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THE MORTALITY AND DISPERSAL OF SARDINE EGGS AND LARVAE

By

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INTRODUCTION

The precision and cost of biological sampling in the ocean are jointly determined by the degree to which the organisms to be sampled are heterogeneously distributed temporally, vertically, and horizontally. Oceanic transport and diffusion, behavior, and mortality continuously change the scale and intensity of patchiness: these changes complicate statistical analysis of population size. We are now attempting to describe each of these spatial and temporal characteristics by simple models of mortality and dispersal. It is the purpose of this paper to describe crude estimates of the rates of mortality and dispersal of sardine eggs and larvae.

Ahlstrom (1954b, p. 101–102) held that the mortality rate of Pacific sardines during the embryonic period was negligible. Sample counts from 1940, 1941, 1950, and 1951 indicated that the mortality rate was of the order of 0·5 % per day. One large tow was censored from this estimate: if it were included, the summed egg counts would have indicated that 2-day-old eggs were more abundant than 1-day-old eggs by more than 10 %. Clearly, this illustrates that conclusions drawn from as many as 50000 eggs taken in 4 years may still be subject to large sampling variability due to patchiness. About 10 % of the eggs in the series were from a single haul.

Taft (1960) concluded that sample counts of sardine eggs "were consistent with the hypothesis that the egg population is distributed according to the negative binomial contagious distribution . . . a logarithmic distribution of patch means and a Poisson distribution of eggs within a patch".

The primary technical difficulty with the negative binomial distribution as applied to pelagic eggs is that the number of samples with no eggs has little meaning since "zero samples" can arise from many sources. Zero samples may be drawn by chance from within a patch (with probabilities related to the sampler width), from between patches and, most importantly, from entirely outside the spawning area. The negative binomial distribution admits only the first of these possibilities. Lloyd (1967) discusses the importance of this to the analysis. In the fluid environment of the ocean, dispersal will *increase* the inter-egg distance within the patch and simultaneously *decrease* the distance between adjacent patches: mortality *increases* the distances between eggs within the patch. Eggs of several days' spawning may co-occur in a sample. All that can be said with certainty about the number of samples with no sardine eggs is that the samples were taken where the horizontal space between some adjacent eggs exceeded the width of the plankton net.

The effective egg survey must result in a useful estimate of the total number of eggs present. This is derived in part from an estimate of the number of eggs per unit area, an estimate of the total area covered by spawning, and an estimate of the duration of the spawning period. The number of eggs per unit area will be an underestimate if the major centers of spawning are missed: the total area covered by spawning will be underestimated unless the possibility of zero samples within spawning areas is evaluated. This estimate is clearly related to the size of the sampler and the length of tow.

DEFINITION OF TERMS

Dispersal—the scattering of objects from a small area over a larger area; centrifugal movements (Lloyd, 1967). Not to be confused "with dispersion which in ecological contexts, has the same meaning as pattern" (Pielou, 1969, p. 125): one must be particularly cautious since "over-dispersed" means "patchy" and is defined as a variance: mean ratio significantly greater than one (Skellam, 1952).

Diffusion—the spread of a substance through a medium. The rate of oceanic diffusion is one means used to explain the dispersal of pelagic eggs in this paper. Since I anticipate other modes of dispersal, I choose to use "dispersal" as the effect and "diffusion" as one of the causes.

Transport—the movement of a mass of water and all that it contains from one geographic region to another. Although transport is not a topic of this paper, it is undoubtedly important to the study of egg mortality and distributions (Hirano and Fujimoto, 1969). I define it here merely to discriminate between transport and dispersal. It is conceivable that a group of objects

