

ESTIMATES OF ABUNDANCE AND MORTALITY OF LARVAL ANCHOVIES (1951-75):  
APPLICATION OF A NEW METHOD

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A method for analysis of egg and larval survey data based upon the maximum likelihood solution for the parameters of a modified negative binomial frequency model for the observed counts is described. The effect of uncontrollable variations in the real or "effective sampler size" and size-dependent levels of aggregation are incorporated as a fundamental part of the estimation procedure. Using this model, we calculated regional-seasonal estimates of abundance and mortality of northern anchovy larvae, *Engraulis mordax*, for the years 1951-75.

As a result of these analyses, we conclude that estimates of average catch, mortality and confidence intervals based upon semi-log regressions of the logarithm of the average standardized catch (rather than the logarithms of the individual observations) with time or age do not differ greatly from the estimates based upon the complete maximum likelihood solutions. Estimates of mean abundance and mortality generally coincided with estimates of the strength of a year-class obtained from fishery data. However, we were unable to consistently detect changes in recruitment using the parameters chosen for this study.

Equations are given for estimating the intensity of sampling required for a desired degree of precision in the relative coefficient of variation  $s_x/\bar{x}$ . The methods described herein may be used for more sophisticated kinds of analyses to: (1) uncover hitherto unrecognized relationships among abundance, aggregation, coverage and mortality which may be indicative of changes in absolute or relative levels of recruitment; and (2) determine the most efficient allocation of effort in the field and laboratory.

INTRODUCTION

Fishery management of short-lived stocks requires frequent estimates of spawning stock size; in addition, short-lived pelagic stocks may require estimates of recruitment. For example, northern anchovy, *Engraulis mordax*, that were prespawners in autumn 1974 comprised only 13% by numbers of the catch in the 1975 season while 90% of the 1959 catch were prespawners in the winter of 1958. Young-of-the-year (0-group) anchovies vary from 1 to 70% of the catch by number. This variation in recruitment to the fishery warrants full life-cycle monitoring for predictive purposes.

It has been shown that egg and larval surveys can be used effectively to monitor relative changes in spawning biomass (Smith, 1972). However, the value of such

data for direct estimates of the abundance of the mature or exploited stock and/or recruitment has yet to be demonstrated. Direct estimates of abundance require, at a minimum, accurate determinations of egg production; and estimates of recruitment require, in addition to egg production estimates, reliable estimates of mortality. Even then, the stock size-recruitment relationship is complex. Recruitment to the stock may be due to areally-or temporally-protracted spawning or to higher than average survival at any prerecruitment stage either inside or outside the population center. Potentially reliable indexes of recruitment strength may consist of estimates of abundance at any or all early life stages, and/or estimates of mortality over restricted or extensive size ranges, and estimates of the extent of the area of spawning.

The conceptual models for estimates of stock abundance from the spawning products have been formulated (e.g., Saville, 1964). But the sampling or statistical considerations which, at least for large scale

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surveys, are primal have received little attention. English (1964) noted that the usefulness of several proposed indexes was severely limited by the lack of knowledge concerning their inherent variability. For statistical reliability, large scale surveys should consider:

- 1) the effect of environmental and behavioral factors on the content of the samples or collections;
- 2) the effect of environmental and behavioral factors on the disposition of the population being sampled; and,
- 3) the temporal-areal allocation of sampling.

The first consideration is central to this paper and concerns the accuracy and precision of stock size and recruitment indexes for the population actually sampled. We attempt to remove the biases and variability due to change in catchability from bias and variability due to the disposition of organisms in the environment. The latter two issues concern the accuracy and precision with which these indexes monitor the total population and can be assessed only in relation to the allocation of sampling and the analysis technique. We use "catchability" in a somewhat restricted sense to represent the probability of capture within the area actually sampled. In the more general interpretation, catchability may include, in addition, the probability of being within the sampling area.

Based on the assumption of a completely effective sampler and using logarithmic transformation of the numbers of fish eggs, English (1964) used the analysis of variance to separate the temporal-spatial (both horizontal and vertical) components of variance and their interactions. He rejected indexes of stock size based on estimates of abundance during short periods or those relying on a few locations over the spawning period because of the complex fluctuations in spawning activity and because of the lack of confidence limits to accompany such indexes. In part to examine this complexity in larval fish, we calculated a series of regional-seasonal estimates of abundance and mortality of anchovy larvae for the years 1951-75. This series was also intended for comparison with other environmental and biological information (see Smith et al., this volume) and to explore the general applicability of the analysis technique. We use the data from one region [(7) Fig. 1] and season (Jan-Mar) of 1969 in the examples of the methods of analysis.

The analyses are based on the negative binomial weighted (NBW) model described by Bissell (1972a) for situations in which the actual size of the sample element was not constant. In his formulation, a weight  $w_i$  is used to define the total likelihood of  $N$  collections

(e.g., counts of larvae)  $x_i$  in terms of the probabilities

$$L = \prod_{i=1}^N \Pr(x_i | m, k, w_i) = \frac{N!}{\prod_{i=1}^N x_i!} \left( \frac{k}{mw_i + k} \right)^k \left( \frac{mw_i}{mw_i + k} \right)^{x_i} \frac{\Gamma(k + x_i)}{\Gamma(x_i + 1)\Gamma(k)}$$

where  $E(x_i) = mw_i$  and  $\text{Var}(x_i) = mw_i(1 + mw_i/k)$ . The resultant parameter estimates  $m$  and  $k$  are appropriate for the case  $w = 1$ .

