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Offshore entrainment of anchovy larvae and its implication for their survival in a frontal region of the Kuroshio

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ABSTRACT: Focusing on an incidence of coastal water entrainment into the Kuroshio frontal region, we looked at the fate of anchovy larvae *Engraulis japonicus* originating from coastal spawning grounds and entrained into the frontal region with the coastal low salinity water. Drifters were released in the low salinity water of the Kuroshio frontal region, and observation and sampling were conducted during drifter tracking from 18 to 21 May 1997. Naupliar copepod abundance and copepod production were high in the low salinity water at an early phase of the tracking, but decreased with elapsed days. Anchovy larvae were most abundant on the coastal side of the Kuroshio, especially in the low salinity water. Their ages estimated from otoliths were consistent with those inferred from the advective transport speed from the coastal spawning ground. The estimated biological mortality rate of first-feeding larvae (less than 7 d old) in the low salinity water was 0.71 d^{-1}, which was high compared to rates previously reported for *Engraulis* spp. This high mortality could have been caused by poor nutritional conditions due to decreasing copepod production and abundance, suggesting that the offshore entrainment of fish larvae originating from coastal water could be unfavorable for their survival. The encounter with a frontal eddy would enhance food production and the subsequent survival of anchovy larvae in the frontal region; otherwise, they may perish due to low food availability.

KEY WORDS: Anchovy larvae · Offshore entrainment · Kuroshio front · Larval survival

INTRODUCTION

Larval transport from spawning to nursery areas is a major factor inducing variability in the larval survival and subsequent recruitment to marine fish populations (Hjørt 1914, Norcross & Shaw 1984). Along the Pacific coast of Japan, most of the pelagic fishes, such as anchovy, sardine and mackerel, spawn in the Kuroshio Current and its coastal water (National Research Institute of Fisheries Science 1995). Since the larval food availability in the offshore Kuroshio water is appreciably low compared to the coastal water (Nakata et al. 1995), interaction between the Kuroshio and its coastal water could be critical to the larval survival for those coastal spawners.

Coastal water is often entrained into the Kuroshio frontal region (Fig. 1), which possibly results in the aggregation of coastal planktonic organisms in the Kuroshio front (Yamamoto et al. 1988, Nakata 1990, Kidachi 1997). Further, cyclonic eddies caused by frontal disturbances of the Kuroshio could enhance primary production and larval prey production in the frontal region (Kimura et al. 1997, Nakata et al. 2000). The plankton aggregation and production enhancement in the frontal region could provide favorable feeding conditions for larval fish in the offshore region. However, the influence of the offshore entrainment of fish larvae originating from the coastal spawning grounds has not yet been fully clarified in the Kuroshio front.

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In addition, it has been reported that larval and juvenile anchovy are broadly distributed to the far east of the Japanese coast, corresponding to a recent increase in the Japanese anchovy stock (Takahashi et al. 2001). This suggests that the larval survival in the offshore water could be of importance, particularly to the anchovy in the Kuroshio region in recent years.

The objectives of this study are to quantify the time changes in the abundance and food availability of anchovy larvae being entrained from the coastal water to the Kuroshio front, and to examine the effect of the interaction between the Kuroshio and its coastal water on larval survival. In this context, we focused on an incidence of coastal water entrainment into the Kuroshio frontal region off the Enshu-nada Sea, one of the major spawning grounds of Japanese anchovy off the Pacific coast of Japan (Funakoshi et al. 1984). The main spawning period of the anchovy in the Enshu-nada Sea is from spring to autumn; the peak frequently occurs in spring (Funakoshi 1990).

The ocean color image (ADEOS/OCTS) of the study area taken on 18 May 1997 is shown in Fig. 1, and demonstrates that coastal water was entrained into the Kuroshio front. Taking this opportunity, we released drifters in the coastal water and sampled larval anchovy along the drifter track from 18 to 21 May 1997, when the drifter moved through the Kuroshio frontal region. During the drifter tracking period, we investigated the time change in the distribution and abundance of anchovy *Engraulis japonicus* larvae and their prey organisms. The nutritional condition, growth and mortality of the anchovy larvae were also estimated.

