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RE-ESTIMATION OF THREE PARAMETERS ASSOCIATED WITH ANCHOVY EGG AND LARVAL ABUNDANCE: TEMPERATURE DEPENDENT INCUBATION TIME, YOLK-SAC GROWTH RATE AND EGG AND LARVAL RETENTION IN MESH NETS

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RE-ESTIMATION OF THREE PARAMETERS ASSOCIATED WITH ANCHOVY EGG AND LARVAL ABUNDANCE: TEMPERATURE DEPENDENT INCUBATION TIME, YOLK-SAC GROWTH RATE AND EGG AND LARVAL RETENTION IN MESH NETS

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ABSTRACT

The estimates of three parameters required for northern anchovy (Engraulis mordax) abundance assessment were updated using new data from 1981 and 1982. These three parameters are incubation time, yolk-sac larval growth, and retention of eggs and larvae in various mesh nets.

The growth data of the yolk-sac anchovy larvae were updated by including a set of new data collected in 1981. This new data set consisted of larval length and age collected at three temperatures: 13.5, 15.0, and 16.5°C. The incubation time was related to the water temperature in a negative exponential form. A Gompertz model was used to describe the growth of yolk-sac anchovy larvae, in which the temperature-dependent growth rate has an exponential form.

The results of a three-vertical-net experiment conducted in March 1982 showed that 0.333 mm mesh was not extrusion-free. The retentions of 0.333 mm Nitex mesh relative to 0.150 mm and 0.075 mm meshes are 0.91 for eggs, 0.63 for larvae \leq 4.0 mm (preserved standard length), 0.95 for larvae = 4.5 mm, and 1 for larvae $>$ 4.5 mm. The retention of eggs and larvae for large meshes can be corrected accordingly.

1. INTRODUCTION AND DATA SOURCES

Quantitative assessment of egg and larval abundances from ichthyoplankton data depends on the use of appropriate correction factors or weights for various parameters, as it is impossible to have a bias-free sampler. These parameters were most recently estimated by Zweifel and Smith (1981) for the northern anchovy. In order to correct for the biases, Zweifel applied a negative binomial weighted model developed by Bissel (1972) (Zweifel and Smith 1981; Hewitt 1982) with each observation weighted by its effective sampler size. Since the completion of their work, new and more complete data have become available at the Southwest Fisheries Center (SWFC) for three of these parameters--incubation time, growth in length of egg through yolk-sac stage larvae, and extrusion of eggs and larvae through the meshes of plankton nets.

New data were collected from a laboratory experiment conducted in 1981 on temperature specific incubation rates and yolk-sac larva growth rates of northern anchovy. In addition, an experiment at sea was conducted in March 1982 to determine retention of anchovy eggs and larvae in three identical net frames, each with a different mesh net. Data from older sources are combined with these data to provide new parameter estimates.

To improve estimates of the relationship between temperature and both incubation time and yolk-sac larval growth and to establish criteria for developmental stages of yolk-sac anchovy, a laboratory experiment was conducted at three temperatures (13.5, 15.0 and 16.5°C) in 1981 using eggs from a captive brood stock. These data were used along with those collected

by David Kramer and employed by Zweifel and Lasker (1976) and Zweifel and Hunter (MS) (at temperatures 14, 17 and 20°C) to develop a revised model for expressing the relationship between yolk-sac larval growth and temperature.

Estimates of retention of anchovy eggs and larvae in small mesh nets were investigated during a week-long field experiment conducted in March 1982 in the Los Angeles Bight at a single station. One hundred forty-two vertical net tows were made using three 25 cm diameter frames each with a Nitex net of different mesh size (0.333, 0.150 and 0.075 mm) mounted on the same wire. These plankton nets are deployed to 70 m depth and retrieved vertically. They are referred to as CalVET nets (CalCOFI vertical nets, Hewitt in press). The anchovy eggs taken in each of the nets were sorted according to their developmental stages and the standard length of the anchovy larvae was measured.

The retention of anchovy eggs and larvae in large mesh nets (0.55 and 0.505 mm vs 0.333 mm) was reexamined. Data from 0.333 mm mesh CalVET tows and 0.505 mm mesh Bongo tows (McGowan and Brown 1966) taken during January-April in 1979-81 along with those used by Lenarz (1972) were included in the analysis to redefine the retention of eggs and larvae in various mesh sizes of plankton nets.

2. METHODS

2.1 Temperature Dependent Incubation Time and Growth of Yolk-Sac Northern Anchovy

In the 1981 laboratory experiment anchovy eggs were incubated at three nominal temperatures (13.5, 15 and 16.5°C) in 10 liter containers in temperature controlled water baths with 20 eggs taken per hour until hatching. After hatching, 20 yolk-sac larvae were taken every 4 hours and 10 of these were measured to determine mean standard live length. The time of the first hatch and approximate time of last hatch were recorded. Because eggs are located at the surface while larvae are usually in the middle depths, both surface and middle depth temperatures were recorded.

At 16.5°C, larvae older than 4.14 days (3.78-3.96mm) were excluded because they began to starve and would bias the growth curve downward. The temperatures used in the analysis were geometric mean surface temperature before hatching and middle depth temperature after hatching, measured every 4 hours. The elapsed time from fertilization, and the measured mean standard live length of anchovy larvae were used along with Kramer's larval data set, reported in Zweifel and Lasker (1976), to fit a temperature dependent growth curve for yolk-sac anchovy larvae (Table 1).

2.2 Retention of Anchovy Eggs and Larvae in Various Mesh Nets

In estimating the abundance of eggs and larvae, one of the sources of bias is their extrusion through the meshes of the net. Extrusion is measured by the ratio of catch retained in a large mesh net to that taken in a smaller mesh net.

Retention of anchovy eggs and larvae in 0.333 mm Nitex mesh compared to

Table 1. Live length (mm) and age from fertilization (days) of yolk-sac larvae at various temperatures (°C). (The predicted length was computed from equation (3)).

AGE (days)	OBSERVED LENGTH (mm)	PREDICTED LENGTH (mm)	SE	TEMP. °C	DATA SOURCE
75	39	35	0.076	13.47	1981
74	59	48	0.073	13.47	
73	61	49	0.063	13.47	
72	82	61	0.059	13.47	
71	82	72	0.047	13.47	
70	93	82	0.042	13.47	
69	06	99	0.038	13.47	
68	24	102	0.037	13.47	
67	26	111	0.036	13.47	
66	13	17	0.036	13.47	
65	34	27	0.036	13.47	
64	43	34	0.036	13.47	
63	55	41	0.035	13.47	
62	70	48	0.035	13.47	
61	63	55	0.034	13.47	
60	56	59	0.033	13.47	
59	28	75	0.032	13.47	
58	47	64	0.031	13.47	
57	62	73	0.030	13.47	
56	52	78	0.029	13.47	
55	93	81	0.028	13.47	
54	12	85	0.028	13.47	
53	87	88	0.028	13.47	
52	67	91	0.028	13.47	
51	13	94	0.029	13.47	
50	17	96	0.030	13.47	
49	7	98	0.031	13.47	
48	14	90	0.033	13.47	
47	22	96	0.033	13.47	
46	12	105	0.033	13.47	
45	12	109	0.033	14.00	
44	34	13	0.033	14.00	
43	40	19	0.031	14.00	
42	64	33	0.030	14.00	
41	64	64	0.029	14.00	
40	79	69	0.028	14.00	
39	95	92	0.027	14.00	
38	70	16	0.045	15.03	
37	80	26	0.040	15.03	
36	11	88	0.033	15.03	
35	12	99	0.033	15.03	
34	84	10	0.032	15.03	
33	47	24	0.031	15.03	
32	62	30	0.027	15.03	
31	78	60	0.027	15.03	
30	41	46	0.027	15.03	
29	11	40	0.027	15.03	
28	73	60	0.027	15.03	
27	66	71	0.026	15.03	
26	77	76	0.025	15.03	
25	96	81	0.024	15.03	
24	11	68	0.023	15.03	
23	22	81	0.023	15.03	
22	46	66	0.023	15.03	
21	63	92	0.023	15.03	
20	58	96	0.023	15.03	
19	79	98	0.020	15.03	
18	11	98	0.015	15.03	
17	99	44	0.033	15.03	
16	94	44	0.035	15.03	
15	73	44	0.038	15.03	
14	66	44	0.041	15.03	
13	55	44	0.044	15.03	
12	88	40	0.047	15.03	
11	97	11	0.050	15.03	
10	15	12	0.050	15.03	
9	77	13	0.055	15.03	
8	47	14	0.058	15.03	
7	47	15	0.058	15.03	
6	63	62	0.040	16.23	
5	80	93	0.033	16.23	
4	80	06	0.029	16.23	
3	96	17	0.027	16.23	
2	11	29	0.027	16.23	
1	33	40	0.027	16.23	
0	46	49	0.027	16.23	
-1	53	55	0.027	16.23	
-2	73	62	0.027	16.23	
-3	96	69	0.026	16.23	
-4	13	78	0.025	16.23	
-5	34	67	0.040	17.00	
-6	50	79	0.035	17.00	
-7	67	14	0.032	17.00	
-8	84	26	0.031	17.00	
-9	80	43	0.030	17.00	
-10	87	53	0.029	17.00	
-11	98	67	0.028	17.00	
-12	79	75	0.027	17.00	
-13	64	83	0.027	17.00	
-14	91	98	0.023	17.00	
-15	16	13	0.059	20.00	
-16	34	25	0.057	20.00	
-17	56	37	0.054	20.00	
-18	74	53	0.050	20.00	
-19	83	75	0.044	20.00	
-20	83	84	0.041	20.00	
-21	07	92	0.040	20.00	
-22	08	98	0.041	20.00	
-23	4	08	0.041	20.00	
-24	4	08	0.041	20.00	

