS TO STAGE AND SIZE FOR ANCHOVY EGGS AND LARVAE

	TEMPERATURE										
AGE	12.0	13.0	14.0	15.0	16.0	17.0	18.0	19.0	20.0	21.0	22.0
I	0.15	0.12	0.10	0.09	0.08	0.07	0.06	0.05	0.05	0.04	0.04
II	0.59	0.49	0.42	0.36	0.31	0.27	0.24	0.22	0.20	0.18	0.16
II	1.03	0.86	0.73	0.63	0.55	0.48	0.43	0.38	0.34	0.31	0.29
IV	1.47	1.23	1.05	0.90	0.78	0.69	0.61	0.55	0.49	0.45	0.41
V	1.92	1.60	1.36	1.17	1.02	0.89	0.79	0.71	0.64	0.58	0.53
VI	2.36	1.98	1.68	1.44	1.25	1.10	0.98	0.87	0.79	0.72	0.66
II	2.80	2.35	1.99	1.71	1.49	1.31	1.16	1.04	0.94	0.85	0.78
II	3.24	2.72	2.31	1.98	1.72	1.51	1.34	1.20	1.09	0.99	0.91
IX	3.69	3.09	2.62	2.25	1.96	1.72	1.53	1.37	1.23	1.12	1.03
X	4.13	3.46	2.94	2.52	2.19	1.93	1.71	1.53	1.38	1.26	1.15
XI	4.57	3.83	3.25	2.79	2.43	2.13	1.89	1.70	1.53	1.39	1.28
TCH	4.71	3.94	3.35	2.88	2.50	2.20	1.95	1.74	1.58	1.43	1.31
ZE	AGE FROM HATCH										
.6	0.2	0.2	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1
.8	0.5	0.4	0.3	0.3	0.2	0.2	0.2	0.2	0.2	0.1	0.1
.0	0.8	0.6	0.5	0.5	0.4	0.4	0.3	0.3	0.3	0.2	0.2
.2	1.1	0.9	0.8	0.7	0.6	0.5	0.5	0.4	0.4	0.3	0.3
.4	1.5	1.3	1.1	0.9	0.8	0.7	0.6	0.6	0.5	0.5	0.4
.6	2.1	1.7	1.5	1.3	1.1	1.0	0.9	0.8	0.7	0.6	0.6
.8	2.9	2.4	2.1	1.8	1.5	1.4	1.2	1.1	1.0	0.9	0.8
.0	4.7	3.9	3.3	2.8	2.5	2.2	1.9	1.7	1.6	1.4	1.3
EDING	9.8	8.2	7.0	6.0	5.2	4.6	4.1	3.6	3.3	3.0	2.7
.2	10.4	8.7	7.4	6.3	5.5	4.8	4.3	3.8	3.5	3.2	2.9
.4	11.4	9.6	8.1	7.0	6.1	5.3	4.7	4.2	3.8	3.5	3.2
.6	12.4	10.4	8.8	7.6	6.6	5.8	5.1	4.6	4.2	3.8	3.5
.8	13.4	11.2	9.5	8.2	7.1	6.2	5.5	5.0	4.5	4.1	3.7
.0	14.3	12.0	10.2	8.8	7.6	6.7	5.9	5.3	4.8	4.4	4.0
.0	18.9	15.8	13.4	11.5	10.0	8.8	7.8	7.0	6.3	5.7	5.3
.0	23.0	19.3	16.4	14.1	12.2	10.7	9.5	8.5	7.7	7.0	6.4
.0	26.9	22.5	19.1	16.5	14.3	12.6	11.1	10.0	9.0	8.2	7.5
.0	30.6	25.7	21.8	18.7	16.3	14.3	12.7	11.4	10.3	9.3	8.5
.0	34.2	28.7	24.3	20.9	18.2	16.0	14.2	12.7	11.5	10.4	9.5
.0	37.7	31.6	26.8	23.0	20.0	17.6	15.6	14.0	12.6	11.5	10.5
.0	41.1	34.4	29.2	25.1	21.8	19.2	17.0	15.2	13.7	12.5	11.5
.0	44.4	37.2	31.6	27.1	23.6	20.7	18.4	16.5	14.9	13.5	12.4
.0	47.7	39.9	33.9	29.1	25.3	22.3	19.8	17.7	16.0	14.5	13.3
0	51.0	42.7	36.2	31.1	27.1	23.8	21.1	18.9	17.1	15.5	14.2
0	54.2	45.4	38.6	33.1	28.8	25.3	22.5	20.1	18.2	16.5	15.1
0	57.5	48.2	40.9	35.1	30.6	26.8	23.8	21.3	19.3	17.5	16.1
0	60.8	50.9	43.2	37.2	32.3	28.4	25.2	22.5	20.4	18.5	17.0
0	64.2	53.7	45.6	39.2	34.1	29.9	26.6	23.8	21.5	19.5	17.9
0	67.5	56.6	48.0	41.3	35.9	31.5	28.0	25.0	22.6	20.6	18.8
0	85.7	71.8	60.9	52.4	45.5	40.0	35.5	31.8	28.7	26.1	23.9
0	107.7	90.2	76.6	65.8	57.2	50.3	44.6	39.9	36.1	32.8	30.1
0	139.2	116.6	99.0	85.1	74.0	65.0	57.7	51.6	46.6	42.4	38.8
0	209.9	175.8	149.2	128.2	111.5	98.0	86.9	77.8	70.2	63.9	58.6

