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THERMAL AND DIURNAL CHANGES IN THE VERTICAL DISTRIBUTION OF EGGS AND LARVAE OF THE PILCHARD (SARDINOPS CAERULEA)¹

By

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INTRODUCTION

Knowledge of the vertical distribution of pilchard eggs and larvae is of interest from two standpoints: first, in adding to the general knowledge of the early life of this species in the sea; and second, in defining the vertical range of its early stages so that regular surveys of the spawning grounds may be designed to sample all strata in which eggs and larvae are to be found. In reference to the second point it was desired if possible to relate vertical distribution to physical characteristics of the sea, so that the depth to which nets must be sent might be predicted. It was felt that the concentration of organisms at a given depth would be controlled chiefly by temperature, density, and light intensity. The analyses described in this paper have been designed to discover and define the relationships between these three variables and the vertical distribution of pilchard eggs and larvae.

METHODS

The field technique employed throughout the experiment was to make at each station successive net hauls, each sampling a layer of water below that of the preceding haul. In 1939, hauls were approximately horizontal. In 1941, however, oblique hauls were adopted to preclude the possibility of missing concentrations of larvae in the gaps between hauls. Each oblique haul extended diagonally from the top of the layer to be sampled by the next haul, to the bottom of the layer sampled by the preceding haul. The “surface” haul was made with

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an open net, while for the others the net was lowered closed to the desired level, hauled for from 15 to 20 minutes, closed, and brought to the surface.

Closing nets used were identical, except for dimensions and materials, with the one described by Leavitt (1935), and the tripping device was the one figured by him in a later paper (Leavitt, 1938, fig. 2). Sizes of nets and materials used are given in the list of stations at the end of this paper.

Temperatures were taken in 1939 with reversing thermometers, and in 1941 with a bourdon-type bathythermograph modified from the one described by Spilhaus (1940).

Water flow was measured in the 1939 hauls by a meter consisting of an impeller and counter. "Stray angle" (departure of the towing wire from the vertical) was measured with a pendulum protractor.

PERIOD AND AREA COVERED

Stations were located within a radius of 120 miles of San Diego, California, and were in an area somewhat to the south and east of the areas of heaviest pilchard spawning as indicated by other surveys. Four series of hauls were made in April, 1939, and seven in April, May and June, 1941. Exact locations, dates, and depths fished are given in the list at the end of the paper.

CLASSIFICATION OF MATERIAL

Eggs and larvae were of course treated separately. Also, to take account of the fact that motility increases with size of larvae, these were divided into two categories: "large" and "small." A dividing line of 8 mm. had previously been used in other work, with which it was desired to compare the results of this analysis. Since this line did not split a mode in the length frequency distribution of larvae in the vertical serial hauls, it was retained for the present study.

Some larvae of the "small" group were lost through the meshes of the one-meter nets used. This, however, does not necessarily invalidate comparisons between numbers caught at different levels with the same net, since the loss should be a constant percentage of the total number caught.

STANDARDIZATION OF HAULS

Because of unavoidable variations in the speed of the ship and time of hauling, the amount of water strained by the net varied from haul to haul, even within a single series. These variations were discounted by putting all the hauls in each series on the basis of a standard volume
of water strained. For the 1939 hauls flow of water through the nets was measured directly by a current meter, but for the 1941 hauls, the relative amount was computed from the formula \( \frac{W_1}{W_2} = \frac{\tan \angle_1}{\tan \angle_2} \), where

\( \frac{W_1}{W_2} \) = the ratio between the amounts of water strained for any two hauls, and \( \angle_1 \) and \( \angle_2 \) = their respective stray angles. Actual volumes of water strained averaged around 400 cubic meters for the one meter nets, and 100 cubic meters for the half-meter nets. The numbers of organisms in the hauls were multiplied by factors \( \left( \frac{V_s}{V_h} \right) \), where \( V_s \) = standard volume of water and \( V_h \) = volume strained in given haul) which made the numbers the same as if the standard volume of water had been strained, and had contained the same concentration of organisms as the water actually strained.