smaller Nitex meshes (0.150 and 0.075 mm) was investigated with the previously mentioned 1982 field experiment. The three 25 cm nets were randomly assigned to port, center and starboard positions, and every 6 hours, two of the nets were switched according to a predetermined system to eliminate possible bias due to net position.

Retention of anchovy eggs and larvae in 0.505 mm Nitex mesh compared to 0.333 mm Nitex mesh was estimated from the larvae taken during January-April in 1979-81 in the 0.505 mm mesh Bongo net and the 0.333 mm mesh CalVET net at stations where both nets were towed. Retention of eggs and larvae in 0.55 mm silk mesh (1 m diameter net) compared to that in 0.333 mm Nitex mesh (0.5 m diameter net) was discussed by Lenarz (1972). In the same study the eggs taken in a 0.505 mm Nitex mesh net were compared to those taken in a 0.333 mm Nitex mesh net (Smith MS) although most of the larvae were neither counted nor measured.

3. RESULTS

3.1 Incubation Time as a Function of Temperature

The incubation time of eggs was first analyzed by Zweifel and Lasker (1976) and was found to be inversely related to the temperature, i.e., the higher the temperature, the shorter the incubation time. The new data on incubation time of anchovy eggs discussed in the Methods section and those used by Zweifel and Lasker (1976) were used to fit an exponential equation expressing the relation between incubation time and incubation temperature (Fig. 1)

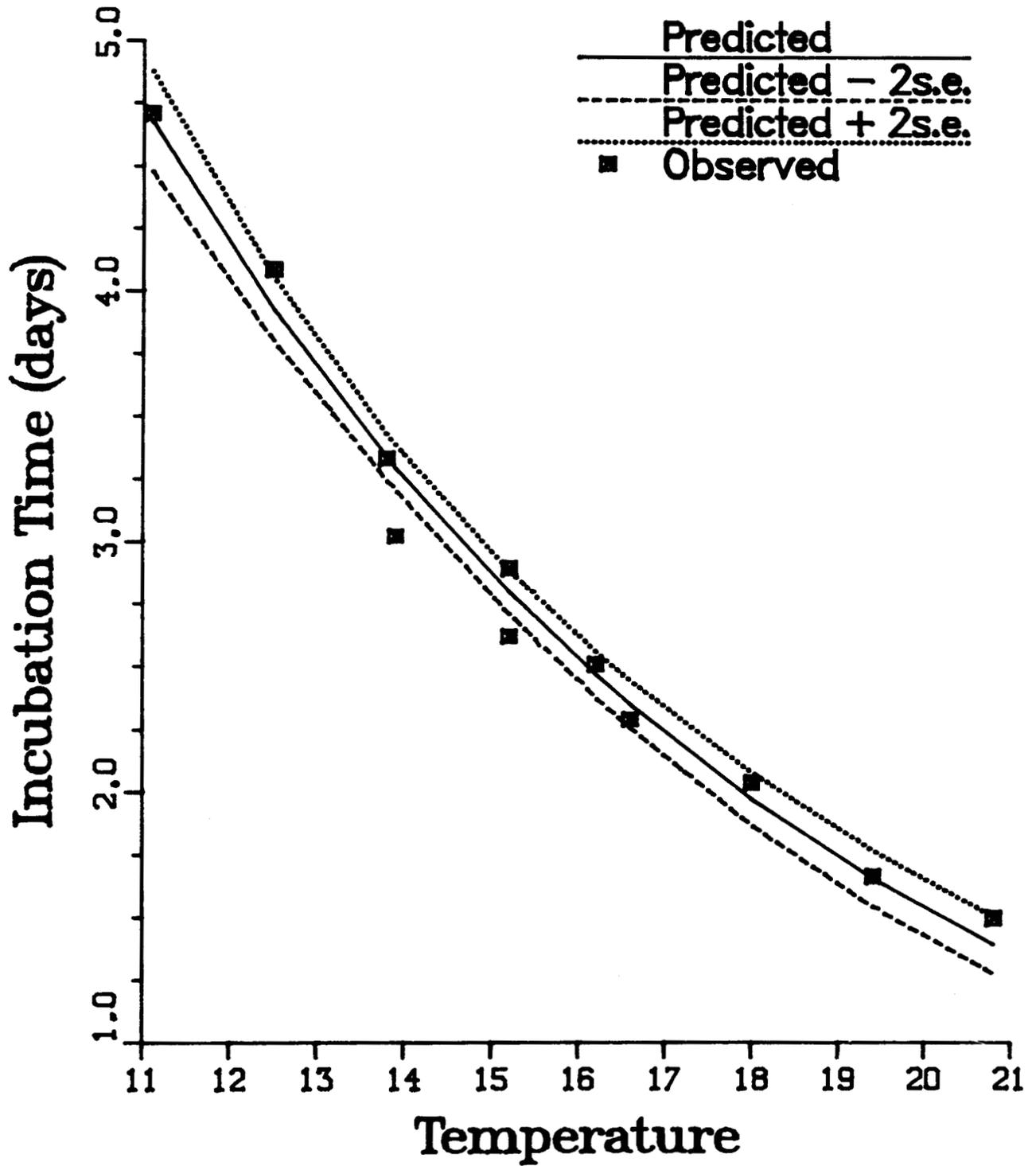


Figure 1. Incubation time (days) of anchovy eggs as a function of temperature (°C).

$$t_I = [18.726e^{-0.125 \text{ temp}}] \quad (1)$$

where t_I is the incubation time in days and temp is the temperature in °C (Fig. 1). Equation (1) can be used to estimate anchovy egg production by adjusting the standing stock of eggs for given average water temperature (Lo In prep.).

