

A Numerical Modeling Study of Japanese Sardine (*Sardinops melanostictus*) Migrations in the Western North Pacific

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Abstract—A two-dimensional individual-based model coupled with fish bioenergetics was developed to simulate the migration and growth of Japanese sardine (*Sardinops melanostictus*) in the western North Pacific. In the model, fish movement is controlled by the feeding migration in addition to passive transport by ocean current. A kinesis is applied to the feeding migration in the modeling approach. Kinesis is a nondirectional, behavioral response to external stimuli in which animals change the speed or frequency of directional changes depending on the intensity of stimuli in their spatial surroundings. The model successfully simulated the observed transport patterns during the egg and larval stages and northward feeding migrations during the juvenile stage in 2005, 2006 and 2007. The model results indicate that both temperature during the larval stage in the Kuroshio Extension and the prey availability during the early juvenile stage in the Kuroshio-Oyashio transitional area are important factors for determining the survival of Japanese sardine in the western North Pacific.

Keywords: Japanese sardine, migration, recruitment success

INTRODUCTION

The stock fluctuations of sardine and anchovy in the western North Pacific are related to interdecadal North Pacific ocean/climate variability (Yasuda *et al.*, 1999). Concerning the population alternation between sardine and anchovy, Takasuka *et al.* (2007) proposed a simple hypothesis, called the “optimal growth temperature hypothesis”. They showed the optimal growth temperature for Japanese sardine larvae is lower than that of Japanese anchovy (*Engraulis*

japonicus), and hence suggested the stock of Japanese sardine increase and anchovy decrease simultaneously during a cooler climate regime. On the other hand, Takahashi *et al.* (2009) suggested that temperature and food availability through the late larval and early juvenile stages in the transitional waters are key factors controlling early growth and hence the population dynamics of sardine and anchovy in the western North Pacific. In the present study we developed a two-dimensional individual-based model coupled with fish bioenergetics in order to simulate migration and growth of Japanese sardine (*Sardinops melanostictus*) in the western North Pacific. Based on the model results we discuss what are the important factors for recruitment success of Japanese sardine during the periods of larval transport and feeding migration of juvenile in the western North Pacific.

METHODS

We developed a horizontal two-dimensional individual-based spatio-temporal model, which is applied to Japanese sardine in the western North Pacific, based on Okunishi *et al.* (2009). The model has a domain of 10°N–50°N and 100°E–160°W in the western North Pacific. The individual-based model is composed of a bioenergetics sub-model and a Lagrangian transport sub-model. The bioenergetics sub-model estimates growth of sardine. The Lagrangian transport sub-model simulates the position of sardine using the ocean current and predicted swimming directions. For oceanic environmental data as the driving force in the model, we used the sea-surface velocities field which was estimated at intervals of seven days with a horizontal resolution of 1/4° by combining satellite altimeter data and sea-surface drifter data (Ambe *et al.*, 2010), sea surface temperature (SST) from NOAA optimum interpolation 1/4 degree daily sea surface temperatures (AMSER + AVHRR) (Reynolds *et al.*, 2007) and daily Chl-a distributions on the Sea-viewing Wide Field-of-view Sensor (SeaWiFS) with the horizontal resolution of 1/12°. Chl-a distributions were used for the prey field of Japanese sardine as forcing data of the bioenergetics sub-model. In the model, fish movement is controlled by the feeding migration combined in addition to passive transport by estimated sea-surface velocity. Two-dimensional trajectories of the simulated fish are computed using an Euler-Lagrangian approach. Swimming speeds and directions during the feeding migration are estimated by a kinesis model based on Humston *et al.* (2000). In the kinesis model, swimming velocity can be modeled considering two components, such as the inertial velocity from the previous time step and some random velocity. The model was carried out for 7 months starting from April 1st to October 31st in 2005, 2006 and 2007 by using realistic oceanic environmental data as the driving force. In the model, spawning points were set as 120 individuals along the southern coast of Japan based on the gridded egg density data from *in situ* observation by Fisheries Research Agency and prefectural fisheries research laboratories in Japan (e.g. Oozeki *et al.*, 2007). We assumed that individual eggs could be spawned from April 1st to April 30th at the spawning points each day if the temperature condition is in the optimal range (15–21°C: e.g., Kuroda, 1991) for spawning of Japanese sardine.

