

Transport and survival of larvae of pelagic fishes in Kuroshio system region estimated with Lagrangian drifters

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ABSTRACT: Transport and survival of larvae of pelagic fishes in the Kuroshio system region were studied using Lagrangian drifter data recorded from 1990 to 2003. A large portion of the drifters from the Kuroshio area south of Japan spread around the Kuroshio Extension up to 170°E, while some moved south to the offshore area of the Kuroshio because of a recirculation gyre. The monthly mean eastward movement from areas south of Japan was approximately 800–900 km, which was smaller than previous numerical estimates. The results of a survival model assuming optimal temperatures for larvae suggest that surface waters during the observation period were too warm for larval Japanese sardine, which has an optimal temperature of 16°C, and the adult abundances did not increase during the observation period. In contrast, the spawning ground temperatures and transport conditions from an area south-west of Japan in April–June matched the requirement for the larval Japanese anchovy, which has an optimal temperature of 22°C. The combined effects of temperature variations due to seasonality and water mass mixing are suggested to play an important role in determining the environmental temperatures that occur in an area.

KEY WORDS: Kuroshio system region, Lagrangian drifter, larvae transport.

INTRODUCTION

In the Kuroshio–Oyashio current system, the main spawning grounds of Japanese sardine *Sardinops melanostictus* and Japanese anchovy *Engraulis japonicus* are located in the East China Sea and the southern coastal area of Japan around the Kuroshio^{1–3} (Fig. 1). Eggs and larvae of these species are advected by the Kuroshio and sometimes reach the Kuroshio Extension region east of Japan by the end of the larval stage.^{4,5} However, the transport is not deterministic but stochastic. Synoptic-scale recirculations formed south of the Kuroshio and the Kuroshio Extension⁶ and mesoscale frontal eddies are likely to be significant for retention and dispersal. The frontal eddies cause large environmental variability during larval transport and play an important role in determining larval food availability.^{7–9}

Stock abundances of the Japanese sardine and anchovy show dramatic out-of-phase fluctuations

on a multidecade time scale. For example, the catch of the Japanese sardine along the Pacific coast of Japan was approximately 2.8×10^6 t in 1988, but it drastically decreased to approximately 50 000 t in 2003. A similar but opposite fluctuation occurs in the anchovy stock: the catch in 2003 was six times larger than in 1998. Since fluctuations occur simultaneously with other sardine and anchovy species in the California Current and Humboldt Current systems, a relationship to large-scale climatic change has been suggested as a fundamental cause.^{10,11} In the Kuroshio–Oyashio current system, strengthening and weakening of the Aleutian low causes cold and warm water environments, respectively. Dominance of the Japanese sardine occurs in cold periods,¹² and the highest abundances of the Japanese anchovy occur in warm periods. These observations indicate that climate change is affecting the recruitment of these pelagic fishes.

In accordance with the stock fluctuations, the distribution of the spawning grounds also changes for both the sardine and anchovy. The spawning grounds are confined to coastal waters when stock abundances are low, but they spread into offshore

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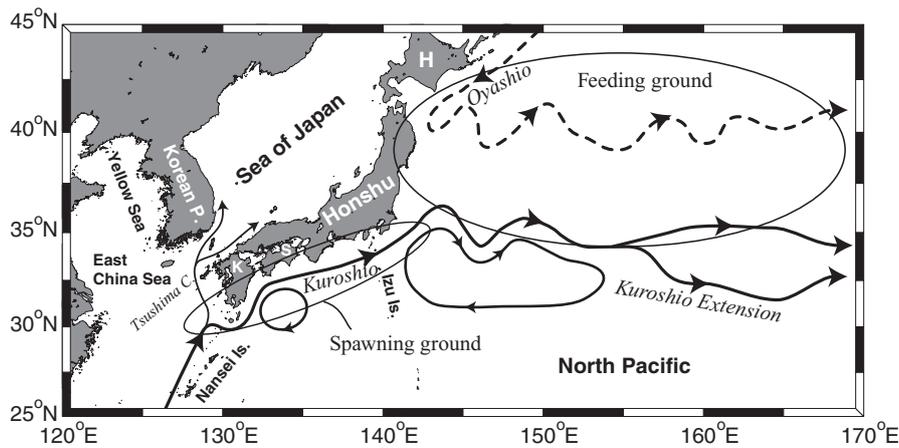


Fig. 1 Schematic illustration of the Kuroshio–Oyashio system region, including recirculation gyres south of the Kuroshio and the Kuroshio Extension, and spawning and feeding grounds of Japanese sardine and Japanese anchovy when the stock abundances were high. H, Hokkaido; S, Shikoku; K, Kyushu.

regions over the Kuroshio in periods when stock abundances are increasing.^{2,13–16} In the latter case, large numbers of larvae are transported downstream to the Kuroshio Extension, and the larvae gradually migrate north to the Kuroshio–Oyashio transition region.^{2,17,18} The larvae transport to the Kuroshio Extension and the subsequent northward migration is inferred to be significant in maintaining high stock abundances, since the collapse of the large sardine stock in the 1980s was caused by a high mortality rate in these life stages until age 1, despite high egg abundance.¹⁹

The summer feeding grounds of the sardine and anchovy until they are one-year old are located in the Oyashio and the Kuroshio–Oyashio transition region, where high primary production usually occurs (Fig. 2). It is considered that larval transport to the Kuroshio Extension is favorable for juveniles that reach this region, but migration success is lower for those transported to the south of the Kuroshio, which is isolated from the regions of high productivity, especially in summer. Kasai *et al.*²⁰ examined the transport and survival of sardine eggs and larvae using an idealized Kuroshio system model and suggested that those transported to the Kuroshio Extension contributed significantly to one-year recruitment. It was concluded that not only the destination of the transported larvae, but also the variability in the mortality rate during transport, was important for recruitment success. Noto and Yasuda²¹ found that there is a significant correlation between the mortality coefficient (equal to $-\log_e S$, where S is the survival rate) of early life stages of Japanese sardine from post larvae to age 1 and the winter sea surface temperatures (SSTs) in the Kuroshio Extension and its southern recirculation area. They reported that the SST reflects the mixed layer depth (MLD), and the winter MLD is a precondition of food availability for larvae transported to that area in spring.

Since the mortality rate usually decreases as the life stage progresses, the growth rate becomes an important factor for recruitment success.^{22–24} Takasuka and Aoki²⁵ investigated the growth rates of Japanese anchovy larvae in different water masses using otolith microstructure analysis and found its optimal temperature range was 21–22°C. In contrast, the range for the Japanese sardine was 15–16°C.²⁶ This large difference suggests that the biological response to temperature change is completely different between the two species. Considering the mortality rates and growth rates of typical marine fish larvae in other regions,^{27–29} temperature is the primary index of larvae survival conditions, including food availability as suggested by Noto and Yasuda.²¹ The temperature history during larval transport in the Kuroshio system region has not been observed, except for a few days of tracking of sardine larvae.^{30,31} However, the observation period of these studies was too short relative to the larval period. It generally takes the Japanese sardine and anchovy several weeks from hatching to yolk absorption, and another one to two months to metamorphose into juveniles.^{2,32} Transport over this time scale (hereafter referred to as a subseasonal time scale) has only been described individually, and the Lagrangian environmental history has not been previously presented.