3.2 Temperature Dependent Growth of Yolk-Sac Northern Anchovy Larvae

After the onset of feeding, growth in sea caught anchovy larvae appears to be independent of water temperature within season (Methot and Kramer 1979; Methot 1981). Thus I have followed the procedure of Methot and Hewitt (1980) and have assumed that only the egg and yolk-sac stages of anchovy growth are temperature dependent and growth over the rest of the larval period (4.1-27 mm) is temperature independent or food dependent. I combined the new data on growth of yolk-sac northern anchovy with the data of Zweifel and Hunter (MS) and estimated the relation between live length and age at 6 temperatures using the Gompertz growth equation (Laird 1969).

$$L_t = L_\infty \left[\frac{L_k}{L_\infty} \right] e^{-\alpha_{\text{temp}}(t-t_k)} \quad (2)$$

where L_t is the live length (mm) at age t days from fertilization.

L_∞ is the asymptotic length (mm) at the age of first feeding,

L_k is the live length (mm) at age t_k

t_k is either the age at hatching, which is temperature dependent incubation time (t_I) or age 0 (t_0)

and α_{temp} is the growth coefficient which is temperature dependent.

Equation (2) was derived from the assumption of the exponential form of the age-dependent instantaneous growth rate. i.e.,

$$\frac{dL_t}{dt} \frac{1}{L_t} = \lambda e^{-\alpha(t-t_k)}$$

$$L_t = L_k e^{\lambda/\alpha} (e^{-\lambda/\alpha}) e^{-\alpha(t-t_k)} \quad (2.1)$$

where λ is the instantaneous growth rate at age t_k . Substituting L_∞ for $L_k e^{\lambda/\alpha}$ and L_k/L_∞ for $e^{-\lambda/\alpha}$ in eq (2.1) produces eq (2). The values of the coefficients for each of 6 temperatures (see Table 1 for data) are with $t_k = t_I$, the incubation time:

temp°C	L (SE) (mm)	L_I (SE) (mm)	α_{temp} (SE)	n
13.47	4.166 (0.117)	3.11 (0.0347)	0.551 (0.090)	30
14.00	4.21 (0.29)	2.27 (0.33)	0.78 (0.38)	7
15.03	4.328 (0.208)	2.86 (0.078)	0.556 (0.1555)	30
16.23	4.287 (0.467)	2.84 (0.0566)	0.9438 (0.417)	11
17.00	4.546 (0.108)	2.406 (0.104)	1.1543 (0.026)	8
20.00	4.152 (0.040)	2.4 (0.0734)	1.71 (0.027)	10

The coefficient α_{temp} is a function of temperature. An exponential curve was fit to $(\alpha_{temp}, temp)$ giving the final version of the length-age relation for yolk-sac anchovy larvae less than 4.1 mm with $t_k = t_0$ and $L_k = L_0$

$$L_t = L_\infty \left[\frac{L_0}{L_\infty} \right] e^{-Ae^{Btemp}(t-t_0)} \quad (3)$$

where $\alpha_{temp} = Ae^{Btemp}$

Equation (3) was simultaneously fitted to all the data collected at 6 temperatures and resulted in the following estimated parameters (Table 1 and Fig. 2):

Parameters	Estimates	(SE)
L_{∞}	4.25 mm	0.093 mm
L_0	0.32 mm	0.17 mm
A	0.11	0.02
B	0.12	0.006

3.3 Retention Coefficients for Anchovy Eggs and Larvae

This section discusses the results of a series of simultaneous vertical tows of 0.333, 0.150 and 0.075mm mesh conducted in March 1982, the estimation of egg retention by nets of two large mesh sizes compared to smaller meshes, and the estimation of the retention of anchovy larvae as a function of preserved standard length.

The following notations are used through the text for the retention rate calculation:

\bar{Y}_{iL} : catch per unit volume of water filtered ($0.05 \text{ m}^3/\text{m}$ depth) for mesh i and egg and larval length L .

$R_{ijL} = \bar{Y}_{iL}/\bar{Y}_{jL}$: the retention rate of mesh i compared to mesh j .

The sample statistics are denoted as \bar{y}_{iL} and \hat{R} for \bar{Y}_{iL} and R

where

$$L = \begin{cases} 0 & \text{for eggs} \\ \text{larval length (mm) (preserved standard length),} & \end{cases}$$

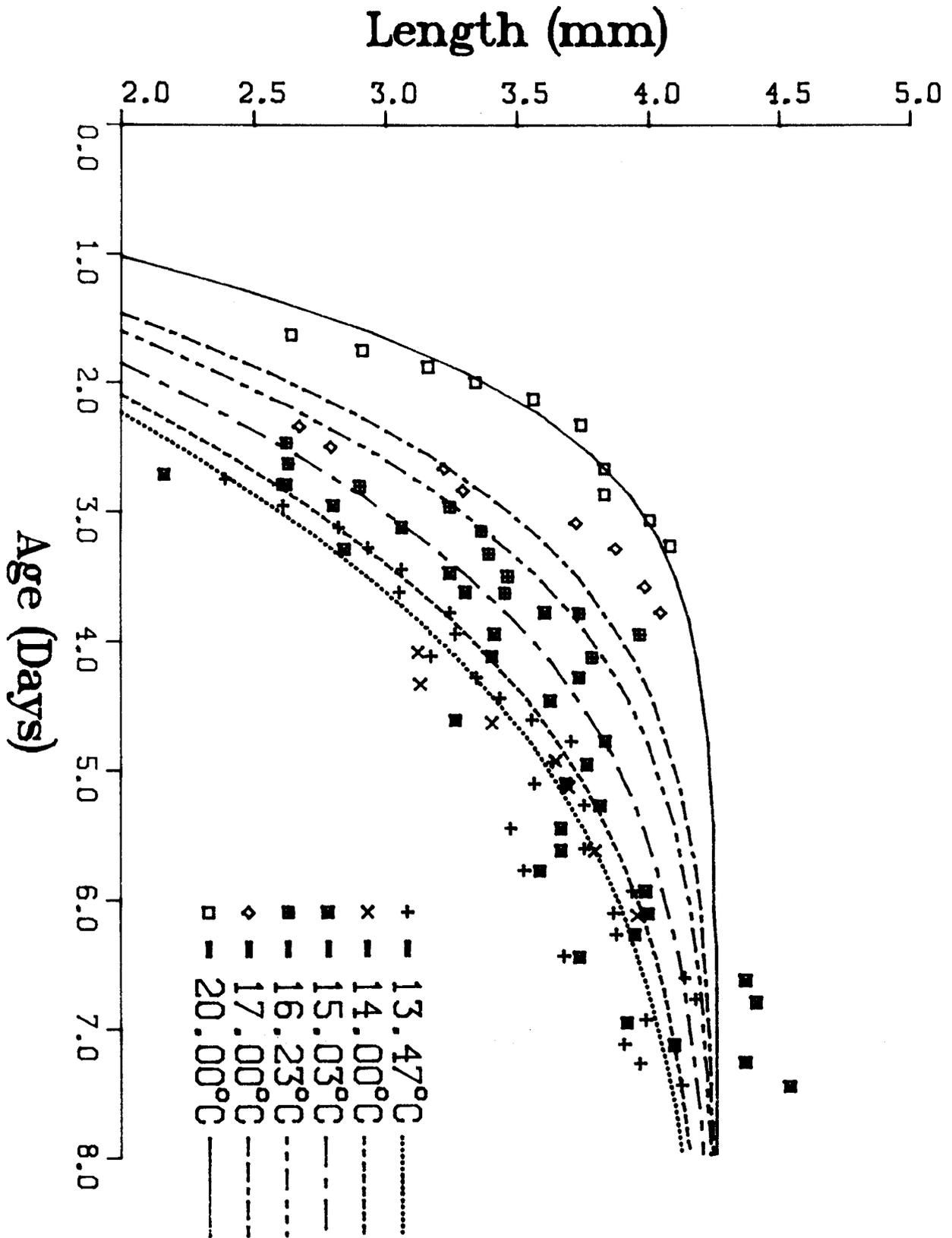


Figure 2. Growth curves of yolk-sac stage of anchovy larvae at various temperatures.