We generalize the application of this model to situations where the sample elements vary in actual as well as "effective" size, i.e., where catchability is influenced by known physical and environmental factors. In our model, the weight  $w_i$  which corresponds to the catch  $x_i$  represents the "effective sampler size" and is determined by the larval size and by conditions local to the area of collection. In this way sample frequencies which are, in reality, an amalgam of observations determined by the vagaries of sampling may be combined and used to estimate the model parameters. Sample to sample comparisons may then be made at some prescribed level (usually  $w = 1$ ) and changes in this "standard" catch with time or size can be used directly as estimates of mortality. Under the model assumptions, methods are described for obtaining maximum likelihood estimates of abundance and mortality with standard errors during the early life history which may then be used to examine the magnitude and pattern of variability in indexes of recruitment strength.

No attempt is made to justify the negative binomial model on a conceptual basis. Bliss (1971) suggests that it is as widely applicable for discrete counts as the normal for continuous data. Others (e.g., Taft, 1960; Roessler, 1973) describe the sample frequencies of a variety of organisms including fish eggs and adult fish. Anderson (1964) considered the model for the catch and effort relationship. An empirical evaluation of its use in the description of larval fish catches was central to this investigation.

#### EFFECTIVE SAMPLER SIZE

Environmental and behavioral factors act together to alter the chance of capture and retention of organisms even for standard gear and operational procedures in all fishery resource surveys. These factors interact to produce what is called the "effective sampler size." For example, avoidance behavior and extrusion through the mesh operate at opposite extremes of the size range to determine a size-specific

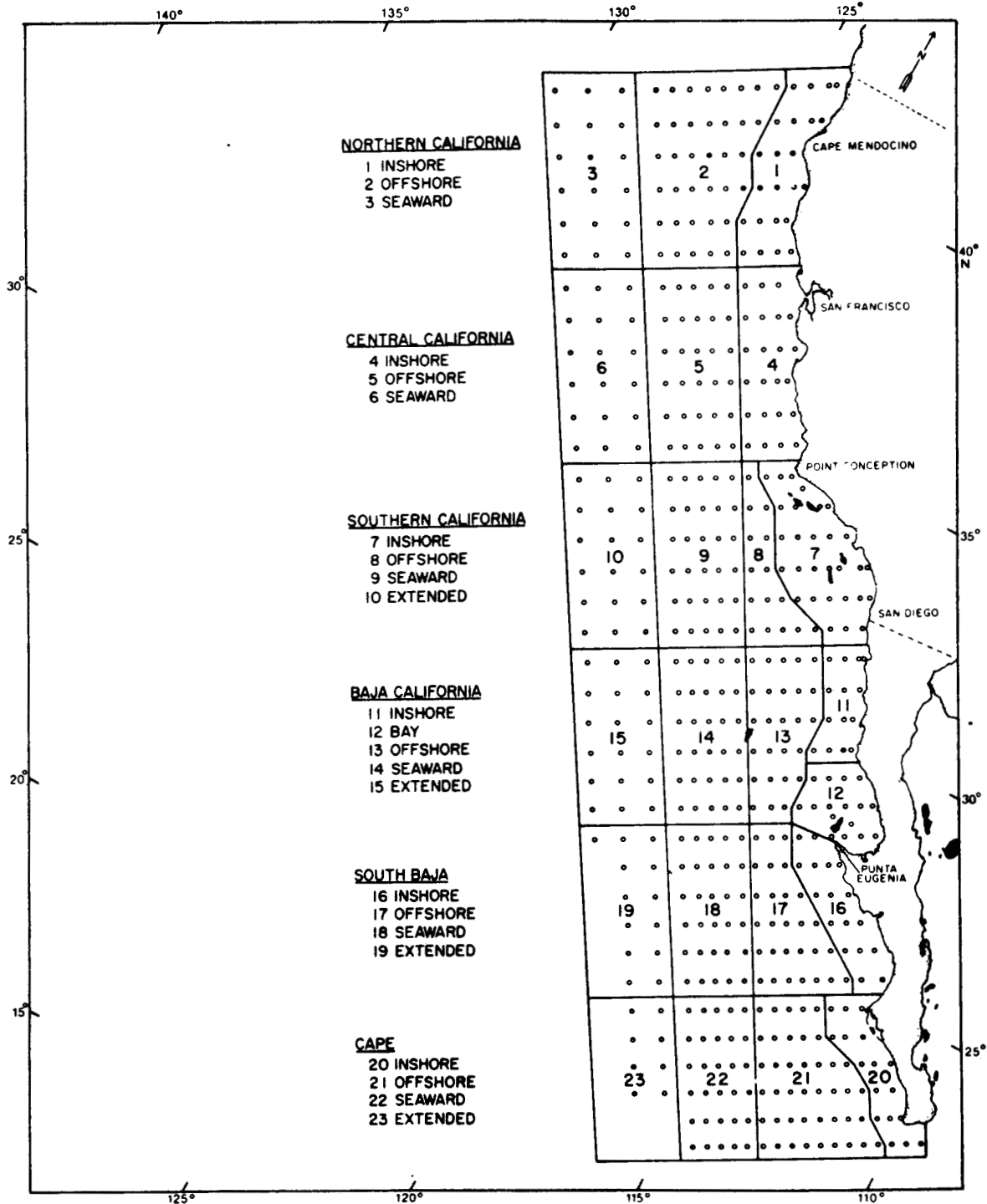


Figure 1. Areal regions used in the analysis of larval catches. o denotes station to be sampled.