In this study, we analyzed drifting buoy data obtained by the Global Drifter Program (GDP) and the World Ocean Circulation Experiment Surface Velocity Program (WOCE–SVP), which both include the position, time, and sea surface temperature for several months in many cases. The main aims of this study are to present subseasonal transport and Lagrangian temperature variability from the Kuroshio area and to examine larval survival, focusing on the Japanese sardine and the Japanese anchovy.

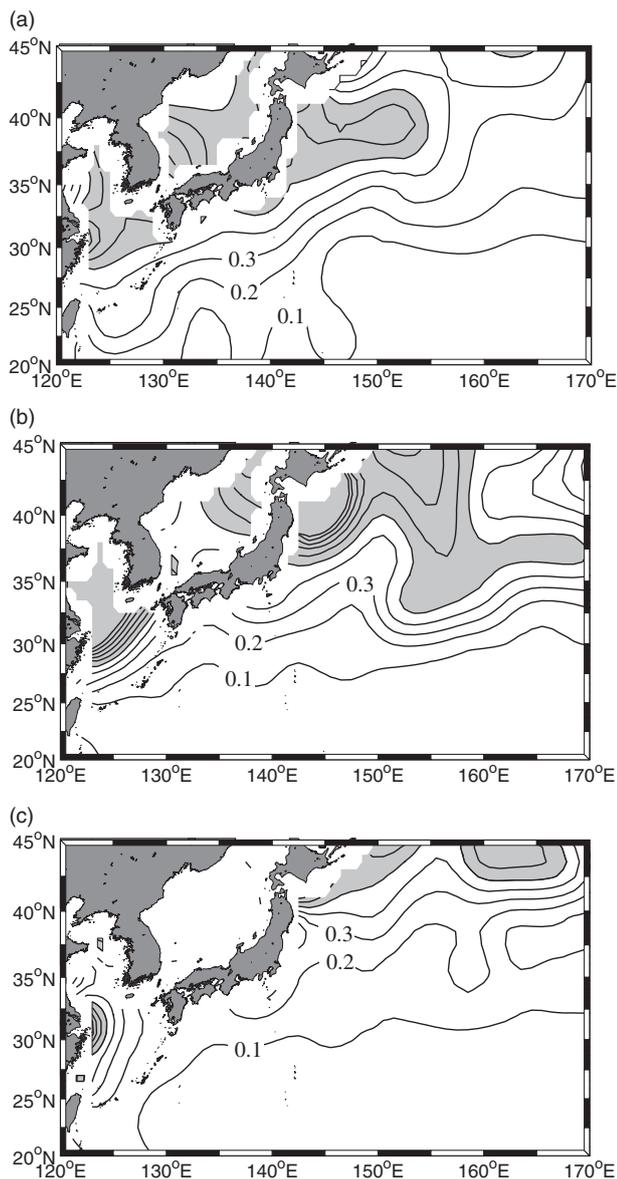


Fig. 2 Climatology of surface chlorophyll concentration profile⁴⁵ averaged in (a) winter (January, February and March), (b) spring (April, May and June) and (c) summer (July, August and September). Contour interval is 0.1 mg/m³. Areas of chlorophyll density >0.5 mg/m³ are shaded; contour lines not drawn for intervals >1.0 mg/m³.

MATERIALS AND METHODS

Lagrangian drifter data

The satellite-tracked Lagrangian drifter data used in this study were collected, processed and archived by the Atlantic Oceanographic and Meteorological Laboratory and Marine

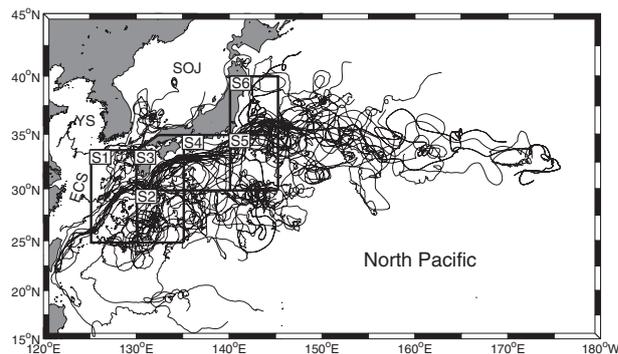


Fig. 3 Target spawning area including six subareas (S1–S6) and trajectories (narrow black lines) of 50 drifters that passed through it. ECS, East China Sea; YS, Yellow Sea; SOJ, Sea of Japan.

Environmental Data Services under GDP and WOCE–SVP. The drifters consisted of a surface buoy equipped with a satellite transmitter, a thermometer and other sensors, and a 15-m drogue below the buoy with a drop-off sensor, to follow the ocean currents isolated from the direct action of waves and wind. It is considered that a depth of 15 m can represent the flow that advects larvae of Japanese sardine and Japanese anchovy, exhibiting diurnal vertical migratory behavior in an epipelagic layer. As for Japanese sardine larvae, Konishi³³ found the distribution in the range of 0–50 m depth, which supports the above consideration. Even if larvae are distributed in deeper layers, the difference is thought to be minor because of the averaging effect of the migration, unless the distribution exceeds the main thermocline depth of several hundreds of meters where vertical shear of oceanic currents becomes significant. The six-hour interval data of the location, sea surface temperature (SST), velocity, and drogue status (either connected to the surface buoy or dropped off) were processed and interpolated using the method described by Hansen and Poulain.³⁴ Temperature measurements were accurate to 0.1°C.³⁵

Fifty drifters that passed through the spawning ground of the Japanese sardine and anchovy in the North Pacific Ocean from January to June, which covers the spawning season, were selected (Fig. 3). The target area was divided into six subareas for statistical analyses of the drifter movement. The starting points for the analyses were selected as the middle of each month (daily mean position at 0:00 hours on the 16th day), if they were in the target area. This resampling time scale is longer than the typical Lagrangian integral time scale of 2–10 days in oceanic areas.³⁶ In this

analysis, 113 Lagrangian data sets were used for a 30-day period, 92 for a 60-day, and 75 for a 90-day period. Because the synoptic-scale path of the Kuroshio south of Japan was straight (nonlarge-meander)³⁷ throughout this period, except for the year 1990, ensemble mean and deviation of movement from one subarea was assumed to be caused by mean flow and eddy components, respectively. Note these eddy components included those caused by temporal path variations such as propagation of small meanders on the quasi-stable path.³⁸

Monthly mean heat fluxes of NCEP/NCAR reanalysis³⁹ from 1990 to 2003 and monthly climatology of mixed-layer depth⁴⁰ were used to estimate contribution of heating and cooling on temperature variation at the Kuroshio area south of Japan (30–35°N, 130–140°E) and the Kuroshio Extension (30–35°N, 145–155°E).