- i and $j = 1$ for 0.075 and 0.150mm Nitex meshes,
2 for 0.333mm Nitex mesh,
3 for 0.505mm Nitex mesh Bongo
4 for 0.505mm Nitex mesh 1 m ring net,
and 5 for 0.55mm silk mesh 1 m ring net.

$RCF_{ijL} = 1/R_{ijL}$: retention correction factor, which was used as a multiplier to correct egg and larva counts.

The basic procedure for computing retention of eggs and larvae of length L from mesh i (compared to mesh 1) for meshes .505 mm and .55 mm ($i \geq 3$) is:

1. $R_{i1L} = R_{i2L} R_{21L}$

with $\text{var}(\hat{R}_{i1L}) = \hat{R}_{i2L}^2 \text{var}(\hat{R}_{21L}) + \hat{R}_{21L}^2 \text{var}(\hat{R}_{i1L})$.

and 2. The retention of larvae (R_{i1L}) was also described as a function of its preserved length (L) for a given mesh size i :

$$R_{i1L} = (1 + e^{A_i + B_i L})^{-1}.$$

The coefficients A_i and B_i are estimated in later sections.

3.3.1 Retention Coefficients of Eggs and Larvae in 0.333mm
Mesh From the Simultaneous Three-Vertical-Net Tows

In order to evaluate whether the three meshes (0.075, 0.150 and 0.333 mm) retain the same amount of eggs and larvae, statistical testing procedures were selected after careful examination of the data. All the egg and larva samples were first sorted and the larvae measured to the nearest 0.5 mm. Thus, each sample contains counts of eggs and larvae of 2.0, 2.5, 3.0, ..., 6.5+ mm, a total of eleven groups. The last length group contains larvae equal or larger than 6.5 mm. I examined the basic statistics (sample mean and standard deviation), the frequency distribution of counts in each group by mesh size (Fig. 3), and the correlation between groups within mesh size.

The basic statistics indicated that within larva length group, the sample standard deviation (s) was proportional to its sample mean (\bar{y}) among meshes, e.g., the ratio, s/\bar{y} , was 1.11 to 1.15 for 2.0 mm, 0.83 to 0.97 for 2.5 mm etc. (Table 4). For each mesh size, the distribution of egg counts was fairly symmetric. The distributions of larva counts between 2.0 and 4.0 mm were skewed, with at most 0.40 of samples containing zero catch, whereas the distributions of larvae ≥ 4.5 mm were highly skewed, with 0.69 to 0.97 of the samples containing zero catch and the maximum count being 8 (Table 2 and Fig. 3). Because all the larvae distributions were skewed, the logarithmic transformation was applied to larva data, $x = \ln(y+1)$, prior to the computation of correlation coefficients. Significant correlation exists between adjacent groups for eggs and larvae ≤ 4.0 mm. The correlation between adjacent groups seems stronger in meshes 0.075 and 0.150 mm than 0.333 mm. As a result, a multivariate analysis of variance (MANOVA) was chosen for eggs and

EGG AND LARVA COUNTS

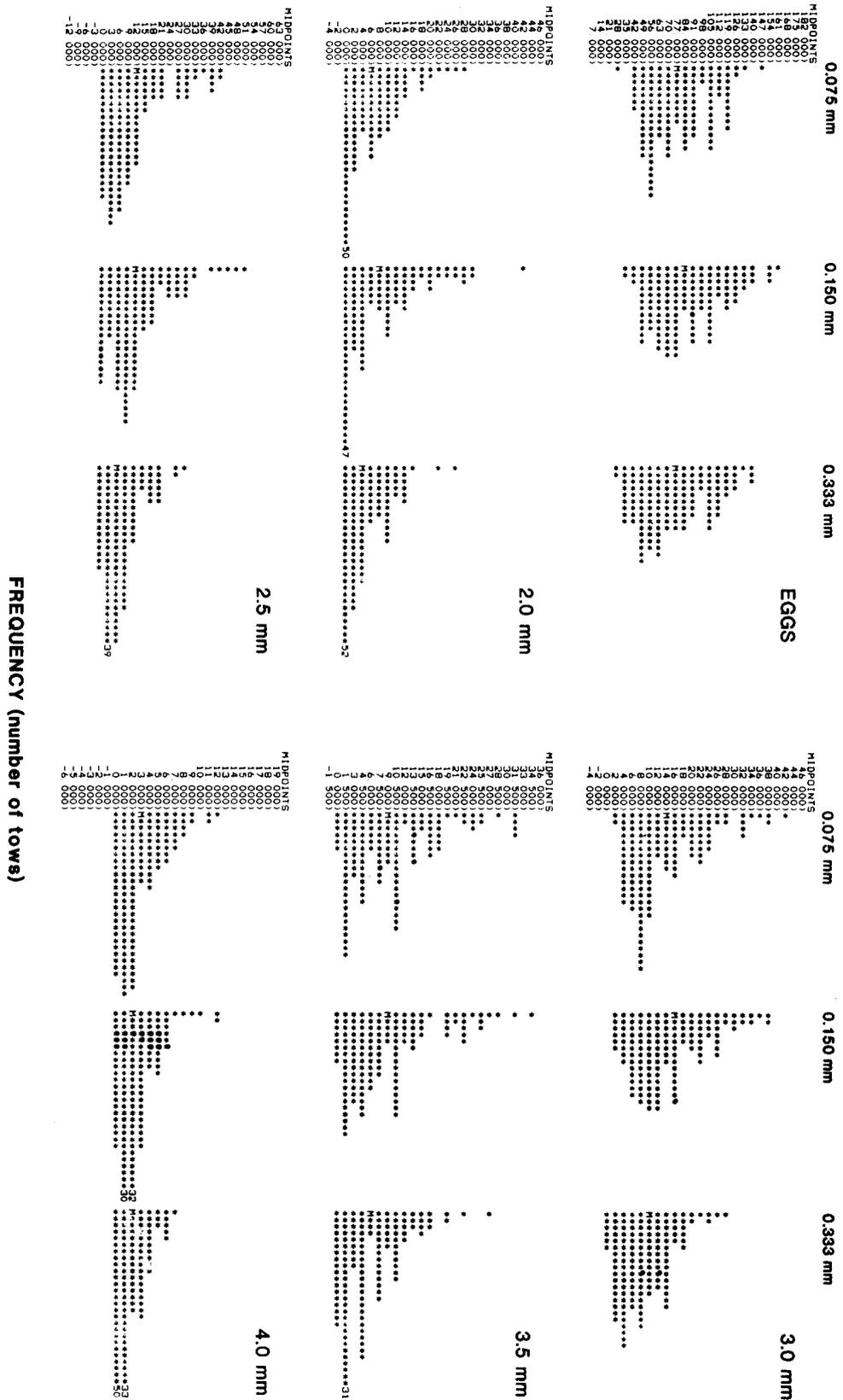


Figure 3A. Frequency distributions of anchovy eggs and larvae by length groups (2-4 mm) for each of three mesh sizes (0.075, 0.150 and 0.333 mm) based upon three-vertical-net experiment, 1982. Sample means are denoted by 'M'. Each dot represents one count. The number at the end is the total frequency for that category.

