MODELING LIFE-STAGE-SPECIFIC INSTANTANEOUS MORTALITY RATES, AN APPLICATION TO NORTHERN ANCHOVY, *ENGRAULIS MORDAX*, EGGS AND LARVAE

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ABSTRACT

Life-stage-specific instantaneous mortality rates (IMRs) are often estimated individually for each life stage of an organism using regression analysis. A single estimation procedure for all life stages may be preferable because it would increase the overall precision of the IMRs and also provide a more realistic mortality model. Two such procedures were developed in this paper. One is single-equation model where regression estimates of all IMRs are obtained by fitting a single survivorship function to the entire data set. The other is the maximum likelihood estimator. These models were compared using northern anchovy egg and larval data. The survivorship functions of each were, respectively, exponential and Pareto functions.

The mortality of marine fish can be described by its survival probability $S(t) = P(T > t) = \exp\left[-\int_0^t \lambda(u)du\right]$, where T is the age of the fish and $\lambda(t)$ is the instantaneous mortality rate (IMR) at age t. During their early life history, pelagic marine fishes pass through a series of life stages: eggs, yolk-sac larval, feeding pelagic larval, juvenile and adult stages. The IMR $\lambda(t)$ could be different for some life stages. Therefore, for I life stages, there may be G distinctive IMRs where $G \leq I$. The IMR $\lambda(t)$ is then a piecewise function (Gross and Clark 1975, p. 20-21; Johnson and Kotz 1976, p. 272-273)

$$\lambda(t) = \begin{cases} \lambda_1(t) & 0 \leq t \leq u_1 \\ \lambda_2(t) & u_1 \leq t \leq u_2 \\ \cdot & \cdot \\ \cdot & \cdot \\ \lambda_g(t) & u_{g-1} \leq t \leq u_g \\ \cdot & \cdot \\ \cdot & \cdot \\ \lambda_G(t) & u_{G-1} \leq t \leq u_G \end{cases}$$

where u_g is the maximum age of mortality stanza g. $\lambda_g(t) \neq \lambda_{\acute{g}}(t)$ for $g \neq \acute{g}$. For example, $\lambda_1(t)$ may be the IMR for egg and yolk-sac larval stages, even though each is a different life stage, and $\lambda_2(t)$ the IMR for feeding larvae. As a result, the conditional survival probability, $S_g(t) = P(T > t | T \geq u_{g-1})$ corresponding to $\lambda_g(t)$, will also be different from $S_{\acute{g}}(t)$ and the survival probability $S(t) = (P\ T > t)$ will be

$$S(t) = \begin{cases} S_1(t) & 0 \leq t \leq u_1 \\ S_1(u_1)S_2(t) & u_1 \leq t \leq u_2 \\ \cdot & \cdot \\ \cdot & \cdot \\ \cdot & \cdot \\ \prod_{d=1}^{G-1} S_d(u_d)S_G(t) & u_{G-1} \leq t \leq u_G \end{cases}$$

The common method for estimating $\lambda_g(t)$'s for marine fishes has been to fit $S_g(t)$ to sample age data separately for each life stage or to assume one common $\lambda(t)$ for all life stages and to fit one $S(t)$ to sample data of all life stages (Hewitt and Brewer 1983). For northern anchovy, *Engraulis mordax*, eggs and larvae <20 d old, the IMR $\lambda(t)$ for eggs and yolk-sac larvae is different from that of the feeding larvae (Lo 1985):

$$\lambda(t) = \begin{cases} \lambda_1(t) = \alpha & 0 < t \leq u_1 \\ \lambda_2(t) = \dfrac{\beta}{t} & u_1 \leq t \leq 20 \end{cases} \quad (1)$$

where u_1 is either the hatching time ($t_h \sim 3$ d) or the age of yolk-sac larvae ($t_{ys} \sim 4.5$ d) with the first feeding as the critical period after which mortality decreased. Either t_h or t_{ys} has been used in various models under different assumptions. If morphological differences cause the changes in mortality rates, t_h is a reasonable separation point between

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egg and larval stages. However, predation, the major cause of mortality in the embryonic period, may be similar for eggs and yolk-sac larvae (Hunter[2]). If this is true, then the end of the yolk-sac stage is a reasonable separation point for the mortality stanza.

The conditional survival probability corresponding to IMR in Equation (1) is

$$S_1(t) = e^{-\alpha t} \qquad t \leqslant u_1 \qquad (2a)$$

and

$$S_2(t) = \left(\frac{t}{u_1}\right)^{-\beta} \qquad u_1 \leqslant t \leqslant 20 \qquad (2b)$$

To assess $S_g(t)$ for $g = 1,2$ in Equation (2), anchovy egg and larval data were first divided into K age groups. The mortality curves (Equation (3)) were fitted to the sample mean counts ($\bar{y}_i$) and mean age (t_i) $i = 1,\ldots,K$:

$$E(\bar{y}_i) = \begin{cases} \theta_0\, S_1[t_i;\, \lambda_1(t)] & t_i \leqslant u_1 \\ \theta_{u_1}\, S_2[t_i;\, \lambda_2(t)] & u_1 \leqslant t_i \leqslant 20 \end{cases} \qquad (3)$$

where θ_t is the expected number of fish at age t. Using separate equations like Equation (3) is unsatisfactory for some applications because separate mortality curves may produce discontinuities at transitions between mortality stanzas (or life stages). The purpose of this paper is to obtain a regression estimator and a maximum likelihood estimator (MLE) of the IMRs ($\lambda(t)$). The regression estimator was based upon a single mortality curve for all early life stages of anchovy, and the MLE was based upon a truncated exponential (Equation (2a)) and Pareto (Equation (2b)) likelihood function of time to death (Lo 1985).

In section on Data, I describe the method of anchovy egg and larval data collection and standardization procedures. The standardization procedures are necessary because the gear and sample sizes used to collect eggs differ from those used to collect larvae. In section on Multi-Equation Model, the current estimation procedures for constructing mortality functions for different life stages are presented. In these procedures separate mortality functions are fitted to the data set for each life stage. In the next two sections, I develop two estimation procedures for the IMRs of different life stages from a single analysis: a single mortality function is constructed which is based on the IMRs of different life stages, and the maximum likelihood estimators of life-stage specific IMRs are described. The MLEs of anchovy eggs and larvae (<20 d) are obtained. The results and the comparisons of various models based on anchovy egg and larval data are given in the last two sections.

DATA

The standardized abundance of anchovy eggs and larvae taken in routine biomass surveys was used to elevate different estimation procedures for mortality rates (Smith 1972; Parker 1980). The variables used in the standardization procedures were extrusion through the net, avoidance of the net mouth, and the variation of the water volume filtered per unit depth (Zweifel and Smith 1981).