catchability. In contrast, a fundamental requirement of all statistical sampling is that the sampler size be constant or at least measurable. Only when it is constant can sample to sample comparisons be made based on the empirical variability; otherwise, expected frequencies and thereby all sampling efforts become inextricably confounded with variations in real abundance of the organism in the environment. In the NBW model, both the mean and variance of each observation are determined by the "effective sample size"  $w_i$ , i.e.,  $E(x_i) = mw_i$  and  $\sigma^2(x_i) = mw_i(1 + mw_i/k)$  where  $w_i$  is determined from other variables measured coincident to the time of collection.<sup>2</sup> Zeros or empty samples are assigned a finite probability of occurrence and treated as real rather than "pseudo" observations. The expected catch under specified "standard" conditions ( $w=1$ ) appropriate for estimates of abundance and mortality, is the parameter  $m$  without recourse to transformation. The parameter  $k$  is an estimate of contagion in the disposition of the sampled organisms.<sup>3</sup> Iterative procedures are required to obtain the maximum likelihood solutions for the parameters  $m$  and  $k$  and the asymptotic variances. The maximum likelihood equations are given by Bissell (1972). Algol coded solutions are available at the SWFC.

Maximum likelihood solutions for the parameters of any mortality relationship using the means ( $m$ ) of several distributions and time or age may be obtained by generalizing the probability function

$$\Pr(x_{ij}) = f(m_i, k_i, w_{ij})$$

to include a relational expression of the individual means with an independent variable(s) e.g.,  $\tilde{m}_i = \theta_1 \exp(-\theta_2 s_i)$  so that the probability of any  $x_{ij}$  is defined as

$$\Pr(x_{ij}) = f[\theta_1 \exp(-\theta_2 s_i), k_i, w_{ij}]$$

Iterative procedures are then employed to obtain the maximum likelihood solution for the parameters and

<sup>2</sup> In an alternative formulation (Bissell 1972b),  $\sigma^2(x_i) = mw_i(1 + \frac{m}{k})$ . We have not, as yet examined this model in our work.

<sup>3</sup> Mathematically, there is no requirement that areas of high or low abundance be contiguous. Larval disposition nearly always exhibits recognizable areal and/or temporal continuity; thus, we interpret the parameter  $k$  as a measure of real contagion. Recently, however, Taylor et al. (1979) have stated that the behaviour of  $k$  (actually  $1/k$ ) is complex in theory and an inconsistent measure of aggregation in practice, whether the negative binomial fits the data or not.

<sup>4</sup> On the basis of larval catches from the period 1951-1969, minimum avoidance of all sizes occurs between 2200 and 2300 h. We used catch at 2300 hours as the standard for all sizes. At least for large larvae the possibility of absolute avoidance cannot be dismissed; thus abundance of these size classes may be underestimated and mortality rates calculated for the entire size range may be too large.

variance-covariance matrix (Zweifel, unpubl. ms.a). Variance estimates for the means are based upon the propagation of error approximation (Deming, 1966, pp. 130). For the simple exponential model above,

$$\text{Var}(\tilde{m}_i) = \exp(-2\hat{\theta}_2 s_i) * [\hat{\text{V}}\hat{\text{a}}\hat{\text{r}}\theta_1 + (\hat{\theta}_1 s_i)^2 \hat{\text{V}}\hat{\text{a}}\hat{\text{r}}\theta_2 - 2\hat{\theta}_1 s_i \hat{\text{C}}\hat{\text{o}}\hat{\text{v}}(\theta_1, \theta_2)]$$

#### METHODS

Numbers of larvae and associated tow data were grouped by station within region and season. The set of samples consisted of oblique plankton tows with a 1m diameter net from below the recorded depth of the anchovy larvae to the surface. A detailed description of the sampling method used is given in Kramer et al., (1972). A statistical summary of the samples is given in Smith (1972). All preserved anchovy larvae in the collection were recorded in length classes given in Table 1, Columns 1-3.

An "effective sampler size" was calculated for each factor thought to seriously bias the estimates of abundance. The most obvious biases are extrusion through the mesh, avoidance of the net mouth, and variation in the amount of water strained per meter of depth. Another less obvious but potentially equally important factor is the influence of water temperature on embryonic growth rate. Size specific and differential growth rates could seriously bias the estimate of duration of the size categories, and thus estimates of absolute or relative abundance and mortality. Methot and Kramer (1979) suggest that possible temperature effects may be less than anticipated because of compensatory effects of food availability and larval behavior.

Avoidance corrections are based upon long term (20 years) catches by size and time of day. Adjustment for the effects of temperature on duration within a size interval are obtained from a temperature dependent growth model developed in the La Jolla Laboratory of NMFS (Zweifel and Lasker, 1976). Escapement through the meshes of the net as a function of larval length is estimated from empirical field data (Lenarz, 1972). A calibrated flowmeter in the net was used to measure the volume filtered per tow. All four bias adjustments were combined for each larval size category in each sample to yield a single "weighting factor." This factor ( $w$ ) was the product of the four separate bias adjustments and was a measure of the "effective sampler size" for a particular collection and size range of larvae. The weighting factor ( $w$ ) is unity when no extrusion takes place, avoidance is minimal<sup>4</sup>, 3.50 m<sup>3</sup> of water were strained per meter of depth, and the temperature at 10 m depth was 16.2° C.