LOG (egg and larva counts + 1)

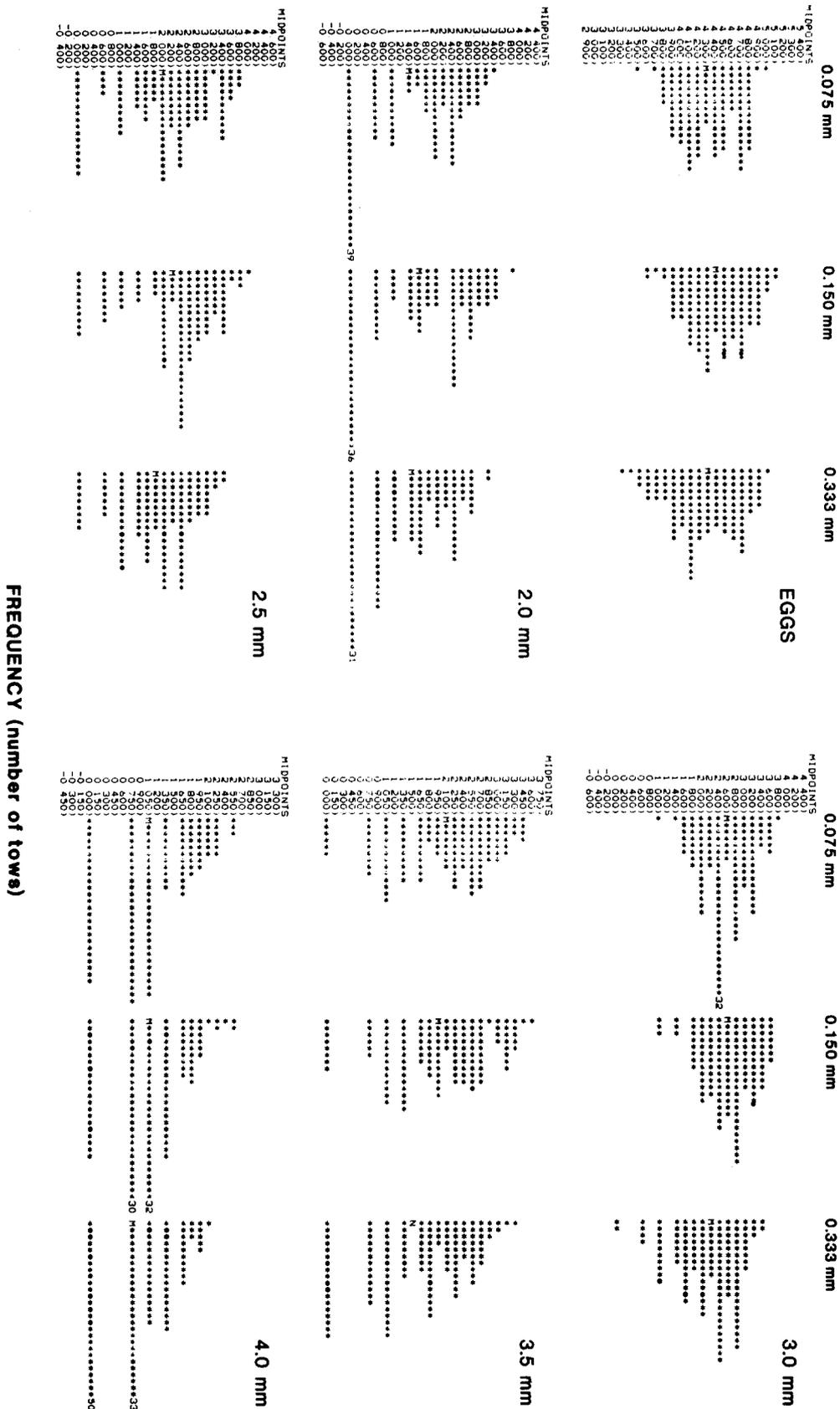


Figure 3B. Frequency distributions of anchovy eggs and larvae by length groups (2-4 mm) for each of three mesh sizes (0.075, 0.150 and 0.333 mm) after log transformation based upon three-vertical-net experiment, 1982. Sample means are denoted by 'M'. Each dot represents one count. The number at the end is the total frequency for that category.

Table 2. Number of samples with zero catch from a total of 140¹ samples for anchovy eggs and larvae by length group, the maximum catch for each of three mesh sizes and the chi-square values for larvae \geq 4.5mm based upon three-vertical-net-experiment, 1982.

	Number of samples with zero catch			Maximum catch			chi-square d.f.=2
	0.075mm	0.150mm	0.333mm	0.75mm	0.150mm	0.333mm	
Eggs	0	0	0				
2.0 mm	42	38	33				
2.5	16	10	9				
3.0	0	0	2				
3.5	7	8	18				
4.0	27	24	52				
4.5	103	97	97	8	3	5	0.83
5.0	111	107	103	5	3	5	1.27
5.5	131	133	136	2	1	1	2.0
6.0	132	130	133	2	1	1	0.6
6.5+	117	102	118	2	3	2	7.24*
							11.94 (d.f.=10)

¹Two samples were discarded because they were spoiled.

*Significant at 5% level.

larvae < 4.5 mm and a chi-square test on the proportion of samples with zero catch among three meshes was chosen for larvae ≥ 4.5 mm to detect the retention difference of three meshes.

For eggs and larvae ≤ 4.0 mm, a two-way (factor) MANOVA was conducted to test whether the mesh sizes of 0.075, 0.150 and 0.333 mm and the position of the three nets (starboard, center and port) had any significant effect on the catches. Because the sample standard deviation of larva counts was proportional to its sample mean within the length group, and the frequency distributions were skewed, a logarithmic transformation $x = \ln(y+1)$ was applied to larva data to equalize the variances and reduce the skewness of the data. The constant "1" was added to the original data for zero observations (Scheffé 1958; Snedecor and Cochran 1969; Li 1965; Aitchison and Brown 1973). Comparison of the variances of transformed data showed that except for larvae of 2.0 mm, the variances within length groups among meshes were not significantly different. Moreover, the distributions of the transformed data were more symmetric than those of the original data (Fig. 3). The results from the two-way MANOVA indicated the net position made no significant difference in catch ($p=0.83$), while mesh size made a significant difference ($p < 0.001$), as did the interaction of mesh size and net position ($p < 0.001$).

Because the interaction of mesh size and net position was significant, a separate MANOVA was run for each of the three positions. It was found that the overall mean catches of eggs and larvae among meshes were significantly different at each position. The univariate tests show that the mean catch was significantly different for eggs and larvae < 4.5 mm with the exception of the mean catch of larvae of 2.0 mm and 2.5 mm on the starboard side which was not significantly different among meshes. The cause of the interaction is

unknown.

Since the position of the net did not affect the catch, a one-way MANOVA was used to evaluate the difference among meshes. The mean catch of anchovy eggs and larvae taken in small mesh nets (0.075 and 0.150mm) was compared to that taken in 0.333mm mesh net, after the mean catch was compared between small meshes (0.075 and 0.150mm). The mean catch of eggs and larvae in the 0.075mm net was significantly different from that in the 0.150mm mesh net ($p=0.04$). However, the significant difference was mainly due to egg counts (catch in 0.150 mm was slightly higher than that in 0.075 mm mesh ($p=0.03$)) whereas all the larvae catches seemed to be the same between these two meshes. Therefore, the catches from these two small meshes were combined to be compared with that of 0.333 mm mesh. The mean catch in the 0.333 mm mesh net was different from both of the small mesh nets (0.075 or 0.150mm) ($p < 0.001$) (Table 3). Hence, eggs and larval anchovy < 4.5 mm appear to be lost by 0.333 mm mesh net presumably by extrusion through the meshes.

To compare the retention of larvae ≥ 4.5 mm among 3 mesh sizes, a 2x3 contingency table was first constructed for each of the 5 groups where the first attribute was mesh size (0.075, 0.150 and 0.333 mm) and the second was catch (zero and non zero). All but the last length group had insignificant chi-square values. Because little correlation exists among the groups, the sum of the 5 chi-square values was used to test the overall retention difference among the mesh sizes. The chi-square value (11.94) was insignificant at 5% level (Table 2). Thus there seems to be no extrusion of larvae ≥ 4.5 mm from 0.333 mm mesh net.

Table 3. One-way analysis of variance of retention of anchovy eggs and larvae (< 4.0 mm, log transformation) in three meshes -- comparison between catches in 0.075 mm and 0.150 mm meshes, and comparison between catches in 0.333 mm and small meshes.