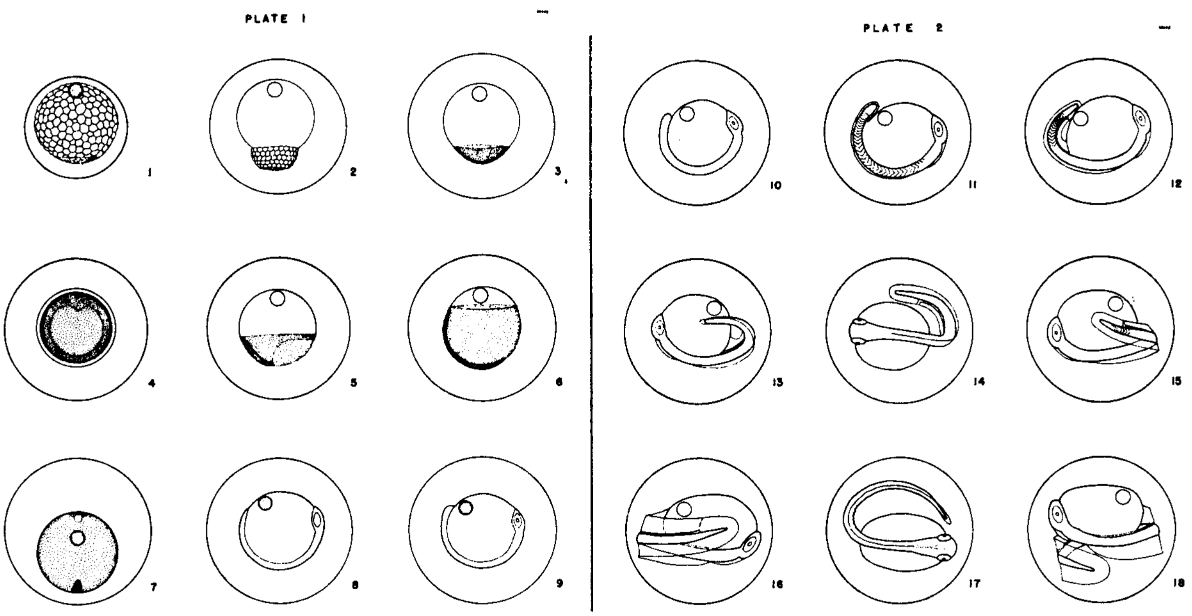

Figure 181. Sardine eggs: (1) stage I; (2) stage II, fairly early; (3) stage II, late; (4) stage III, intermediate, dorsal view; (5) stage IV, beginning; (6) stage V, beginning; (7) stage V, immediately before closing of blastopore, ventral view; (8) stage VI, early; (9) stage VI, late; (10) stage VII, early; (11) stage VII, late; (12) stage VIII, late; (13) stage IX, late; (14) stage X, early, dorsal view; (15) stage X, early; (16) stage XI, early; (17) stage XI, intermediate, dorsal view; (18) stage XI, late. From Ahlstrom 1943.

could retain the same microdistribution while being transported. By dispersal I mean changes in the microdistribution without reference to changes of geographic distribution caused by transport. By microdistribution, I mean the scale of size important to numbers per unit sample; by geographic distribution, I mean the scale of size important to the total distribution of the species and its eggs.

ORIGIN OF DATA

The sardine egg data reported here represents all sardine eggs collected in standard hauls on CalCOFI cruises from January 1951 to December 1959. Approximately 90 cruises were conducted during this period and 14000 standard plankton samples were taken. Of these, 1349 samples yielded about 200000 sardine eggs which have been sorted, staged, assigned a day of spawning and standardized to a unit surface area to correct small differences in towing procedure. Refer to Ahlstrom (1966) for a description of the annual surveys, cruises, and towing techniques.

METHOD OF DETERMINING THE AGE OF SARDINE EGGS

Following the sorting of all sardine eggs from the plankton sample, each egg was characterized as to state of embryonic development and assigned a stage number according to the description and drawings of Ahlstrom (1943). (Plates I and II of that publication are reproduced here as Figure 181 due to the difficulty some may have in obtaining the original).

The original data on the influence of temperature on the rate of development of sardine eggs to four selected stages is reproduced here as Figure 182 (Ahlstrom, 1943). Virtually all eggs are spawned between 2000 and 0400 hours thus the stage of development and the 10 meter temperature (SIO, 1962–1965) collected with each plankton tow may be used to establish the day of spawning. Of the egg counts reported here, those collected between 1951 and 1957 have been published (Ahlstrom, 1953, 1954a, 1958, 1959a; Ahlstrom and Kramer, 1955, 1956, 1957) while those for 1958 and 1959 are not yet published. Eggs collected subsequent to 1959 have been staged but not aged. In Figure 183, I have redrawn the temperature development curves to illustrate the method by which the day of spawning and the hour of sampling can be used to deduce the age of the egg to within about 6 hours. For the purpose of this paper, the time 0 to 2000 hours and the category "Aa" is the 6-hour interval immediately following 2000. Each successive 6 hours is labelled "b", "c", and "d" while the succeeding days are labelled "B", "C", and "D". The numbers used are the total numbers of staged eggs:

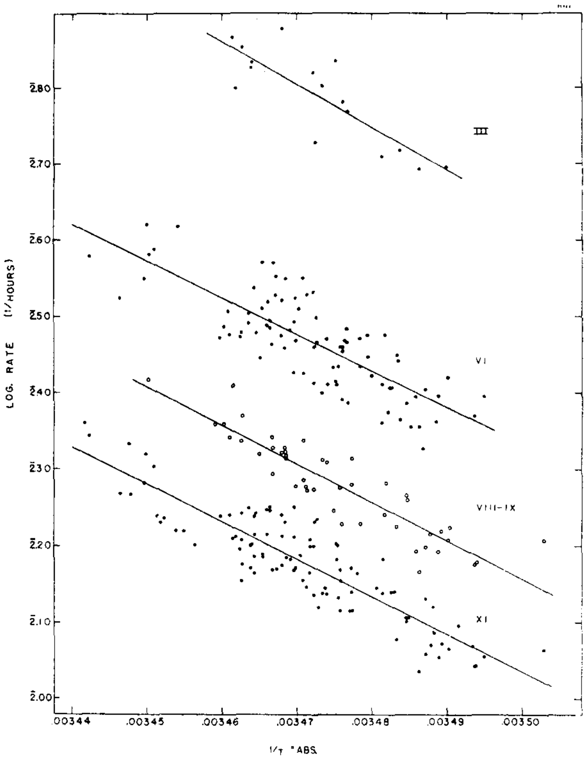

Figure 182. Temperature dependent development rate. (Reproduced without change from Ahlstrom, 1943)

the division into "normal" and "abnormal" categories was ignored since Ahlstrom (personal communication) feels that most abnormalities are due to damage in the net tow, wash down of the samples, and preservation.

The number of eggs in each stage was divided by three so that the numbers represent the number of eggs per 3·33 m² sea surface rather than the number of eggs per 10 m². The standard haul factor used to convert eggs per tow to eggs per 10 m² is normally distributed about 3, thus most sample counts represent the eggs in an oblique net tow under 3·33 m² of sea surface.

RESULTS

Table 101 lists the summaries of egg data by quarter-day intervals from 1951 to 1959. The first half of the table uses as the number of samples, all samples taken which contained any stage sardine egg, in which the accompanying water temperature (10 m) indicated eggs had not yet hatched. The second half of the table includes as the number of samples only those which contain eggs in that stage.