Table 3. Abundance classes of 3.75 mm larvae taken in the first quarter of 1969 in the southern California inshore Region 7 with average effective sampler size," age at 16.2° C, and corrections for bias due to temperature, volume of water strained, avoidance and extrusion.

Lower-Mark-Upper	No. of stations	Weight <sup>a</sup>	Age <sup>b</sup>	Temp <sup>c</sup>	Vol. <sup>d</sup>	Avoid <sup>e</sup>	Escape <sup>f</sup>
0	6	1.28	7.02	3.20	.88	.73	.63
1	2	1.04	8.75	3.99	.73	.56	.63
2	3	.85	6.10	2.78	.89	.54	.63
3	1	1.10	8.30	3.78	.91	.51	.63
4	2	1.53	7.55	3.44	.87	.80	.63
7	2	.96	6.40	2.92	.94	.56	.63
9	1	1.06	8.24	3.76	.95	.47	.63
10	1	1.79	8.62	3.93	.97	.74	.63
14	1	.75	7.73	3.53	.97	.35	.63
16- 21-32	5	1.21	7.49	3.42	.89	.64	.63
33- 43-64	6	1.63	7.12	3.24	1.10	.74	.63
65- 99-128	13	1.21	6.96	3.17	.94	.65	.63
129-205-256	8	.93	6.84	3.12	.87	.54	.63
257-329-512	10	1.28	6.68	3.04	1.19	.58	.63
513-771-1024	5	1.55	6.62	3.02	.93	.88	.63
1025-343-2048	1	.80	6.59	3.01	.83	.51	.63

<sup>a</sup> Average product of individual weighting components.

<sup>b</sup> Calculated from equations obtained from laboratory growth experiments. Temperature Specific Equations for growth and development of anchovy, *Engraulis mordax*, during embryonic and larval stages.

<sup>c</sup> Calculated as estimated time in size interval/standard time = 2 days.

<sup>d</sup> Calculated as estimated volume of water strained/standard volume = 3.5 m<sup>3</sup> per meter depth.

<sup>e</sup> Calculated as long term catch by hour/standard or maximum catch at 2300 h.

<sup>f</sup> Determined from mesh retention study of Lenarz (1972).

#### EXAMPLE

We use the numbers of 3.75 mm larvae collected during January, February and March of 1969 from the southern California inshore Region 7 as shown in Figure 1 to illustrate the steps required to calculate larval abundance from numbers of larvae per sample and associated data. Station by station larval counts together with the mid-time of haul, temperature at 10 m depth and standard haul factor (10/volume strained/depth) are shown in Table 2. In Table 3, the same data are grouped by classes of abundance. Grouping by abundance class is convenient, but is not a requirement of the NBW analysis. It is used here to average out the effects of the weighting factors. Preliminary investigation suggests that the effect on parameter estimates is minimal but further investigation is needed. O'Carroll (1962) assigned the interval frequency at the mid-point rather than the average. For each abundance class, the average bias correction for the four separate components, the average combined weight calculated as the average product of the individual components, and the estimated age at 16.2° C are shown.

Calculations analogous to those in Table 3 are required for each size class included in estimates of larval mortality. These bias corrections can significantly alter estimates of abundance at any size as well

as the pattern of mortality from size class to size class. In Table 4, we show the uncorrected average number of larvae per sample  $\bar{x}$  and the parameter estimates  $\hat{m}$  and  $\hat{k}$  with standard errors for all larval sizes (Jan-Mar, Region 7). The ratios  $\hat{x}/\hat{m}$  indicate the effect of the weighting technique on estimated larval abundances; for these collections, a maximum (about two-fold) alteration occurs in the class of smallest larvae.

Estimated abundances  $\hat{m}_i$  assuming a constant instantaneous rate of size (average live length) — related mortality ( $\theta_2$ ) over the entire size range, i.e.

$$\hat{m}_i = \theta_1 \exp(-\theta_2 s_i)$$

are also shown in Table 4 for the 16 smallest classes of sized larvae (January-March, Region 7, 1969). These estimates were obtained from the complete maximum likelihood solution where

$$\hat{\theta}_1 = 1780.05, \hat{\theta}_2 = 0.4717, \sqrt{\text{Var}\hat{\theta}_1} = 275.10 \text{ and}$$

$$\sqrt{\text{Var}\hat{\theta}_2} = 0.0159$$

The 2.50 mm size class has many more larvae than would be expected assuming continuity in the mortality relationship (Fig. 2). This class (<4 mm live size) precedes the "critical period" of first feeding larvae. (4-5 mm live size) whose biological importance has

Table 4. Estimates of the parameters of the negative binomial weighted model in the analysis of anchovy larvae taken during the first quarter of 1969 in Region 7.