MATERIALS AND METHODS

Observations of the Kuroshio front off the central Pacific coast of Japan were made from RV 'Hakuho-Maru' from 18 to 22 May 1997. Four drifters were released in the coastal water marked by low salinity, and tracked from 16:10 h on 18 May, to 06:21 h on 21 May, for 46 to 54 h. The drifters were composed of a surface buoy and a 2×5 m drogue centered at a depth of 18 m below the sea surface. The drifter's position was monitored using the ship's radar linked to a global positioning satellite system (GPS). Following the drifters, physical and biological surveys were conducted at night along 3 transects (Fig. 2; Line 1, Stns D1 to D6; Line 2, Stns D13 to D18; Line 3, Stns D25 to D28). The drifters were retrieved after the Day 2 survey (Line 3). A fourth transect (Line 4, Stns D29 to D34) was conducted along the same longitudinal section as Line 3 to describe detailed physical and biological structure on a wider spatial scale. Along each transect, temperature and salinity were measured by a Seabird CTD (Seabird Electronics) deployed to 500 m depth. The CTD data were depth-averaged into 1 m depth strata. Larvae were collected using the Ocean Research Institute (ORI) net with 1.6 m diameter and 0.33 mm mesh size (Omori 1965). The ORI net was fitted with a flowmeter to estimate the volume filtered and towed for 3 to 5 min at a speed of 1 m s^{-1}. The larval sampling was conducted in the surface layer (ca. upper 2 m depth), where most of anchovy larvae were found in the Kuroshio and its coastal area at night (Nakata et al. 2000). Larval abundance was standardized to number of individuals under 1000 m^3. Up to 40 individuals of the anchovy larvae in the sample were

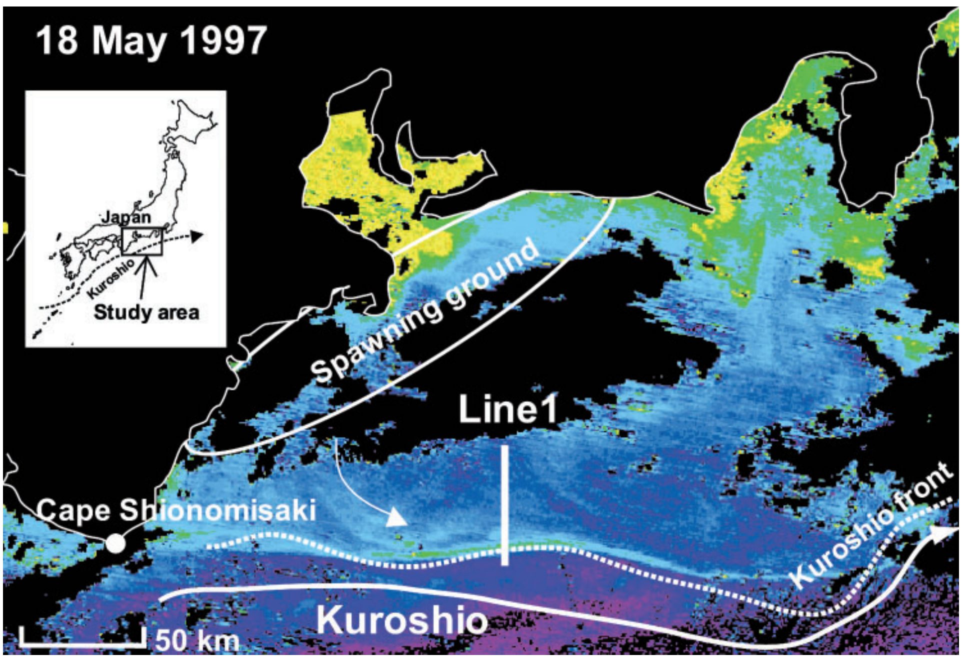

Fig. 1. Satellite ocean color images in the Enshu-nada Sea taken by Midori on 18 May 1997. Location one of the survey transects (Line 1) and the coastal spawning ground of anchovy in this region are shown. Dashed line indicates the position of the Kuroshio front inferred from the satellite SST image. Black areas indicate land or cloud

