Japanese Anchovy Egg Accumulation at the Sea Surface or Pycnocline—Observations and Model

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Near surface vertical distributions of Japanese anchovy eggs (isolated and pelagic) were studied at western Wakasa Bay, Japan. Samples were collected in horizontal tows with four plankton nets simultaneously operated at different four depths of 0, 0.5, 1.0, and 2.0 m. The egg concentration was found to decrease exponentially with depth. The egg concentration profile can be explained by considering the balance of the eggs’ ascent and vertical diffusion. Taking further into account vertical difference in rising/sinking rates of the eggs, a clear accumulation of the eggs on a pycnocline, observed elsewhere, also can be explained. Vertical eddy diffusivity in the surface layer in a calm sea was 1–10 cm² s⁻¹, as estimated from the egg concentration profile and the velocities of the eggs in the vertical direction.

1. Introduction

The distribution of fish eggs and larvae is one of the most pressing problems in fisheries science (Lasker, 1987). A prerequisite to any program of quantitative sampling of plankton organisms is a knowledge of their depth distribution (Ahlstrom, 1959). I believe that knowledge of physical processes which determine egg/larval vertical distribution is important when predicting egg/larval horizontal drift in relation to their survival and subsequent recruitment.

Besides a number of descriptive work on vertical distribution of floating organisms, reviewed by Banse (1964), Smayda (1970), Zaitsev (1971), and Russell (1976), attempts to explain the physical processes controlling the vertical distribution of floating fish-eggs and larvae are not many. Although there exist a few exceptions adopting one-dimensional models incorporating egg buoyancy for explaining field data (Sundby, 1983; Page et al., 1989; Westgård, 1989), observations on the vertical distribution in those studies were with rather coarse resolution over 5 m or more, and physical consideration on fine-scale distribution of fish eggs and larvae is scarce. This scarcity is due to some difficulties in acquiring data in situ; fish eggs and larvae in the sea are usually found in a smaller concentrations than those of phytoplankton and invertebrate zooplankton that in situ observations could not always provide satisfactory vertical resolutions to allow detailed physical analysis. Nevertheless, considering that phytoplankton and zooplankton concentrations in situ have already been revealed to vary within only 0.2 m in the vertical direction (Owen, 1981), we have to notice that there are some possibilities of serious underestimation of the egg concentration at a certain level when we examine vertical distributions of fish eggs using ordinary plankton-nets; it possibly arises when the resolution exceeds only a few meters.

In the present study, I showed that the concentrations of floating eggs of marine fish sometimes vary drastically within only a half meter in the vertical direction, and attempted to understand the physical processes in the vertical distributions of the eggs, aiming to explain how
egg buoyancy controls their vertical distributions, to discuss the effect of the egg rising/sinking rates varying in the vertical direction due to the depth distribution of water density around the eggs, and to estimate the vertical eddy diffusivity according to the egg concentration profiles and the rising/sinking rates of the eggs.

2. Materials and Methods

2.1 Samplings

Near surface vertical distributions of plankton were observed at western Wakasa Bay, the Sea of Japan, on the daytime (8:00–12:15) of 30 July 1981 (Fig. 1) under blue sky and a calm sea (0–1 Beaufort wind scale) with negligible tidal current. Plankton from different 4 depths near the sea surface (0–2 m) was successfully sampled at 8 sites within a 10 km area. The samplings were made with “Ladder Nets” (M. Ueno, unpublished), which can simultaneously collect plankton from several levels within a few meters near the surface (Fig. 2). This is a modified gear of a push-net system (Miller, 1973). The “Ladder Nets” consists of two ladder-like frames of steel with several 30 cm × 60 cm rectangles for attaching plankton nets. The frames were rigged at both sides of the front part of a boat and held perpendicular to the sea surface during collection. The research boat (12-m long and 4.4 metric tons) “Shiranami-maru” of the Faculty of Agriculture, Kyoto University, was conveniently small enough for the sampling procedure below.