Effect	Variate	Sum of squares	d.f.	Mean squares	F (d.f.)	P
.075 mm vs. .150 mm	All ¹	TSQ = 13.67			2.25 (6,397)	0.04
Univariate Tests					(1,402)	
	eggs	3793.13	1	3793.13	5.01	0.03
	2.0 mm	1.68	1	1.68	1.44	0.23
	2.5	2.69	1	2.69	2.96	0.09
	3.0	0.25	1	0.25	0.68	0.41
	3.5	0.33	1	0.33	0.44	0.51
	4.0	0.11	1	0.11	0.25	0.62
.075 mm & .150 mm vs. .333 mm	All ¹	TSQ = 114.14			18.79 (6,397)	0.000 ²
Univariate tests					(1,402)	
	eggs	4419.34	1	4419.34	5.84	0.02
	2.0 mm	2.93	1	2.93	2.52	0.11
	2.5	7.19	1	7.19	7.93	0.005
	3.0	18.89	1	18.89	51.35	0.000
	3.5	15.79	1	15.79	20.95	0.000
	4.0	11.71	1	15.79	20.95	0.000
Error	eggs	304141.94	402	756.57		
	2.0	467.95	402	1.16		
	2.5	364.70	402	0.91		
	3.0	147.90	402	0.37		
	3.5	303.01	402	0.75		
	4.0	177.77	402	0.44		

¹Multivariate analysis. TSQ is Hotelling T² statistic

²p<0.0001

Anchovy eggs and larvae taken in the two small mesh nets (0.075 and 0.150mm) were combined to produce the mean catch for eggs and larvae by length classes. (No log transformation was used for computing catch ratios.) These data were used as the basis for estimating the retention of eggs and larvae in large mesh nets in the latter sections. The retention coefficients of eggs and larvae by 0.5 mm and 1 mm length classes in 0.333 mm Nitex mesh are in Table 4. Relative to small meshes, the 0.333 mesh retains 0.91 of anchovy eggs and 0.63 of anchovy larvae < 4.5 mm length.

3.3.2 Retention Coefficients for Various Mesh Nets and Life Stages of Northern Anchovy

The retention of anchovy eggs and larvae was estimated for two mesh sizes (0.55mm silk and 0.505mm Nitex) on two frames (1 m ring net and Bongo net). To be consistent with the sampling scheme of the current egg production method (Stauffer and Picquelle 1980), the retention of eggs was reestimated for the first 4 months and CalCOFI central regions (regions 4, 7, 8, 9, and 11) (Huppert et. al. 1980). All egg catches in ring nets and Bongo nets were standardized to the sampling unit used for CalVET net catches ($0.05\text{m}^3/\text{m}$ depth).

Because no larval catch data were available for the 0.505mm Nitex 1 m ring net, the larvae taken in Bongo and CalVET net tows were combined with the three-vertical-net experiment data to arrive at an estimate of larval retention in 0.505 mm Nitex mesh net.

Table 4. Sample mean catch of anchovy eggs and larvae in small meshes, (\bar{y}_{1L}) and 0.333mm (\bar{y}_{2L}), and retention coefficients (R_{21L}) for eggs and larvae by 0.5 mm length grouping and alternative 1 mm length grouping based upon three-vertical net experiment 1982 (n=140). Standard errors are in parentheses.

(1)	(2)	(3)	(4) ¹	(5)	(6) ²	
	Mean catch \bar{y} (SE)	Mean catch \bar{y} (SE)	Mean catch in small meshes \bar{y}_{1L}	Mean catch .0333mm \bar{y}_{2L} (SE)	R_{21L} (SE)	
	.075mm	.150mm				
eggs	78.57 (2.10)	86.12 (2.40)	82.34	75.22 (2.40)	0.91 (0.01)	
2.0mm	5.66 (0.55)	7.54 (0.73)	6.6	4.49 (0.42)	0.68 (0.04)	} 0.63
2.5	10.81 (0.89)	12.33 (0.89)	11.57	7.42 (0.52)	0.64 (0.03)	
3.0	13.86 (0.72)	14.85 (0.72)	14.36	9.17 (0.50)	0.64 (0.02)	
3.5	9.34 (0.64)	8.61 (0.62)	8.97	5.71 (0.44)	0.64 (0.03)	
4.0	2.87 (0.23)	2.50 (0.20)	2.69	1.55 (0.14)	0.57 (0.06)	
4.5	0.46 (0.09)	0.43 (0.06)	0.44	0.42 (0.07)	0.95 (0.16)	
5.0	0.26 (0.05)	0.30 (0.05)	0.28	0.40 (0.07)	1.43 (0.27)	
5.5	0.08 (0.03)	0.05 (0.02)	0.06	0.03 (0.01)	0.44 (0.26)	
6.0	0.06 (0.02)	0.07 (0.02)	0.07	0.05 (0.02)	0.74 (0.31)	
6.5+	0.18 (0.04)	0.32 (0.05)	0.25	0.2 (0.04)	0.80 (0.18)	
2.5 ³ mm			32.53 ³	21.09	0.65 (0.02)	
3.75			11.66	7.26	0.62 (0.03)	
4.75			0.73	0.82	1.13 (0.14)	
5.75			0.13	0.08	0.60 (0.19)	
6.5+			0.25	0.20	0.80 (0.18)	
2.25 ⁴ mm			18.17 ⁴	11.91	0.66 (0.03)	
3.25			23.32	14.89	0.64 (0.02)	
4.25			3.13	1.97	0.63 (0.05)	
5.25			0.35	0.43	1.24 (0.22)	
6.0			0.07	0.05	0.74 (0.31)	
6.5+			0.25	0.20	0.80 (0.18)	

¹(4)=[(2)+(3)]/2

²(6)=(5)/(4)

³2.5 mm = 2.0 mm + 2.5 mm + 3.0 mm, 3.75 mm = 3.5 mm + 4.0 mm etc.

⁴2.25 mm = 2.0 mm + 2.5 mm, 3.25 mm = 3.0 mm + 3.5 mm etc.

3.3.2.1 Retention Coefficient for Eggs in 0.55mm Silk Mesh

1 m Ring Nets (\hat{R}_{510}) and 0.505mm Nitex Mesh 1 m Ring Nets (\hat{R}_{410})

A one-meter (1 m) ring net of 0.55mm silk mesh was the standard CalCOFI plankton net from 1951-1968. In 1969, the silk mesh was replaced by Nitex. This 0.505mm Nitex mesh 1 m ring net was used until 1978 when the Bongo frame was introduced for ichthyoplankton surveys (Smith and Richardson 1977). Smith (MS) estimated the retention of anchovy eggs in 0.55 and 0.505 mm mesh 1 m ring nets by comparing their catches to that of the 0.5 m diameter 0.333 mm mesh ring net. A seasonal difference in egg retention seems to exist probably because of seasonal changes in egg size. The retention of eggs in 0.55 and 0.505 mm mesh nets relative to that taken by the 0.333 mm mesh net (Smith MS) are shown below:

	Winter	Spring	Summer	Fall	Mean
0.55mm \hat{R}_{520}	0.29	0.27	0.08	0.13	0.24
(1966) \hat{RCF}_{520}	3.44	3.70	13.07	7.45	4.25
0.505mm \hat{R}_{420}	0.40	0.28	0.09	0.26	0.33
(1969) \hat{RCF}_{420}	2.47	3.53	11.72	3.89	3.00

Analysis of the data of Jan-April from the 1966-68 mesh experiment (75 paired tows with positive catches from either net or both nets (0.55 and 0.333mm)) and the 1982 three-vertical-net experiment indicated that the retention of anchovy eggs in 0.55mm silk mesh compared to the 0.333mm Nitex mesh and small mesh (0.075 or 0.150mm Nitex mesh) was 0.3 (\hat{R}_{520}) and 0.27 ($\hat{R}_{510} = 0.30 \times 0.91$) respectively. In order to correct the egg counts in 0.55mm silk mesh net, the egg counts must be multiplied by the retention correction factor 3.62 (SE = 0.65) (Table 5).