Table 101. Sardine eggs taken on CalCOFI cruises during 1951–59 listed by days. Number per standard haul (number under 3·33 m² sea surface)

	t (days)	Σ_x	Σ_{x^2}	N	$\bar{x}$	s^2
Total hauls:						
Aa	0·125	4189	3029289	313	13·38	9529·57
Ab	0·375	25867	43721493	349	74·12	120127·29
Ac	0·625	29022	119479682	351	82·68	334514·38
Ad	0·875	20145	30532617	336	59·96	87536·77
Ba	1·125	27669	149045615	312	88·68	471356·44
Bb	1·375	20928	15843916	346	60·49	42255·29
Bc	1·625	23064	62303932	341	67·64	178658·73
Bd	1·875	18985	15434595	317	59·89	45245·54
Ca	2·125	8997	3408633	266	33·82	11714·43
Cb	2·375	8945	1975863	286	31·28	5951·22
Cc	2·625	14243	17966433	270	52·75	63996·61
Cd	2·875	6758	2801476	199	33·96	12989·78
Da	3·125	979	95875	91	10·76	948·25
Db	3·375	1310	542808	53	24·72	9815·94
Dc	3·625	718	174438	41	17·51	4046·61
Dd	3·875	65	1301	13	5·00	81·33
Positive hauls:						
Aa	0·125	4189	3029289	57	73·49	48597·04
Ab	0·375	25867	43721493	161	160·66	247284·89
Ac	0·625	29022	119479682	189	153·56	611825·49
Ad	0·875	20145	30532617	204	98·75	140607·38
Ba	1·125	27669	149045615	217	127·51	673692·71
Bb	1·375	20928	15843916	224	93·43	62280·91
Bc	1·625	23064	62303932	254	90·80	237982·80
Bd	1·875	18985	15434595	228	83·27	61029·78
Ca	2·125	8997	3408633	192	46·86	15638·95
Cb	2·375	8945	1975863	208	43·00	7686·88
Cc	2·625	14243	17966433	188	75·76	90306·81
Cd	2·875	6758	2801476	147	45·97	17060·22
Da	3·125	979	95875	61	16·05	1336·05
Db	3·375	1310	542808	32	40·94	15780·00
Dc	3·625	718	174438	26	27·62	6184·41
Dd	3·875	65	1301	8	8·13	110·41

THE EVIDENCE FOR SARDINE EGG MORTALITY

The sample mean in the upper half of Table 101 shows a significant downward trend (rank correlation coefficient $-0{\cdot}8$, $n = 11$) from the second quarter of the first day through the last quarter of the third day. The first quarter of the first day was eliminated due to bias caused by spawning during the period: the last day was eliminated since more than half the stations had been omitted due to hatching temperature. The product-moment correlation coefficient of the sample mean number of eggs and time after hatching is $-0{\cdot}78$ and is significantly different from zero. The

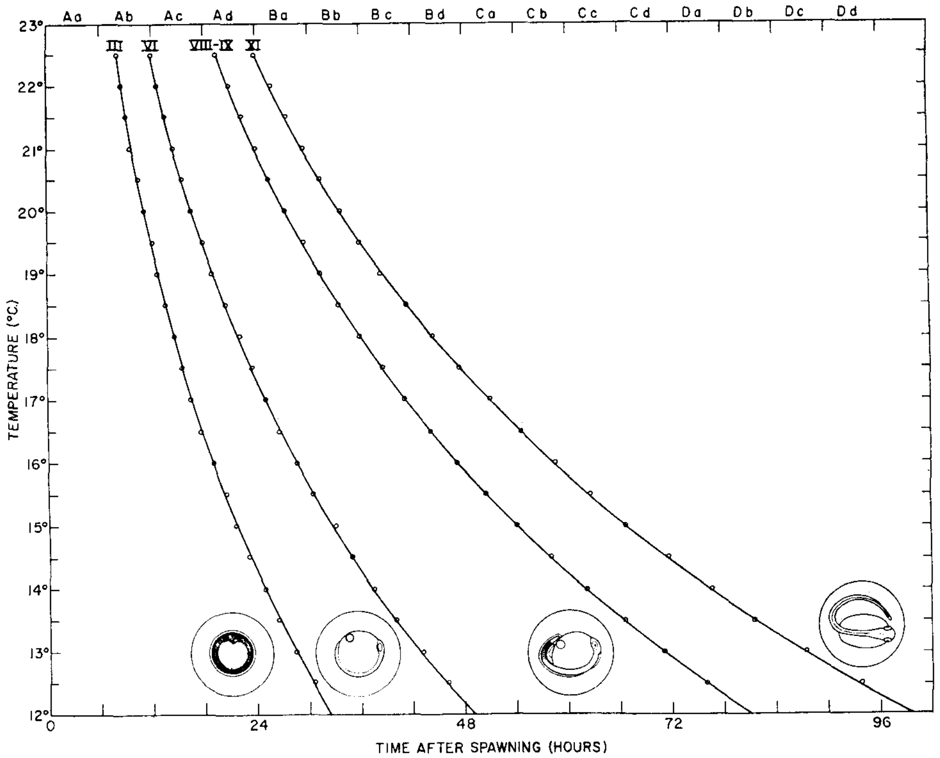

Figure 183. $y = a + bx$ where x is temperature in degrees Celsius, y is the $\log_{10}$ of time in hours and a takes values of 2·22101 (stage III), 2·39977 (stage VI), 2·61754 (stage VIII–IX) and 2·70825 (stage XI). The slope 'b' was the common value, −0·05897. Standard error of estimates 0·03 to 0·04.

strength of these coefficients lends support to the idea that the apparent mortality is not a result of the decidedly non-normal and changing frequency distributions which give rise to the observed arithmetic means.