Optimal temperature model

Consider survival from time t_0 to t_1 , which corresponds to the start and end of a life stage. The survival rate is then given as equation 1:

$$S_1 = \frac{N_1}{N_0} = \exp\left\{-\int_{t_0}^{t_1} m dt\right\} \quad (1)$$

where m is the mortality rate, and N_0 and N_1 are abundances at t_0 and t_1 , respectively.

Variables t_0 and t_1 have the following relationship (equation 2) with growth rate g for a given parameter ΔL representing growth during a model life stage (for example, increase in body length):

$$\Delta L = \int_{t_0}^{t_1} g dt \quad (2)$$

Note that m and g are independent of the growth level (for example, body length) during the stage. Considering the dominant effect of temperature on the survival, we assumed dependence of the variables m and g only on temperature as:

$$m = m_0 \times \exp\left(\frac{[T - T_0]^2}{[2\sigma^2]}\right) \quad (3a)$$

$$g = g_0 \times \exp\left(-\frac{[T - T_0]^2}{[2\sigma^2]}\right) \quad (3b)$$

where m_0 , g_0 , T_0 and σ are the minimum mortality rate, maximum growth rate, optimal temperature, and the width of the optimal temperature window, respectively. If m_0 , g_0 and the temperature are constant during the stage, the effects of m and $1/g$ on

survival are the same. However, variability in temperature has stronger effects on the former: an instantaneous high mortality rate can be fatal, whereas an instantaneous low growth rate causes little extension of the stage duration.

In this study, transport and survival of larval patches in an early life stage were examined using drifter data. The patches were considered hatched at the start points of the drifters, and passively transported with them because the swimming ability of larvae is negligible compared with the oceanic flows. The egg period of 1–3 days was not considered in the survival model. The duration of the model life stage was specified by $\Delta t_0 = \Delta L/g_0$ (minimum duration from hatching to a standard growth level). Substituting this formulation, equation 2 is simplified as equation 4:

$$\Delta t_0 = \int_{t_0}^{t_1} \exp\left\{-\frac{(T - T_0)^2}{(2\sigma^2)}\right\} dt \quad (4)$$

The integrands can be interpreted as nondimensional growth rates whose maximum is 1. Three cases, $T_0 = 16, 19,$ and 22°C , were examined with fixed other parameters of $\Delta t_0 = 30$ days, $m_0 = 0.2/\text{day}$ and $\sigma = 3^\circ\text{C}$. Temperature ranges were selected with reference to the spawning temperature ($11\text{--}21^\circ\text{C}$ for Japanese sardine² and $15\text{--}26^\circ\text{C}$ for Japanese anchovy⁴¹), and the optimal growth temperature (16.2°C for Japanese sardine²⁵ and 22.0°C for Japanese anchovy²⁶), and the minimum duration was chosen regarding typical time scale of larval stages of approximately one to two months. As for the minimum mortality rate of $0.2/\text{day}$, we referred to estimated mortality rates of $0.34/\text{day}$ for Japanese sardine in the Kuroshio area⁴² and $0.25/\text{day}$ (range $0.14\text{--}0.36/\text{day}$)¹⁶ for Japanese anchovy in the Kuroshio Extension and the Kuroshio–Oyashio transition region. Integrations of growth and mortality were carried out for 92 larval patches for 60 days at most, until time integration of nondimensional growth rate reached Δt_0 (equivalent to when integration of growth rate reached ΔL). Sixty days calculation was long enough for survival examination because the survival rates after 60 days were 0.00006% at most, far lower than maximum survival rate of approximately 0.25% at 30 days. Even though detailed biology such as fertility, mortality after larval stages, and predation pressure is needed to evaluate number of recruits, results of different optimal temperature cases in our model were simply compared because the drastic regime shift from Japanese sardine to Japanese anchovy was related to the high mortality rate of Japanese sardine in early life stages.¹⁹

RESULTS

Movement and Lagrangian temperature variability

A large portion of the drifters from the Kuroshio area south of Japan and the southern part of the

East China Sea spread around the Kuroshio Extension up to 170°E, while some moved south to the offshore area of the Kuroshio (Fig. 4). Anticyclonic circulation south of the Kuroshio or the Kuroshio Extension suggested that the drifters were trapped in recirculation gyres. Ekman transport due to westerly winds might be responsible for the

