The Dependence of Yearly Recruitment of Japanese Sardine *Sardinops melanostictus* on Survival in the Kuroshio-Oyashio Transition Region

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We have numerically modeled the transport and survival processes of Japanese sardine eggs and larvae *Sardinops melanostictus* in the Kuroshio-Oyashio region to investigate the dependence of yearly recruitment of the sardine on the mortality rate during the early life stages. The model covers from 130°E to 160°E and simulates the Kuroshio Current and wind-induced current resulting from the winter monsoon in a simple way. As a biological process, natural mortality of the eggs and larvae is parameterized by area and year, considering the oceanographic condition such as the extent of southward intrusion of the Oyashio. The year-to-year variations in the amount of survivors simulated by the model are compared to that of one-year sardine stock based on the field data. The variation in the abundance of one-year old sardine is well correlated to that of the surviving juveniles off the east but not the south of Japan, both of which are calculated by the model. This indicates that the survival condition after the postlarval period off the east coast of Japan, which is strongly affected by the Oyashio, could play an important role in determining the year class strength. A strong year class can be formed by the numerous juveniles transported to the east and/or by the good survival condition in the eastern offshore region of Japan.

Key words: recruitment, sardine, numerical model, Kuroshio-Oyashio Transition area, survival, simulation

The catch of Japanese sardine *Sardinops melanostictus* in 1994 was about one million tons and comprised 15% of the total catch around Japan. It is used as food for many kinds of cultured fish such as yellow-tail *Seriola quinqueradiata*, in addition to being used for human consumption. Moreover, sardine is considered to be an important species to the ocean ecosystem around Japan because of its large biomass. On the other hand, it is also well known that sardine's stock exhibits a very wide variation over a period of several decades. The catch of sardine around Japan has exponentially increased since 1973 and was at a high level of more than four million tons in the early 1980s. However, since 1989 it has started to decline. Large variations in the stock are consistent with information from a 16th century document. The mechanism of these changes have not yet been clarified.

It is widely noted that the transport of eggs and larvae from the spawning grounds to their nurseries is one of the most important physical factors which determine the recruitment of pelagic fish stocks. In recent years, therefore, increased attention has been focused on the simulation of egg and larval transport to understand the mechanism behind the variability of pelagic fish stocks. In regard to the Japanese sardine, Kasai *et al.* numerically modeled the advection and diffusion of Japanese sardine eggs and larvae in the south of Japan to examine the effects of larval transport on the recruitment. Their results indicated that the spawning location and the offshore drift current induced by the winter monsoon during the spawning period had a significant effect on the survival of sardine larvae. They also obtained a significant correlation between the year-to-year variation in larval survival rates estimated from the numerical experiment and those estimated from the field data.

However, their study still has a limitation. Recent studies have revealed that the larval survival of Japanese sardine within one month after spawning off the southern coast of Japan did not always correlate with the sardine's year class strength. In addition, Sugisaki reported that many postlarvae and juveniles of sardine were caught in the far east offshore of the Japanese Pacific coast. These studies indicate that the larvae transported far east offshore are still alive and may be able to recruit. If larvae and juveniles were abundant in the east offshore of Japan, the Oyashio could affect the survival of sardine larvae because the Oyashio Current is richer with nutrients compared to the Kuroshio water. Kodama *et al.* suggested that the population of one-year old sardine was correlated with the Oyashio southward intrusion. The experimental period of Kasai *et al.* was only 20 days after spawning and their model area only extended to 145°E, which were too short and too small respectively, to simulate the recruitment of sardine. Their model could simulate the abundance of larvae off the southern coast of Japan, but not the year class strength.

In this study, therefore, a numerical model is developed, which covers the area extending from the Kuroshio to the Oyashio and the Kuroshio-Oyashio Transition areas. The
model simulates the number of sardine survivors each year during 1978-1988, which is then compared to that of one-year-old sardine previously estimated from the catch off the east coast of Hokkaido. This study aims to look at the contribution of the survivors in the Kuroshio-Oyashio Transition area to the recruitment in comparison with that off the southern coast of Japan. The implication of the egg and larval transport for the determination of the year class strength is also discussed.