he times of egg stages given here are based upon the descriptions of Ahlstrom (1943) for e sardine Sardinops caerulea and the identification of these stages by David Kramer in our boratory. Only those stages identified in Table 2 were used to define the time and stage lationship. All estimates are based upon equation 8 with parameters as given in the text, ge . Beyond hatching, estimated times are days from hatch.

K	2.67	.17	9	2.69	2.34	17.0
	2.79	.14	9	2.93	2.50	
	3.22	.22	10	3.15	2.67	
	3.29	.18	10	3.34	2.84	
	3.72	.08	9	3.55	3.09	
	3.87	.16	10	3.68	3.29	
	3.98	.14	10	3.82	3.59	
	4.04	.10	10	3.89	3.79	
J	3.78	.15	15	4.02	3.94	18.0
	3.86	.17	15	4.04	3.78	18.8
	4.22	.18	83	4.09	4.78	
	4.37	.26	55	4.25	5.78	
	5.34	.77	60	5.34	7.78	
	5.97	.73	52	5.94	8.78	
	6.64	.59	59	6.56	9.78	
	7.02	.78	36	7.21	10.78	
	7.82	.89	102	7.89	11.78	
	8.43	.87	95	8.60	12.78	
	9.01	.89	107	9.32	13.78	
	9.54	.92	88	10.06	14.78	
	10.38	.90	82	10.82	15.78	
	10.88	1.05	46	11.60	16.78	
	11.35	1.08	24	12.39	17.78	
	12.32	1.36	63	13.18	18.78	
K	2.64	.30	9	2.58	1.63	20.0
	2.91	.23	9	2.85	1.75	
	3.16	.30	9	3.09	1.88	
	3.34	.15	10	3.28	2.00	
	3.56	.12	9	3.46	2.13	
	3.74	.16	9	3.66	2.33	
	3.83	.14	9	3.87	2.67	
	3.83	.19	8	3.94	2.87	
	4.00	.13	8	3.99	3.07	
	4.08	.10	8	4.03	3.27	

* In addition to our data (H) and that of Kramer (K) a few additional measurements of yolk-sac larvae (J) made by Jerde (unpub) at 15 and 18° C were also included.