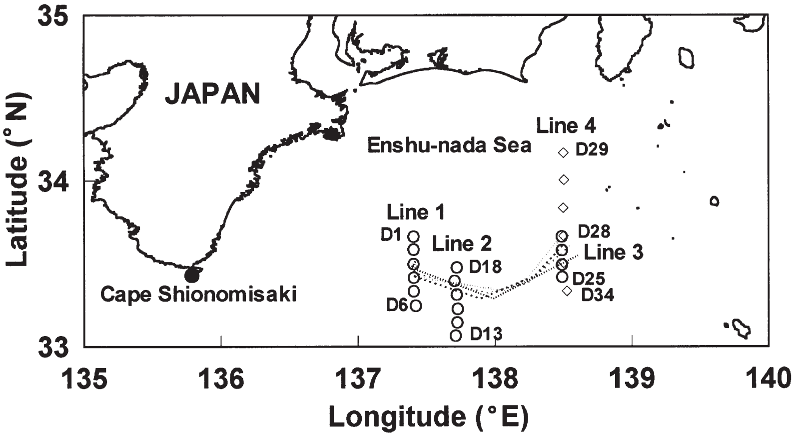

Fig. 2. Transects (Lines 1 to 4) and stations (Stns D1 to D34) for the CTD observation and the collection of fish larvae and their prey organisms across the Kuroshio front in the Enshu-nada Sea from 18 to 22 May 1997. Dashed lines indicate drifter trajectories

immediately sorted on the ship for the analyses of nucleic acid content and otoliths, then the larvae were stored in sucrose solution (0.25 M sucrose, 1 mM EDTA, 20 mM Tris-HCL, pH 7.5) at −80°C until the analyses were conducted. A small portion of zooplankton collected with the ORI net was stored on the fine mesh gauze at −80°C for the nucleic acid analysis of adult female copepods. The remains of larval and plankton samples were preserved in 2.5% seawater glutaraldehyde. Larval prey (mainly naupliar copepods) were collected from the surface water (0 to 0.3 m) using a bucket simultaneously with the ORI net deployment, since naupliar copepods were most abundant in the surface layer in the Kuroshio and its coastal water (Okazaki et al. 2002). The larval prey samples (1 l) were fixed in 5% seawater formalin after concentration by a plankton net with 0.020 mm mesh. Nutrient and chl *a* concentrations of the water samples were also determined and reported by Kasai et al. (2002). The total number of net tows and larval prey samplings were 18 and 20, respectively. The sampling was conducted once at each station due to time constraints, because all samplings along one transect had to be completed during the night to reduce potential bias associated with net avoidance by the larvae.

In the laboratory, fish larvae were sorted from the preserved samples. The standard length (SL) of anchovy larvae, the most dominant species, was measured, and naupliar copepods in the water samples were counted without identifying species.

We use *Paracalanus* sp. for nucleic acid analysis of female copepods. This species is one of the dominant copepods in the Kuroshio frontal region (Hirota 1995). The quantities of DNA and RNA in the individual anchovy larva and 10 adult female *Paracalanus* sp. from each station were determined by the fluorescence technique described by Clemmesen (1993) and further modified by Sato et al. (1995). Specimens were homogenized in 0.4 ml of Tris-SDS buffer (0.05 M Tris, 0.1 M NaCl, 0.01 M EDTA, 2% SDS, pH 8.0) containing Proteinase K (0.2 mg ml^{-1}) using a shaking mill for 1 h, and fluorescence-photometric measurements were subsequently made using ethidium bromide (EB). In total, 164 individual anchovy larvae and 15 samples of *Paracalanus* sp. were analyzed for their RNA:DNA ratios.

For the otolith processing method we followed Watanabe & Kuroki (1997). Prior to otolith extraction, the standard length of each larval anchovy was measured to the nearest 0.1 mm. Sagittal otoliths were dissected out and mounted on a glass slide with enamel resin. A total of 123 otoliths were examined. We counted the total number of daily growth rings and measured the radius of each ring using an otolith measurement system (RATOC System Engineering) consisting of a light microscope, a CCD camera, video monitor and an image analyzer controlled by a computer. We determined allometric parameters for each fish by using the biological intercept method (Campana 1990). The SL of anchovy at the first ring deposition was fixed at 4 mm for the biological intercept, referring to Takita (1988). Tsuji & Aoyama (1984) verified the daily deposition of otolith growth rings in Japanese anchovy after the 3rd to 4th day from hatching when larvae start feeding. Therefore, daily age of each anchovy larva was calculated as the number of rings plus 3.