Table 5. Sample mean catch of eggs in large meshes (\bar{y}_{i0}) and 0.333mm (\bar{y}_{20}), retention coefficients compared to both 0.333mm (\hat{R}_{i20}) and small meshes (\hat{R}_{i11}) and retention correction factor (\hat{RCF}^1) in January-April. Standard errors are in parentheses.

Mesh Size (i)	Year	Mean Catch		n	\hat{R}_{i20}	\hat{R}_{210}	\hat{R}_{i10}	\hat{RCF}^1 (SE)
		\bar{y}_{i0} (SE)	\bar{y}_{20} (SE)					
.55 mm silk 1 m ring net (5)	1966-68	15.65 (1.93)	51.53 (8.07)	75	.30	0.91	0.27	3.62 (0.65)
.505 mm Nitex 1 m ring net (4)	1969	18.63 (3.34)	51.60 (9.41)	82	.36	.91	.33	3.04 (0.49)
.505 mm Nitex Bongo net (3)		2.69 (0.38)	31.52 (5.32)	116	.09	.91	.08	12.76 (2.56)
	1980	3.17 (0.87)	32.29 (9.14)	35	.10	.91	.09	11.19
	1981	2.48 (0.39)	31.19 (6.56)	81	.08	.91	.07	13.82

\hat{RCF}^1 may not equal to $1/\hat{R}_{i10}$ due to rounding errors.

The analysis of the data of the first four months from the 1969 mesh experiment (82 paired tows with positive catches from either net or both nets (0.505mm and 0.333mm Nitex)) and the 1982 three-vertical-net experiment indicated that the retention of eggs in nets of 0.505mm Nitex mesh compared to 0.333mm and small meshes was 0.36 (\hat{R}_{420}) and 0.33 ($\hat{R}_{410} = 0.36 \times 0.91$) respectively. In order to correct the egg counts in 0.505 Nitex mesh net, the egg counts must be multiplied by the retention correction factor 3.04 (SE = 0.49) (Table 5).

3.3.2.2 Retention Coefficients for Eggs in 0.505mm Nitex Mesh Bongo Net (\hat{R}_{310})

The 1 m ring frame was replaced by the Bongo frame as the standard CalCOFI gear in 1978, because it reduced net avoidance by large larvae (Smith and Richardson 1977). The retention of eggs by the Bongo and ring frames with the same mesh size were believed to be equivalent but this appears not to be the case.

To estimate the retention of eggs and larvae in the 0.505mm Nitex mesh Bongo net, data from Bongo and CalVET net tows consisting of 116 stations with positive catches from either net or both nets were used in the analysis. All Bongo catches were standardized to the CalVET 0.05m³/m depth sample unit (Table 5). The retention of eggs in 0.505mm mesh compared to 0.333mm (\hat{R}_{320}) was 0.09. The retention of eggs in the Bongo net compared to the small mesh (\hat{R}_{310}) was $0.09 \times 0.91 = 0.08$ (Table 5). In order to correct the egg catch in the 0.505mm Nitex mesh Bongo net, one has to multiply the catch by the retention correction factor 12.76 (SE = 2.56). In other words, the small mesh (0.075 or 0.150mm mesh) retains almost 13 times more eggs than the Bongo net

and 3 times more than the 0.505mm Nitex mesh 1 m ring net. It appears that the Bongo gear is about 1/4 as effective as the 1 m ring with the same net material. Because data were collected in different years, one may speculate that the retention difference between Bongo and 1 m ring frame of 0.505mm mesh could be due to different egg sizes.

3.3.2.3 Retention Coefficients for Larvae in 0.55mm

Silk Mesh 1 m Ring Nets (\hat{R}_{51L})

As mentioned in an earlier section, prior to 1969, the standard CalCOFI net was the 0.55mm silk mesh 1 m ring net. From larval data collected in the 1966-1968 mesh experiment, 26 tows were selected by Lenarz (1972) for his analysis of retention. Due to loss of the raw data sheets, only the data from 19 tows are available for reexamination of the retention of anchovy larvae by length class (Table 6). The retention of larvae in 0.55mm mesh net was calculated according to the formula:

$$\hat{R}_{51L} = \hat{R}_{52L} \hat{R}_{21L} \quad (4)$$

where \hat{R}_{21L} is assumed to be 1 for $L > 4.50\text{mm}$ because no significant difference was found between catches of 0.333mm mesh (\bar{y}_{2L}) and that of the small meshes (\bar{y}_{1L}) (Table 4). The seeming decrease of retention of larvae larger than 4.5mm in the three-vertical-net experiment could be caused by avoidance of larvae or may be due to random error. The retention of larvae compared to 0.333 mesh net (\hat{R}_{52L}) is assumed to be 1 for $L \geq 6.5$ mm.

The logistic equation that describes the relation between retention of

Table 6. Sample mean catch of larvae in 0.55mm silk mesh 1 m ring net (\bar{y}_{5L}) and 0.333mm Nitex mesh 0.5m ring net (\bar{y}_{2L}), and their retention coefficients compared to both 0.333mm mesh (\hat{R}_{52L}) and small meshes (\hat{R}_{51L} and \hat{R}_{21L}) based on data from January-April 1966-1968 mesh experiment, and 1982 three-vertical-net experiment, 1982.

(1) Preserved length (L) (mm)	(2) Mean catch in .55 mm (\bar{y}_{5L})	(3) Mean catch in .333mm (\bar{y}_{2L})	(4) \hat{R}_{52L}	(5) \hat{R}_{21L}	(6) ² \hat{R}_{51L}	(7) ³ R^*_{51L}
2.5	0.45	1.50	0.30	0.65	.19	.14
3.75	0.42	0.72	0.58	0.62	.36	.39
4.75	0.45	0.59	0.77	(1.13) ¹	.77	.66
5.75	0.34	0.39	0.87	(.60)	.87	.86
6.5+	0.80	0.80	0.99	(.80)	.99	1.00
2.25	0.13	0.67	.20	.66	.13	.11
3.25	0.48	1.17	.41	.64	.26	.28
4.25	0.45	0.58	.77	.63	.48	.53
5.25	0.41	0.53	.77	(1.23)	.77	.77
6.00	0.19	0.24	.79	(.73)	.79	.88
6.5+	0.80	0.80	.99	(.80)	.97	1.00

n = 19

¹() was substituted by 1 in computing (6).

²(6) = (4) x (5)

³(7) is computed from equation (5).

larvae (\hat{R}_{51L}) and preserved length (L), (Table 6 and Fig. 4) is:

$$\hat{R}_{51L} = \begin{cases} [1 + e^{4.53 - 1.098L}]^{-1} & \text{for } L < 6.5\text{mm} \\ 1 & \text{for } L \geq 6.5\text{mm} \end{cases} \quad (5)$$

3.3.2.4 Retention Coefficients for Larvae in 0.505mm Nitex Mesh Bongo Nets (\hat{R}_{31L})

The Bongo net has been used to collect larvae during CalCOFI ichthyoplanktonic surveys since 1978. I used the 1979-1981 Bongo-CalVET data to estimate the retention of anchovy larvae in the 0.505mm Nitex mesh net. A total of 383 stations had samples from both Bongo and CalVET nets (147 from 1979, 96 from 1980, and 140 from 1981). A weighted negative binomial was used to estimate average catch for each larval length class (Zweifel and Smith 1981). The Bongo net catch was further standardized to the 0.05m³/m depth sampling unit (Table 7). The catch ratio of the 0.505mm mesh Bongo net to the small mesh net (\hat{R}_{31L}) was calculated according to the formula: $\hat{R}_{31L} = \hat{R}_{32L} \times \hat{R}_{21L}$. The retention coefficient (\hat{R}_{31L}) and the corresponding preserved length (L) were fitted to a logistic model which estimates the retention of larvae of given preserved length (L) (Table 7 and Fig. 4):

$$\hat{R}_{31L} = \begin{cases} [1 + e^{3.965 - 0.9357L}]^{-1} & \text{for } L < 6.5\text{mm} \\ 1 & \text{for } L \geq 6.5\text{mm} \end{cases} \quad (6)$$

4. CONCLUSION AND DISCUSSION

Both new temperature-dependent incubation time function (eq 1) and growth function for yolk-sac anchovy larvae (eq 3) are improvements over the past

Table 7. Sample mean catch of larvae in .505mm Nitex mesh Bongo net (\bar{y}_{3L}) and 0.333mm Nitex mesh CalVET net (\bar{y}_{2L}) and their retention coefficients compared to both 0.333mm mesh (\hat{R}_{32L}) and small meshes (\hat{R}_{31L} and \hat{R}_{21L}) based upon CalCOFI cruise data in January-April 1979-1981, and three-vertical-net experiment, 1982.