The northern anchovy spawning area lies off central and southern California and Baja California. The sampling area was divided into 23 regions covering 17.566×10^{11} m^2 (Fig. 1). The central anchovy stock is enclosed by 8 regions (4, 5, 7, 8, 9, 11, 13, and 14) with a total of 5.703×10^{11} m^2 (Duke[3]). In this paper, I study the mortality of egg and larva of central anchovy stock. Anchovy eggs and larvae are sampled by net tows and each tow is a sampling unit. Every year, m_1 egg tows, vertical tows of 0.333 mm mesh with 25 cm diameter mouth opening, and m_2 larval tows using an oblique plankton net of 0.505 mm mesh with 60 cm diameter mouth opening are made. Ages were assigned to life stages using stage specific growth curves (Methot and Hewitt 1980[4]; Lo 1983). The standardized number of larvae in each group was divided by the time that larvae remained at a particular length to yield the sample mean daily larval production per unit area (0.05 m^2). A weighted mean per unit area for the entire survey area (8 regions) was calculated: $\bar{y}_i = \sum_r w_r \bar{y}_{ir}$ where w_r was the weight for region r and $\sum_r w_r = 1$ (Table 1) (Lo 1985) and $\bar{y}_{ir}$ was the sample mean count for i^{th} age group in region r. I considered only larvae smaller than 10 mm (20 d old) because for anchovy larvae larger than 10 mm, the

[2]J. R. Hunter, Fishery Biologist, Southwest Fisheries Center La Jolla Laboratory, National Marine Fisheries Service, NOAA, P.O. Box 271, La Jolla, CA 92038, pers. commun. July 1983.

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[4]Methot, R. D., and R. P. Hewitt. 1980. A generalized growth curve for young anchovy larvae; derivation and tubular example. Southwest Fish. Cent. Admin. Rep. No. LJ-80-17. National Marine Fisheries Service, NOAA, P.O. Box 271, La Jolla, CA 92038.

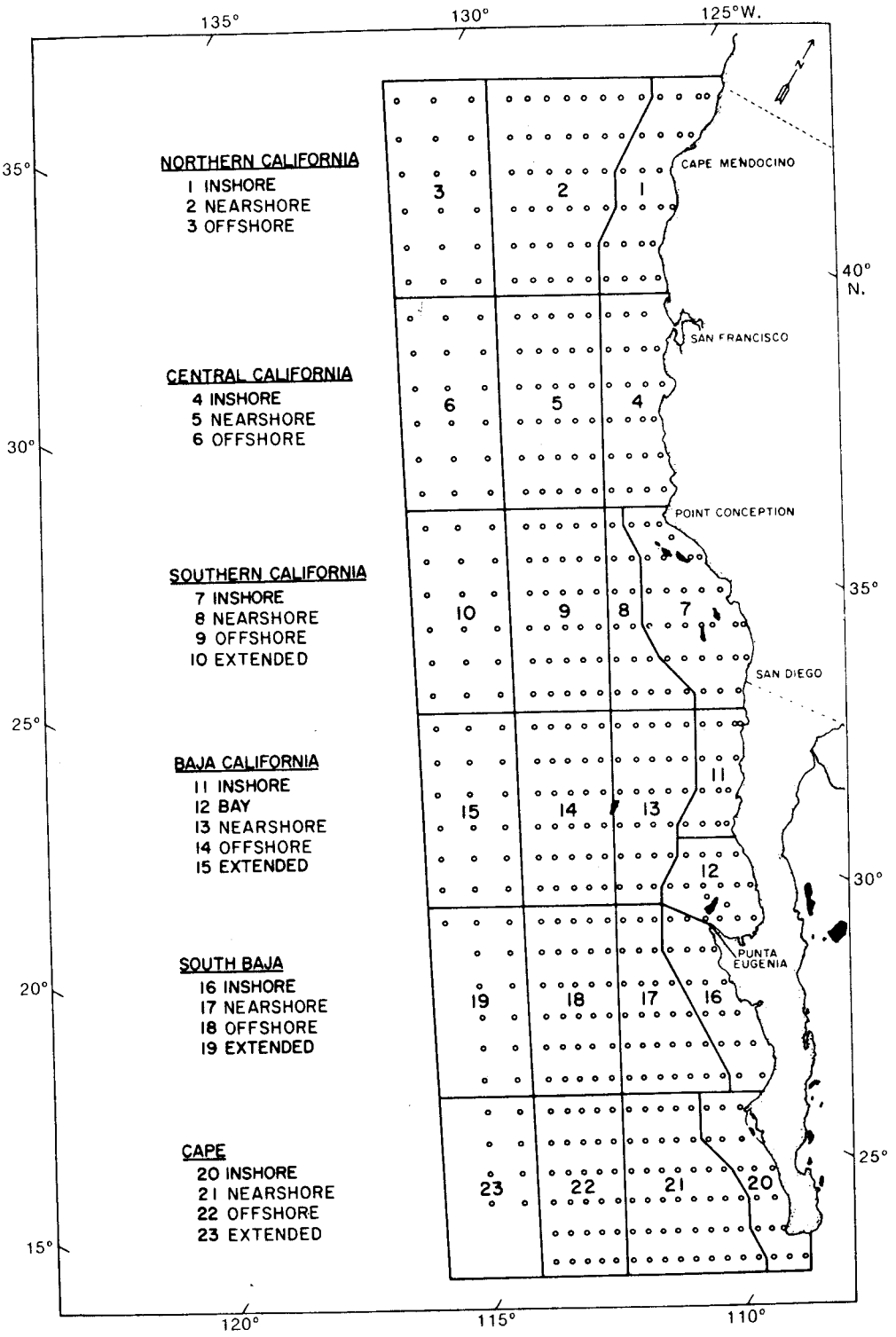

FIGURE 1.—Sampling area for estimating mortality of northern anchovy eggs and larvae (<20 d) with sampling stations denoted by the open circles, and regions denoted by numbers.

TABLE 1.—Group data of anchovy eggs and larvae: Sample mean daily production ($\bar{y}_i$) at age t_i, days for regression estimators and sample mean daily death (n_i) for maximum likelihood estimators (MLEs) of egg and larval mortality.