Because of the great range in numbers of organisms (from 6 to 6000 in a single series of hauls) they could not be represented graphically on the same scale. Since the change in concentration from one series to another was not of interest, but only the changes from haul to haul within a series, the graphing difficulty was overcome by representing each vertical series by a polygon of equal area. To do this, the product of numbers of organisms by thickness of layer sampled was obtained for each haul. These products were summed for each station, and the original counts of organisms were multiplied by factors which made the sum of such products a constant for all stations. Besides overcoming the graphing difficulty, this computation placed the numbers at each level for all of the stations on a comparable basis, permitting direct comparison of catches at different levels even though they were not taken at the same station.

To avoid excessive random variability from small numbers, series containing less than 100 eggs, 50 small larvae or 5 large larvae were omitted from the analysis.

In order to construct the polygons mentioned above, it was necessary to compute the average depth for each haul. For the 1939 hauls, when the stray angle was measured two or three times during a haul, the angles were simply averaged and the depth computed from the average angle and the length of the towing wire. In 1941, when angles were measured each minute during a haul, it was possible to construct a plot of the course of each haul (Figure 34). Average depths were computed from the plots by measuring the area bounded by each one and its baseline, and dividing by the length of the baseline.
EFFECT OF TEMPERATURE

Inspection of the vertical profiles for relative numbers of eggs and larvae, together with the corresponding temperature profiles (Figure 35) indicates a possible relationship between temperature and vertical distribution. Such a relationship could arise as the result of the seeking of an optimum temperature by the larvae, and by the adult fish which lay the eggs. Since pelagic fish eggs tend to remain in water of the same specific gravity as that in which they were fertilized (Walford, 1938) the vertical distribution of eggs should tend to reflect that of the parent fish at the time of spawning. This relationship is complicated by vertical turbulence above the thermocline, which tends to disperse passive bodies like fish eggs.

Whatever the nature of the relationship between temperature and the distribution of pilchard eggs, the larvae may be expected to respond directly to changes in temperature, since they are capable of locomotion. Again the relationship is probably complicated by other factors, such as the amount of fodder organisms present.

To measure the correlation between temperature and concentrations of eggs and larvae, the relative numbers were plotted as regressions on degrees Centigrade (Figure 36). Hauls above a depth of 10 meters were omitted because of the reversals in egg and larvae profiles which often occurred in that layer. Also excluded were zero hauls below the first. Inclusion of either of these two categories of hauls would
Figure 35. Relative numbers of eggs and larvae taken at each depth. Broken line shows temperature. For the large larvae two series taken around noon have been omitted because of the effect of light. They are shown in Figure 37.
obscure the decrease from the maximum concentrations down to zero, which is the point of chief interest in the regressions insofar as they are to be used in determining the depth of net hauls for regular surveys. Correlation coefficients were .590 for eggs, .557 for small larvae, and .548 for large larvae, corresponding to probabilities of .010, .041 and .024 of chance occurrence. Combining these probabilities by the method of Fisher (1936, p. 105) indicates that the result, as a whole, is highly significant ($P = .0009$).

Of special interest in the foregoing correlations are the intersections of the computed regression lines with their baselines, since these should indicate the temperature below which we would not expect to find eggs or larvae. The indicated minimum temperatures are 10.5°
for eggs, 12.4° for small larvae, and 12.0° for large larvae. Since the regressions for large and small larvae were found by Fisher's (1936 p. 146) t test not to differ significantly in slope, they were combined, giving an indicated minimum of 12.0° for both size categories.

**DIURNAL CHANGES**

To determine the extent and nature of diurnal changes in the vertical distribution of pilchard larvae, two special pairs of serial hauls were run in June, 1941, the first of each pair being occupied around midnight, and the other around noon. Due to unavoidable movements of the vessel the two members of each pair were not located at exactly the same point geographically, but approximately the same position was maintained and they were probably in water of similar characteristics.