The mortality rate (Z) during the drifter tracking was estimated for anchovy larvae below 20 d of age as:

$$Z = \frac{\ln(C_{t_1}) - \ln(C_{t_2})}{t_2 - t_1}$$

where C_{t_1} is the density of the cohort at time 1 (t_1), C_{t_2} is the density of the same cohort at time 2 (t_2). The larval cohorts were divided into 2 groups: first-feeding larvae and post first-feeding larvae (hereafter post larvae). The mortality rate was estimated for each group, based on the data from the first transect (Line 1, Fig. 1) at Day 0 and the third transect (Line 3, Fig. 1) at Day 2, taking the larval growth from Day 0 to Day 2 into account. The age range of the first-feeding larvae at Day 0 was less than 5 d old and that of the post larvae was 6 to 18 d old.

We further defined the high salinity water associated with the Kuroshio (psu > 34.55, referred to hereafter as 'the Kuroshio water'), moderate salinity water (34.35 < psu < 34.55) and low salinity water (psu < 34.35), referring to Kasai et al. (2002).

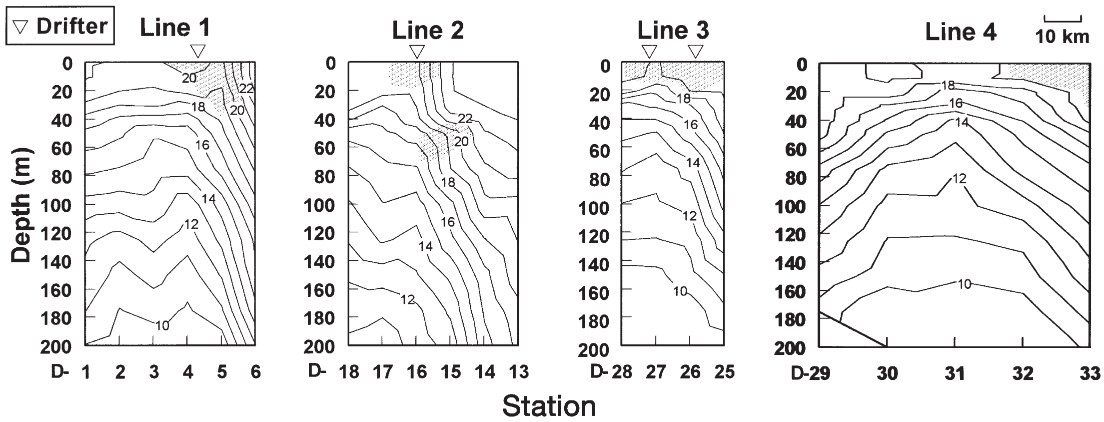

Fig. 3. Vertical profiles of temperature, together with distribution of low salinity water (indicated by the shaded area) across the Kuroshio front measured along transects (Lines 1 to 4; Stns D1 to D6, D13 to D18, D25 to D28 and D29 to D33, respectively) in the Enshu-nada Sea from 18 to 22 May 1997. Open triangles denote the drifter position. Note: no CDT observations for Stn 34

RESULTS

Cross-frontal distributions of physical and biological properties

Large horizontal temperature gradients between the Kuroshio and coastal water were detected along Lines 1 and 2, indicating the location of the Kuroshio front (Fig. 3). It is noteworthy that the low salinity water existed at the northern edge of the front. The position of the drifter coincided well with that of the low salinity water for each transect, indicating that the drifter represented the horizontal movement of the low salinity water. The average speed of the drifters moving toward the east was about 0.56 m s^{-1}.