For each sampling, four nets (0.33 mm mesh opening) were simultaneously pushed with the boat at a constant speed of 0.5 m s⁻¹ for 10 min; the boat moved horizontally 300 m during each sampling accordingly. The levels of the center of net-attached mouth below the sea surface were

![Map showing the study site. Numerals denote the order of each observation conducted from the southern point to the north (8:00–12:15). Plankton samples were successfully collected at 8 points (solid circles and triangles) through simultaneous 10 min (300 m) tow with 4 nets at different levels near the surface (0, 50, 100 and 200 cm). Temperature and salinity were measured at 7 points indicated by both solid and open circles. At the open circle (number as 3) only temperature and salinity measurement was accomplished.](image-url)
Fig. 2. Sampling gear “Ladder Nets”, which collects plankton simultaneously from different levels near the surface. Dimensions are in centimeters.

maintained at 0.1 and 1 m on the port side and at 0.5 and 2 m at the starboard side. The upper bar of the net-mouth for the uppermost level was kept several centimeters above the sea surface so that about 80% of the mouth area was in the water; this will be referred to as the “surface level” hereafter. While sampling, the gear was kept well clear of the bow wave of the boat. A flow meter was attached at the mouth of each 4 nets to estimate the water volume filtered. Samples were bottled and preserved in buffered 10% formaldehyde-seawater solution immediately after each collection.

2.2 Water temperature and salinity measurement

Water temperature and salinity were measured at seven points shown in Fig. 1, using a thermo-salinograph (Type ST-1D of Tsurumiseiki Co.) at 0, 0.5, 1.0, 1.5, and 2.0 m below the sea surface. Water densities corresponding to the temperature and salinity measurements were computed.

2.3 Sorting and counting

All fish eggs and larvae were sorted and counted under a microscope in the laboratory. The present study deals with two types of fish eggs captured abundantly. One type is of Japanese anchovy Engraulis japonicus, and the other, not being able to be identified but likely to belong to a single species (referred to as “Type-1” hereafter). Detailed characteristics of these two are shown in Table 1. The number of eggs were converted to “concentration”, i.e., the individual number per 100 m³ corresponding to the actual sampled volume (43–76 m³) of seawater.
Table 1. Characteristics of eggs examined.

<table>
<thead>
<tr>
<th>Type</th>
<th>Dimensions in mm (shape)</th>
<th>Developmental stage*</th>
<th>Oil globule</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Engraulis japonicus</em></td>
<td>0.6 × 0.6 × 1.2 (ellipsoid)</td>
<td>A–B</td>
<td>0</td>
</tr>
<tr>
<td>Type-1</td>
<td>0.85–0.95 (sphere)</td>
<td>A</td>
<td>1</td>
</tr>
</tbody>
</table>

*Developmental stage A: from spawning until germ ring reached near the equatorial position, B: after the end of stage A and before separation of tail from yolk surface.

3. Results

3.1 Vertical distribution of eggs

Japanese anchovy egg concentration had a tendency of exponential decrease with increasing depth (Fig. 3). Type-1 eggs were apparently concentrated at the surface level but scarce at lower levels (Fig. 4). The difference between the two may primarily be due to the differences in their physical properties, because the eggs are not locomotive and both the anchovy and Type-1 eggs were captured in the same collections. Ascending/descending velocity due to species-specific and/or developmental stage-specific density, shape, and dimensions may control the vertical distributions of eggs (Sundby, 1983).

3.2 Model of egg vertical distribution

Vertical profiles of particle concentration in water column over a wide area can be explained by considering the balance of their vertical velocity versus water and vertical flux by eddy diffusion (e.g. Okubo, 1980). Sundby (1983) applied a similar treatment to explain vertical distributions of pelagic fish eggs. Also for the present case, such one-dimensional model can be adopted to consider the egg vertical distribution, because: (1) The vertical scale of the present observation was 2 m, (2) The eggs treated here was assumed to rise 0.02–0.1 cm s⁻¹, as will be shown later in the following text, (3) Japanese anchovy in natural waters is known to spawn near surface, and (4) The spawning time of this fish is limited within few hours before midnight (Azeta, 1981; Fukuura, 1983; Kawaguchi et al., 1990) and hence we can regard the eggs captured during the research must pass over eight hours in the water column taking the time of day (08:00–12:15) when the samplings are done, so that such eggs could be considered to have passed enough time for vertical dispersion to allow us to approximate their vertical distribution in the surface layer in nearly steady state.