1980							1981						
Regression estimators			MLE				Regression estimators			MLE			
i	t_i	$\bar{y}_i$	i	t_i	$\bar{y}_i$	[1]n_i	i	t_i	$\bar{y}_i$	i	t_i	$\bar{y}_i$	n_i
1	0.41666	1.57	1	0.41666	1.57		1	0.41666	1.33				
										1	0.6666	1.665	
2	0.91666	1.21	2	0.91666	1.21	0.36	2	0.91666	2.00				
										2	1.6666	1.33	0.335
3	1.41666	1.07	3	1.41666	1.07	0.14	3	1.41666	1.19				
4	1.91666	0.64					4	1.91666	1.47				
5	2.41666	0.88	4	2.1666	0.76	0.31	5	2.41666	1.11	3	2.41666	1.11	0.22
6	3.05	0.74	5	3.05	0.74	0.02	6	[2]2.91666	0.60				
										4	3.008	0.915	0.195
7	5.6	0.37	6	5.6	0.31	0.37	7	3.10	1.23				
8	9.06	0.21	7	9.06	0.21	0.16	8	5.98	0.44	5	5.98	0.44	0.475
9	11.40	0.16	8	11.40	0.16	0.05	9	9.45	0.25	6	9.45	0.25	0.19
10	13.98	0.10	9	13.98	0.10	0.06	10	11.97	0.16	7	11.97	0.16	0.09
11	16.00	0.086	10	16.00	0.086	0.014	11	14.37	0.10	8	14.37	0.10	0.06
12	18.63	0.012	11	18.63	0.072	0.014	12	16.53	0.10	9	16.53	0.10	0
							13	18.56	0.08	10	18.56	0.08	0.02

1982							1983						
Regression estimators			MLE				Regression estimators			MLE			
i	t_i	$\bar{y}_i$	i	t_i	$\bar{y}_i$	n_i	i	t_i	$\bar{y}_i$	i	t_i	$\bar{y}_i$	n_i
1	0.41666	0.84					1	0.41666	1.78	1	0.41666	1.78	
			1	0.6666	1.21								
2	0.91666	1.57					2	0.91666	1.02				
										2	1.1666	1.67	0.11
3	1.41666	0.76					3	1.41666	2.31				
			2	1.6666	0.93	0.28							
4	1.91666	1.10					4	1.91666	0.99	3	1.91666	0.99	0.68
5	2.41666	0.61					5	2.41666	0.92	4	2.41666	0.92	0.07
			3	3.42	0.64	0.29							
6	4.42	0.67					6	3.82	0.68	5	3.82	0.68	0.24
7	8.00	0.23	4	8.00	0.23	0.41	7	7.03	0.16	6	7.03	0.16	0.52
8	11.07	0.14	5	11.07	0.14	0.09	8	9.97	0.11	7	9.97	0.11	0.05
9	13.62	0.08	6	13.62	0.08	0.06	9	12.34	0.08	8	12.34	0.08	0.03
10	15.74	0.06	7	15.74	0.06	0.02	10	14.60	0.05	9	14.60	0.05	0.03
11	18.13	0.05	8	18.13	0.05	0.01	11	16.73	0.0405	10	16.73	0.0405	0.01
							12	18.88	0.0375	11	18.88	0.0375	0.003

[1]$n_i = \bar{y}_{i-1} - \bar{y}_i$. [2]Used in MLE only.

avoidance of the net becomes a serious bias.

Region	$nm^2 \times 10^{-3}$	$n^2 \times 10^{-10}$	w_r
4	18	6.105	0.107
5	29	9.878	0.174
7	20	6.896	0.119
8	12	4.116	0.072
9	29	9.878	0.174
11	9	3.171	0.054
13	21	7.122	0.125
14	29	9.866	0.174
Total	167	57.031	1.00

The sample mean daily production of eggs and larvae per 0.05 m^2 ($\bar{y}_i$) with its age (t_i) constituted the data base for regression estimates of IMRs of eggs and larvae in MEM and SEM. Mean daily production represent eggs for 0.17 d (4 h) $< t_i \leq$ 3 d, and larvae for 3 d $< t_i \leq$ 20 d; $i = 1, \ldots K$, where K is the total number of age groups. The sample age structure ($\bar{y}_i$, t_i) reflects that of a single cohort under the assumption of steady production over the survey period (Seber 1980). The same data set was also used to generate the sample mean number of eggs or larvae lost per day between two adjacent age groups ($n_i = \bar{y}_{i-1} - \bar{y}_i$). The statistics n_i's were used directly in the MLE. Normally, sample totals were used instead of sample means in MLE. I used n_i's because anchovy eggs and larvae were sampled with different nets and because the number of egg tows was different from that of larvae.

MULTI-EQUATION MODEL (MEM)

In the current estimation procedures, separate mortality curves are constructed (Equation (3)) for

the IMRs ($\lambda(t)$) of anchovy eggs and larvae. If the life-stage-specific IMR is the main objective, the MEM is an easy method for obtaining the estimates of IMRs. The mortality curves (Equation (3)) are nonlinear functions of age (t). The IMRs can be estimated by either nonlinear regression (NR) or linear regression (LR) after the data set ($\bar{y}_i$, t_i) is transformed. The NR is based upon the assumption that the errors are additive. The observed mean daily production ($\bar{y}_i$) relates to the conditional survival probability as

$$\bar{y}_i = \theta_0 S_1[t_i; \lambda_1(t)] + e_{1i}$$

$$= \bar{y}_0 e^{-\alpha t_i} + e_{1i} \qquad t_i \leqslant u_1 \qquad (4a)$$

$$\bar{y}_i = \theta_{u_1} S_1[t_i; \lambda_2(t)] + e_{2i}$$

$$= \bar{y}_{u_1}\left(\frac{t}{u_1}\right)^{-\beta} + e_{2i} \qquad u_1 \leqslant t_i \leqslant 20 \qquad (4b)$$

where $u_1 = t_h \sim 3$ d old. Nonlinear regression estimation procedures provided by standard statistical packages such as BMDP statistical software (Dixon et al. 1983) are then used to estimate the parameters of IMRs, i.e., α and β.

The LR assumes that the errors are multiplicative. The observed daily production ($\bar{y}_i$) relates to the conditional survival probability in the form of

$$\bar{y}_i = \theta_{u_{g-1}} S_g(t_i; \lambda_g(t))\, e_{gi} \qquad \text{for } g = 1,2.$$

The logarithm of both sides of the equation yields two linear functions

$$\ln(\bar{y}_i) = A - \alpha t_i + \in_{1i} \qquad t_i \leqslant u_1 \qquad (5a)$$

$$\ln(\bar{y}_i) = B - \beta \ln\left(\frac{t_i}{u_1}\right) + \in_{2i} \qquad u_1 \leqslant t_i \leqslant 20. \qquad (5b)$$

Equation (5a) is then fitted to data set ($\ln(\bar{y}_i)$, t_i for $t_i \leqslant u_1$), and Equation (5b) is fitted to data set ($\ln(\bar{y}_i)$, $\ln(t_i/u_1)$ for $u_1 \leqslant t_i \leqslant 20$ d) to estimate α and β.