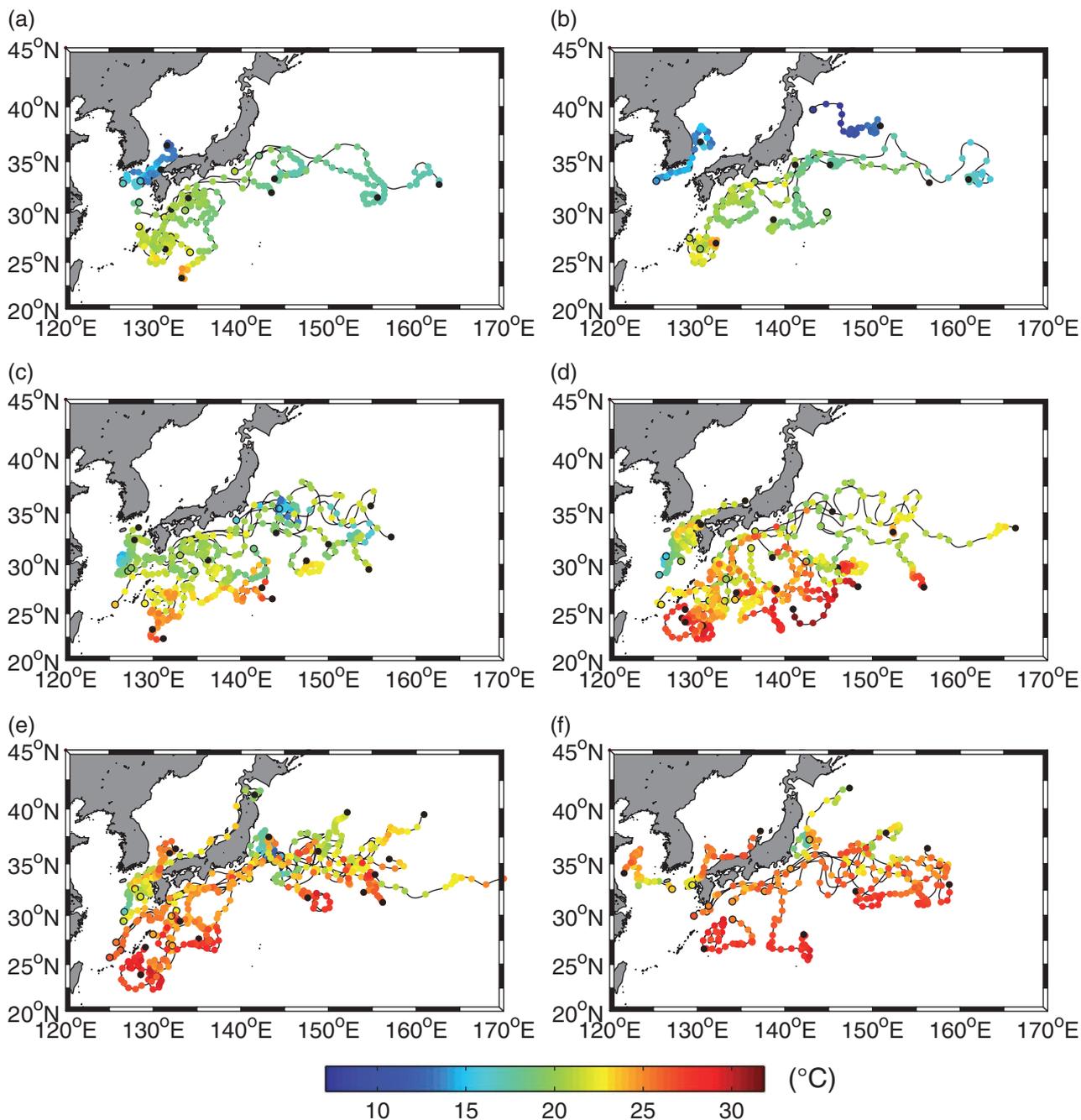


Fig. 4 Trajectories and Lagrangian temperature evolutions of 90 days from (a) January, $n = 10$, (b) February, $n = 8$, (c) March, $n = 13$, (d) April, $n = 17$, (e) May, $n = 17$ and (f) June, $n = 10$. n , number of individuals. Start point, day 0 (○), end point, day 90 (●).

southward shift from the main path of the Kuroshio Extension to the recirculation gyres, although seasonality of wind stress was not clearly reflected in the movements of the drifters. On the northern side of the Kuroshio Extension, several drifters intruded northward from spring (May) to summer (June) (Fig. 4e,f). It is inferred that these movements were caused by the northward movement of warm eddies and streamers.⁴³ Drifters in the northern part of the East China Sea moved north-east, and some of them entered the Sea of Japan, except for the one that moved north-west to the Yellow Sea.

Although subseasonal movements showed a stochastic tendency, Lagrangian temperatures were more deterministic. Initial temperatures in the Kuroshio area south of Japan were approximately 17–22°C in winter (January–March) and 20–25°C in spring (April–June), and a seasonal fluctuation caused by atmospheric heating or cooling was observed. However, it is recognized that the trajectories of drifters exhibiting stochastic behavior also had a significant effect. There was a cooling tendency for drifters that moved from the Kuroshio area to the Kuroshio Extension, but the effect of seasonal heating was dominant for those that stayed in areas south of the Kuroshio. As the drifters moved into the Kuroshio Extension, temperatures fell greatly in winter (Fig. 4a–c), and the rise was suppressed in spring (Fig. 4d–f). Figure 5 shows the initial temperature and mean variation of Lagrangian temperatures from initial temperature during the first 30 days in the North Pacific, and heat flux contribution of Eulerian temperature variation estimated from heat flux and mixed layer depth. The initial temperature was approximately 20°C in January, and it dropped to its lowest level of 18–19°C in February and monotonically rose to 23–24°C in June (Fig. 5a). Part of the seasonal warming or cooling pattern seen in the heat flux contribution of Eulerian temperature variation (Fig. 5c) appeared in the Lagrangian one with a mean amplitude of approximately 1.8°C (Fig. 5b). Calculating mean variation of drifters moving more and less than 5°E separately, we estimated that the mean cooling effect caused by eastward movement and the warming effect by retention seen in Figure 4 were –1.0 and +0.6°C, respectively. The largest difference in the variation between the two groups was 3.3°C, which occurred from May to June (Fig. 5b). Because temperature rise (fall) estimated from heat flux and mixed layer depth were smaller (larger) in the Kuroshio area south of Japan than in the Kuroshio Extension, this difference was not caused by heating or cooling.

To obtain the characteristics of subseasonal transport from various spawning grounds,

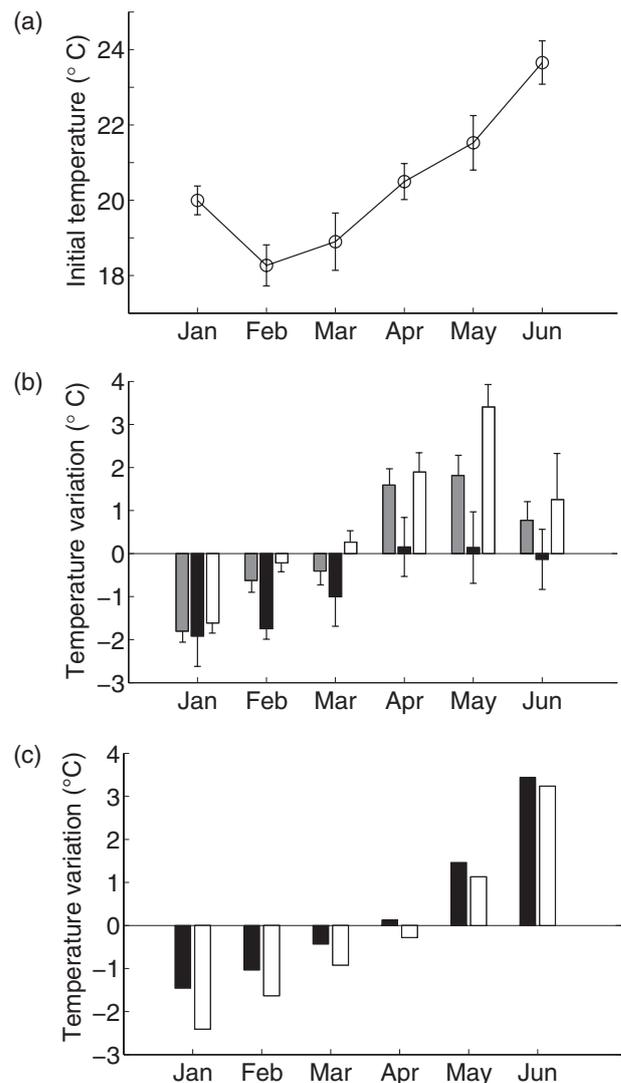


Fig. 5 Monthly mean of (a) initial temperature, (b) variation of Lagrangian temperature after 30 days for drifters in the North Pacific ($n = 81$) and (c) contribution of heat flux on temperature variation. A drifter in extremely cold water around 40°N in February (Fig. 4b) is eliminated from the averages. In (b), calculations were made for all drifters (gray), those whose eastward movement was more than 5°E (black), and those whose eastward movement was less than 5°E (white). Error bars, standard errors. In (c), calculations were made for the Kuroshio Extension 30–35°N 145–155°E (black), and the Kuroshio area south of Japan 30–35°N, 130–140°E (white).