Further evidence for mortality in the embryonic stages of sardine is given by comparison of the Ahlstrom data from 1950 and 1951 (1954) with his data collected between 1951 and 1959. In Table 102, I have compared the evidence from which Ahlstrom concluded that mortality was negligible to similar data from the years 1951–1959. The elimination of the first 8 hours and the first 6 hours after spawning is justified on the grounds that some spawning is going on during that period: the 2-hour difference between the Ahlstrom (1954b) figures and the ones reported here are regarded as unimportant. In 1950, 82 samples contained sardine eggs at some stage, 4199 eggs were spawned 8 to 32 hours previous to sampling and 4215 were spawned 32·1 to 56 hours previous to sampling. In 24 hours the mean number per standard sample stayed the same (51·20 to 51·40). In the uncensored estimate of 1951 the mean number per standard sample rose from 97·50 (119 samples) to 134·12, a gain of 38% in 24 hours. The censored estimate (by elimination of a single large egg sample) showed a decline from 81·88 (118 samples) to 75·11 per standard haul: down −8% in 24 hours. In the figures for 1951–1959 are included the uncensored totals for 1951, and the mean per standard station changed from 76·19 (1348 samples) to 56·67 (1270 samples) in 24 hours; the mean density at any time may be estimated from these two points, as follows: —

$$N_t = N_0 \exp(-Zt)$$
$$N_t = 95{\cdot}15 \exp(-0{\cdot}2956t)$$

where N_t is the mean density of eggs in number per 3·33 m^2 at time t
N_0 is the mean density of eggs at time zero
Z is the instantaneous mortality rate per day
t is the time in days.

It is important that the absolute difference in the total number of eggs is greater than any single (102 703 to

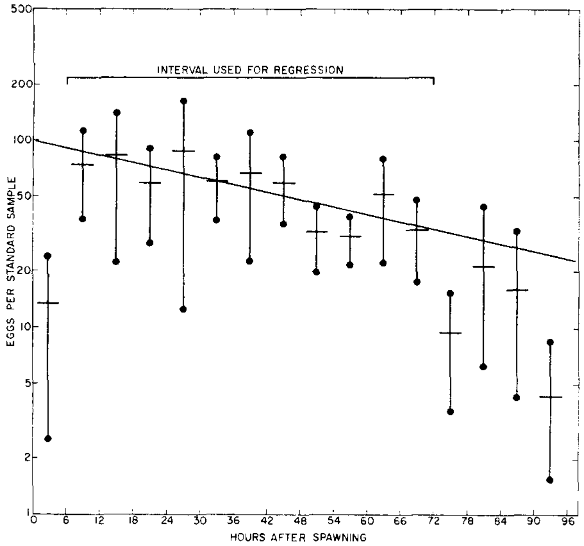

Figure 184. Sample means and an estimate of the 95% fiducial limits [$\pm 1{\cdot}96\, s/\sqrt{(n)}$] for all samples which contain any stage sardine egg, 1951–59. (Table 101). The line is a least squares fit to the log of sample means from 6 to 72 hours. Time zero is 2000 hours.

71974) sample (maximum sample, 1959–1959, 10333 eggs per standard sample).

It seems likely from the above that significant mortality does occur in the embryonic stage. Because the rate is determined from only two points, the rate of 0·3 per day is not to be taken as an accurate slope. To gain a sense of the crude mortality rate, I have plotted the sample means and an estimate of the 95% confidence limits, for each of the 16 categories, in Figure 184. The formula for the curve is (11 points, Ab–Cd)

$$N_t = 94{\cdot}02 \exp(-\,0{\cdot}3074)$$

This rate of mortality, 0·3074 per day over 3 days, does not differ markedly from the 0·2956 of the first 2 days of fully recruited eggs (Table 102): the standard error for the mortality rate derived from two points is not evaluable but for the 11 point curve the standard error is 0·087 (for method of fitting line and determining standard error see Conway, Glass and Wilcox, 1970).

THE EVIDENCE FOR SARDINE EGG DISPERSAL

The importance of dispersal was first indicated by the increased proportion of positive egg samples with time (Table 103, Fig. 185) after spawning. Other evidence includes a) the rate of decline in the mean number of eggs per positive sample exceeds the mortality rate (Table 101, Fig. 186); b) the change with time of the frequency distribution of mean distance between nearest neighbor eggs while the frequency distribution of eggs per sample remains relatively stable (Fig. 187); c) the decline in the Lloyd (1967) "patchiness" (Table 105) ratio; and d) the decrease with time of the probability of obtaining a "large" sample of eggs (Tables 104, 106).

Table 102. Comparison of crude sardine egg mortality estimates

Period	Age	Number of eggs	Number of stations[1]	Mean	Percent difference
1950	8–32 hr.	4199	82	51·20	–
	32·1–56	4215	–	51·40	–
1951	8–32 hr.	11602	119	97·50	–
Uncensored	32·1–56	15960	–	134·12	+38%
1951	8–32 hr.	9662	118	81·88	–
Censored	32·1–56	8863	–	75·11	–8%
1951–59	6–29 hr.	102703	1348	76·19	–
	30–54	71974	1270[2]	56·67	–26%

[1] Number of stations with any stage sardine egg.

[2] 78 stations removed from consideration since eggs would not be anticipated at that temperature due to hatching.

The rate of dispersal for sardine egg patches for the first day after spawning is reflected by the change in proportion of samples which are positive, given by:

$$P_d = 38{\cdot}05t^{0{\cdot}2332}$$

where P_d is the proportion of samples which are positive, and t is the time in days.

Table 103 shows that the proportion of samples which are positive stabilizes after a day and a half and I presume that this is due to the development of spaces between eggs such that a sampler may pass between eggs in a patch. The dispersal rate is clearly distinguishable from the increased probability of positive samples due to spawning (Early, Table 103) immediately after 2000 hours (Fig. 185):

$$P_s = 6{\cdot}08t^{3{\cdot}1223}$$

where P_s is the percent positive samples in the first 7 hours of spawning.