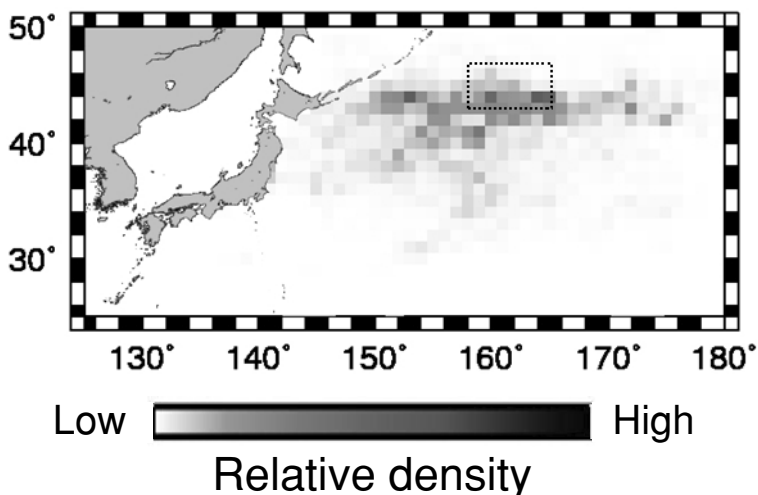


Fig. 1. Fish distribution (density) in autumn (September–October) in the model. Relative density shows averaged density in 2005, 2006, 2007. Rectangle in dotted line shows high density region in autumn in observation data (Kawabata *et al.*, 2008).

RESULTS

In the model, simulated larvae and early-juveniles, which have no or weak swimming capability, are transported eastward from the spawning region to 160°E until May by the strong Kuroshio Current. In autumn (September–October), many fish migrate to the cold water below 14°C, and experience relatively high Chl-a ($>0.5 \text{ mg m}^{-3}$) conditions in the model. The model reproduces the observed fish distribution during juvenile stage in autumn (Fig. 1).

Sizes of fish at October 31st (end of simulation) have a wide range. Larger fish have a higher probability of survival following on “the bigger is better hypothesis” (Miller *et al.*, 1988). Therefore, the model results of fish size-distribution can be important information to investigate the factors regulating recruitment success of sardine. Here, we divided individual fish into three size groups based on body length of fish at the end of simulations (BL_{END}), such as small-fish-group ($BL_{\text{END}} < 7 \text{ cm}$), medium-fish-group ($7 \leq BL_{\text{END}} \leq 9 \text{ cm}$) and large-fish-group ($BL_{\text{END}} > 9 \text{ cm}$). We assumed that the population in large-size group has a higher probability for recruitment success. Individual fish in the large-size-group are exposed to near the optimal temperature of sardine (about 16–17°C) at 30 day-age (Fig. 2). Super-individual fish in the large-size-group are exposed to near the optimal temperature at 60 and 90 day-age. But, SST experienced by the small and medium-size-groups are higher than the optimal temperature of sardine at 30 day-age (larval stage) and 60 day-age (early juvenile stage), respectively. Chl-a of the individual locations in the large-size-group remain at relatively high concentration ($>0.4 \text{ mg m}^{-3}$ on average) at 30, 60 and 90

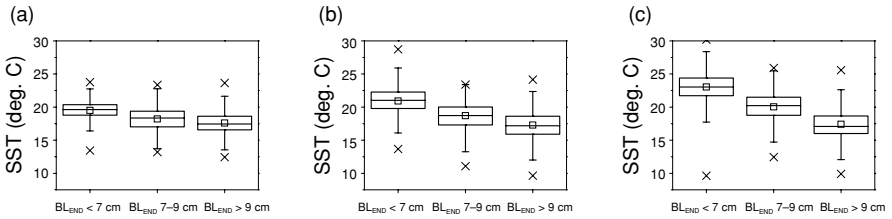


Fig. 2. Box-whisker plot of SST (sea surface temperature) on the individual fish location at each size group ($BL_{END} < 7$ cm, $7 \leq BL_{END} \leq 9$ cm, $BL_{END} > 9$ cm) in 2005, 2006 and 2007 in the model. Left panel (a) shows the result at age 30 days (larval stage). Center panel (b) shows the result at age 60 days (early juvenile stage). Right panel (a) shows the result at age 90 days (juvenile stage). The center line in the box shows the median. The bottom and top of the box shows the 25th and 75th percentiles. The square shows the mean. The cross shows the minimum or maximum value. The whiskers show the 1.5 times value of box length.