SINGLE-EQUATION MODEL (SEM)

The SEM consolidates all the conditional survival probabilities ($S_g(t)$) from each mortality stanza into a single equation. It not only eliminates discontinuities at transitions between life stages, but also improves the precision of overall mortality estimates because of the large sample size. Moreover, the SEM makes it possible to estimate the IMR for life stages where data are scarce.

Based upon Equation (2), $S(t_i)$ of anchovy eggs and larvae is

$$S(t_i) = \begin{cases} S_1(t_i) & t_i \leqslant u_1 \\ S_1(u_1)S_2(t_i) & u_1 \leqslant t_i \leqslant 20 \end{cases}$$

or

$$S(t_i) = \begin{cases} S_1(t_i)S_2(u_1) & t_i \leqslant u_1 \\ S_1(u_1)S_2(t_i) & u_1 \leqslant t_i \leqslant 20 \end{cases}$$

where $S_1(u_1) = P(T > u_1 | T \geqslant 0) = e^{-\alpha u_1}$, $S_2(u_1) = P(T > u_1 | T \geqslant u_1) = 1$, and $u_1 = t_{ys} = 4.5$ d. Thus by creating two new independent variables x_{1i} and x_{2i} such that

$$x_{1i} = \begin{cases} t_i & t_i \leqslant u_1 \\ u_1 & u_1 \leqslant t_i \leqslant 20 \end{cases}$$

and

$$x_{2i} = \begin{cases} u_1 & t_i \leqslant u_1 \\ t_i & u_1 \leqslant t_i \leqslant 20 \end{cases}$$

it follows that $S(t_i) = S_1(x_{1i})S_2(x_{2i})$ and the mortality curve can be written as

$$E(\bar{y}_i) = \theta_0 S_1(x_{1i})S_2(x_{2i}) = \theta_0 e^{-\alpha x_{1i}}\left(\frac{x_{2i}}{u_1}\right)^{-\beta}. \qquad (6)$$

The data set for fitting Equation (6) looks like

age group (i)	*age* (t_i)	$\bar{y}_i$	x_{1i}	x_{2i}	
1	t_1	$\bar{y}_1$	t_1	u_1	
2	t_2	$\bar{y}_2$	t_2	u_1	
.	.	.	.	.	
.	.	.	.	.	
.	.	.	.	.	
					$u_1 = 4.5$ d
i	t_i	$\bar{y}_i$	$\bar{u}_1$	t_i	
.	.	.	.	.	
.	.	.	.	.	
k	t_k	$\bar{y}_k$	$\bar{u}_1$	t_k	

In order to use Equation (6) to estimate the IMRs of eggs and larvae in Equation (1), a combined data

set ($\bar{y}_1$, x_{1i}, x_{2i}), which includes all the data from each life stage and the maximum ages of mortality stanzas (u_g's), is important to ensure the accuracy of the estimates of the IMRs. The determination of u_g's depends primarily on the changes of the mortality rates, which may be related to the changes in morphology or behavior that affects mortality rates. In the best fit of the SEM, however, the end points of morphological patterns may not correspond to the maximum ages. Three life stages were identified for anchovy eggs and larvae, with the end point of mortality stanza 1 being the average age of yolk-sac larvae (u_1 = 4.5 d). In the MEM, the hatching time (t_h) was used, but, the best fit of the SEM occurred when u_1 = 4.5 d. Two mortality stanzas were assigned to three life stages of anchovy (<20 d) because from the existing data, no evidence for a change in the IMRs within a life stage existed although the data may not have been adequate to detect such changes.

The regression estimates of the IMRs for the SEM can be obtained by either NR or LR as described in the previous section. If NR is used, Equation (6) is fitted to the data set ($\bar{y}_i$, x_{1i}, and x_{2i}) directly to obtain estimates of parameters of $\lambda_1(t)$ and $\lambda_2(t)$. Because the variance of egg data is larger than that of larvae, a weighted NR (WNR) would be preferable. If errors are assumed to be multiplicative, taking the logarithm of both sides of the Equation (6) yields

$$\ln(\bar{y}_i) = A - \alpha x_{1i} - \beta \ln\left(\frac{x_{2i}}{u_1}\right) + \in_i. \qquad (7)$$

The data set ($\ln(\bar{y}_i)$, x_{1i}, and $\ln(x_{2i}/u_1)$) is then used to estimate α and β through linear least squares regression.

MAXIMUM LIKELIHOOD ESTIMATOR (MLE)

The MLE is presented here as an alternative method of estimating IMRs. Because the data used for mortality estimators are grouped by age, I followed the procedures described by Kulldorff (1961) and McDonald and Ransom (1979) for grouped data. Here, $N_i = Y_{i-1} - Y_i$ (number of deaths between ages t_{i-1} and t_i) of a single cohort are multinomial variables, each with probability

$$P_i = S(t_{i-1}) - S(t_i).$$

The likelihood function of N_i's for the whole life cycle (i = 1, ..., I, and Y_I = 0) is

$$L(N_i, P_i(z'); i = 1, \ldots, I) \propto \prod_{i=1}^{I} P_i(z')^{N_i}$$

$$= \prod_{i=1}^{I} [S(t_{i-1}) - S(t_i)]^{N_i} \qquad (8)$$

where z is the parameter vector in $\lambda(t)$. The derivatives of the logarithm of likelihood function with respect to the parameters z's are set equal to zero. Solutions to the simultaneous equations

$$\frac{\partial \ln L}{\partial z_i} = 0$$

are MLEs of z, if certain conditions are satisfied (Kulldorff 1961). In marine fish only the IMRs of a few life stages are considered because of the lack of data. It is then necessary to compute the conditional probability

$$P_i = P(t_{i-1} \leqslant T < t_i \mid T \in D)$$

$$= [S(t_{i-1}) - S(t_i)]/P(T \in D)$$

where D is the domain of ages of life stages considered.