ensemble means and standard deviations of the movement of drifters from six subareas (Fig. 3) for periods of 30, 60 and 90 days are shown in Figure 6. Transport from the Kuroshio area south of Japan (S3 and S4) at 30 days was advective. Mean \pm standard deviation of eastward movements were 680 ± 520 km (or 880 ± 480 km after

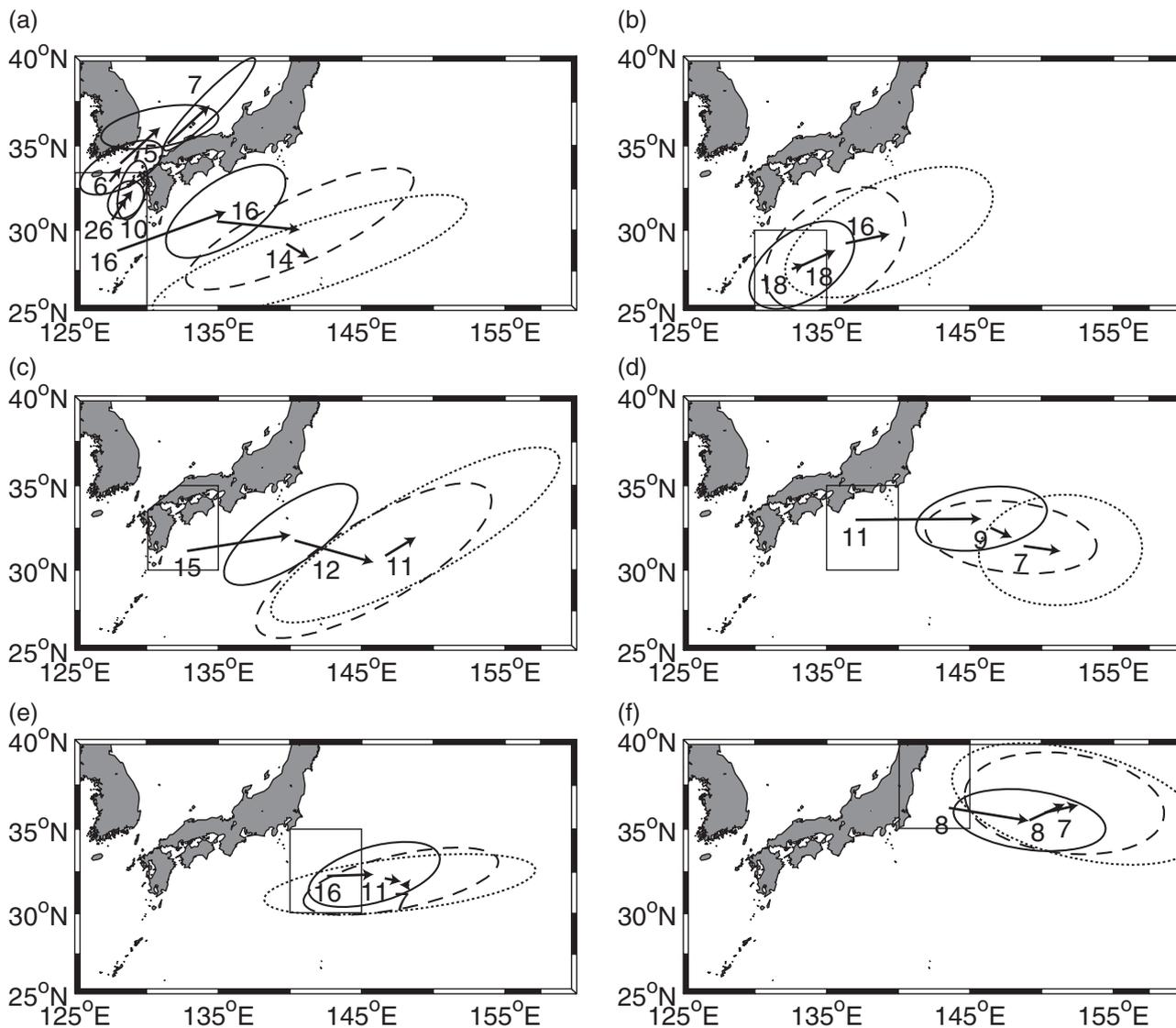


Fig. 6 Means (arrows) and standard deviations (ellipses) of movement in 30 days (solid lines), 60 days (dashed lines) and 90 days (dotted lines) for subareas (a) S1, (b) S2, (c) S3, (d) S4, (e) S5 and (f) S6. Statistics were calculated for data from January to June, and numbers of data are shown at the start points. In S1, statistics were separately calculated for subgroups for different destinations: the North Pacific (east of 130°E or south of 25°N), the Sea of Japan (north of 35°N), and S1 and its eastern side. No drifters moved into the Sea of Japan in 30 days.

eliminating those that had a westward component) and 810 ± 510 km from S3 and S4, respectively, and generally downstream to the Kuroshio Extension and its southern flank. However, they were dispersed from mean flow after 60 days by recirculation gyres as shown in Figure 4. The distribution of drifters from S4 slightly shifted southward after 60 days, and they spread widely in the recirculation region of the Kuroshio Extension, which is also seen for those from S5. Although a similar movement occurred for some from S3, others moved offshore to the south of 30°N (Fig. 3), and the standard deviation ellipses were skewed and elongated.

Migration of drifters from the offshore area of the Kuroshio (S2) was less advective (the mean eastward movement was 60 ± 410 km at 30 days) than those from S3 and S4, and most of the drifters stayed south of Japan in the period of 60 days (Fig. 4b). The dispersive tendency of drifters from north of the Kuroshio Extension (S6) seems to be caused by eddy activities including temporal variability of the axis of the Kuroshio (Fig. 4e,f). In the East China Sea and the water around the Nansei Islands (S1), the means and standard deviations were given for three subgroups divided for each period by their destination (Fig. 6a): (i) the North

Pacific (east of 130°E or south of 25°N); (ii) the Sea of Japan (north of 35°N); and (iii) S1 including its eastern side. Transport to the North Pacific occurred mostly by the main stream of the Kuroshio in 30 days, and offshore movement crossing the stream became significant after two months, as seen from S3, which is a downstream subarea along the Kuroshio (Fig. 6c). Drifters in the northern area of the East China Sea moved to the Sea of Japan after 60 days.