Model

We have modified our egg and larval advection and diffusion model, which was previously developed to simulate the year-to-year variation in the larval survival of Japanese sardine.9) As the first modification, the model basin is extended from 145°E to the 160°E (Fig. 1). For simplicity, we assumed that the Kuroshio flows in a straight (non-meander) and there is no other current than the wind-induced drift current, because the large variation of the Kuroshio path has only a negligible effect on the offshore transport of Japanese sardine larvae in the previous model.9) Only the effect of the meso-scale eddies and tongues protruding from the Kuroshio in association with the variation in the Kuroshio's path with time scales less than a few months is included in the model. Kasai13) showed that when the Kuroshio took a large meandering path, the meso-scale warm water from the Kuroshio often intruded into coastal areas such as the Enshu-nada Sea (ENS) which is one of the most important nursery grounds for sardine larvae. The time scale of the intrusion was less than a few months. It was also estimated that 60% of the eggs and larvae in the Kuroshio frontal region were transported to the coastal area accompanied with warm water. This condition is imposed in our present model. The Prompt Report of Oceanographic Conditions, published biweekly by the Japan Maritime Safety Agency, is used to determine the type of the Kuroshio path. The path is defined as a contour of 15°C at a depth of 200 m.16)

The main spawning period of the Japanese sardine is from December to March. During this period, strong westerly or northwesterly monsoons prevail, which possibly causes offshore transport of the eggs and larvae.9,33) The offshore velocity of wind-induced current is calculated by substituting the monthly averaged wind velocity at meteorological stations along the Pacific coast for the wind term of the bulk formula. The wind velocity data (observed at 850 mb at 9 h and 21 h) obtained from Kagoshima, Shionomisaki, and Tatenoi are used as wind conditions from 130°E to 135°E, from 135°E to 140°E and from 140°E to 160°E, respectively. The current velocity in the model is then given by the vector sum of the geostrophic Kuroshio Current and Ekman drift components.

In this study, eggs and larvae of the Japanese sardine are treated as passive and conservative drifters; they are distributed near the surface, depths shallower than 100 m.16) Hence, the advection-diffusion equation of the eggs and larvae is expressed by:

\[
\frac{\partial C}{\partial t} + \frac{\partial}{\partial x}\left( uC - \kappa \frac{\partial C}{\partial x} \right) + \frac{\partial}{\partial y}\left( vC - \kappa \frac{\partial C}{\partial y} \right) = -\alpha C \quad (1)
\]

where \(C\) is the concentration of eggs and larvae, \(u\) and \(v\) are the velocities in \(x\) and \(y\) directions respectively, \(\kappa\) is the horizontal eddy diffusivity, and \(\alpha\) is the mortality rate of eggs and larvae.

The sardine egg and larval distribution has been observed every year since 1978 by the Japan Fisheries Agency.17,18) We used these data to detect the initial egg distribution each year.

The values of mortality rate and diffusivity used in the model are listed in Table 1 and shown in Fig. 2. In this paper, we call areas to the west and east of 140°E of the model basin the south and east of Japan, respectively. In the coastal and the Kuroshio regions in the south of Japan, the mortality rate \(\alpha\) is given as 0.15 d\(^{-1}\).10) This value is also applied to the Kuroshio extension area in the south of Japan. It takes about one month to be transported to the east of Japan for larvae. The amount of postlarvae with body length of 10 mm, corresponding to larvae 20-30 days old, is on the order of \(10^{13}\) and that of one-year-old sardine is on the order of \(10^{10}\). Hence, apparent mortality including the decline in the larval density due to offshore transport is estimated as 1/60 ln (1000) = 0.12 from 30 to 90 days. Therefore, in the northern side of the Kuroshio Extension area (Kuroshio-Oyashio Transition area), the mortality rate \(\alpha\) is fixed at 0.05 for Case 1 from 30 to 90 days after spawning, while it varies within a range of 0.005-0.1 depending on the extent of southward intrusion of the Oyashio for the other cases. Figure 2(a) shows