Because I considered only the IMRs of anchovy eggs and larvae of ages >4 h (0.17 d) and <20 d, the conditional probabilities are computed from a truncated exponential and Pareto survival probability (Equation (2)) (Gross and Clark 1975, p. 128-132):

$$P_i = P(t_{i-1} < T \leqslant t_i \mid t_1 < T \leqslant 20)$$

$$= (S(t_{i-1}) - S(t_i))/(S(t_1) - S(20))$$

$$P_i = \begin{cases} \dfrac{e^{-\alpha t_{i-1}} - e^{-\alpha t_i}}{e^{-\alpha t_1} - e^{-\alpha u_1}\left(\dfrac{20}{u_1}\right)^{-\beta}} & t_i \leqslant u_1 \\ \dfrac{e^{-\alpha u_1}\left[\left(\dfrac{t_{i-1}}{u_1}\right)^{-\beta} - \left(\dfrac{t_i}{u_1}\right)^{-\beta}\right]}{e^{-\alpha t_1} - e^{-\alpha u_1}\left(\dfrac{20}{u_1}\right)^{-\beta}} & u_1 \leqslant t_i \leqslant 20. \end{cases} \qquad (9)$$

Then the likelihood function of N_i's for anchovy eggs and larvae of ages <20 d is

$$L \propto \prod_{i=2}^{k} P_i^{N_i} = \left[\prod_{i=2}^{k} (S(t_{i-1}) - S(t_i))^{N_i} \right] / \left[S(t_1) - S(20) \right]^{\sum_{i=2}^{k} N_i}$$

and

$$\ln(L) = \sum_{i=2}^{k} [N_i \ln(P_i)] = \sum_{i=2}^{c} [N_i \ln(P_i)] + \sum_{i=c+1}^{k} [N_i \ln(P_i)] \tag{10}$$

where $N_i = m(\bar{y}_{i-1} - \bar{y}_i) = m \cdot n_i$ and c is max(i) for $t_i \leqslant 3$ d (u_1). Substituting Equation (9) for P_i in Equation (10) yields

$$\ln(L) = \sum_{i=2}^{c} N_i \ln\left(e^{-\alpha t_{i-1}} - e^{-\alpha t_i}\right) + \sum_{c+1}^{k} \left[N_i(-\alpha u_1 + \beta \ln u_1) + N_i \ln(t_{i-1}^{-\beta} - t_i^{-\beta}) \right]$$

$$- \sum_{i=2}^{k} N_i \ln\left[e^{-\alpha t_1} - e^{-\alpha u_1} \left(\frac{20}{u_1}\right)^{-\beta} \right]. \tag{11}$$

Solving simultaneous equations $\frac{\partial \ln L}{\partial \alpha} = 0$ and $\frac{\partial \ln L}{\partial <}$ for α and β gives their MLEs.

The asymptotic variance-covariance (ASVAR-COV) of MLEs of α and β was computed according to Kulldorff (1961, p. 86-87):

$$\begin{bmatrix} \text{As var}(\alpha) & \\ \text{As cov}(\alpha,\beta) & \text{As var}(\beta) \end{bmatrix}\Bigg|_{\hat{\alpha},\hat{\beta}} = (1/N) \begin{bmatrix} a_{11} & \\ a_{21} & a_{22} \end{bmatrix}\Bigg|_{\hat{\alpha},\hat{\beta}} = (1/N)\, A_{\hat{\alpha},\hat{\beta}}$$

$$= -\frac{1}{N} \begin{bmatrix} \sum_{i=2}^{k} P_i \frac{\partial^2 \ln P_i}{\partial \alpha^2} & \\ \sum_{i=2}^{k} P_i \frac{\partial^2 \ln P_i}{\partial \alpha \partial \beta} & \sum_{i=2}^{k} P_i \frac{\partial^2 \ln P_i}{\partial \beta^2} \end{bmatrix}^{-1}\Bigg|_{\hat{\alpha},\hat{\beta}} \tag{12}$$

For detailed derivation of the MLEs, see the Appendix.

Conceptually, abundance declines monotonically with increasing age, but this may not occur in the sample. Although its absence does not complicate regression analysis, corrections are required when the MLEs are used. The MLEs are functions of sample totals $N_i = (\bar{y}_{i-1} - \bar{y}_i)m$, $N_i \geqslant 0$, and can also be expressed as function of sample proportions N_i/N (Equations (A1) and (A2)), which are equal to the ratios of differences of sample mean daily productions $(\bar{y}_{i-1} - \bar{y}_i)/(\bar{y}_1 - \bar{y}_k) = n_i/n$ (see Appendix). The quantity $n_i = N_i/m$ is the sample mean daily death between two adjacent groups. The MLEs require $N_i \geqslant 0$. Due to sampling error, it is possible to observe more individuals in the older group than the adjacent younger group, i.e., $\bar{y}_{i-1} < \bar{y}_i$. If so, some adjacent groups

$(\bar{y}_i, t_i)$ have to be combined so that $\bar{y}_i > \bar{y}_{i'}$ for $t_i < t_{i'}$. The ratio n_i/n can be used in place of N_i/N to compute the MLEs. This correction is inappropriate if the reason for $\bar{y}_i > \bar{y}_{i'}$, for $t_i < t_{i'}$ is that individuals were evicted from the sampling area or immigrated into it, as such movements violate the assumption of a stationary population.

Although n_i's are sufficient for computing point estimates of the MLE, the total number of deaths between ages t_1 and t_k ($N = m(\bar{y}_1 - \bar{y}_k)$ is required for computation of the ASVAR-COV of the MLEs. N can then be used to determine minimum number of tows (m_1) for the youngest stage through $m_1\bar{y}_1 \doteq N$ for a given precision of the MLE. Although the sample size for eggs may differ from that of larvae, an equal number of sample sizes is assumed to compute the ASVAR-COV. The minimum number of egg tows can be determined by $m_1 = N/\bar{y}_1$.

RESULTS

Both the MEM and the SEM were fitted to the basic data ($\bar{y}_i$, t_i; 0.17 d $< t_i \leq$ 20 d) collected from 1980 to 1983, using NR and LR (Table 1, Fig. 2). The point estimates and their asymptotic standard errors are listed in Table 2 and Figure 3. NR and LR produced similar estimates of the IMRs for the MEM. When the SEM was applied to the combined egg and larval data, the WNR was also used to compute the IMRs in addition to NR and LR because of the inequality of the variances among life stages. The variance of egg counts was higher than that of larvae because eggs were more patchily distributed than larvae. Because of this, the inverse of the variances of sample means of eggs and larvae was used as the weights for the WNR. The estimates from the WNR were similar to those from LR and the standard errors from both methods were lower than those from NR.