Survival by optimal temperature model

Survival rates and destinations of larval patches from the spawning grounds that were estimated by the model of optimal temperatures of 16°C (Case I), 19°C (Case II) and 22°C (Case III) are shown in Figures 7–9. In Case I, survival rates were generally low and no patch had a survival rate greater than 0.1%, except for two patches from the northern East China Sea in January and April, and one from the east of the Izu Islands. Surface water temperatures in the western North Pacific during the observation period of 1990–2003 were higher than 16°C in the whole area of this study. Survival rates were greatly improved in Case II. There were high survival rates for larvae put in January, February and March from areas along the Kuroshio south of Japan (Fig. 8a–c). As a result, 18 patches had a survival rate higher than 0.1% in these three months. Transport of these survivors was mainly eastward, which was the downstream direction along the axis of the Kuroshio, whereas some from south of Shikoku (S3) and the southern flank of the Kuroshio Extension (S5) showed a slight southward or westward movement, as shown in Figures 4 and 6. In Case III, there were 11 patches with a survival rate higher than 0.1% for the whole period (Fig. 9). Seven patches were in the first four months (January–April) from waters around the Nansei Islands (southern part of S1, and S2), which stayed there after the stage, but the others in the last three months (April–June) were from the Kuroshio south of Shikoku (S3), the Kuroshio Extension (S5), or the northern East China Sea (S1). Even though the high survival rates (> 0.1%) were lower than for Case II, this case shows that a larger number of cases of intermediate survival (0.01–0.1%) appeared from the south of Japan (S3 and S4) and the Kuroshio Extension (S5) in the last three months (April–June).

As the feeding grounds of juveniles are located north of the Kuroshio Extension, where high productivity occurs even in summer (Fig. 2), the destination of larval patches should be close to this high production area for migration success in juve-

nile stages. In Case II, transport of model patches with high survival rates was mainly toward the region along the axis of the Kuroshio or the Kuroshio Extension region from January to March, which is located on the southern periphery of the high production area (Fig. 8) and hence, preferable for juvenile survival. On the other hand, in Case III, model patches at 25–30°N from February to April with high survival in the model larval stage were far from the area of high production. Thus, they would not reach the feeding ground in the later stages (Fig. 9). Therefore, we narrowed the good spawning grounds for juvenile survival in Case III to a region south-east of Japan (S4 and S5) in April, May and June

DISCUSSION

The spawning grounds of Japanese sardine and Japanese anchovy spread across a wide area with high abundance, and dense egg patches were often observed in areas south of Shikoku and Kyushu (S3) and the waters south-east of Japan (S4 and S5), which are their main spawning grounds. The sub-seasonal transport fields obtained in this study suggest that the movement of larvae from these areas was mainly toward the Kuroshio Extension and its southern flank, but some from S3 were advected by a recirculation gyre south of Shikoku. Heath *et al.*⁴⁴ showed by particle-tracking experiments that the duration of transport to the Kuroshio Extension from an area corresponding to S3 in this study (~1000 km) in 1993 and 1994 was approximately two to three weeks, which was shorter than the results of our study (880 ± 480 km in 30 days for those moving along the Kuroshio from S3). In a previous model,⁴⁴ the flow field reconstructed from the observations was not time-dependent and the retention effect of mesoscale eddies was underestimated. This difference in transport duration becomes a problem when estimating survival, because it has a close relation to migration success in later stages. In the Kuroshio Extension and its southern flank, transport became less advective and the larval patches would be dispersed in wide areas along the current. It is inferred that the surface water masses of the stream are transported toward a recirculation gyre by the combined effects of Ekman transport and frontal disturbances, and are mixed in the gyre by chaotic advection.

It was observed that the surface temperatures of the main spawning grounds were approximately 18–20°C in winter and 20–24°C in spring, and the mean Lagrangian temperature variability from those areas showed a seasonal amplitude of

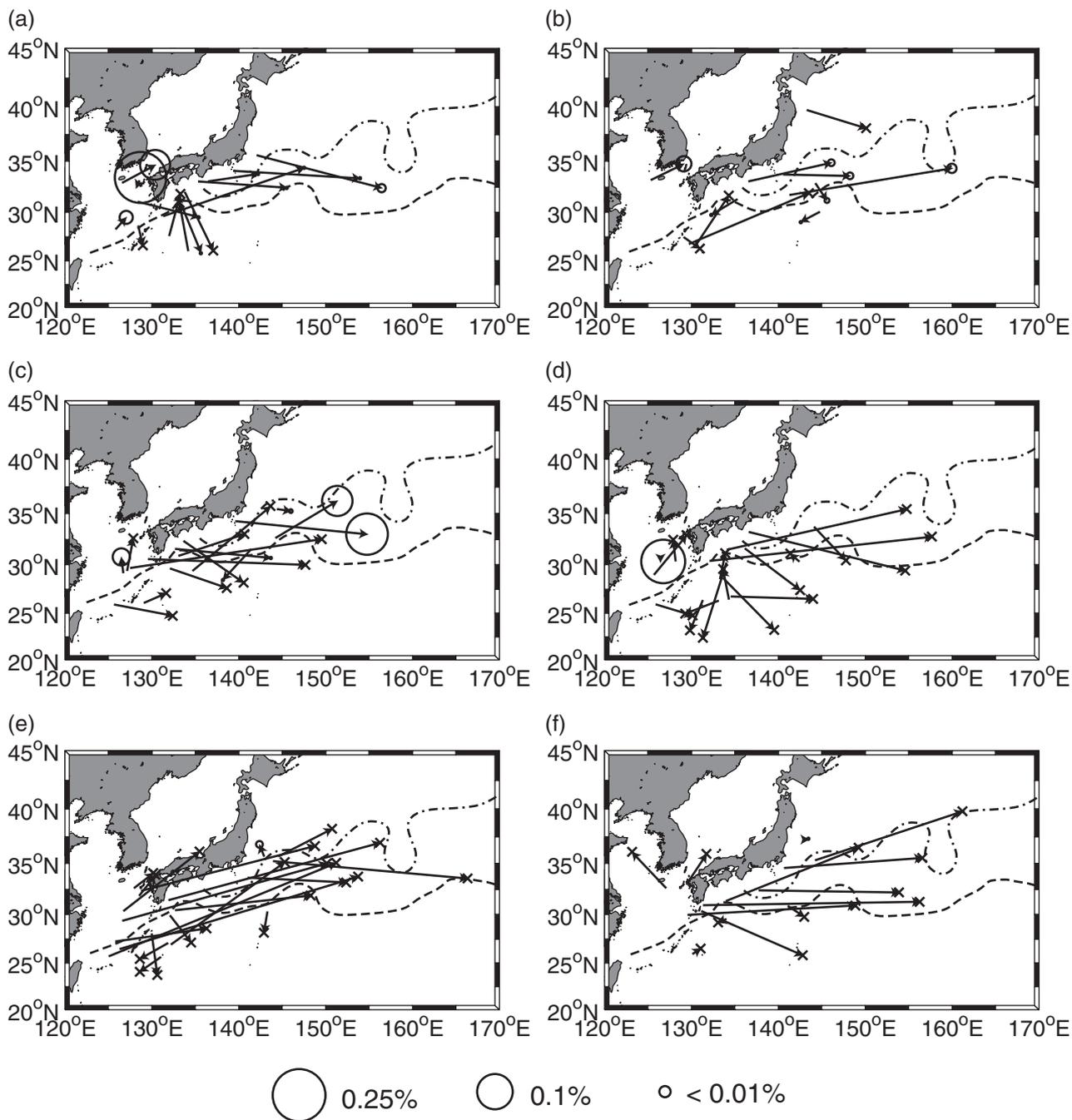


Fig. 7 Survival rates and transport of model larval patches estimated from the middle of (a) January, (b) February, (c) March, (d) April, (e) May and (f) June for Case I ($T_0 = 16^\circ\text{C}$). End points (○): rates are shown by the area of (○). Position after 60 days if the duration of the stage was >60 days (×). Arrows show movements in the model life stage.