The decline in the mean number of eggs per positive sample is at a higher rate than could be explained by mortality alone (Table 101, Fig. 186):

$$N_{t+} = 194{\cdot}13 \exp(-\,0{\cdot}5038t)$$

where N_{t+} is the sample mean number of eggs per positive sample per 3·33 m^2 surface area.

Table 103. Percentage of samples positive for sardine eggs taken on CalCOFI cruises during 1951–59, listed by days

	t (days)	Number of samples	Number of positive samples	Percent positive samples	Confidence limits (%)
Aa	0·125	313	57	18	±4
Ab	0·375	349	161	46	5
Ac	0·625	351	189	54	5
Ad	0·875	336	204	61	5
Ba	1·125	312	217	70	5
Bb	1·375	346	224	65	5
Bc	1·625	341	254	74	5
Bd	1·875	317	228	72	5
Ca	2·125	266	192	72	5
Cb	2·375	286	208	73	5
Cc	2·625	270	188	70	5
Cd	2·875	199	147	74	6
Da	3·125	91	61	67	10
Db	3·375	53	32	60	13
Dc	3·625	41	26	63	15
Dd	3·875	13	8	62	28
Samples within the first 9 hours					
1 hr.	0·042	106	7	7	5
3 „	0·125	105	19	18	7
5 „	0·208	102	31	30	9
7 „	0·292	109	48	44	9
9 „	0·375	123	56	46	9

The rate of − 0·5038 (S. E. 0·075) per day exceeds the mortality rate (0·3074; S. E. 0·087). The difference is explained by the fact that the rate of dispersal exceeds the rate of aggregation, if any (such as surface convective cells) exists.

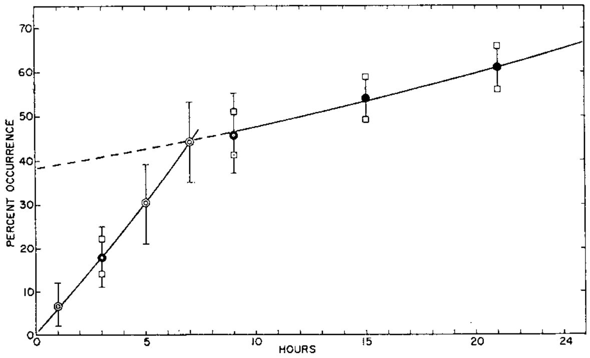

Figure 185. The percent occurrence of sardine eggs in the day of spawning. Solid circles are the percent occurrence of 6 hour intervals plus an estimate of the 95% fiducial limits $[+1{\cdot}96\surd(pq/n-1)$ squares$]$. Open circles are the percent occurrence of sardine eggs in 2 hour intervals and an estimate of the 95% limits (bars). The dashed line is the extension of the least squares estimate of $\log_{10}$ percent occurrence on time between 6 and 30 hours. The solid line near the origin (2 000 hours) is the least squares estimate of the percent occurrence over the first eight hours.

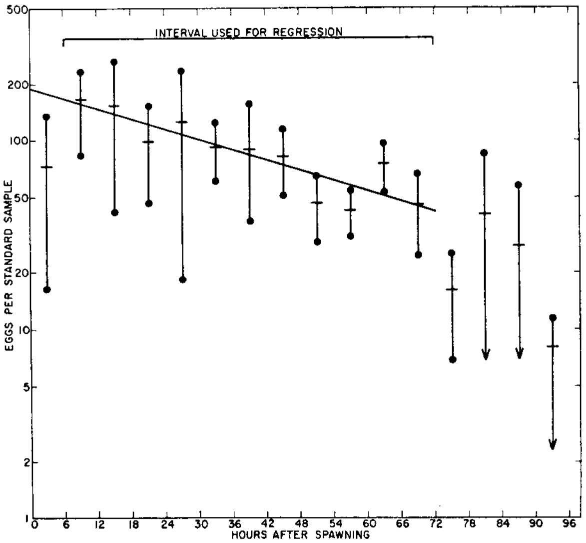

Figure 186. Sample means and an estimate of the 95% fiducial limits $[+1{\cdot}96\, s/\surd(n)]$ for all samples positive for that particular stage age, 1951–59. (Table 101, positive samples). The line is the least squares fit to the $\log_{10}$ of sample means from 6 to 72 hours, time zero is 2 000 hours.

The characteristic of Pacific sardine egg patchiness is that most eggs occur in a few large samples (Tables 104, 106). Most positive samples contain relatively few eggs. A rule-of-thumb for this species is that 90% of the eggs occur in about 10% of the positive samples. The results of 349 samples taken between the hours of 0200 and 0800 are shown in Figure 187. The summary of the three stages of eggs taken in these samples (Ab, Bb, Cb)—Table 101 — shows the change of the sample mean number per standard sample to be 74, 60, and 31 eggs (regression estimate 86, 61, and 43 eggs respectively) at 24 hour intervals. While the number of eggs per sample changes gradually and retains the same form (b) the frequency distribution of percent of eggs (a) shifts from mean nearest neighboring category, of less than 2·5 cm, to the 5 cm category.

Lloyd (1967) proposed the following measure of "mean crowding", which is the number of other individuals per quadrat per individual:—

$$\overset{*}{m} = \sum_{i=1}^{N} x_i/N \qquad (6)$$

where $\overset{*}{m}$ = population estimate of mean crowding
N = number of individuals
x_i = number of other individuals that are located with the individual in the same quadrat.