Class	Average live size (mm)	Actual counts		NBW estimates				Constant instantaneous mortality $\tilde{m}_s = \hat{\theta}_1 e^{-\hat{\theta}_2 S}$		
		$\bar{x}$	s	$\hat{m}$	$s_m$	$\hat{k}$	$s_k$	$\tilde{m}$	k	Var in $\tilde{m}$
250	3.23	338.05	620.50	801.83	176.189	0.310	0.0461	387.51	0.268	0.0118
375	4.49	176.77	253.51	159.06	30.631	0.403	0.0613	213.86	0.393	0.0086
475	5.57	91.58	109.07	111.47	20.894	0.428	0.0690	128.51	0.424	0.0065
575	6.62	52.77	61.88	56.94	9.906	0.500	0.0829	78.22	0.480	0.0050
675	7.65	31.80	38.56	40.67	7.050	0.506	0.0869	48.06	0.500	0.0040
775	8.67	17.25	21.33	24.69	4.100	0.567	0.1040	29.72	0.556	0.0036
875	9.68	11.29	15.50	16.68	3.048	0.471	0.0929	18.47	0.468	0.0037
975	10.68	8.29	13.20	12.54	2.690	0.345	0.0739	11.51	0.344	0.0044
1075	11.68	5.43	9.72	9.74	2.016	0.380	0.0859	7.18	0.359	0.0055
1175	12.68	2.46	5.55	4.74	1.122	0.312	0.0878	4.49	0.311	0.0071
1275	13.67	1.73	5.04	3.77	1.289	0.145	0.0450	2.80	0.141	0.0092
1375	14.67	1.08	3.66	2.11	0.840	0.111	0.0407	1.75	0.110	0.0118
1475	16.17	0.65	2.29	1.16	0.460	0.112	0.0488	0.86	0.106	0.0167
1575	16.65	0.32	1.23	0.52	0.281	0.064	0.0381	0.68	0.063	0.0185
1725	18.15	0.25	0.84	0.24	0.100	0.137	0.0847	0.34	0.129	0.0247
1925	20.16	0.17	0.85	0.13	0.088	0.046	0.0340	0.13	0.045	0.0348

been the subject of considerable study and speculation. For the biological point of view size classes, 2.50 and 3.75 mm are subject to increased variability due to the unpredictable nature of the time of first feeding and the subsequent rapid increase in growth.

Several authors, e.g. Lasker (1975, 1978) and Hunter (1976) have documented the importance of food density as well as the capacity for high survival with minimum growth. Thus, departure from the "average" environmental condition may give rise to greater or lesser numbers of larvae in either the "critical period" or those adjoining. Failure to find food will increase the numbers remaining in the small (2.50 mm) size class and decrease the observed number of the 3.75 mm class. Above average feeding conditions promoting growth will tend to decrease the observed number in the non-feeding (2.50 mm) category and increase numbers in the 3.75 and subsequent size classes. Figure 2 (inset) shows the average or standard (16.2° C) growth relationship for newly hatched to 6 mm larvae together with similar curves for 13° and 19° C. To the extent that variations in food availability can be equated to changes in ambient temperature and thus to growth, the potential for increased variability in observed counts exists. In the next section, we show that even the large discrepancies in 2.50 mm class larvae may be more apparent than real.

#### CONFIDENCE INTERVALS

Establishment of useful limits or intervals requires a stable population and a representative sample from

that population, neither of which can be assured in natural environments. In fact, it has been recognized (Taylor 1971, pp. 363; Taylor et al., 1979, pp. 290) that most sample frequency distributions are largely empirical in nature. For example, the negative binomial frequencies can arise from a variety of conceptual formulations or empirically by random sampling over a gradient (Taylor, 1971, pp. 362). Variations in absolute or "effective" sampler size may give rise to sample frequencies which reflect changes in catchability as well as areal-temporal disposition; then samples become an amalgam of observations and not even non-parametric methods of analysis are appropriate. As an alternative to confidence limits, Kempthorne (1967) and more recently Easterling (1976) propose the use of consonance regions or intervals which depend only upon the model formulation for the observed sample. This approach determines limits on the parameters of the frequency distribution such that the goodness of fit is contained within specified probability limits. While this seems the more realistic approach, it has so far been largely ignored by statisticians and biologists alike. We have not, as yet, explored the applicability of consonance regions to the Negative Binomial Weighted (NBW) analysis, although an examination of these kinds of alternatives seems essential to any major advance in the application of realistic statistical procedures to natural or uncontrollable populations.

We have used the NBW model analysis to separate the effects of catch-ability and disposition. The recommendations for confidence intervals are based upon simulations from completely specified binomial, Pois-

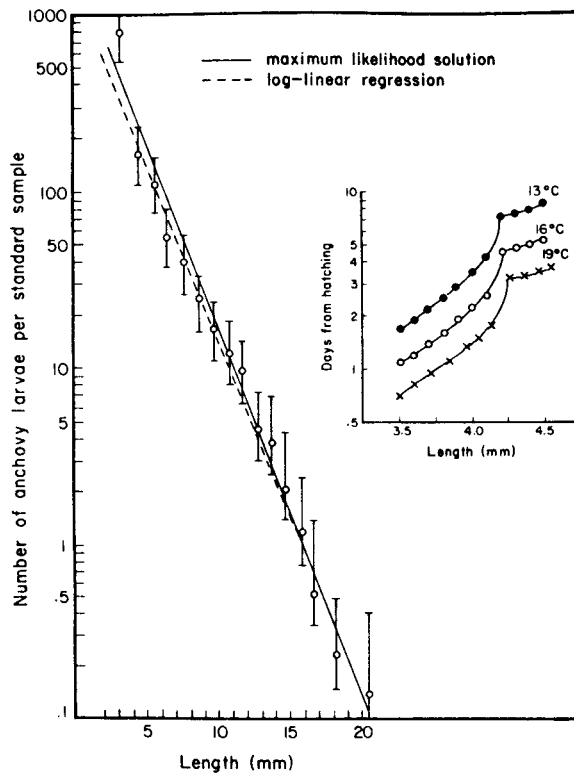


Figure 2. Estimates of the mean per standard sample ( $\hat{m}$  of the NBW analysis) for 16 size classes of anchovy larvae with confidence intervals. Coefficients of the mortality relationship were estimated from both the NBW analysis (1780.05, 0.4717) and the regular log-linear regression (1855.10, 0.4740). Inset describes growth at three temperatures at the onset of feeding (4.28 mm).