One of the chief differences between the night and day hauls was that the former contained many more large larvae than the latter (Figure 37). This could result from any one of three causes: (1)
location of the day hauls in an area of lesser concentration than the
night hauls, as a result of movement of the ship through the water
between the two series; (2) migration of most of the larvae below the
levels fished, during the daytime; (3) dodging of the net by the larvae,
in the daytime.

The first explanation is a highly improbable one, since the larger
catches at night have been observed many times previously, for other
plankton organisms and larvae of other species of fish. Also, our
regular surveys of the spawning grounds show the night catches of
larvae to be consistently larger than the day.

The second explanation has been most widely entertained by others
investigating vertical migrations. For instance, it was advanced by
E. S. Russel (1928) to explain the larger catches of clupeoid and
gobioid larvae at night, but he was later forced to abandon it when
subsequent daylight hauls near the bottom (Russel, 1930) did not
average larger catches than the ones in the upper layers of water.
For our own data, the taking of at least two blank hauls (Figure 37)
below those which contained any larvae argues against the proba-
bility of a concentration of larvae below the levels sampled.

Elimination of the first two explanations leaves only the third—
dodging of the net in the daytime. Russel (1926) and Johansen (1925)
admit this possibility, but doubt that fish larvae could swim fast
enough for successful dodging. On this point it may be well to con-
sider how fast it would be necessary for larvae to swim in order to get
out of the way of the net. All nets towed in the conventional manner
give warning of their approach by means of the piece of line which
attaches them to the towing wire. In our gear this line was about 5
meters long, while our average speed of towing was around 50 cm. per
second. The larvae would thus have about 10 seconds to swim out
of the way. Since the maximum distance they would have to swim
would be the radius of the net, or 50 cm., a swimming rate of 5 cm.
per second would be sufficient if the direction of swimming were
favorable. This does not seem an incredible rate for pilchard larvae
of the size in question (over 8 mm. in length). Likewise it does not
seem unreasonable that they should swim away from the center of
disturbance, and therefore in a direction favorable to escape from the
oncoming net.

In the day hauls the large larvae were not only less numerous than
in the night hauls, but also appeared to be distributed in somewhat
deeper levels. A greater relative number of larvae at the deeper levels
in the daytime than at night might result from more successful dodging
of the net in the better illuminated upper layers of water. A greater
absolute number, however, could result only from downward migration in the daytime, providing the overall concentration were not greater. Such a downward migration might well occur as a result of negative phototropism. Comparison of the night and day hauls for stations 2452 and 2454 (Figure 37) reveals that there actually were more larvae at the deeper levels in the day hauls. Four larvae were taken in the day series at 59 meters, and one at 73 meters, while none were taken at either of these levels in the night series. The significance of these differences was tested by means of Bayes' theorem (using the formulation of Pearson, 1930, page lxx) considering a success the presence of a larva at the indicated depth, and assuming the same overall concentration for day and night (in other words assuming that the lesser numbers in the upper layers in the daytime were due to dodging of the net). The computation gave values of $P$ of .06 at 59 meters and .50 at 73 meters. The latter, of course, does not indicate a significant difference between day and night hauls, but the former, closely approaching the conventional significance level of .05, gives some indication of an actually deeper distribution in the daytime.

In applying this result to the prediction of vertical distribution, a knowledge of the penetration of light at various times of day is necessary. Unfortunately, no empirical data for the area of our survey are available, and we are forced to argue by analogy with data collected elsewhere. G. L. Clarke (1934) has shown in his graphs that submarine irradiation in the Atlantic Ocean reaches nearly its maximum value shortly after sunrise, and is maintained there until shortly before sunset. Accordingly, extension of the regular hauls below 73 meters between sunrise and sunset would seem to be necessary in order to make sure of sampling all strata in which larvae were to be found.

**SUMMARY AND CONCLUSIONS**

Analysis of catches of pilchard eggs and larvae taken in serial hauls in 1939 and 1941 indicates the following relationships and effects:

1. A positive correlation of concentrations of eggs and larvae with temperature, at least within the range of 10° to 17° c.
2. An apparent dodging of the nets by the larger larvae, in the layers of water which are illuminated in the daytime.
3. A negative phototropism for the larger larvae.