The WNR estimates of egg IMRs from the SEM were more precise than estimates from the MEM, whereas the most precise estimates of larval IMRs were provided by the MEM using NR. The SEM was more precise than the MEM for eggs but not for the larvae, because the variance of eggs was larger than that of larvae. Thus, when eggs and larvae were combined in an SEM, the variance around the single equation was smaller for the eggs and larger for the larvae. Nevertheless, the SEM produced larval IMRs with reasonable precision when the WNR was used. Therefore, the SEM WNR is suitable for ap-

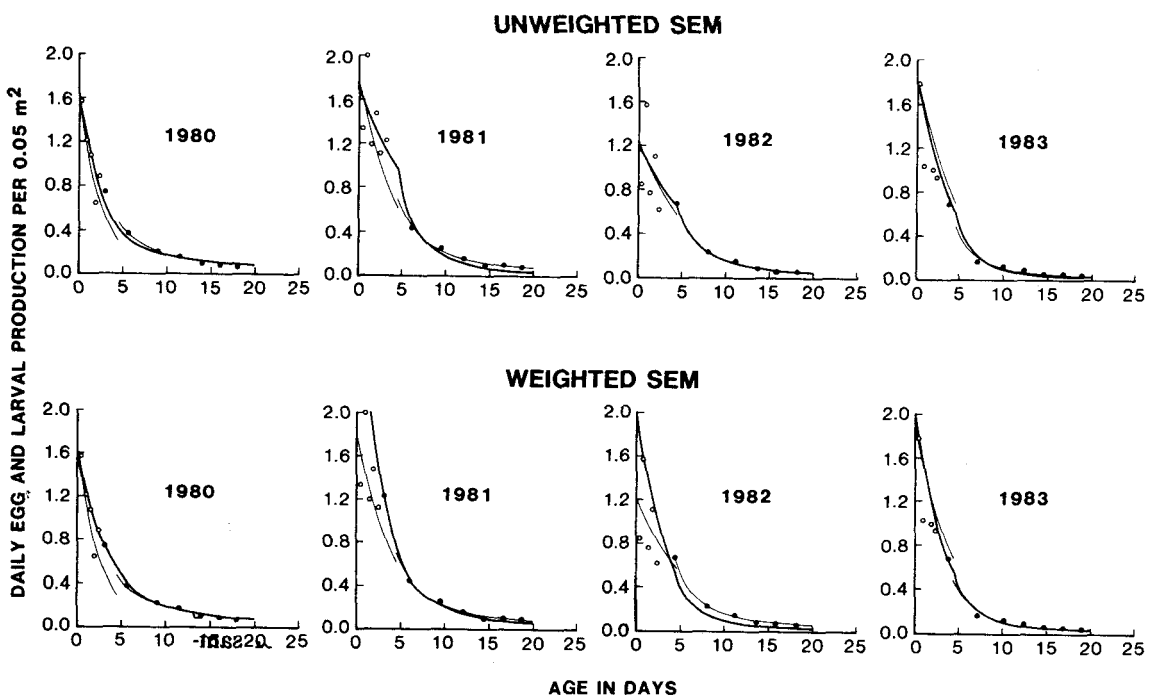

FIGURE 2.—Observed daily anchovy egg and larval production/0.05 m² (○ = eggs, ● = larvae), and the mortality curves from the MEM (two short curves) and SEM (single curve) using unweighted and weighted nonlinear regression for 1980-83 field collected data.

TABLE 2.—Estimates from multi-equation model (MEM), single-equation model (SEM), and maximum likelihood estimator (MLE) for anchovy egg and larval mortality ($\hat{\alpha}$ and $\hat{\beta}$), and their standard error (SE) based upon 1980-83 field data where K is number of age groups and m is number of tows used in each model. For both MEM and SEM, nonlinear regression (NR), linear regression (LR) and weighted nonlinear regression (WNR) estimates are given.

	Egg mortality			Larval mortality		
	$\hat{\alpha}$	SE	$K(m)$	$\hat{\beta}$	SE	$K(m)$
1980						
MEM						
NR	0.39	0.103	5(961)	1.22	0.0314	7(199)
LR	0.35	0.13		1.32	0.06	
SEM						
NR	0.32	0.05	12(1,160)	1.06	0.41	12(1,160)
WNR	0.25	0.02		1.33	0.06	
LR	0.24	0.05		1.36	0.13	
MLE	0.36	0.012	11(961)	1.28	0.09	11(961)
		0.016	(500)		0.12	(500)
		0.02	(300)		0.16	(300)
		0.03	(199)		0.27	(199)
1981						
MEM						
NR	0.13	0.16	5(1,134)	1.53	0.032	7(403)
LR	0.13	0.15		1.54	0.06	
SEM						
NR	0.13	0.07	12(1,537)	2.19	0.96	12(1,537)
WNR	0.33	0.06		1.70	0.18	
LR	0.20	0.05		1.64	0.15	
MLE	0.24	0.008	10(1,134)	0.96	0.06	10(961)
		0.01	(500)		0.08	(500)
		0.02	(300)		0.11	(300)
		0.01	(403)		0.10	(403)
1982						
MEM						
NR	0.17	0.26	5(992)	1.81	0.036	6(96)
LR	0.19	0.24		1.87	0.065	
SEM						
NR	0.14	0.10	11(1,088)	1.77	1.46	11(1,088)
WNR	0.13	0.04		1.83	0.36	
LR	0.12	0.07		1.85	0.20	
MLE	0.24	0.008	8(992)	1.20	0.08	8(992)
		0.01	(500)		0.11	(500)
		0.015	(300)		0.14	(300)
		0.03	(100)		0.25	(100)
1983						
MEM						
NR	0.23	0.29	5(850)	2.05	0.11	7(78)
LR	0.27	0.25		1.80	0.10	
SEM						
NR	0.26	0.19	12(928)	2.45	2.71	12(928)
WNR	0.30	0.05		2.23	0.28	
LR	0.33	0.08		1.84	0.22	
MLE	0.32	0.007	11(850)	2.48	0.10	11(850)
		0.01	(500)		0.14	(500)
		0.013	(300)		0.18	(300)
		0.02	(80)		0.35	(80)

plications where it is preferable to estimate IMRs for egg and larvae simultaneously (e.g., simulation studies of mortality at all life stages). The SEM is preferable for modeling the mortality curves through all life stages because it eliminates the multiple estimates that occur at the endpoint of each life stage (Fig. 2). In addition, the SEM allows estimation of the IMRs for all life stages even when data for some life stages are inadequate for independent estimation of a life-stage-specific IMR. In comparing NR and LR, the estimates of IMRs from these two procedures were similar, despite the different assumptions about the error term. One complication of using LR is that the abundance for any