son and negative binomial distributions (Zweifel, Unpubl. ms. b) and from simulations from known mortality relationships, e.g., where  $\hat{m}_i = \theta_1 \exp(-\theta_2 S)$ . The former suggest that for the three models the distribution of the sample mean  $\bar{x}$  is more closely approximated by the log-normal than the normal distribution, i.e., that the upper (UCL) and lower (LCL) confidence limits determined as

$$\text{LCL} = \bar{x} \exp(-Z_p \sqrt{\text{Var} \ln \bar{x}})$$

and

$$\text{UCL} = \bar{x} \exp(Z_p \sqrt{\text{Var} \ln \bar{x}})$$

where

$$\widehat{\text{Var}} \ln \bar{x} = \ln(1 + \text{Var} \bar{x} / \bar{x}^2)$$

and  $Z_p$  is the standard normal deviate such that  $P_r(Z > Z_p) = p/2$ , more nearly account for the asymmetries in the distribution of the sample mean for small sample sizes. As the sample size increases, the two

become indistinguishable. Simulations of the mortality relationship indicated that the instantaneous mortality coefficient ( $\theta_2$ ) obtained from the maximum likelihood solutions were essentially normally distributed while the estimates  $\theta_1$  and  $\hat{m}$  were skewed and more closely approximated by a log-normal distribution. Detailed results will be presented in a separate paper.

In Table 5 we use equations (7) and (8) and the maximum likelihood estimates for the 16 smallest classes of sized larvae (Jan-Mar, Region 7, 1969) to calculate the 95% confidence limits for the estimates  $\hat{m} = \theta_1 \exp(-\theta_2 S)$ , i.e. where  $\bar{x} = \hat{m}$  and  $\text{Var} \bar{x}$  is estimated from equation (4). For comparison, we calculate the same limits using the simple regression of  $\ln \hat{m}$  on average size. These and other results suggest that the simpler procedure may provide estimates equally as useful as those derived from the complete maximum likelihood solution. Confidence limits calculated for an individual observation using the regression equation shows that the number of 2.50 mm class larvae is just slightly greater than the upper 95% limit.

#### ESTIMATES OF ABUNDANCE AND MORTALITY

##### ABUNDANCE

In a period of development and rapid growth of fish eggs and larvae, vulnerability to capture by the plankton net changes continuously and rapidly. When the areal-temporal distribution of the spawning population is extensive, changes in catchability due to behavioral and environmental factors may greatly alter both the bias and variability in the catches. To estimate the standing stocks apart from changes in catchability, we used the NBW model to estimate the abundance of each size of larvae together with standard errors for each region and season for the years 1951-75. The parameter estimates  $\hat{m}$  for these analyses thus represent the catch which would have been expected for the standard or ideal sampler.

##### MORTALITY

For the steady state model<sup>5</sup> the variability inherent in estimates of mortality due to the spatial heterogeneity of the spawning habit of schooling pelagic fish (Smith, 1973) and subsequent dispersion from the centers of spawning has not as yet been separated from

<sup>5</sup> On a population basis, the overall steady-state may not occur; spawning rate may not be continuous (Hunter and Goldberg, 1980), and the mortality rate may not be constant. Lenarz (1973) reported "catch curves" for some larvae of the California Current area and specified conditions for interpreting mortality rates. Under some conditions (Ahlstrom, 1954) it may be possible to trace "cohorts" of larvae as would be indicated by the analysis of the fate of a single short-term spawning.



Table 5. The 95% confidence limits of sample estimates by size-class using propagation of error and logarithmic slope approximations.

Size class	Size live (mm)	$\ln \hat{m} = a + b \cdot \text{Size}$								
		Propagation of error			Mean			Predicted		
		LCL	m	UCL	LCL	m	UCL	LCL	UCL	
2.50	3.23	311.84	387.51	481.54	309.60	397.89	511.34	210.12	753.43	
3.75	4.49	177.66	213.86	251.44	176.73	219.13	271.72	117.26	409.51	
4.75	5.57	109.37	128.51	151.00	109.23	131.42	158.13	71.01	243.22	
5.75	6.62	67.90	78.22	90.10	68.36	79.94	93.49	43.54	146.78	
6.75	7.66	42.38	48.06	54.58	42.92	48.86	55.63	26.78	89.15	
7.75	8.68	26.37	29.73	33.52	27.12	30.15	33.51	16.60	54.74	
8.75	9.68	16.35	18.47	20.86	17.23	18.78	20.47	10.37	33.99	
9.75	10.69	10.08	11.51	13.14	10.81	11.64	12.53	6.44	21.04	
10.75	11.69	6.20	7.19	8.34	6.74	7.25	7.80	4.01	13.10	
11.75	12.68	3.79	4.49	5.31	4.18	4.54	4.93	2.51	8.21	
12.75	13.68	2.32	2.81	3.40	2.55	2.83	3.13	1.56	5.13	
13.75	14.68	1.41	1.75	2.18	1.55	1.76	1.99	.97	3.21	
14.75	16.17	.67	.86	1.12	.74	.87	1.02	.47	1.60	
15.75	16.66	.52	.69	.90	.58	.69	.82	.37	1.27	
17.25	18.15	.25	.34	.46	.27	.34	.42	.18	.64	
19.25	20.17	.09	.13	.19	.10	.13	.17	.07	.25	

variations in catchability. As noted above, this may be accomplished by incorporating the mortality function into the NBW analysis. In the regional-seasonal series reported here, the simple exponential model  $\tilde{m} = \theta_1 \exp(-\theta_2 S)$  was adequate for the size range 3–20 mm<sup>6</sup>. Even so, in some cases, variations in sampling intensity prevented a maximum likelihood solution for mortality. To provide a continuous series, the mortality estimates are based upon the relationship of the log-transformed NBW estimates  $\hat{m}$  and the estimated mid-live size at 16.2° C. As indicated in the section on confidence intervals, it does not appear that either bias or variability differ greatly for the alternative solutions.