Such relationships with physical conditions as have been indicated by the present study may, of course, hold true only for the particular set of oceanographic conditions prevailing at the times and places where the data were gathered. For instance, the relationship between the horizontal distribution of pilchard eggs and temperature as indi-
cated by our regular spawning surveys for 1941 was quite different from that found in 1940. However, the data for the present study were gathered in two different years (1939 and 1941) and over a considerable area, so that they may permit of some generalization.

It may have been noted that the concentrations of eggs and larvae are correlated with depth as well as temperature, since the latter two are themselves highly correlated. However, there are some instances where the deeper extension of warm water corresponds with a deeper distribution of eggs or larvae (cf. Figure 35). Also, there is some logical basis for a correlation with temperature, which might act either as the cause of direct reaction of the larvae, or as an indicator of density differences affecting the distribution of eggs.

It is not intended to argue that temperature itself necessarily controls the vertical distribution of pilchard eggs and larvae. Their location may be determined by complex reactions of the spawners to a combination of physical conditions, including salinity, fodder food, density etc. To the extent that these would induce spawning in a homologous portion of the layer of water above the thermocline, temperature may be merely an indicator and not a cause. This, of course, does not detract from the usefulness of temperature as a guide to vertical distribution.

As a basis for predicting the proper depths to which to send nets on regular surveys, the regressions of egg and larvae concentrations on temperature indicate that hauls should be made deep enough to go below temperatures of 10.5° C. for eggs and 12.0° for larvae. Distribution of the large larvae during the daytime shows the need for fishing to a depth greater than 73 meters between sunrise and sunset.

PILCHARD EGGS AND LARVAE TAKEN IN VERTICAL SERIAL HAULS BY "E. W. SCRIPPS"

Data are given in the following order: Station number; date; time interval; latitude; longitude; type of net; depth interval for each haul; numbers of eggs; length and number of larvae for larvae of each .5 mm. interval of length. Time of day is given to the nearest hour with the hours numbered consecutively from 1 for 1 AM to 24 for midnight. Depths are in meters and lengths of larvae in millimeters.

Example: (Station) 1832; (Month) 4/ (Day) 10/ (Year) 41; (Start) 11h- (End) 15h: (North latitude) 33:13; (West longitude) 118:26; (Type of net) B; (Upper limit of stratum fished, depth) 0- (Lower limit of stratum fished, depth) 13: (Number of eggs taken) E 181; (Larvae) L: (Length) 2.5, (Number) 3; (Length) 3.0, (Number) 35; (length) 3.5, (Number) 4; (Limits) 17-26: (Number of eggs) E 103:
(Larvae) L: (Length) 2.5, (Number) 22; (Length) 3.0, (Number) 366; etc.

Net types are as follows: Type A is a closing net of one meter diameter mouth; made of No. 24XXX grit gauze, with the last half meter of No. 56XXX grit gauze; and with a detachable "cod end" of No. 56XXX grit gauze. Type B is a closing net of one-half meter diameter mouth; made of No. 40XXX grit gauze, with the last 65 cm of No. 56XXX grit gauze. Type C is a closing net of one meter diameter of mouth; made of cotton scrim with openings approximately 1 mm. square, with the last half meter of No. 56XXX grit gauze; and with detachable "cod end" of No. 56XXX grit gauze. Approximate sizes of openings of XXX grit gauzes are: No. 24, 1.10 mm., No. 40, .65 mm.; No. 56, .47 mm.

F8A; 4/19/39; 3h-9h; 32:48, 117:42; A; 0–3: E 1877; L: 4.0, 1; 4.5,1; 5.0,4; 5.5,2; 7.0,2; 8.0,1; 9.5,1; 6–8: E 2879; L: 4.0,1; 4.5,3; 5.0,7; 6.0,1; 6.5,2; 7.0,1; 7.5,1; 8.0,2; 9.0,2; 10.0,1; 10.5,1; 7–16: E 3878; L: 3.0,2; 3.5,1; 4.0,3; 4.5,8; 5.0,9; 5.5,2; 6.0,2; 17–25: E 1265; L: 5.0,1; 8.0,1; 30–34: E 56; L: 0; 44–46: E 5; L: 0; 45–60: E 0; L: 4.5,2; 108–115: E 6; L: 0.