Table 104. Frequency distribution of samples of sardine eggs taken on CalCOFI cruises, 1951–59, by mean space between nearest neighbors and mean number per standard sample. (Number under 3·33 m² sea surface)

Mean space between nearest neighbors	Eggs/sample	Aa	Ab	Ac	Ad	Ba	Bb	Bc	Bd	Ca	Cb	Cc	Cd	Da	Db	Dc	Dd	Total
1 cm........	3705–33333	0	1	1	0	2	0	1	0	0	0	1	0	0	0	0	0	6
2	1334–3704	1	5	4	3	0	2	1	2	0	0	0	0	0	0	0	0	18
3	681–1333	1	4	2	0	1	6	3	4	2	0	1	1	0	1	0	0	26
4	413–680	1	5	6	8	5	7	4	7	3	2	5	3	0	0	0	0	56
5	276–412	2	3	6	4	3	3	6	6	3	5	4	2	0	0	1	0	48
6	198–275	1	7	6	4	9	7	7	3	3	6	4	3	1	0	0	0	61
7	149–197	0	2	6	3	6	3	3	8	2	8	6	4	0	0	0	0	51
8	116–148	1	3	5	7	1	9	3	7	3	5	4	5	0	2	1	0	56
9	93–115	0	3	4	7	3	9	8	3	4	6	2	0	0	1	0	0	50
10	77–92	1	5	3	6	3	3	9	4	3	1	11	4	1	1	0	0	55
11	64–76	1	4	3	4	5	6	2	4	4	2	3	2	1	0	0	0	41
12	54–63	1	2	1	3	8	4	8	4	9	5	6	1	1	0	1	0	54
13	47–53	1	3	5	1	2	3	5	8	3	4	2	3	1	0	0	0	41
14	41–46	0	4	2	7	4	8	7	2	3	5	5	1	0	0	0	0	48
15	36–40	0	5	2	2	5	2	6	4	4	1	3	0	0	0	0	0	34
16	32–35	0	5	2	5	3	4	3	2	2	3	2	2	0	0	0	0	33
17	28–31	1	1	3	1	4	3	5	2	5	6	3	1	1	1	1	1	39
18	25–27	0	2	2	6	3	3	1	1	4	5	2	3	2	0	0	0	34
19	23–24	0	2	3	1	5	2	1	5	2	2	4	1	0	0	2	0	30
20	21–22	1	1	5	3	3	2	5	2	1	4	2	2	3	0	0	0	34
21	19–20	1	2	2	3	1	1	2	4	3	2	3	1	3	1	0	0	29
22	17–18	1	2	4	5	2	4	5	3	4	2	5	0	1	0	0	0	38
22·5–23·1.....	16	2	0	3	4	3	1	2	2	1	1	1	1	2	1	0	0	24
23·2–23·9.....	15	1	0	2	1	1	3	1	0	2	2	1	4	2	0	0	1	21
24·0–24·7.....	14	0	2	3	0	1	2	3	5	5	2	1	2	0	0	0	0	26
24·8–25·7.....	13	0	0	3	0	3	1	6	4	3	3	2	5	1	0	0	0	31
25·8–26·8.....	12	1	1	2	4	5	2	7	0	4	6	5	1	0	1	0	0	39
26·9–28·1.....	11	1	0	4	2	3	3	3	4	2	2	2	2	1	0	1	0	30
28·2–29·5.....	10	3	3	1	3	2	5	3	3	3	6	3	3	2	0	0	0	40
29·6–31·2.....	9	0	4	8	5	5	2	2	5	10	6	2	3	2	1	0	1	56
31·3–33·2.....	8	1	7	3	4	3	4	3	2	5	7	1	6	4	1	0	0	51
33·3–35·7.....	7	1	4	5	6	6	3	8	6	10	4	8	2	0	0	0	0	63
35·8–38·8.....	6	2	1	6	5	5	9	6	8	3	2	3	2	3	2	0	0	57
38·9–42·9.....	5	2	5	2	7	6	5	12	8	6	3	7	7	1	3	2	0	76
43·0–48·7.....	4	5	7	6	10	12	11	6	11	9	10	10	7	3	2	2	0	111
48·8–57·6.....	3	6	9	6	14	15	16	17	16	12	14	14	13	3	3	2	2	162
57·7–74·4.....	2	5	17	22	12	17	19	22	21	16	28	13	15	9	4	2	1	223
74·5–129·0....	1	12	30	36	44	52	47	58	48	34	38	37	35	13	7	11	2	504
129·1 – Infinity	0	256	188	162	132	95	122	87	89	74	78	82	52	30	21	15	5	1488
Total.........		313	349	351	336	312	346	341	317	266	286	270	199	91	53	41	13	3884

The sample estimate was calculated by the formula:

$$\overset{*}{x} = \bar{x}[(s^2/\bar{x}) - 1] \tag{7}$$

The ratio of the sample estimate for mean crowding $\overset{*}{x}$ and the sample estimate of the mean is equivalent to the reciprocal of the negative binomial k and is described by Lloyd (loc. cit.) as a measure of "how many times as 'crowded' an individual is on the average, as it would have to be if the same population had a random distribution". "Patchiness" declines with time (rank difference correlation coefficient = $-0{\cdot}4$, $n = 16$).