The analyses included one fit to the first six size groups if present—one fit to the larger 12 size groups if present—and a fit to all size groups present. Cruises were conducted no more frequently than monthly and the maximum estimated age from spawning of 15 mm

larvae is approximately 30 days at 16.2° C. Consequently, under a steady state model, each size group up to 15 mm may be used to estimate total egg production by the spawning population.

## RESULTS

We examined only the simplest hypotheses concerning the relationship of larval abundance and mortality to recruitment strength. On average, estimates of mean abundance and mortality coincided with estimates of the strength of a year-class obtained from fishery data as reported by Smith et al. (this volume). The median mortality coefficient calculated from embryonic and early larval sizes for years above and below average strength were 0.24 and 0.32, respectively. The average abundance of 15 mm larvae interpolated from the analysis of larger larvae indicated differences between these same years.

Nevertheless, except for a few extreme cases, we were unable to quantitatively detect changes in recruitment potential from the average regional-seasonal estimates of embryonic or post-embryonic mortality or the abundance of 15 mm larvae. The failure may be an inherent problem in sampling the late larvae; or the determination of recruitment level may be established in subsequent months of development and survival of larvae, post-larvae, and juveniles. It is also possible that increased recruitment may come from high survival in certain (e.g., nearshore) regions rather than from general increases over the total geographic area.

Relatively small areal-temporal strata<sup>7</sup> (20 000 square miles over 3 months) often yielded estimates of abundance and mortality which were biologically and

<sup>6</sup> Analyses over extensive ranges of size or age or from life stage to life stage indicate, however, that time or size dependent mortality rates such as those defined by the equation

$$dN_t/dt = (a + \beta \rho^t) N_t \text{ or } N_t = N_0 e^{k(R^t - 1) - ct}$$

are required to estimate the decline in the observed counts.

<sup>7</sup> Some of the arbitrarily selected strata used in this study contained more gradients or large-scale heterogeneity than could adequately be described by the NBW model, at least with the weighting factors used herein. These strata cannot be determined a priori nor changed retrospectively; their discovery was in fact an important objective of this study. It should be noted, however, that smaller strata exhibiting statistical coherence are more subject to the effects of drift into and away from the strata of birth altering the estimates of mortality in contiguous areas or seasons.

Table 6. Seasonal estimates of anchovy larval mortality (number per mm) in Region 7 for the years 1951-75 and estimates of relative year-class strength<sup>a</sup>.

	Jan-Mar	Apr-Jun	Jul-Sep	Oct-Dec	Year-class strength
1951	.05	.38	.29	.33	-2.76
1952	.25	.27	.22	.33	-.66
1953	.35	.25	.47	.48	1.98
1954	.47	.42	.29	.45	3.30
1955	.44	.40	.23	.14	-1.92
1956	.36	.43	.26	.28	-2.82
1957	.44	.45	.26	.34	-2.94
1958	.51	.40	.32	.45	-.42
1959	.48	.41	.29	.30	4.08
1960	.47	.37	.24	.09	.42
1961	.59	.47	.30	.09	-.30
1962	.56	.43	.33	.25	.96
1963	.58	.28	.31	.32	3.42
1964	.44	.41	.31	.30	1.62
1965	.67	.49	.50	—	-2.34
1966	.50	.55	.38	.43	-3.12
1967	—	.34	.31	—	.60
1968	.48	.53	—	—	.60
1969	.47	.56	.44	.47	.72
1970	—	—	—	—	3.18
1971	—	—	—	—	1.14
1972	.50	.53	.42	.42	1.44
1973	—	—	—	—	.48
1974	—	—	—	—	3.66
1975	.49	.72	.49	.50	-4.68

<sup>a</sup>Based on the average normalized contribution of 1,2,3 and 4 year old fish to the commercial catch.

statistically reasonable. Mortality estimates from one stratum (Region 7) within the population center were remarkably stable over large changes in estimated year-class strength (Table 6). These results suggest (a) that pooling of mortality information over years and/or seasons may provide more precise estimates of abundance and; (b) that concentration of sampling within the population center may preclude the detection of important changes in recruitment potential.

#### SAMPLE SIZE

English (1964) noted that concentration of sampling effort in time or space is hazardous unless the spawning behavior of the population is well understood. The non-random distribution of eggs and larvae insures that the inherent variability changes with levels of abundance and makes extrapolation of sampling requirements difficult.