F8B; 4/19/39; 15h–19h; 32:48, 117:44; A; 0–2: E 2892; L: 5.5,1; 6.5,1; 7.0,1; 15–17: E 1359; L: 3.5,1; 4.5,1; 29–35: E 88; L: 0; 53–58: E 8; L: 0; 68–72: E 0; L: 0; 164–183: E 4; L: 0.

F9A; 4/20/39; 2h–8h; 32:30, 117,32; A; 0–5: E 52; L: 3.5,6; 4.0,1; 4.5,2; 5.0,4; 5.5,6; 6.0,1; 6.5,3; 7.0,2; 12–14: E 194; L: 6.0,1; 28–32: E 54; L: 0; 45–57: E 1; L: 6.0,1; 56–59: E 1; L: 0; 109–*: E 7; L: 0.

F9B; 4/20/39; 9h–13h; 32:29, 117:39; A; 0–2: E 940; L: 5.5,2; 6.0,4; 6.5,5; 7.0,7; 8.0,3; 8.5,1; 9.0,1; 9.5,2; 10.0,1; 11.0,1; 14–*: E 4137; L: 3.5,1; 4.0,6; 5.0,1; 6.0,1; 57–66: E 6; L: 0; 126–149: E 4; L: 0.

1832; 4/10/41; 11h–15h; 33:13, 118:26; B; 0–13: E 181; L: 2.5,3; 3.0,35; 3.5,4; 17–26: E 103; L: 2.5,22; 3.0,366; 3.5,187; 4.0,2; 4.5,6; 5.5,1; 28–39: E 11; L: 2.5,1; 3.0,47; 3.5,31; 4.0,2; 4.5,6; 5.0,2; 41–55: E 0; L: 0; 53–66: E 0; L: 3.0,2; 3.5,2; 69–83; E 0; L: 2.5,1; 3.5,1; 5.0,1.

2046; 4/30/41; 17h–21h; 32:29, 119:26; B; 0–3: E 0; L: 3.0,3; 3.5,3; 4.0,1; 4.5,2; 5.0,33; 5.5,36; 6.0,9; 6.5,1; 7.0,1; 9.5,1; 6–12: E 0; L: 3.5,2; 4.0,2; 4.5,2; 5.0,31; 5.5,51; 6.0,55; 6.5,20; 7.0,3; 7.5,4; 8.0,2; 8.5,2; 9.0,1; 9.5,1; 10.0,2; 14.0,1; 15–25: E 0; L: 2.5,1; 3.0,1; 3.5,2; 4.0,1; 4.5,3; 5.0,27; 5.5,37; 6.0,74; 6.5,23; 7.0,9; 7.5,5; 8.0,5; 8.5,2; 9.0,2; 9.5,2; 10.5,1; 14–29: E 0; L: 3.0,2; 3.5,11; 4.0,11; 4.5,12; 5.0,38; 5.5,29; 6.0,15; 6.5,3; 28–43: E 0; L: 2.5,3; 3.0,19; 3.5,30; 4.0,16; 4.5,11; 5.0,25; 5.5,3; 6.0,6; 6.5,3; 7.5,1; 44–62: E 3; L: 2.5,1; 3.0,13; 3.5,11; 4.0,4; 4.5,1; 5.0,1; 65–92: E 18; L: 6.0,1.