Following Sundby (1983), we can explain the steady-state distribution of eggs in the vertical direction as:

\[
KdS/dz - w(z)S = 0
\]

where \(K\) is a virtual diffusivity (cm² s⁻¹) in the vertical direction which incorporates the effects
of various processes arising from the averaging such as small scale vertical advection (Okubo, 1980); $S$, the concentration of eggs; $z$, the distance from the sea surface (cm), and $w(z)$, the vertical component of the egg velocity ($\text{cm s}^{-1}$, positive downward) as a function of $z$. Here, averaging over a large area, we may ignore the effects of horizontal advection and diffusion. Although, there may exist depth variation in the $K$ value in the actual condition, I simply consider the value constant through the depth range treated here because no marked discontinuities were found in the depth distributions of water density (Fig. 5).

Integrating Eq. (1) in the most simple cases when both $K$ and $w(z)$ are constant, we obtain the distribution of the egg concentration by Eq. (2),

$$S(z) = S_0 \exp \left( \frac{w}{K} z \right)$$

(2)
where $S_0$ is the egg concentration at the sea surface.

Equation (2) gives a good fit for the exponential decrease with depth of the in situ vertical profiles of the anchovy egg concentrations described above. Five of the eight profiles are significantly fit by curves of exponential decrease with depth (Table 2), and hence it is assumed that, in this study area during the observation, the egg concentration had a tendency of exponential decrease with depth. The values of $w/K$, ranging from $-0.0084$ to $-0.0098$ cm$^{-1}$ giving exponential curves as good fits for the actual profiles (Table 2), may permit us to assume that the relation between $w$ and $K$ in the study area is somewhat stable during the observation. Given the relation of $w/K$ ranging from $-0.0084$ to $-0.0098$ cm$^{-1}$ was realistic, the $K$ value could be assessed knowing the $w$.

Applying Stokes’ Law, we can estimate the velocity using Eq. (3),

$$w = \frac{\Delta \rho g D^2}{18 \eta}$$

(3)

where $\Delta \rho$ is the excess density of an egg compared with the medium seawater; $g$, the gravitational acceleration; $D$, the egg diameter and $\eta$, the molecular viscosity of seawater. Here, because the anchovy eggs are ellipsoid with 0.12 cm, 0.06 cm, and 0.06 cm in the three axes (Fukuhara, 1983), the $D$ value in Eq. (3) should be 0.08 cm (the diameter of a sphere with the same volume as this ellipsoid). Because at low Reynolds number, the resistance against this sphere ranges 95–110% of that of the ellipsoid (McNown and Malaika, 1950), we can practically assume this sphere well represents the egg motion in the viscous fluid.

As $\Delta \rho$ estimation, I adopted the value ranging $-5 \times 10^{-4}$ to $-4 \times 10^{-3}$ g cm$^{-3}$ to substitute into Eq. (3), because (1) Japanese anchovy eggs in their early to middle developmental stages, for over 20 h, are known to be $5 \times 10^{-4} - 4 \times 10^{-3}$ g cm$^{-3}$ less dense than the seawater in which they were spawned (Tanaka, 1990a, c), which may be true within a considerable range of salinity (May, 1974), and (2) although the salinity of the medium at the time of fertilization affects the buoyancy of a floating fish-egg until hatching, transferring the fertilized egg to a different density will alter its buoyancy to only a limited extent (May, 1974). The viscosity $\eta$ is about 0.01 g cm$^{-1}$s$^{-1}$ for
Table 2. Fitting curves to anchovy egg concentration profile of each site and that averaged over whole site, as an exponential function of depth: \( S(z) = S(0)\exp(w/K)z \), as described by Eq. (2) in text. Regression curves were computed with a least squares program. Asterisks under \( P \) denote statistical significance of each regression according to the correlation coefficient \( r \) between actual data and those on each fitting curve on each sampled depth (*: over 95% significant, **: over 99%).