![Fig. 1. Schematic view of the Kuroshio and Oyashio Currents, and configuration of the model basin.](image)

Black arrows indicate inlet and outlet for the Kuroshio. ENS and KOT denote Enshu-nada Sea and Kuroshio-Oyashio Transition area, respectively. 'South' and 'East' mean the area off the southern and eastern coast of the Japanese Islands, respectively.

<table>
<thead>
<tr>
<th>Area</th>
<th>South of Japan</th>
<th>East of Japan</th>
</tr>
</thead>
<tbody>
<tr>
<td>(\alpha) (d(^{-1}))</td>
<td>(\kappa) (cm(^2) s(^{-1}))</td>
<td>(\alpha) (d(^{-1}))</td>
</tr>
<tr>
<td>Coastal area</td>
<td>0.15</td>
<td>10(^6)</td>
</tr>
<tr>
<td>Kuroshio-Oyashio</td>
<td>---</td>
<td>---</td>
</tr>
<tr>
<td>Transition area</td>
<td>0.15</td>
<td>10(^6)</td>
</tr>
<tr>
<td>Kuroshio region</td>
<td>0.5</td>
<td>10(^6)</td>
</tr>
</tbody>
</table>

\(\alpha\) = mortality rate of sardine eggs and larvae; \(\kappa\) = eddy diffusivity coefficient. \(\star\) denotes that mortality rate varies depending on the Oyashio southward intrusion. See Fig. 2.
the relationship between the southern limit of the Oyashio and the ratio of the abundance of one-year old sardine to that of the egg. This suggests that more sardine larvae could survive when the Oyashio extended more southward and spread more widely. In Case 2, therefore, the mortality rate is reduced in proportion to the Oyashio southward intrusion. The mortality of larvae might not remain constant during the northward migration; larvae could experience higher mortality during the metamorphosis stage. This means that the southward intrusion of the Oyashio may not always affect the larval mortality linearly as in Case 2. In addition, the Kuroshio front and the secondary Kuroshio front usually exist around 36°N and 38°N, respectively. Larvae must experience large temperature changes when they cross the fronts during the northward migration. It could cause the great difference in mortality. Hence, as a trial, a step function as seen in Fig. 2(b) (Case 3) is applied to represent the change in the mortality rate corresponding to the extent of the Oyashio intrusion. The position of the Oyashio is defined as a 5°C contour at a depth of 100 m. We determine the southern limit of the Oyashio as the average of the most southern latitude of the Oyashio in each month between February and June, during which sardines are transported to the east of Japan. In both of the south and east of Japan, the mortality rates in the offshore areas are set to be constant and larger than those in the coastal or the Kuroshio area. Mortality rates in all experimental areas are fixed constant in time; from 0 d to 90 d.

The eddy diffusivity coefficient, \( \kappa \), is estimated to be \( 10^6 \) cm\(^2\) s\(^{-1}\) in the coastal and offshore areas south of Japan and Kuroshio-Oyashio Transition area, by taking the grid size into consideration. On the other hand, in the Kuroshio region, \( \kappa \) is taken as \( 10^7 \) cm\(^2\) s\(^{-1}\) off the southern coast of Japan and \( 10^8 \) cm\(^2\) s\(^{-1}\) in the Kuroshio Extension area, because the Kuroshio usually takes an unstable path in the Kuroshio Extension area (Table 1). The grid interval of the model is taken to be 10 km and the time step is 30 minutes.