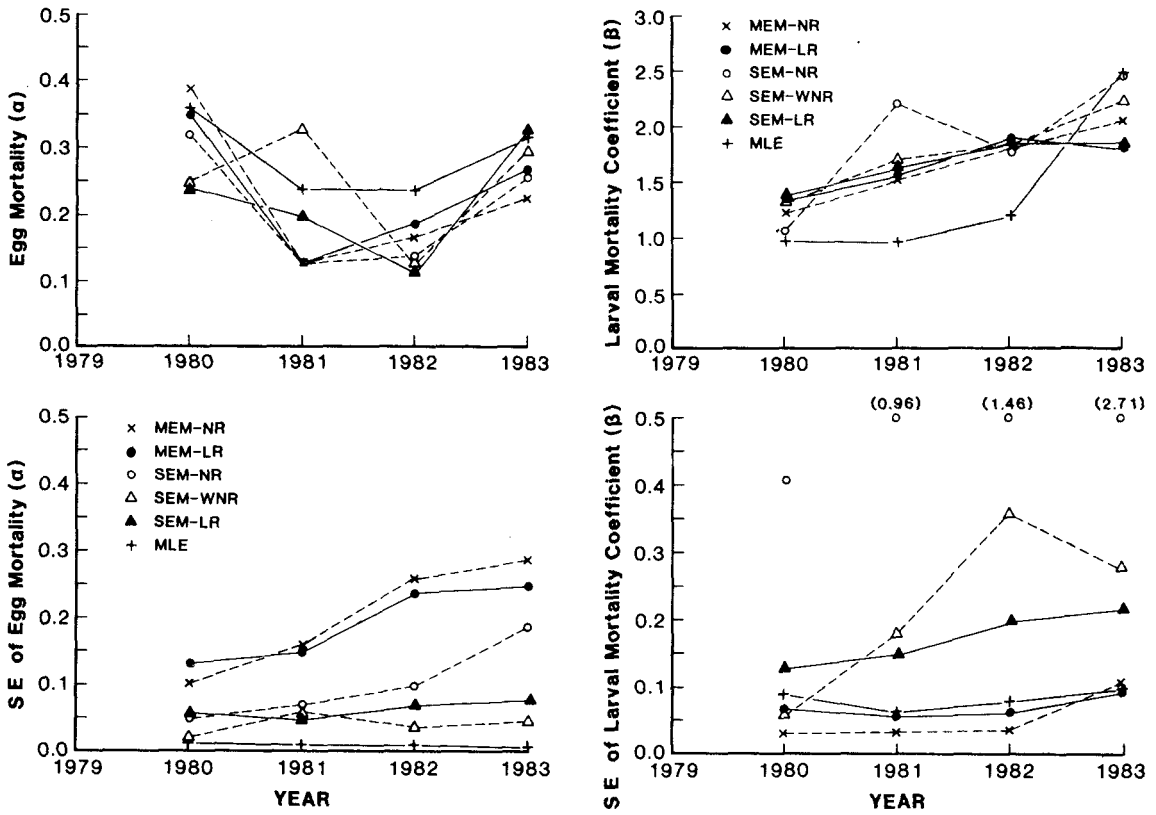

FIGURE 3.—Estimated anchovy egg mortality ($\hat{\alpha}$), larval mortality coefficient ($\hat{\beta}$), and their standard error (SE) using multi-equation model (MEM), single-equation model (SEM), and maximum likelihood estimator (MLE) for 1980-83.

specific age needs to be transformed back to the original unit. Direct inverse transformation may bias the estimates. Thus, the LR may not be appropriate for biomass estimation or other applications where a transformation back to original units is required.

In addition to the above regression models, the MLEs of egg and larval IMRs were also computed based on the data set $n_i = \bar{y}_{i-1} - \bar{y}_i$, $i = 1, \ldots k$ (Equations (A1) and (A2), Table 1). The ASCOVVAR for anchovy egg and larval mortality rates requires the total number of eggs and larvae that died between ages 4 h and 20 d from the sample (N). It is not possible to obtain N directly from $m\bar{y}_1$ (i.e. $N \doteq m\bar{y}_1$) because eggs and larvae are sampled with different nets and in different regions. Anchovy eggs have a more concentrated and patchy distribution than larvae which are less numerous and distributed more uniformly throughout the entire survey area because of the diffusion of larvae after hatching (Hewitt 1982). Zero density of eggs was assumed for the offshore regions where eggs were not sampled to compute the weighted average egg production $\bar{y}_i = \sum_r w_r \bar{y}_{ir}$. I then divided $m_1\bar{y}_1$ by the proportion of area sampled ($q = \sum_r w_r$ where w_r's are summed over the regions where egg tows were taken) to obtain sample daily death N in $[t_1, t_k)$. Thus, $N = m_1\bar{y}_1/q$; q ranges from 0.53 to 0.82 for 1980-83. Four sets of sample sizes were considered: $m = m_1$, 500, 300, m_2 where m_1 is the actual number of egg tows and m_2, actual number of larval tows (Table 2). For any given N, one obtains the ASVAR-COV of α and β by dividing a_{ij} by N where a_{ij}'s are the elements in matrix A of Equation (12).

The MLE point estimates $\hat{\alpha}$ and $\hat{\beta}$, were between the estimates yielded by the SEM and the MEM in most cases. The precision of the MLE for egg IMR was higher than that of the regression estimates. The standard error of the MLE of the larval IMR was between those of the MEM and SEM regression estimates (Table 2, Fig. 3).

DISCUSSION

All the estimates of instantaneous mortality rates (IMR) discussed in this paper were computed from age (stage) frequency data. To ensure the unbiasedness of the estimates, three assumptions have to be met: a stationary population, reliable growth curves, and accurate samplers. Any violation of these assumptions will cause biases in the mortality estimates. Nets usually do not retain fish of all sizes because some small fish extrude through the net and some large fish avoid the net. Thus the estimates of size-specific retention rates are essential correction factors for the catch. If fish migrate at a significant rate, either the migration rate should be estimated or the sampling area should be expanded to eliminate migration problems, for migration violates the assumption of a stationary population and thus biases the mortality. Because growth curves are normally used to assign age to stage of eggs and larvae, biased growth curves would lead to inaccurate age assignments which definitely would bias the mortality estimates.

Although modeling the mortality rates of the early life stages of anchovy is the focus of this paper, I have shown that the SEM (Fig. 2) can be applied to any continuous process whose parameters are life-stage specific and generally estimated separately. For example, many allometric relations such as the growth curves may have different instantaneous growth rates for different life stages. A single continuous growth curve for the whole life cycle is possible using the SEM which allows greater latitude of modeling life-stage-specific growth rates than modeling the instantaneous growth rate for the whole life cycle as proposed by Schnute (1981). However, the SEM does require knowledge of the forms of instantaneous rates and the endpoint of each mortality stanza (or life stage).