<table>
<thead>
<tr>
<th>Site</th>
<th>( S(0) )</th>
<th>( w/K ) (cm(^{-1}))</th>
<th>( r )</th>
<th>( P )</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>163</td>
<td>-0.00887</td>
<td>0.960</td>
<td>*</td>
</tr>
<tr>
<td>2</td>
<td>182</td>
<td>-0.0124</td>
<td>0.907</td>
<td></td>
</tr>
<tr>
<td>4</td>
<td>91</td>
<td>0.00263</td>
<td>0.657</td>
<td></td>
</tr>
<tr>
<td>5</td>
<td>224</td>
<td>-0.00892</td>
<td>0.981</td>
<td>*</td>
</tr>
<tr>
<td>6</td>
<td>83</td>
<td>-0.00178</td>
<td>0.638</td>
<td></td>
</tr>
<tr>
<td>7</td>
<td>1763</td>
<td>-0.00979</td>
<td>0.959</td>
<td>*</td>
</tr>
<tr>
<td>8</td>
<td>1099</td>
<td>-0.00835</td>
<td>0.980</td>
<td>*</td>
</tr>
<tr>
<td>9</td>
<td>1201</td>
<td>-0.00955</td>
<td>0.997</td>
<td>**</td>
</tr>
<tr>
<td>Whole</td>
<td>597</td>
<td>-0.00843</td>
<td>0.979</td>
<td>*</td>
</tr>
</tbody>
</table>

seawater ranging from 20–30°C and 30–35 ppt (Sverdrup et al., 1942), and \( g = 980 \) cm s\(^{-2}\). Substituting these values into Eq. (3), we can estimate \( w \) ranging from \(-0.02 \) to \(-0.1 \) cm s\(^{-1}\), suggesting that the eggs rise slowly. Recent study showed this estimate realistic (Tanaka, 1990c). The variation in the \( w \) values between 0–2 m from the sea surface in the study area could not exceed 0.02 cm s\(^{-1}\) because the water density variation in the vertical direction was \( 0.42 \times 10^{-3} \pm 0.19 \times 10^{-3} \) g cm\(^{-3}\) (standard deviation) (Fig. 5). Thus it is practically appropriate here to assume the \( w \) constant in this layer.

When \( w \) ranges from \(-0.02 \) to \(-0.1 \) cm s\(^{-1}\), we can roughly estimate the virtual vertical eddy diffusivity \( K \) to be 2–10 cm\(^2\)s\(^{-1}\) since \( w/K \) is approximated from \(-0.008 \) to \(-0.01 \) cm\(^{-1}\). The \( K \) values are realistic considering the previous estimates for surface layers (Okubo, 1970).

The apparent accumulation of Type-1 eggs at the surface level can also be explained using the above treatment, assuming that these eggs ascend rather swiftly due to the larger size than that of anchovy eggs. For this profiles, however, it does not seem worth trying to get good fits because the vertical gradient in egg concentration near the surface level is rather steep compared with the vertical resolution of this sampling gear.

Further, when the vertical velocity \( w(z) \) is not constant (varies with depth), Eq. (1) is solved as:

\[
S(z) = S_0 \exp \left\{ K^{-1} \int_0^z w(z) \, dz \right\}. \tag{4}
\]

Assuming that the seawater density increases linearly with depth, we can expect \( w(z) \) to linearly decrease with depth as:

\[
w(z) = w_0 - cz, \tag{5}
\]

where \( w_0 \) is the downward velocity at the sea surface, \( c \) is a positive constant. This assumption
may be appropriate because seawater density usually increases with depth and, according to Stokes’ Law, downward velocity of a particle at a low Reynolds’ number increases linearly with its excess density over the surrounding seawater (in this case, the increase in seawater viscosity due to decreasing temperature and increasing salinity was neglected). The Reynolds’ number about the anchovy eggs usually does not exceed unity based on actual measurements of egg dimensions, ascending or descending velocity of the eggs (Tanaka, 1990a, c).