approximately 1.8°C , which was caused by atmospheric heating or cooling. However, cooling and warming of approximately -1.0 and $+0.6^\circ\text{C}$ was recorded by drifters that moved eastward for more and less than 5°E , respectively. Since the eastward movement corresponds to transportation from areas south of Japan to the Kuroshio Extension

region but heating or cooling showed the opposite tendency (Fig. 5c), it is considered that horizontal mixing with cold water originating from the Oyashio, across the front of the Kuroshio Extension, is responsible for the cooling.⁷ In contrast, retention in a recirculation gyre south of Japan seems to contribute to warming through mixing

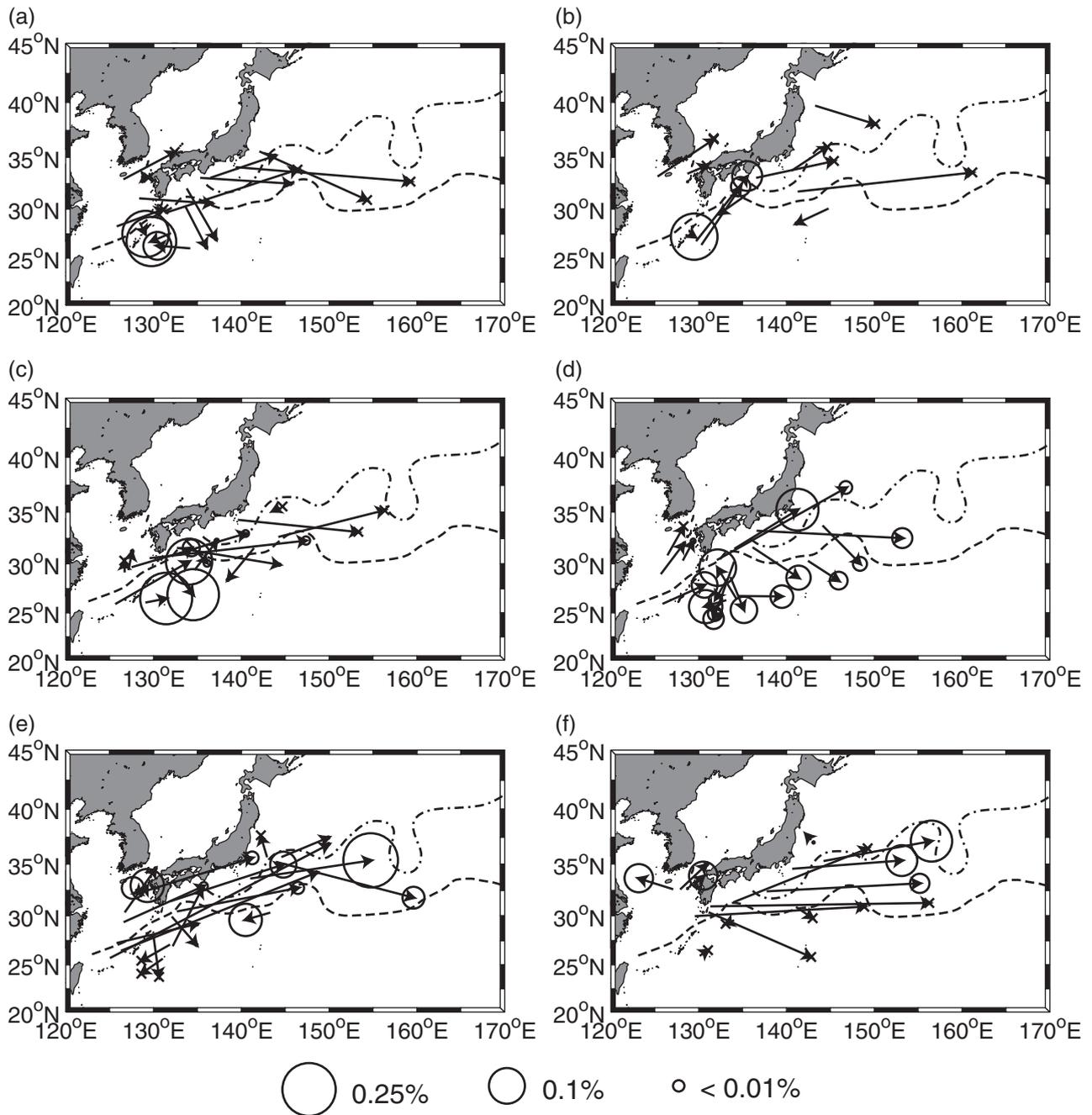


Fig. 8 Same as Figure 7 but for Case II ($T_0 = 19^\circ\text{C}$).

with relatively warm water. A combination of seasonality and cooling (warming) caused by mixing results in strong (weak) cooling in winter and weak (strong) warming in spring, respectively (Fig. 5b).

The survival model showed that high survival and preferable transport took place for many larval patches in Case II ($T_0 = 19^\circ\text{C}$), but survival was generally low in Case I ($T_0 = 16^\circ\text{C}$) and temporal and spatial conditions were limited in

Case III ($T_0 = 22^\circ\text{C}$). Considering the observed spawning and optimal growth temperatures, the optimal temperatures for the survival of the Japanese sardine and anchovy were 16°C ²⁶ and 22°C ,²⁵ respectively. Although it has been proposed that a decrease in the abundance of Japanese sardine in the late 1980s was related to the warming of the western North Pacific,²¹ our model results suggest that warm water temperatures in the oceanic spawning grounds could have prevented an