In this study, the determination of a cutoff point between life stages was based upon examination of the empirical data and biological implications. It is conceivable to include the cutoff point (u_1) as one of the parameters in both SEM and MLE (Matthews and Farewell 1982). The cutoff point can then be estimated directly through the models. Matthews and Farewell considered the exponential mortality curve with one cutoff point and obtained MLE of the cutoff point (change point). For anchovy egg and larvae, the cuttoff point for the eggs and larvae up to 20 d old was easily determined from the IMR and age data (Lo 1985). Estimation of the cutoff point through SEM or MLE would be laborious and any improvement may be minimal. However, the estimates through the models would eliminate the problem of whether u_1 should be hatching time or the age of yolk-sac larvae.

Comparison of these two regression models with the MLEs based on anchovy egg and larval data indicated that the point estimates of the IMRs were similar. The SEM using WNR provided the most precise egg IMR which was nearly the same as the MLE. The MEM, using NR, provided the most precise estimates of larval IMR's. The regression estimators of the IMR's are easier to compute than the MLEs, yet they require larger sample sizes than the MLEs. If money is not a constraint, the SEM is preferred to the MLE. Otherwise, the MLE should be used. Based upon 1980 anchovy egg and larval data, 300 tows for eggs and larvae each (a total of 600 tows) could guarantee MLEs of α and β with cv = 0.10. The current sampling design (egg tows $\sim$ 1,000) seems to use an excessive number of egg tows for the MLEs of egg and larval IMRs. If the larval IMR is the only parameter to be estimated, the MEM is recommended.

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APPENDIX

The two partial deviations of ln L (Equation (11)) are

$$\frac{\partial \ln L}{\partial \alpha} = N \sum_{i=2}^{c} \frac{N_i}{N}\left[\frac{-t_{i-1} - t_i e^{-\alpha\Delta_i}}{1 - e^{-\alpha\Delta_i}}\right] - u_1 \sum_{i=c+1}^{k} \frac{N_i}{N} + t_1 - (u_1 - t_1)\left[e^{\alpha(u_1 - t_1)}\left(\frac{20}{u_1}\right)^{\beta} - 1\right]^{-1} = 0 \quad \text{(A1)}$$

$$\frac{\partial \ln L}{\partial \beta} = N \sum_{i=c+1}^{k} \frac{N_i}{N}\left[\ln u_1 + \frac{-\ln t_{i-1} + \left(\frac{t_i}{t_{i-1}}\right)^{-\beta} \ln t_i}{1 - \left(\frac{t_i}{t_{i-1}}\right)^{-\beta}}\right] - \ln\left(\frac{20}{u_1}\right)\left[e^{\alpha(u_1 - t_1)}\left(\frac{20}{u_1}\right)^{\beta} - 1\right]^{-1} = 0 \quad \text{(A2)}$$

where $\Delta_i = t_i - t_{i-1}$ and $u_1 \sim 3$.

Both Equations (A1) and (A2) depend on the proportion N_i/N rather than the absolute counts (N_i's). In order to have a unique solution of α and β, it is necessary to have

$$\frac{\partial^2 \ln L}{\partial \alpha^2} < 0 \quad \text{and} \quad \frac{\partial^2 \ln L}{\partial \beta^2} < 0. \quad \text{(A3)}$$

Moreover, the conditions

$$\lim_{\alpha \to 0} \frac{\partial \ln L}{\partial \alpha} > 0, \quad \lim_{\alpha \to \infty} \frac{\partial \ln L}{\partial \alpha} < 0$$

and (A4)

$$\lim_{\beta \to 0} \frac{\partial \ln L}{\partial \beta} > 0, \quad \lim_{\beta \to \infty} \frac{\partial \ln L}{\partial \beta} < 0$$

guarantee a positive solution of α and β. Equation (A3) leads to the following constraints

$$1 < \frac{\left[e^{\alpha(u_1 - t_1)} \left(\frac{20}{u_1}\right)^{\beta} - 1 \right]^2}{(u_1 - t_1)^2 \left(\frac{20}{u_1}\right)^{\beta} e^{(u_1 - t_1)\alpha}} \sum_{i=2}^{c} \frac{N_i}{N} \left(\frac{t_i - t_{i-1}}{1 - e^{-\alpha(t_i - t_{i-1})}} \right)^2 e^{-\alpha(t_i - t_{i-1})} \tag{A5}$$

and

$$1 < \frac{\left[e^{\alpha(u_1 - t_1)} \left(\frac{20}{u_1}\right)^{\beta} - 1 \right]^2}{\left[\ln \left(\frac{20}{u_1}\right) \right]^2 \left(\frac{20}{u_1}\right)^{\beta} e^{\alpha(u_1 - t_1)}} \sum_{i=c+1}^{k} \frac{N_i}{N} \frac{\left(\frac{t_i}{t_{i-1}}\right)^{-\beta} \left[\ln \frac{t_i}{t_{i-1}} \right]^2}{\left[1 - \left(\frac{t_i}{t_{i-1}}\right)^{-\beta} \right]^2}. \tag{A6}$$

After algebraic manipulation, it was easy to see that Equation (A4) was true for this truncated exponential and the Pareto MLE. We used an iterative procedure to select the MLE of α and β, which satisfies not only Equation (A3) but also the constraints of Equations (A5) and (A6).

The partial derivations in each entry of matrix A (Equation (12)) are

$$\frac{\partial^2 \ln P_i}{\partial \alpha^2} = - \left(\frac{\Delta_i}{e^{\alpha \Delta_i} - 1} \right)^2 e^{\alpha \Delta_i} + (u_1 - t_1)^2 \frac{\left(\frac{20}{u_1}\right)^{\beta} e^{\alpha(u_1 - t_1)}}{\left[e^{\alpha(u_1 - t_1)} \left(\frac{20}{u_1}\right)^{\beta} - 1 \right]^2}$$

$$\frac{\partial^2 \ln P_i}{\partial \beta^2} = \frac{\left[\ln \left(\frac{20}{u_1}\right) \right]^2 \left(\frac{20}{u_1}\right)^{\beta} e^{\alpha(u_1 - t_1)}}{\left[e^{\alpha(u_1 - t_1)} \left(\frac{20}{u_1}\right)^{\beta} - 1 \right]^2}$$

and

$$\frac{\partial^2 \ln P_i}{\partial \alpha \partial \beta} = \frac{(u_1 - t_1) \left(\frac{20}{u_1}\right)^{\beta} e^{\alpha(u_1 - t_1)} \ln \left(\frac{20}{u_1}\right)}{\left[e^{\alpha(u_1 - t_1)} \left(\frac{20}{u_1}\right)^{\beta} - 1 \right]^2}.$$