* Only one stray angle reading.
1943; 5/2/41; 20h-24h; 32:50, 118:18; C; 0-4: E 90; L: 3.0,1; 5.0,20; 5.5,30; 6.0,32; 6.5,20; 7.0,38; 7.5,43; 8.0,53; 8.5,48; 9.0,33; 9.5,17; 10.0,19; 10.5,6; 11.0,14; 11.5,13; 12.0,7; 12.5,4; 13.0,5; 13.5,3; 14.0,1; 14.5,1; 15.0,2; 7-13: E 16; L: 4.0,1; 4.5,4; 5.0,21; 5.5,19; 6.0,12; 6.5,6; 7.0,10; 7.5,9; 8.0,14; 8.5,15; 9.0,23; 9.5,13; 10.0,26; 10.5,12; 11.0,7; 11.5,11; 12.0,15; 12.5,9; 13.0,7; 13.5,6; 14.0,3; 14.5,3; 15.0,1; 16.0,1; 17-26: E 1; L: 4.5,1; 5.0,2; 5.5,1; 6.0,1; 7.0,1; 9.5,1; 11.5,1; 12.5,1; 13.5,1; 25-33: E 1; L: 4.5,1; 11.5,1; 12.0,1; 14.0,2; 14.5,1; 15.5,1; 30-53: E 0; L: 11.5,1; 52-73: E 0; L: 0; 68-98: E 0; L: 0; 97-142: E 0; L: 0.

2452N; 6/17-18/41; 22h-3h; 32:23, 117:52; C; 0-3: E 1; L: 11.0,1; 12.0,5; 12.5,4; 13.0,3; 13.5,3; 14.0,2; 14.5,1; 15.5,1; 18.5,1; 7-12: E 0; L: 8.5,1; 13.5,1; 14.0,1; 15-24: E 0; L: 9.0,2; 11.0,2; 11.5,1; 12.0,1; 12.5,2; 13.0,1; 13.5,1; 15.0,2; 22-35: E 0; L: 13.0,1; 36-52: E 0; L: 10.5,1; 11.5,1; 14.5,1; 48-84: E 0; L: 0; 57-101: E 0; L: 0; 90-146: E 0; L: 0.

2452D; 6/18/41; 9h-14h; 32:17, 117:52; C; 0-3: E 0; L: 0; 6-12: E 0; L: 0; 14-21: E 0; L: 0; 25-36: E 0; L: 11.5,1; 38-43: E 0; L: 11.5,1; 12.5,1; 52-67: E 0; L: 17.5,1; 18.0,1; 68-81: E 0; L: 18.0,1; 96-152: E 0; L: 0; 125-156: E 0; L: 0.

2454N; 6/18-19/41; 21h-2h; 32:12, 118:38; C; 0-4: E 8; L: 4.5,1; 5.0,2; 6.0,1; 6.5,2; 7.0,1; 9.0,1; 9.5,1; 10.0,1; 10.5,3; 12.5,1; 18-25: E 1; L: 4.5,1; 5.0,2; 6.0,1; 6.5,2; 8.5,1; 9.0,2; 10.5,1; 11.0,1; 12.0,1; 12.5,1; 18-25: E 1; L: 5.0,1; 7.5,1; 8.0,1; 9.0,3; 9.5,4; 10.0,1; 11.0,2; 12.0,2; 12.5,1; 13.0,1; 13.5,1; 14.0,2; 14.5,2; 15.0,1; 24-32: E 0; L: 4.5,5; 5.0,2; 5.5,1; 7.0,2; 8.5,1; 9.0,2; 9.5,3; 11.0,5; 11.5,3; 12.0,3; 12.5,3; 13.0,4; 17.5,1; 38-52: E 0; L: 10.0,1; 11.0,2; 12.5,1; 52-69: E 0; L: 0; 66-108: E 0; L: 0; 90-149: E 0; L: 0; 122-208: E 0; L: 0.

2454D; 6/19/41; 8h-13h; 32:10, 118:39; C; 0-3: E 3; L: 6.0,1; 10.0,2; 12.0,1; 12.5,1; 7-14: E 1; L: 0; 17-25: E 0; L: 4.5,1; 6.0,3; 6.5,1; 10.0,1; 23-36: E 0; L: 4.0,2; 4.5,4; 5.5,2; 13.0,1; 36-47: E 0; L: 5.0,1; 12.0,1; 52-69: E 0; L: 21.0,1; 26.0,1; 70-85: E 0; L: 0; 99-121: E 0; L: 0; 120-198: E 0; L: 0.
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