We consider the case where estimates of the negative binomial parameters  $m_1$  and  $k_1$  are available from sampling the time and area of peak spawning. Under the model the coefficient of variation ( $S_{\bar{x}}/\bar{x}$ ) of the

sample mean  $C_1$  is  $\sqrt{(1/n_1 m_1 + 1/n_1 k_1)}$  where  $n_1$  is the number of samples or collections. For an alternative plan, the corresponding expression is

$$C_2 = \sqrt{(1/n_2 m_2 + 1/n_2 k_2)}$$

For fixed intervals of sampling (both in time and space) expansion of the sampling grid outside the area of peak spawning reduces both the mean  $m_2$  and coefficient of contagion  $k_2$ , approximately by the ratio  $\sqrt{(n_1/n_2)}$ . Adjusting the algebra, we obtain

$$C_2/C_1 = \sqrt[4]{(n_1/n_2)}$$

Thus a doubling of the sample size obtained by increasing the sampling area, i.e.,  $n_2=2n_1$  may be expected to decrease the relative standard error by only 16% to  $\sqrt[4]{(1/2)} = 0.84$ . Similarly a ten-fold increase in area gives  $C_2/C_1 = 0.56$  i.e., less than 50% reduction. On the other hand, a four-fold decrease ( $n_2=n_1/4$ ) increases the ratio by only 40%. Changes in sampling intensity, i.e. where  $m_2=m_1$  and  $k_2=k_1$  alter the ratio  $C_2/C_1$  as  $\sqrt{(n_1/n_2)}$ . Within the area of peak

spawning, for example, a four-fold increase in sample size will be required to reduce the relative coefficient of variation by half. Thus the  $a$ -fold change in sampling intensity required for a  $b$ -fold change in range in order to attain a  $P$  percent change in the relative coefficient of variation is determined by the relationship

$$(1-P/100) = a^{1/2} b^{1/4}$$

The solutions for a given  $P = 0(25)75$  and  $b = 0.25, 0.50, 1(1)4$  are shown in Table 7. Taylor, et al. (1979) examined the density of  $k$  and showed that  $m$  and  $k$  are not functionally independent. That interaction has not been considered here. The form of the relationship if known, could lead to more precise estimates of the sampling requirements.

The relationship for fixed  $k$ ,  $m_2 = am_1$  and  $n_2 = bn_1$  is

$$C_2/C_1 = \sqrt{\left[ \frac{1}{b} \left( 1 - \frac{a-1}{an_1 m_1 C_1^2} \right) \right]}$$

While approximate, these relationships indicate the intensity of sampling effort required for specified precision in the estimates of abundance and mortality and thus for indexes of stock size and recruitment.

#### DISCUSSION

In this paper we describe a statistical model for the expected frequencies of the catches of eggs and larvae taken in large scale oceanic surveys which permits sample to sample comparisons and which is robust against changes in both the form of the underlying distribution and the mechanisms which determine them. The negative binomial distribution on which the analyses are based is suited without change to the Poisson at one extreme and the Poisson log-normal at the other extreme of "patchy" disposition. Patterns of mortality and dispersal and subsequent reaggregation common in the life cycle of pelagic schooling fish can be analyzed without change of the underlying distributional model. The effects of uncontrollable variations in the "effective sampler size" and size and density

Table 7. Estimates of the  $a$ -fold change in sampling intensity required for a  $b$ -fold change in sampling range in order to attain a  $P$  percent change in the relative coefficient of variation  $S_z/\bar{x}$ .

P	b					
	.25	.50	1	2	3	4
0	2.0	1.4	1.0	.70	.58	.50
25	3.6	2.5	1.8	1.2	1.0	.89
50	8.0	5.6	4.0	2.8	2.3	2.0
75	32.0	22.6	16.0	11.3	9.2	8.0

dependent levels of aggregation are incorporated as a fundamental part of the estimation procedure.

Using the NBW analysis, bias corrections for size, water filtered, time of day, and growth can be augmented by other as yet unquantified correction factors without fundamental change in the analysis. Existing correction factors can be separately or jointly evaluated for impact on sample variance and requirements for careful conduct or planning of tows can be relaxed or tightened as deemed appropriate. Alternative sampling designs (including fractional sorting) can be examined from existing data with known impact on both the estimates of standard error of density and the geographic area of occurrence. Empirical approaches can be attempted; multivariate and numerical classification techniques using the estimates of abundance, aggregation, coverage and mortality may uncover hitherto unrecognized relationships which are indicative of changes in absolute or relative recruitment.

The lack of simple relationships among abundance, survival and recruitment strength is not surprising: e.g., critical geographic or temporal scales may exist for determining mortality rates at different stages of the life cycle and incorporating them into a useful estimate of the level of recruitment. The existence of such scales may be explored experimentally (e.g., by intensive surveys of small subareas of the larval distribution) to detect local differences in larval survival and to forecast the impact of those differences on the recruitment of the young to the fishable stock (see e.g., Lasker, this volume) or by retrospective data analysis. The success or failure of either will be determined by the variability inherent in the sampling process and the sampling effort. In uncontrolled environments, variability is due to (a) changes in the effectiveness of the sampler, (b) the sampling design and intensity, (c) the method of analysis, and (d) the areal-temporal disposition of the population. In this paper we have addressed the first three of these issues from a statistical point of view. The last issue is variable but not statistical, i.e., it is basically unpredictable. No amount of statistical information can determine the practical risks involved in limiting the sampling range. Restriction of sampling to population centers without corresponding changes in sampling intensity may decrease rather than increase precision in the estimators. We have attempted to provide estimates of the cost (in terms of sample size) of limiting the sample range without significantly impairing the reliability of the results.

#### ACKNOWLEDGMENTS

The authors are deeply indebted to Reuben Lasker, John Hunter and Gary Stauffer, whose critical ques-

tioning and editing have helped to simplify the description of both intent and content of this study. Special thanks are due to Julie Shoemaker and Lorraine Prescott for their skill and patience in the typing of several drafts.

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