TABLE 5

ESTIMATED DAYS TO STAGE AND SIZE FOR ANCHOVY EGGS AND LARVAE

	TEMPERATURE										
STAGE	12.0	13.0	14.0	15.0	16.0	17.0	18.0	19.0	20.0	21.0	22.0
I	0.15	0.12	0.10	0.09	0.08	0.07	0.06	0.05	0.05	0.04	0.04
II	0.59	0.49	0.42	0.36	0.31	0.27	0.24	0.22	0.20	0.18	0.16
III	1.03	0.86	0.73	0.63	0.55	0.48	0.43	0.38	0.34	0.31	0.29
IV	1.47	1.23	1.05	0.90	0.78	0.69	0.61	0.55	0.49	0.45	0.41
V	1.92	1.60	1.36	1.17	1.02	0.89	0.79	0.71	0.64	0.58	0.53
VI	2.36	1.98	1.68	1.44	1.25	1.10	0.98	0.87	0.79	0.72	0.66
VII	2.80	2.35	1.99	1.71	1.49	1.31	1.16	1.04	0.94	0.85	0.78
VIII	3.24	2.72	2.31	1.98	1.72	1.51	1.34	1.20	1.09	0.99	0.91
IX	3.69	3.09	2.62	2.25	1.96	1.72	1.53	1.37	1.23	1.12	1.03
X	4.13	3.46	2.94	2.52	2.19	1.93	1.71	1.53	1.38	1.26	1.15
XI	4.57	3.83	3.25	2.79	2.43	2.13	1.89	1.70	1.53	1.39	1.28
HATCH	4.71	3.94	3.35	2.88	2.50	2.20	1.95	1.74	1.58	1.43	1.31
SIZE	AGE FROM HATCH										
2.6	0.2	0.2	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1
2.8	0.5	0.4	0.3	0.3	0.2	0.2	0.2	0.2	0.2	0.1	0.1
3.0	0.8	0.6	0.5	0.5	0.4	0.4	0.3	0.3	0.3	0.2	0.2
3.2	1.1	0.9	0.8	0.7	0.6	0.5	0.5	0.4	0.4	0.3	0.3
3.4	1.5	1.3	1.1	0.9	0.8	0.7	0.6	0.6	0.5	0.5	0.4
3.6	2.1	1.7	1.5	1.3	1.1	1.0	0.9	0.8	0.7	0.6	0.6
3.8	2.9	2.4	2.1	1.8	1.5	1.4	1.2	1.1	1.0	0.9	0.8
4.0	4.7	3.9	3.3	2.8	2.5	2.2	1.9	1.7	1.6	1.4	1.3
FEEDING	9.8	8.2	7.0	6.0	5.2	4.6	4.1	3.6	3.3	3.0	2.7
4.2	10.4	8.7	7.4	6.3	5.5	4.8	4.3	3.8	3.5	3.2	2.9
4.4	11.4	9.6	8.1	7.0	6.1	5.3	4.7	4.2	3.8	3.5	3.2
4.6	12.4	10.4	8.8	7.6	6.6	5.8	5.1	4.6	4.2	3.8	3.5
4.8	13.4	11.2	9.5	8.2	7.1	6.2	5.5	5.0	4.5	4.1	3.7
5.0	14.3	12.0	10.2	8.8	7.6	6.7	5.9	5.3	4.8	4.4	4.0
6.0	18.9	15.8	13.4	11.5	10.0	8.8	7.8	7.0	6.3	5.7	5.3
7.0	23.0	19.3	16.4	14.1	12.2	10.7	9.5	8.5	7.7	7.0	6.4
8.0	26.9	22.5	19.1	16.5	14.3	12.6	11.1	10.0	9.0	8.2	7.5
9.0	30.6	25.7	21.8	18.7	16.3	14.3	12.7	11.4	10.3	9.3	8.5
10.0	34.2	28.7	24.3	20.9	18.2	16.0	14.2	12.7	11.5	10.4	9.5
11.0	37.7	31.6	26.8	23.0	20.0	17.6	15.6	14.0	12.6	11.5	10.5
12.0	41.1	34.4	29.2	25.1	21.8	19.2	17.0	15.2	13.7	12.5	11.5
13.0	44.4	37.2	31.6	27.1	23.6	20.7	18.4	16.5	14.9	13.5	12.4
14.0	47.7	39.9	33.9	29.1	25.3	22.3	19.8	17.7	16.0	14.5	13.3
15.0	51.0	42.7	36.2	31.1	27.1	23.8	21.1	18.9	17.1	15.5	14.2
16.0	54.2	45.4	38.6	33.1	28.8	25.3	22.5	20.1	18.2	16.5	15.1
17.0	57.5	48.2	40.9	35.1	30.6	26.8	23.8	21.3	19.3	17.5	16.1
18.0	60.8	50.9	43.2	37.2	32.3	28.4	25.2	22.5	20.4	18.5	17.0
19.0	64.2	53.7	45.6	39.2	34.1	29.9	26.6	23.8	21.5	19.5	17.9
20.0	67.5	56.6	48.0	41.3	35.9	31.5	28.0	25.0	22.6	20.6	18.8
25.0	85.7	71.8	60.9	52.4	45.5	40.0	35.5	31.8	28.7	26.1	23.9
30.0	107.7	90.2	76.6	65.8	57.2	50.3	44.6	39.9	36.1	32.8	30.1
35.0	139.2	116.6	99.0	85.1	74.0	65.0	57.7	51.6	46.6	42.4	38.8
40.0	209.9	175.8	149.2	128.2	111.5	98.0	86.9	77.8	70.2	63.9	58.6