We input these conditions into the model and calculate the distribution of the larvae for 90 days after the December, January, February, and March spawning. The number of yearly survivors from 1978 to 1988 is obtained by averaging the number of survivors after 30 and 90 days from each month. The numerical results are compared with the field data on the amount of one-year old sardine migrating to the east coast of Hokkaido previously estimated by Wada.23)

**Results**

The numbers of survivors one month after spawning in the total experimental area are calculated by the numerical model and presented in Fig. 3, together with the numbers of postlarvae less than 10 mm in total length collected at sea by the Japan Fisheries Agency. It is clear that the year-to-year variation in the larval abundance calculated by the model correlates well with that in postlarval abundance (\( r=0.97, p <0.0001 \)). This indicates that the number of survivors during the first month is decided by the egg abundance and transport. The result coincides with those by Watanabe et al.10) and Kasai et al.9) However, the number of survivors does not correlate with that of one-year old sardine (\( r=0.16 \)). This implies that the factors affecting survival after the postlarval period are more important in determining the year class strength.10) Only the effects of wind-induced current or the spawning position, which were regarded as important for the larval survival in the previous study,9) would be insufficient for determining the year class strength of sardine.

Figure 4 shows the numbers of surviving juveniles 90 days after spawning for each case. The correlation coefficients remain low between the year-to-year variations calculated by the model for all the total experimental area (Figs 4a–c) and those estimated from the field data on the amount of one-year old sardines (Table 2). However, the amount of surviving juveniles off the east coast of Japan (Figs 4d–f) show relatively high correlations with that of one-year old sardine (Table 2). This indicates that the sur-
Recruitment of Sardine

Fig. 3. Year-to-year variation in the abundance of (a) sardine larvae at 30 days after spawning calculated by the model, and (b) postlarvae up to 10 mm in total length estimated by the field data.

Fig. 4. Year-to-year variation in the abundance of sardine larvae at 90 days after spawning calculated by the model.

Table 2. Correlation coefficients and probability values between the year-to-year variations in sardine stock estimated by the field data and model results

<table>
<thead>
<tr>
<th>Case</th>
<th>Correlation</th>
<th>P-Value</th>
</tr>
</thead>
<tbody>
<tr>
<td>Case 1 All</td>
<td>0.122</td>
<td>0.7278</td>
</tr>
<tr>
<td>Case 2 All</td>
<td>0.328</td>
<td>0.3353</td>
</tr>
<tr>
<td>Case 3 All</td>
<td>0.432</td>
<td>0.1905</td>
</tr>
<tr>
<td>Case 1 East</td>
<td>0.241</td>
<td>0.4874</td>
</tr>
<tr>
<td>Case 2 East</td>
<td>0.421</td>
<td>0.2037</td>
</tr>
<tr>
<td>Case 3 East</td>
<td>0.670</td>
<td>0.0219</td>
</tr>
</tbody>
</table>

'All' and 'East' mean the stock in the total experimental area and off the east coast of Japan, respectively.

Survival in the Kuroshio-Oyashio Transition area plays an important role in the recruitment. In addition, higher correlation coefficients are obtained when the mortality is set to be changed by the Oyashio intrusion. Feeding conditions during postlarval and juvenile stages, which could be notably affected by the Oyashio, are considered to play an important role in determining the year class strength.

The year-to-year variation in the number of juveniles transported to the east of the Japanese Islands is shown in Fig. 5c. Comparing the number of juveniles off the east coast of Japan (Fig. 5c) with the egg or larval abundance in the south of Japan in each year (Figs 3a, 3b, and 5a), contribution of the larvae transported to the east (Fig. 5c) to all surviving juveniles (Fig. 5d) increased after 1985; a large number of larvae are transported to the east in 1985, 1986, and 1988 in the model. One of the reasons for this increase in the transport was the offshore shift of the spawning area. In 1988, however, the abundance of survivors off the east coast of Japan at 90 d decreased in conjunction with the northward retreat of the Oyashio (Fig. 5b, 5c, and 5d). In 1983, on the other hand, many sardine survived until 90 d despite the smaller number of larvae transported to the east than the other years. In this model, good recruitment was supported by the good survival conditions off the east coast of Japan in some years and by the abundance of the larvae transported eastward in other years. The year class strength would be determined by the survival conditions in the Kuroshio-Oyashio Transition area and/or the abundance of transported larvae to the area.