(1) Preserved length (mm)	(2) Mean catch in .505mm Bongo (\bar{y}_{3L})	(3) Mean catch in 0.333mm (\bar{y}_{2L})	(4) \hat{R}_{32L}	(5) \hat{R}_{21L}	(6) \hat{R}_{31L}	(7) R^*_{31L}
1979 (n=147)						
2.50	1.02	4.81	0.21	0.65	0.14	0.16
3.75	0.50	3.86	0.13	0.62	0.08	0.39
4.75	0.40	1.02	0.39	1.13	0.44	0.62
5.75	0.32	0.78	0.41	(.60)	0.41	0.80
1980 (n=96)						
2.25	0.36	1.36	0.26	0.66	0.17	0.13
3.25	1.35	3.47	0.38	0.64	0.25	0.28
4.25	0.87	0.64	1.36	0.63	0.86	0.50
5.25	0.89	0.34	2.62	(1.23)	(2.62)	0.72
6.25+	0.68	0.23	--	--	--	--
1981 (n=140)						
2.25	0.89	1.93	0.46	0.66	.30	0.13
3.25	2.24	5.59	0.43	0.64	0.27	0.28
4.25	1.30	2.14	0.61	0.63	0.38	0.50
5.25	1.03	0.71	1.45	(1.23)	(1.45)	0.72
6.25+	0.82	--	--	--	--	--

¹(6) = (4) x (5)

²(7) is computed from equation (6)

³() was substituted for computation

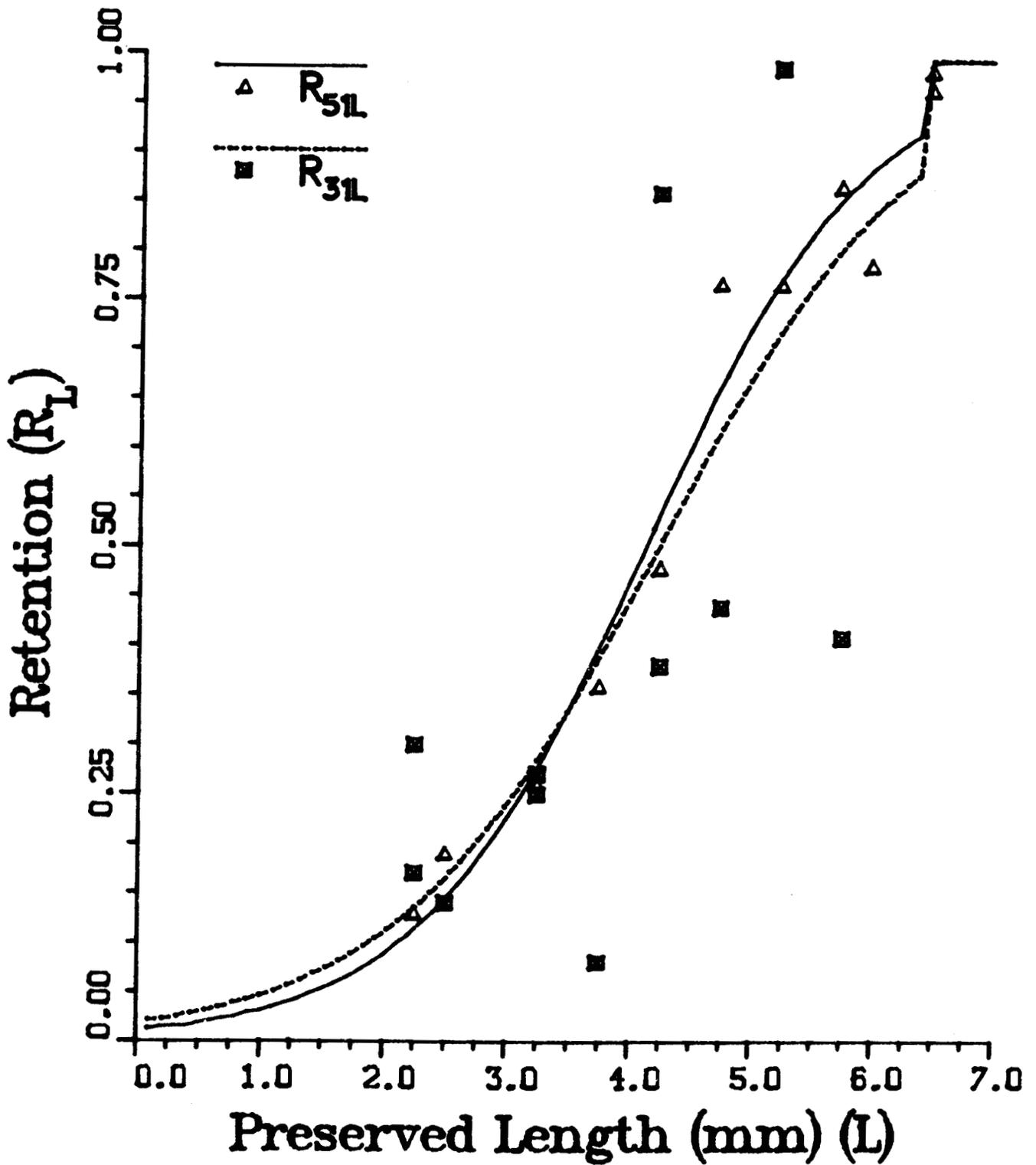


Figure 4. Retention of anchovy larvae in 0.55 mm silk mesh 1 m ring net (R_{51L}) and in 0.505 mm Nitex mesh Bongo net (R_{31L}) compared to small meshes. Solid line is from equation (5) and dotted line is from equation (6).

models (Zweifel and Lasker 1976; Zweifel and Hunter MS; and Methot and Hewitt 1980) because they have much simpler forms and are based upon a larger data set, covering a wider temperature range.

The analysis of catch data from the three-vertical-net experiment (simultaneous tows of 0.075, 0.150, and 0.333mm nets) indicated that eggs and larvae were extruded from 0.333mm mesh which was previously believed to be extrusion free. The retention of anchovy eggs and larvae in 0.333mm mesh are 0.91 for eggs, 0.63 for larvae \leq 4.0mm, 0.95 for larvae = 4.5mm, and 1.0 for larvae $>$ 4.5mm. The retention rate of eggs and larvae in 0.333mm compared to small meshes (average catches of 0.075 and 0.150mm mesh) together with that of large meshes (0.55 and 0.505mm) compared to 0.333mm gives a much less biased estimate of retention of eggs and larvae than those previously reported (Smith MS; Lenarz 1972; Zweifel and Smith 1981; Hewitt 1982). There seems to be little difference in retention of larvae between 0.55 mm silk mesh and 0.505 mm Nitex mesh.

The final estimates of anchovy egg retention in 0.55 mm silk, 0.505 mm 1 m Nitex ring nets and 0.505mm Bongo nets are 0.27, 0.33, and 0.08, respectively. A large difference exists in retention between the two 0.505mm mesh nets but the reason for this difference is unknown; this effect should definitely be studied in future field experiments. Correction for larval extrusion through the 0.333mm mesh net alters the estimates of larval abundance, and consequently changes the shape of the larval mortality curve from one with a constant apparent instantaneous mortality rate to one with an age dependent instantaneous mortality rate (Lo In Prep.).

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