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[1] The times of egg stages given here are based upon the descriptions of Ahlstrom (1943) for the sardine Sardinops caerulea and the identification of these stages by David Kramer in our laboratory. Only those stages identified in Table 2 were used to define the time and stage relationship. All estimates are based upon equation 8 with parameters as given in the text, page . Beyond hatching, estimated times are days from hatch.

Table 6. Average weight and length at hatch of anchovy eggs passed and retianed by a 560 m filter for the same spawning batch.

Expt.		Average egg weight (mg)	N	Average size at hatch (mm)	N
1	Caught	.0303	(150)	4.08	(25)
	Passed	.0244	(150)	3.68	(25)
2	Caught	.0304	(150)	4.15	(25)
	Passed	.0268	(150)	3.99	(25)

TABLE 7

DAILY GROWTH RATES(MM) BY SIZE FOR LARVAL ANCHOVY

	TEMPERATURE										
ZE	12.0	13.0	14.0	15.0	16.0	17.0	18.0	19.0	20.0	21.0	22.0
.6	0.79	0.94	1.11	1.29	1.49	1.69	1.91	2.13	2.36	2.60	2.83
.7	0.75	0.90	1.06	1.23	1.42	1.61	1.82	2.03	2.25	2.47	2.70
.8	0.71	0.85	1.00	1.17	1.34	1.53	1.72	1.92	2.13	2.34	2.55
.9	0.67	0.80	0.94	1.10	1.26	1.43	1.62	1.81	2.00	2.20	2.40
.0	0.62	0.75	0.88	1.02	1.18	1.34	1.51	1.68	1.87	2.05	2.24
.1	0.58	0.69	0.81	0.94	1.09	1.24	1.39	1.56	1.72	1.89	2.07
.2	0.53	0.63	0.74	0.86	0.99	1.13	1.27	1.42	1.58	1.73	1.89
.3	0.48	0.57	0.67	0.78	0.90	1.02	1.15	1.28	1.42	1.56	1.71
.4	0.42	0.50	0.59	0.69	0.80	0.91	1.02	1.14	1.26	1.39	1.51
.5	0.37	0.44	0.52	0.60	0.69	0.79	0.89	0.99	1.10	1.21	1.32
.6	0.31	0.37	0.44	0.51	0.58	0.66	0.75	0.83	0.92	1.02	1.11
.7	0.25	0.30	0.35	0.41	0.47	0.54	0.60	0.67	0.75	0.82	0.90
.8	0.19	0.23	0.27	0.31	0.36	0.41	0.46	0.51	0.56	0.62	0.68