Discussion

The number of surviving juveniles off the east coast of Japan at 90 d is at the similar level to the southern coast by the model calculation (compare Fig. 4c with 4f). This indicates that a large number of larvae are transported to the east. It is therefore reasonable that many juveniles are caught in the far eastern area of the Japanese Islands as shown in Sugisaki's observation. The ratio will not change even if the calculation is continued after 90 d in this model, because the majority of the larvae in the Kuroshio area are already transported to the Kuroshio Extension area at 90 d.

It is reasonable that the sardine's survival is enhanced by the Oyashio intrusion, because primary and secondary production are increased by nutrient-rich water originating from the north when the Oyashio extends southward. For example, Kotani and Odate showed that...
zooplankton biomass off the east coast of Sanriku area in summer negatively correlates with the sea surface temperature. This indicates that the Oyashio southward intrusion possibly affects the food condition for sardine larvae and juveniles. In addition, Tomosada\textsuperscript{25}) reported that the sardine catch off the east coast of Japan increased when the water temperature was relatively low. Recruitment failure in 1988 has been considered to initiate the decline of sardine stock in 1990s. Our model results show that numerous larvae were transported to the east of Japan but could not survive in the Kuroshio-Oyashio Transition area in 1988 due to the Oyashio northward retreat. The large variability of the sardine stock could depend on the survival of larvae and juveniles in the Kuroshio-Oyashio Transition area. In addition, it is worth notice that a higher correlation obtained from Case 3 than from the other cases. The mortality indicated by the step function means that the survival rate changes remarkably if the Oyashio intrudes some latitude (36°N and 38°N). Furthermore, there would be both critical and non-critical areas for survival of sardine on the way to the east coast of Hokkaido from the Kuroshio Extension area. The actual mortality or survival rates in the Kuroshio-Oyashio transition region have not been measured. It is essential to detect the rates in the open ocean and detailed observation is needed.

The recruitment of sardine calculated by the model is also low in 1980 and does not correspond to the amount of one-year old sardine based on the field data (compare Fig. 5d with 5e). This suggests that the relation between water temperature and mortality in the Kuroshio-Oyashio Transition area should be considered in more detail. Here we analyze some existing data observed in 1980 by Iwate Prefectural Fishery Station, by way of an example to see the relation. Figure 6 shows the year-to-year variations in average temperatures at depths less than 100 m in summer. Temperature at Stn. 6 was low in 1980, in comparison with those at the other stations. Since the cold water from the north decreased the temperature, the food condition at Stn. 6 would be better than those at the others. Not only the area off Iwate, but also other offshore areas in the Kuroshio-Oyashio Transition area might have a good feeding condition for larvae in 1980 corresponding to smaller scale variations in the Oyashio intrusion as seen around Stn. 6, and this possibly led to a high survival rate. More detailed studies on the distributions of sardine larvae and juveniles, their prey, and predators interacting with meso- or small-scale physical features, especially off the east coast of Japan, are necessary to understand the survival process of sardine larvae.

In this study, the mortality rate was not assumed to vary by year off the southern coast of Japan, because the precise values are not yet known. The mortality rate may change with time and space. Nakata \textit{et al.}\textsuperscript{26}) reported that the meandering of the Kuroshio possibly depresses the production of food organisms for the larvae. However, a
large cyclonic circulation develops when the Kuroshio takes a meandering path. The upwelling of nutrient-rich water associated with the circulation is believed to activate primary and secondary production. Zenitani27) incubated sardine eggs and larvae in different temperatures and found that the survival rate could be highest at 19°C compared with at 15°C or 23°C. This implies that the temporary change in the Kuroshio path could affect the survival of sardine larvae through the ambient temperature. To estimate the actual mortality rate resulting from the environmental changes in the Kuroshio, more observational data on sardine larvae and their prey are required.

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