Even though the periphery of the egg patches spreads rapidly, most eggs remain closely spaced near the origins of the patches (discounting transport). Table 106 lists the 24 largest samples of the 9-year series. The list includes all samples where the mean horizontal space between nearest neighbors was less than 2·5 cm. Although these 24 samples represent only 0·6% of the samples taken, they contained 37·5% of the eggs. There is no obvious order of rank and age, thus the absolute size of these samples appears to be due to chance. The probability of obtaining these samples does change with time, however:

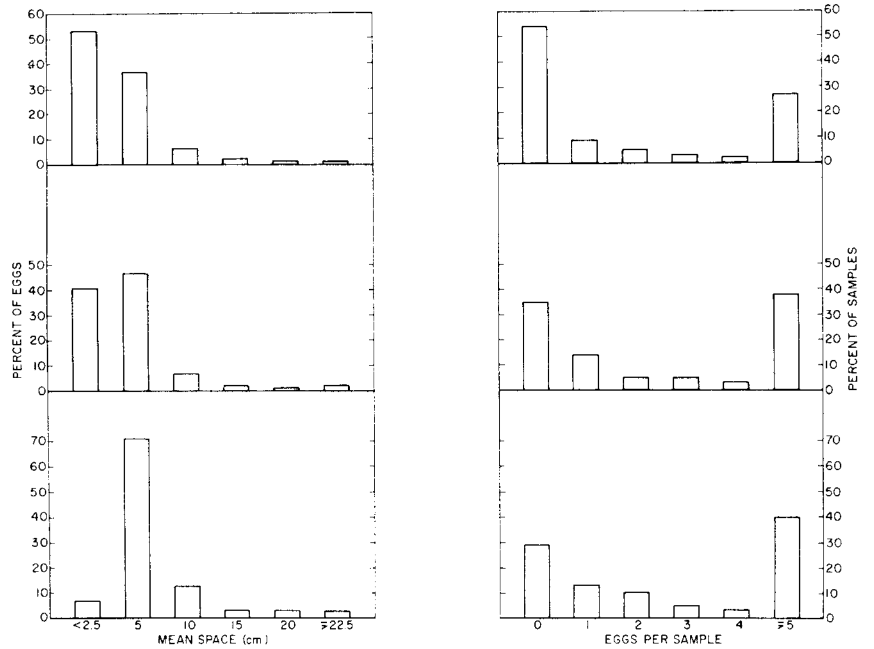

Figure 187. Frequency distribution of eggs (a) and samples (b) at 9·33 and 57 hours after spawning. Part "a" is the percent of the eggs in each mean space category (mean space equivalents in numbers per m^2 in Table 104). Part "b" is the percent of samples in "eggs per sample" categories.

Table 105. Estimate of mean crowding of sardine eggs taken on CalCOFI cruises during 1951–59, listed by days

	Time t	Mean density $\bar{x}$	Variance s^2	Variance /mean $s^2/\bar{x}$	Mean crowding $\overset{\bullet}{x}$	Patchiness rates $\overset{\bullet}{x}/\bar{x}$
Aa	0·125	13·38	9529·57	712·22	724·60	54·16
Ab	0·375	74·12	120127·29	1620·71	1693·83	22·85
Ac	0·625	82·68	334514·38	4045·89	4127·57	49·92
Ad	0·875	59·96	87536·76	1459·92	1518·88	25·33
Ba	1·125	88·68	471356·44	5315·25	5402·93	60·93
Bb	1·375	60·49	42255·29	698·55	758·04	12·53
Bc	1·625	67·64	178658·73	2641·32	2707·96	40·03
Bd	1·875	59·89	45245·54	755·48	814·37	13·60
Ca	2·125	33·82	11714·43	346·38	379·20	11·21
Cb	2·375	31·28	5951·22	190·26	220·54	7·05
Cc	2·625	52·75	63996·61	1213·21	1264·96	23·98
Cd	2·875	33·96	12989·78	382·50	415·46	12·23
Da	3·125	10·76	948·25	88·13	97·89	9·10
Db	3·375	24·72	9815·94	397·08	420·80	17·02
Dc	3·625	17·51	4046·61	231·10	247·61	14·14
Dd	3·875	5·00	81·33	16·27	20·27	4·06

Table 106. Large samples of sardine eggs 1951–1959

Rank	Density (number/sample)	Age	
1	10333	Ba	1·125 days
2	10204	Ac	0·625 ,,
3	7097	Bc	1·625 ,,
4	6665	Ba	1·125 ,,
5	4077	Ab	0·375 ,,
6	3854	Cc	2·625 ,,
7	3610	Ad	0·875 ,,
8	3163	Ab	0·375 ,,
9	2797	Ad	0·875 ,,
10	2654	Bc	1·625 ,,
11	2507	Ad	0·875 ,,
12	2479	Bd	1·875 ,,
13	2206	Ab	0·375 ,,
14	2190	Bb	1·375 ,,
15	1940	Ac	0·625 ,,
16	1800	Bd	1·875 ,,
17	1699	Ac	0·625 ,,
18	1698	Bb	1·375 ,,
19	1504	Ac	0·625 ,,
20	1481	Ab	0·375 ,,
21	1453	Ab	0·375 ,,
22	1363	Ac	0·625 ,,
23	1352	Aa	0·125 ,,
24	1348	Ab	0·375 ,,

Day	$\underline{\underline{N}}$	N_+	%
0·5	11	350	3·1
1·0	5	421	1·2
1·5	4	478	0·8
2·0	2	420	0·5
2·5	1	396	0·3

where Day is the time in days after spawning,

$\underline{\underline{N}}$ is the number of large samples (> 1333 per standard sample)

N_+ is the number of positive samples

% is the percent of positive samples which are large.

Table 104 indicates that the large samples are part of a continuous distribution in sample sizes.

Considerations of oceanic diffusivity (Okubo, 1968) would suggest that the smaller the scale of the patch, the slower would be the rate of diffusion. Okubo has fitted a curve to existing diffusion experiments and the following formula describes the scale dependent effect:

$$Ka = 0{\cdot}0103L^{1{\cdot}19}$$

where Ka = the apparent diffusivity in $\text{cm}^2\ \text{sec}^{-1}$
L = the scale of the patch in cm.