.9	0.13	0.15	0.18	0.21	0.24	0.27	0.30	0.34	0.38	0.41	0.45
.0	0.06	0.07	0.09	0.10	0.12	0.13	0.15	0.17	0.18	0.20	0.22
.1	0.19	0.23	0.27	0.31	0.36	0.41	0.46	0.51	0.57	0.62	0.68
.2	0.19	0.23	0.27	0.31	0.36	0.41	0.46	0.52	0.57	0.63	0.69
.3	0.19	0.23	0.27	0.32	0.37	0.42	0.47	0.52	0.58	0.64	0.70
.4	0.20	0.24	0.28	0.32	0.37	0.42	0.48	0.53	0.59	0.65	0.71
.5	0.20	0.24	0.28	0.33	0.38	0.43	0.48	0.54	0.60	0.66	0.72
.6	0.20	0.24	0.28	0.33	0.38	0.43	0.49	0.54	0.60	0.66	0.72
.7	0.20	0.24	0.29	0.33	0.38	0.44	0.49	0.55	0.61	0.67	0.73
8	0.21	0.25	0.29	0.34	0.39	0.44	0.50	0.56	0.62	0.68	0.74
9	0.21	0.25	0.29	0.34	0.39	0.45	0.50	0.56	0.62	0.69	0.75
0	0.21	0.25	0.30	0.35	0.40	0.45	0.51	0.57	0.63	0.69	0.76
0	0.23	0.28	0.33	0.38	0.44	0.50	0.56	0.62	0.69	0.76	0.83
0	0.25	0.30	0.35	0.41	0.47	0.53	0.60	0.67	0.74	0.82	0.89
0	0.26	0.31	0.37	0.43	0.50	0.56	0.64	0.71	0.79	0.86	0.94
0	0.27	0.33	0.39	0.45	0.52	0.59	0.66	0.74	0.82	0.90	0.99
0	0.28	0.34	0.40	0.47	0.54	0.61	0.69	0.77	0.85	0.93	1.02
0	0.29	0.35	0.41	0.48	0.55	0.63	0.71	0.79	0.87	0.96	1.05
0	0.30	0.36	0.42	0.49	0.56	0.64	0.72	0.80	0.89	0.98	1.07
0	0.30	0.36	0.42	0.49	0.57	0.65	0.73	0.81	0.90	0.99	1.08
0	0.30	0.36	0.43	0.50	0.57	0.65	0.74	0.82	0.91	1.00	1.09
0	0.31	0.36	0.43	0.50	0.58	0.66	0.74	0.82	0.91	1.00	1.10
0	0.31	0.36	0.43	0.50	0.58	0.65	0.74	0.82	0.91	1.00	1.09
0	0.30	0.36	0.43	0.50	0.57	0.65	0.73	0.82	0.91	1.00	1.09
0	0.30	0.36	0.42	0.49	0.57	0.65	0.73	0.81	0.90	0.99	1.08
0	0.30	0.36	0.42	0.49	0.56	0.64	0.72	0.80	0.89	0.98	1.07
0	0.26	0.30	0.36	0.42	0.48	0.55	0.62	0.69	0.76	0.84	0.92
0	0.20	0.24	0.28	0.32	0.37	0.42	0.48	0.53	0.59	0.65	0.71
0	0.12	0.15	0.17	0.20	0.23	0.26	0.30	0.33	0.37	0.40	0.44
0	0.03	0.04	0.05	0.06	0.06	0.07	0.08	0.09	0.10	0.11	0.12