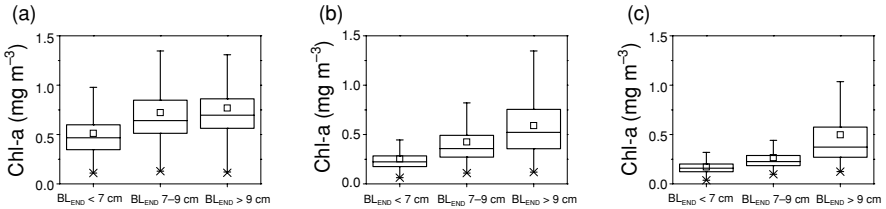


Fig. 3. Box-whisker plot of Chl-a concentration on the individual fish location at each size group ($BL_{END} < 7$ cm, $7 \leq BL_{END} \leq 9$ cm, $BL_{END} > 9$ cm) in 2005, 2006 and 2007 in the model. Details of the panels are same as Fig. 2.

day-age (Fig. 3). Chl-a of the individual locations in the small-size-group and medium-size-group decrease over time. But, there are unclear differences of Chl-a of the individual locations between medium-size-group and large-size-group at 30 age-day (Fig. 3). The difference of Chl-a of the fish locations become clear at 60 day-age (Fig. 3). Individual fish in the large-size-group, which experience near optimal temperature and high Chl-a, have a large growth rate at 30, 60 and 90 day-age (not shown). At that time, fully grown individuals in the large-size-group have a high swimming ability depending on fish size. Therefore, they can search for high prey densities and near optimum temperature regions. This ability accelerates growth and migration to northern region (Oyashio region), where Chl-a concentration is high.

DISCUSSION

Fish in the small-size group in the model, which are transported to the offshore side of the Kuroshio by 30 days, could not have a normal growth rate in the model (not shown). This is because these fish are exposed to higher SST (Fig.

2) than the optimal temperature of sardine (16–17°C), in which larvae of Japanese sardine grow faster (Takasuka *et al.*, 2007). Zenitani *et al.* (1996) reported the instantaneous mortality rate of early stage larvae in the offshore region was very high (0.83–1.11 day⁻¹). The main cause of larval mortality is predation, and vulnerability to predation trends to decrease with larval growth (Butler and Pickett, 1988). Larval fish mortality depends on size (Miller *et al.*, 1988; Bailey and Houde, 1989) and growth rate (Anderson, 1988; Takasuka *et al.*, 2003, 2004). Takasuka *et al.* (2007) showed that the optimal growth temperature of Japanese sardine larvae is lower than that of Japanese anchovy (*Engraulis japonicus*), and hence suggested that the stock of Japanese sardine increase and anchovy decrease simultaneously during a cooler climate regime. They pointed out that ambient temperature during larval stage is an important factor for the larval survival. The model results are consistent with Takasuka *et al.* (2007). On the other hand, Takahashi *et al.* (2008, 2009) suggested that food availability and survival processes during the early juvenile stage in the Kuroshio-Oyashio transitional area is a key factor for the recruitment abundance of sardine for the Pacific stock. The model result also showed that fish having a high growth rate (large-fish-group) experienced high forage condition during the early juvenile stage (Fig. 3). This result suggests that the prey condition is one of the important factors for determining the growth rate during the early juvenile stage. Fish having a high growth rate (large-fish-group) could migrate to northern region (Oyashio region) with a high prey density (>0.5 mg m⁻³) and low SST field (<14°C). Only full-grown fish might escape the high predation risk by top predators, such as the skipjack tuna *Katsuwonus pelamis*, which migrate to the Kuroshio-Oyashio transitional area during summer and autumn. Therefore, the model result indicates that the prey condition in the Kuroshio Extension of sardine is an important factor controlling the recruitment abundance of sardine in the western North Pacific as Takahashi *et al.* (2008, 2009) pointed out. In conclusion, our results provide a potential mechanism for recruitment success of Japanese sardine, which is consistent with both Takasuka *et al.* (2007) and Takahashi *et al.* (2008, 2009).

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