Substituting Eq. (5) into Eq. (4), we obtain:

\[
S(z) = S_0 \exp \left\{ K^{-1} \left\{ \int_0^z (w_0 - cz) dz \right\} \right\}
\]

\[
= S_0 \exp \left\{ K^{-1} \left( w_0z - 0.5cz^2 \right) \right\}. \tag{6}
\]

This equation can explain the vertical profile of egg concentration within a linearly stratified layer. Adopting arbitrary values for \( w_0, c \) and \( K \), we can get various profiles of egg concentration, some of which well fit the actual data below.

Figures 6 and 7 show some results derived by substituting practical values for \( w_0, c \) and \( K \). Here, we can see two types of egg concentration profile resembling those in situ. In the first case, when \( w_0 < 0 \) (eggs have upward velocities up to the surface), the profile shows a higher ratio of decrease in concentration with depth than the simple exponential curve obtained when \( w(z) = w_0 = \text{const.} \) (Fig. 6). With this treatment, we could get any fits to the in situ data.

In the second case, Eq. (6) can give another profile with a peak at the level where eggs attain neutral buoyancy when \( w_0 > 0 \), i.e., eggs near the surface descend, become neutrally buoyant at a level, and those below the level ascend (Fig. 7). This computed profile resembles that with a clear peak at a pycnocline (Fig. 8), observed by Sekiguchi et al. (1989) in Ise Bay. Such a case can be observed in situ as this bay where near surface was clearly affected by river water. Due to the physiological reasons described before, floating fish-eggs spawned below the pycnocline should be negatively buoyant when transferred into the upper less-dense layer.

Another model also can well explain the profile by Sekiguchi et al. (1989). The vertical

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**Fig. 6.** Vertical profile of egg concentration according to Eq. (6). The thin line: when \( w(z) = w_0 = -0.05 \) cm s\(^{-1}\); the thick line: when \( w(0) = -0.05 \) cm s\(^{-1}\), \( w(200) = -0.1 \) cm s\(^{-1}\) and \( K = 2 \) cm\(^2\) s\(^{-1}\).
Fig. 7. Vertical profiles of egg concentration according to Eq. (6) when \( w(0) = 0.1 \text{ cm s}^{-1} \), \( w(300) = 0 \text{ cm s}^{-1} \) and \( K = 2 \text{ cm}^2 \text{s}^{-1} \). Here, the \( z \) axis ranges from 0 to 1500 cm to compare this figure with Fig. 8.

Fig. 8. Vertical profile of Japanese anchovy egg concentration and water density (re-drawn after Sekiguchi et al., 1989, and their original data). Solid circles joined by thick lines are mean values of 4 replicate samplings. Horizontal bars show \( \pm \) standard deviation ranges about the mean values. Thin line within shaded area is the averaged water density profile at the 4 sampling sites; the shaded area denotes \( \pm \) standard deviation range.

Profile of water density in Fig. 8 shows the water columns above and below the sharp pycnocline respectively are fairly homogeneous. The pycnocline, with a change in water density from 1.017 to 1.022 g cm\(^{-3}\) between 3 and 4 m below the sea surface, should be too sharp for the eggs to pass and hence regarded as a strict boundary in the vertical distribution of the eggs. We can assume here, according to the mentions above, that the density of anchovy egg was adjusted slightly smaller than the water below the pycnocline, but that it cannot be positively buoyant in the upper layer because of the considerably low water density there. Then we may assume that the downward velocities of the eggs above and below the pycnocline, respectively, were a positive constant \( w_1 \), and a negative constant \( w_2 \), and on the pycnocline, zero. Then, we can draw profiles
peaked at the pycnocline as:

\[
S(z) = S(a) \exp \left( \frac{w_1}{K_1}(z-a) \right) \quad (0 < z < a)
\]

\[
S(z) = S(a) \exp \left( \frac{w_2}{K_2}(z-a) \right) \quad (a < z)
\]

(7)

where \(a\) is the level of the pycnocline from the sea surface; \(S(a)\), the egg concentration at the pycnocline; \(K_1\) and \(K_2\), the vertical eddy diffusivity above and below the pycnocline, respectively.