TABLE 7

DAILY GROWTH RATES(MM) BY SIZE FOR LARVAL ANCHOVY

SIZE	TEMPERATURE										
	12.0	13.0	14.0	15.0	16.0	17.0	18.0	19.0	20.0	21.0	22.0
2.6	0.79	0.94	1.11	1.29	1.49	1.69	1.91	2.13	2.36	2.60	2.83
2.7	0.75	0.90	1.06	1.23	1.42	1.61	1.82	2.03	2.25	2.47	2.70
2.8	0.71	0.85	1.00	1.17	1.34	1.53	1.72	1.92	2.13	2.34	2.55
2.9	0.67	0.80	0.94	1.10	1.26	1.43	1.62	1.81	2.00	2.20	2.40
3.0	0.62	0.75	0.88	1.02	1.18	1.34	1.51	1.68	1.87	2.05	2.24
3.1	0.58	0.69	0.81	0.94	1.09	1.24	1.39	1.56	1.72	1.89	2.07
3.2	0.53	0.63	0.74	0.86	0.99	1.13	1.27	1.42	1.58	1.73	1.89
3.3	0.48	0.57	0.67	0.78	0.90	1.02	1.15	1.28	1.42	1.56	1.71
3.4	0.42	0.50	0.59	0.69	0.80	0.91	1.02	1.14	1.26	1.39	1.51
3.5	0.37	0.44	0.52	0.60	0.69	0.79	0.89	0.99	1.10	1.21	1.32
3.6	0.31	0.37	0.44	0.51	0.58	0.66	0.75	0.83	0.92	1.02	1.11
3.7	0.25	0.30	0.35	0.41	0.47	0.54	0.60	0.67	0.75	0.82	0.90
3.8	0.19	0.23	0.27	0.31	0.36	0.41	0.46	0.51	0.56	0.62	0.68
3.9	0.13	0.15	0.18	0.21	0.24	0.27	0.30	0.34	0.38	0.41	0.45
4.0	0.06	0.07	0.09	0.10	0.12	0.13	0.15	0.17	0.18	0.20	0.22
4.1	0.19	0.23	0.27	0.31	0.36	0.41	0.46	0.51	0.57	0.62	0.68
4.2	0.19	0.23	0.27	0.31	0.36	0.41	0.46	0.52	0.57	0.63	0.69
4.3	0.19	0.23	0.27	0.32	0.37	0.42	0.47	0.52	0.58	0.64	0.70
4.4	0.20	0.24	0.28	0.32	0.37	0.42	0.48	0.53	0.59	0.65	0.71
4.5	0.20	0.24	0.28	0.33	0.38	0.43	0.48	0.54	0.60	0.66	0.72
4.6	0.20	0.24	0.28	0.33	0.38	0.43	0.49	0.54	0.60	0.66	0.72
4.7	0.20	0.24	0.29	0.33	0.38	0.44	0.49	0.55	0.61	0.67	0.73
4.8	0.21	0.25	0.29	0.34	0.39	0.44	0.50	0.56	0.62	0.68	0.74
4.9	0.21	0.25	0.29	0.34	0.39	0.45	0.50	0.56	0.62	0.69	0.75
5.0	0.21	0.25	0.30	0.35	0.40	0.45	0.51	0.57	0.63	0.69	0.76
6.0	0.23	0.28	0.33	0.38	0.44	0.50	0.56	0.62	0.69	0.76	0.83
7.0	0.25	0.30	0.35	0.41	0.47	0.53	0.60	0.67	0.74	0.82	0.89
8.0	0.26	0.31	0.37	0.43	0.50	0.56	0.64	0.71	0.79	0.86	0.94
9.0	0.27	0.33	0.39	0.45	0.52	0.59	0.66	0.74	0.82	0.90	0.99
10.0	0.28	0.34	0.40	0.47	0.54	0.61	0.69	0.77	0.85	0.93	1.02
11.0	0.29	0.35	0.41	0.48	0.55	0.63	0.71	0.79	0.87	0.96	1.05
12.0	0.30	0.36	0.42	0.49	0.56	0.64	0.72	0.80	0.89	0.98	1.07
13.0	0.30	0.36	0.42	0.49	0.57	0.65	0.73	0.81	0.90	0.99	1.08
14.0	0.30	0.36	0.43	0.50	0.57	0.65	0.74	0.82	0.91	1.00	1.09
15.0	0.31	0.36	0.43	0.50	0.58	0.66	0.74	0.82	0.91	1.00	1.10
16.0	0.31	0.36	0.43	0.50	0.58	0.65	0.74	0.82	0.91	1.00	1.09
17.0	0.30	0.36	0.43	0.50	0.57	0.65	0.73	0.82	0.91	1.00	1.09
18.0	0.30	0.36	0.42	0.49	0.57	0.65	0.73	0.81	0.90	0.99	1.08
19.0	0.30	0.36	0.42	0.49	0.56	0.64	0.72	0.80	0.89	0.98	1.07
25.0	0.26	0.30	0.36	0.42	0.48	0.55	0.62	0.69	0.76	0.84	0.92
30.0	0.20	0.24	0.28	0.32	0.37	0.42	0.48	0.53	0.59	0.65	0.71
35.0	0.12	0.15	0.17	0.20	0.23	0.26	0.30	0.33	0.37	0.40	0.44
40.0	0.03	0.04	0.05	0.06	0.06	0.07	0.08	0.09	0.10	0.11	0.12