By use of the rate of increase of positive stations (Smith, MS.) in Table 103, the scale of patch involved in the dispersal of sardine eggs appears to be of the order of 10's to 100's of meters patch diameter. One can say with reasonable certainty, that the scale of diffusion which affects the dispersion of sardine egg numbers per unit area and is the major source of variance, is not the sort that one would expect from the spawning of single or small groups of females nor that expected by the spawning of huge shoals of fish schools over kilometers and 10's of kilometers.

THE MORTALITY AND DISPERSAL OF SARDINE LARVAE

We have attempted in a preliminary way to align larval and egg time series to days after spawning as corrected by hatching and yolk sac growth by temperature. A series of all 171 samples in 1955 indicates that larval apparent mortality increases somewhat immediately after hatching, but most changes can be attributed to escapement through the meshes of the net (Ahlstrom, 1954b):

1955	day	$\bar{x}_r$	$\bar{x}_e$	$\%_e$
	3	32·56	32·56	
	4	23·11	11·42	65 %
	5	16·41	6·31	45 %
	6	11·65	3·79	40 %

where $\bar{x}_r$ = predicted value at 29% per day
$\bar{x}_e$ = measured value
$\%_e$ = estimated rate.

Lenarz (this vol.) estimates the overall larval mortality rate at approximately 0·1 per day. We anticipate that extensions of this technique and new laboratory rearing data will allow improvements for this estimate. There is no apparent difference in the rate of dispersal of early larvae as compared to eggs. Patchiness exists for the individual larva through at least the 7th day: for the 1955 data, more than 3/4 of the larvae were spaced less than 20 cm from the mean nearest neighbor.

DISCUSSION

Although the main objective of this paper was to use the observed distributions of sardine eggs at differing ages to improve the precision of biological sampling and analysis per unit cost, there are important leads in these results for the study of sardine mortality and pelagic ecology in general. Following the discussion on sampling in the presence of patchiness and dispersal, I will briefly relate the dispersal and mortality of sardine eggs and larvae to oceanic conditions of life.

SAMPLING AND ANALYSIS

The general finding of this paper is that sardine eggs are spawned in a mosaic pattern of fish school proportions, and the eggs at the perimeter subsequently disperse to a condition of randomness in a large "corona" around a concentrated "centrum". The size of the centrum appears to be of the order of 10's of meters diameter while the size of the "corona" rapidly shifts from one to several hundred meters after spawning. Horizontal mean space between nearest neighbor eggs is of the order of 1 or 2 cm at spawning and changes to 15 to 20 cm mean space between most, several-day old larvae.

The implications for sampling strategy at sea are clear. Large numbers of small samples, each covering a unit square metre will rapidly yield a catch size distribution which defines the amount of open area between patches in a spawning area, the mean density of the randomly placed eggs in the "corona" and a sample estimate of the negative binomial k. It seems likely that samples of this kind will not yield useful rates of such gradual phenomena as mortality until a thousand or so positive samples have been taken. Considering the relative sizes of the "corona" and "centrum" no practical tow length could be envisaged which would be long enough to stabilize the variance mean ratio at unity. Larger scales of "patchiness", such as groups of schools of spawning adults, may well defeat the purpose of lengthening the tow.

Some statistical purpose would be served by making "zero" tows less likely. The 30 to 40% of the spawning area which appears to be free of eggs in 3·33 m² samples might have only 5 to 10% negative tows with 10 m² samples. Certainly this would reduce the "zero" labelling of an 8000 square mile area represented by a single negative tow in a spawning area.

In the analysis of egg concentrations, I can see no useful analytical purpose in contouring discontinuous distributions of egg counts for single stations as suggested by Sette and Ahlstrom (1948). The scale of patchiness suggested by these data would cause local fluctuations of several orders of magnitude between adjacent stations, and the assumption of contour continuity would not hold.

SARDINE MORTALITY IN THE EMBRYONIC STAGE

The daily rate of −0·31 for sardine egg mortality is unexpectedly high. Comparison with the negligible rate held by Ahlstrom (1954) by similar techniques, yields a 26 per cent change in the first two fully recruited days. I conclude that the egg mortality rate of −0·31 (S.E. 0·087) is demonstrably higher than the 0·1 per day rate postulated by Lenarz (this vol.) for sardine larvae. Both egg and larval mortality rates depend on the assumption that station temperatures at 10 m depth are representative of the actual temperature of development. We are now beginning a study of temperatures throughout the upper mixed layer for an estimate of the possible magnitude of error in this assumption. Marr (1956) proposes three mortality rate curve types for early stages. I believe that the crude rates of mortality derived here support his "type two" curve and gradually change from 0·3 to 0·1 per day in the first few weeks of life. Further studies and samples are obviously needed on this point, however. Intuitively, I feel that the "critical" period type curve if occurring should have been more obvious from the extensive set of data.

ECOLOGICAL CONSIDERATIONS OF DISPERSAL AND MORTALITY

The universal nature of patchiness in pelagic invertebrates (Clutter, 1969) and fish eggs and larvae tempts one to speculate that the "mean crowding" elucidated by Lloyd (1967) should be considered as an index of "mean adaptive aggregation" for pelagic animals. Among the adaptive properties of patchiness for larval fish is the rate at which the subsequent behaviour and schooling may develop from chance contacts (Breder, 1967; Shaw, 1963). Van Olst and Hunter (1970) find that interfish distances of anchovy larvae in the laboratory close rapidly from three body lengths spacing at 30 mm length to less than one body length space at 70 mm length. The ontogeny of these reactions to other fish must be affected by dispersal rates encountered during the planktonic stage.

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