Figure 9 shows some examples of egg concentration profile when \(a = 300\, \text{cm}, w_1 = 0.1\, \text{cm s}^{-1}, w_2 = -0.1\, \text{cm s}^{-1}\), and various \(K_1\) and \(K_2\). The \(a\) value was based on the position of the peak seen in Fig. 8. The tentative values for \(w_1\) and \(w_2\) in Fig. 9 is realistic; substituting \(\Delta \rho = \pm 3 \times 10^{-3}\, \text{g cm}^{-3}\) into Eq. (3) considering the difference in water density \(5 \times 10^{-3}\, \text{g cm}^{-3}\) between the two layers, we get \(-0.1\) and \(+0.1\, \text{cm s}^{-1}\) for the \(w\) values in layers above and below the pycnocline, respectively.

It is obvious that, in this model, the sharpness of the egg concentration peak at the pycnocline increases with increasing \(w_1\) and decreasing \(w_2, K_1\) and \(K_2\). If \(w_1\) and \(w_2\) are appropriate here, we can see both \(K_1\) and \(K_2\) between 1 and 10 cm² s⁻¹ give better fits for actual data by comparing Figs. 8 and 9.

These estimates of \(K_1\) and \(K_2\) do not differ in terms of order from those attained under a calm weather and negligible tidal stirring at Wakasa Bay as described above. Also, when Sekiguchi et al.’s (1989) sampling was conducted, the weather was fairly calm (H. Sekiguchi, personal communication) and tidal current was negligibly weak (after their description). Thus the values of 1–10 cm² s⁻¹ may be realistic for near surface layer about 0–10 m or so under a calm weather with little tidal stirring.

From vertical distributions and buoyancies of eggs from pelagic fishes in the North Sea, Sundby (1983) had already estimated the \(K\) value under windless conditions to be about 80 cm²

![Fig. 9. Vertical profile of egg concentration according to Eq. (7) when \(w_1 = 0.1\, \text{cm s}^{-1}, w_2 = -0.1\, \text{cm s}^{-1}\) and various \(K_1\) and \(K_2\). The thin line, thick line, and dashed line respectively are obtained when both \(K_1\) and \(K_2\) are 2, 10, and 100 cm² s⁻¹.](image-url)
s$^{-1}$. This is rather large compared with my estimates for a calm sea, and this is due to the differences in physical factors depending on study sites, seasons, and vertical scales in consideration.

4. Discussion

It is natural to consider that to understand floating particle distributions in the sea, we have to understand the physical properties of object particles together with distribution survey as stated by Sundby (1983). Now the use of considering the depth variation in egg rising/sinking rate due mainly to the increase in water density with depth should be taken into account. Various physical properties may additionally affect the egg rising or sinking, such as depth variation in molecular viscosity of seawater. How these affect the egg distribution is to be examined further. However, if eggs are surrounded by some chemical substances existing in seawater or exuded from the eggs themselves, the velocities might become higher than the estimates above. Thus, detailed discussion considering small variations in physical properties alone would not be sufficient without knowledge about physiological characters of object organisms particle; the distribution of living particle cannot be fully understood if we treat it as merely a non-living particle. Studies on the distributions of biotic particles like pelagic fish-eggs require further knowledge about their biological properties, for example, the buoyancy of the eggs are not always uniform during development; some species increase in egg density drastically during a few hours before hatching (Tanaka, 1990a, b; Tanaka et al., 1991); after hatching their locomotion should also be taken into account. Lastly, I would like to stress that studies on the mechanisms of the distributions of biotic particles are more complex than that of abiotic ones, requiring both physical, biological, and chemical, which are, interdisciplinary approaches.

5. Conclusions

Accumulation of Japanese anchovy *Engraulis japonicus* eggs at the sea surface and their exponential decrease with depth between 2 m were exemplified through a set of well designed field observations using a depth-discrete plankton sampler. This tendency in the vertical profile was physically explained with a one-dimensional model by considering the balance of the eggs’ ascent and vertical diffusion. Knowing the egg rising rate, we could roughly estimate the vertical eddy diffusivity in the surface layer to be 1–10 cm$^2$ s$^{-1}$. Taking into account the vertical difference in rising/sinking rates of the eggs, the model can further explain a previous observation showing the egg accumulation on a pycnocline. It was stressed that physical consideration alone is not always enough for understanding the mechanism of the spatial distributions of biotic particles such as fish eggs.

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