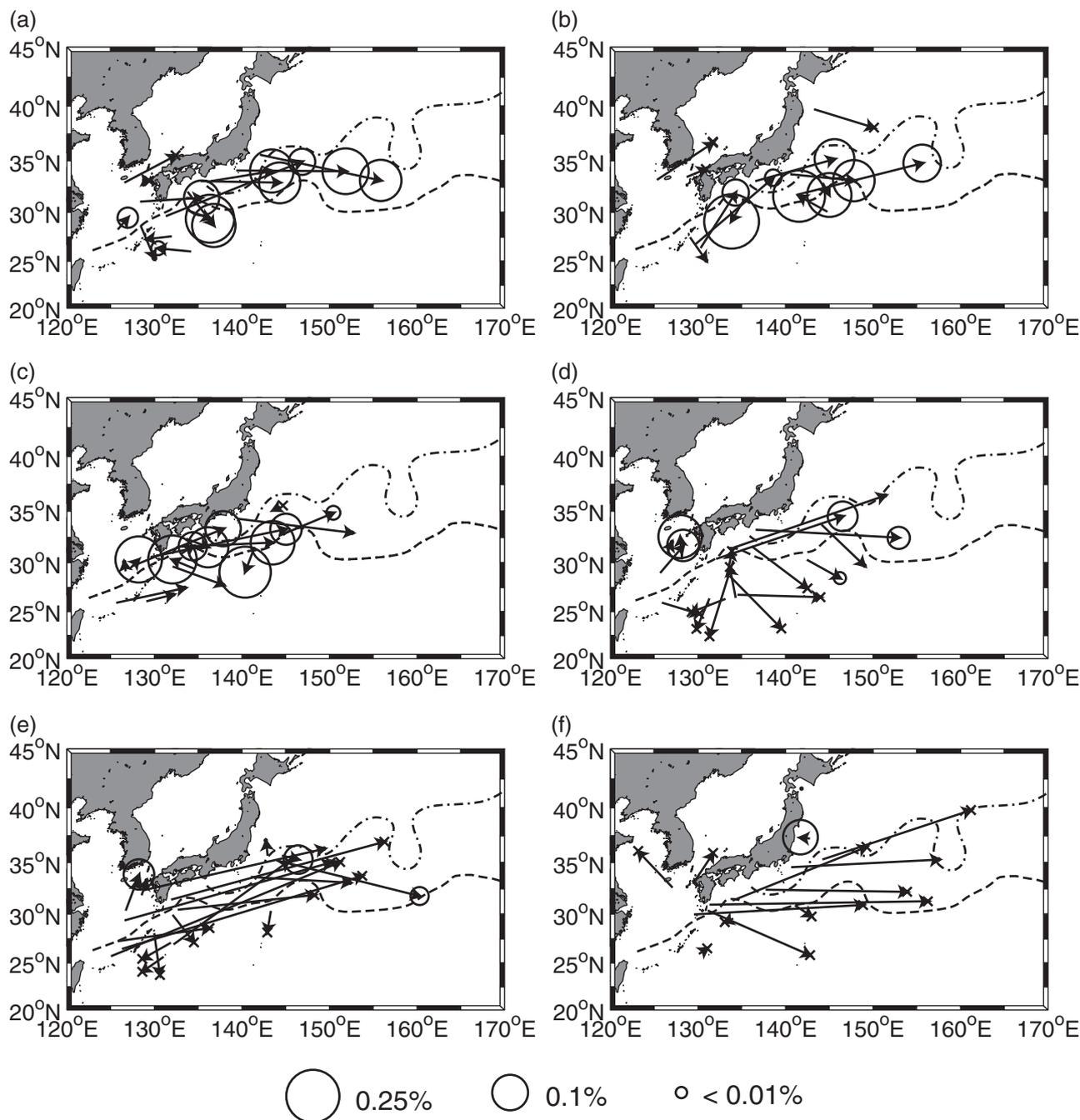


Fig. 9 Same as Figure 7 but for Case III ($T_0 = 22^\circ\text{C}$).

increase in stock abundance of the Japanese sardine from 1990 to 2003 (Fig. 5a). The temperatures of the spawning grounds were approximately 20°C in January and $18\text{--}19^\circ\text{C}$ in February and March. In Case II, atmospheric cooling lowered the mean temperature to close to the optimal temperature of 19°C for January, while the temperature was kept around 19°C through the model larval period for February and March

by the effect of retention (Fig. 5b), resulting in a high survival rate. Some data from February and March marked almost the highest survival of larvae in the model. As for Case III, which has simulated survival of the Japanese anchovy, a preferable spawning ground was found in an area south-east of Japan (S4 and S5) in spring. It is implied that the balance of seasonal (atmospheric) heating and mixing with cold water kept

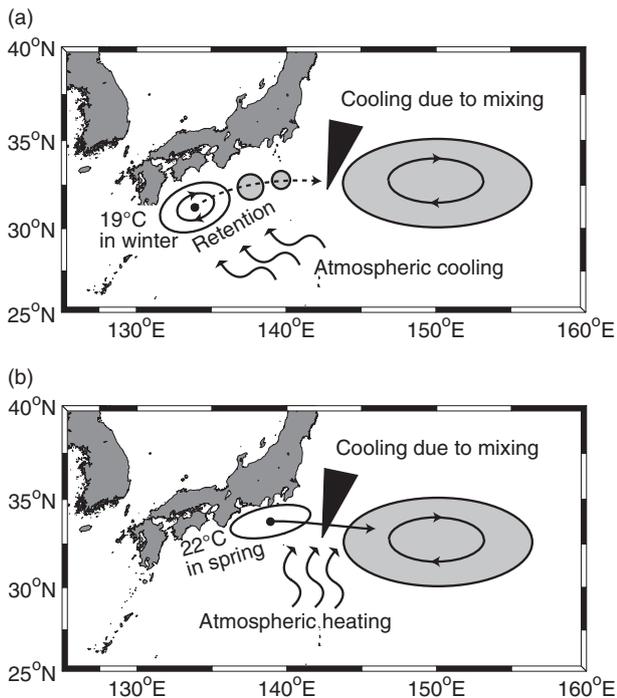


Fig. 10 Preferable survival scenarios for (a) cool water species and (b) warm water species suggested by the model as optimal temperature cases of $T_0 = 19^\circ\text{C}$ and $T_0 = 22^\circ\text{C}$, respectively. The main spawning grounds are formed in (a) western and (b) eastern areas south of Japan, and the larval patches are (a) trapped in a recirculation gyre and (b) advected to the Kuroshio Extension. In (a) and (b), optimal temperatures are kept preferable because differential atmospheric forcing (cooling in winter and heating in spring) is balanced by the effect of mixing with different waters. Open and shaded ellipses indicate spawning and feeding grounds; thin arrows, black arrowheads are atmospheric and mixing effects during transport, respectively.

the environmental temperatures at an optimal level (Fig. 5b), and contributed greatly to maintaining the stock abundance of the Japanese anchovy at a high level. It is considered that the successful transport in Cases II and III represent typical survival scenarios of cool and warm water species in the Kuroshio system region, respectively (Fig. 10). Although the Japanese anchovy was considered a warm water species in the observation period of 1990–2003, we assume that the Japanese sardine was a cool water species in the relatively cold period from the late 1970s to 1980s.

In this study, we showed the subseasonal transport from the Kuroshio system region using Lagrangian drifter data, and identified temporal and spatial conditions of spawning and transport for the Japanese sardine and anchovy. Even though

selection of a season and an area will determine the temperature history to some degree in advance, retention and mixing caused by recirculation gyres and frontal disturbances of the Kuroshio and the Kuroshio Extension caused stochastic temperature variability. Therefore, large-scale climatic change may be the primary cause of fluctuations in stock abundance; however, bimodality of paths of the Kuroshio south of Japan and variability of intensity of the recirculation of the Kuroshio Extension are also important, because they will alter the retention time scale and water exchange across the fronts.

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