TABLE 8. MEAN SIZE AT AGE OF NORTHERN ANCHOVY LARVAE AT 16 C. WHERE THE NUMBER OF LARVAE(15) WAS SEPARATED INTO 5 GROUPS OF 3 LARVAE REPRESENTING THE 10TH, 30TH, 50TH, 70TH, AND THE 90TH PERCENTILES. ESTIMATED VALUES ASSUME A LOG-NORMAL DISTRIBUTION OF INITIAL GROWTH RATES A_0

	OBS	EXP	OBS	EXP	OBS	EXP	OBS	EXP	OBS	EXP
4	3.79	3.69	3.92	3.74	4.05	3.77	4.12	3.81	4.28	3.86
6	3.79	4.35	3.99	4.43	4.28	4.49	4.49	4.55	4.77	4.64
8	4.67	5.06	5.26	5.18	5.46	5.27	5.68	5.36	6.14	5.51
10	4.73	5.82	5.78	5.99	6.11	6.12	6.70	6.25	7.29	6.45
12	6.04	6.63	7.22	6.86	7.45	7.03	7.65	7.20	8.18	7.47
14	7.70	7.48	8.91	7.78	9.43	7.99	9.85	8.21	10.08	8.56
16	9.57	8.37	10.27	8.74	10.64	9.00	10.92	9.28	11.43	9.71
18	9.29	9.30	10.78	9.73	11.43	10.05	11.99	10.39	13.21	10.92
20	10.69	10.24	11.20	10.76	11.67	11.14	12.69	11.54	13.53	12.18
22	12.27	11.20	13.39	11.81	14.14	12.25	14.75	12.73	15.54	13.47
24	11.76	12.17	12.93	12.87	14.84	13.38	16.05	13.93	16.80	14.80
26	12.37	13.15	13.95	13.94	14.37	14.53	15.31	15.15	16.94	16.14
28	15.63	14.13	17.73	15.02	18.48	15.68	19.37	16.38	20.11	17.50
30	15.12	15.10	18.62	16.09	19.15	16.82	19.52	17.61	20.36	18.86
32	14.93	16.07	16.94	17.15	18.15	17.96	19.41	18.83	20.39	20.22
34	17.59	17.01	19.18	18.20	19.65	19.09	20.58	20.04	21.47	21.56
36	15.21	17.94	19.18	19.23	20.30	20.20	22.45	21.23	24.08	22.89
38	17.73	18.85	20.49	20.24	22.03	21.28	22.91	22.40	24.27	24.20
40	20.35	19.73	22.31	21.22	23.47	22.34	24.83	23.55	25.67	25.48
42	23.33	20.59	24.27	22.18	24.69	23.37	25.57	24.66	27.72	26.73
44	21.75	21.42	23.85	23.10	24.50	24.37	25.62	25.74	26.60	27.94
46	17.36	22.22	21.70	23.99	23.89	25.33	26.37	26.78	29.03	29.12
48	23.15	22.98	25.20	24.85	26.83	26.26	27.21	27.79	29.59	30.25
50	24.73	23.72	26.65	25.68	27.91	27.15	29.77	28.76	32.25	31.34
52	22.17	24.42	24.69	26.46	26.83	28.01	29.49	29.68	32.57	32.39
54	27.63	25.10	28.60	27.22	28.93	28.83	29.90	30.57	31.30	33.39
56	28.27	25.74	29.80	27.94	31.63	29.61	32.57	31.42	34.03	34.35
58	26.20	26.34	29.57	28.62	31.20	30.35	32.90	32.23	39.10	35.27
60	26.97	26.92	30.03	29.27	33.00	31.06	35.27	33.00	37.33	36.14
62	29.83	27.47	31.30	29.89	32.90	31.73	34.77	33.73	37.77	36.96
64	29.07	27.99	30.68	30.47	33.80	32.36	37.43	34.42	39.48	37.75
66	26.87	28.47	30.37	31.02	31.20	32.96	33.40	35.07	38.60	38.49
68	25.93	28.94	30.40	31.54	34.17	33.53	35.70	35.69	38.43	39.19
72	27.83	29.78	31.03	32.50	34.10	34.56	37.13	36.82	39.33	40.48
74	26.40	30.16	32.07	32.93	35.27	35.04	36.97	37.34	40.20	41.07
GET	15.2		15.8		16.2		16.9		17.9	