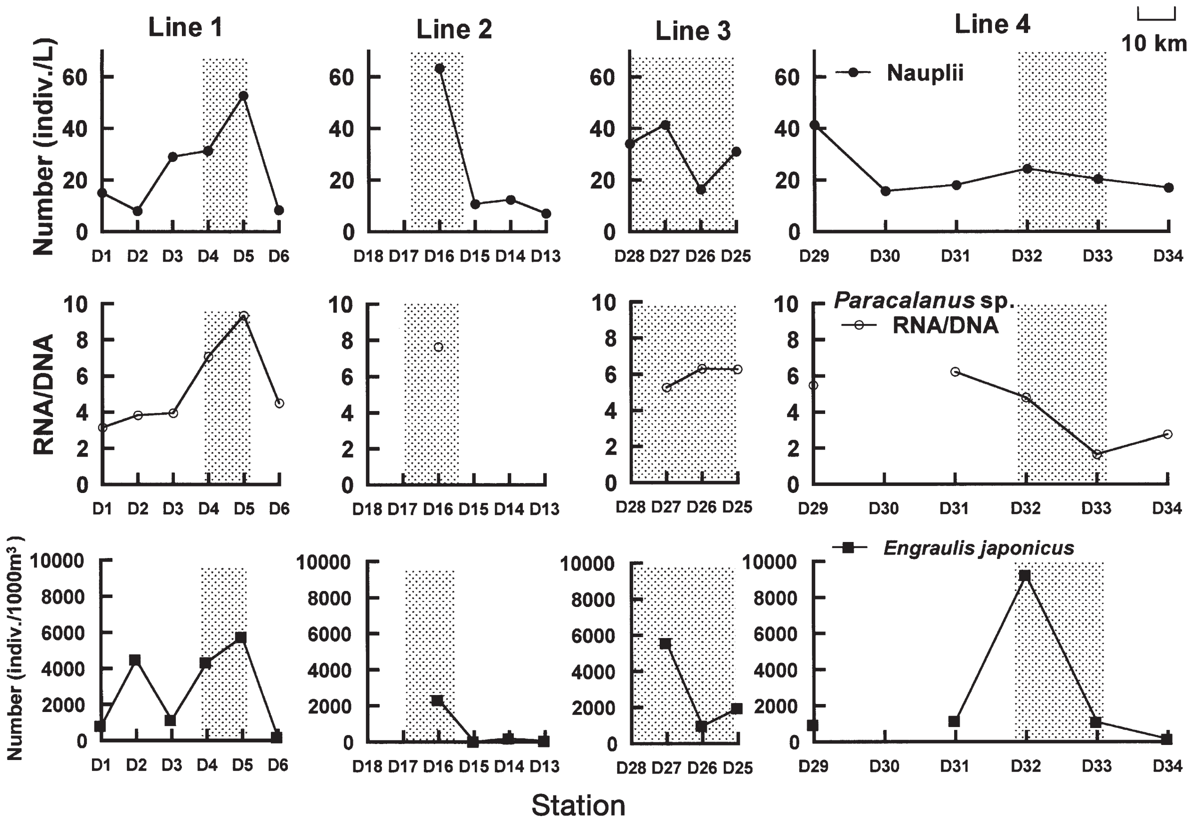

Fig. 4. Distributions of naupliar copepod abundance, RNA:DNA ratios of female *Paracalanus* sp. and abundance of anchovy larvae across the Kuroshio front measured along transects (Lines 1 to 4; Stns D1 to D6, D13 to D18, D25 to D28 and D29 to D34, respectively) in the Enshu-nada Sea from 18 to 22 May 1997. Shaded areas denote the low salinity water

The 14°C isotherm decreased in depth from 80 m (Line 1) to 50 m (Line 3) during the tracking, and a marked dome-shape isotherm distribution was found along Line 4; this suggests that a marked upwelling induced by a frontal eddy occurred in the latter transects (Lines 3 to 4), and that the low salinity water could be entrained from the Kuroshio front to the edge of the frontal eddy by its cyclonic motion.

Naupliar abundance was appreciably higher in the low salinity water along Lines 1 and 2; however, it decreased in the latter transects where the differences in the abundance were not clear between the low salinity water and the surrounding water (Fig. 4). The RNA:DNA ratios of female *Paracalanus* sp. showed a marked peak in the low salinity water along Line 1, indicating that copepod egg production was high in the low salinity water (Nakata et al. 1994, Saiz et al. 1998). However, the RNA:DNA ratios decreased with time, corresponding to the temporal decline in the naupliar abundance.

Anchovy larvae were most abundant on the coastal side of the Kuroshio, especially in the low salinity water, and rapidly decreased in the Kuroshio water (Fig. 4). Since the low salinity water in the Kuroshio frontal region originated from the coastal region, as inferred from the ocean color image taken during the survey period (Fig. 1), the anchovy larvae that collected in the low salinity water could have been entrained from the coastal spawning ground.

Nutritional condition and growth of larvae

Positive correlations were found between naupliar abundance and mean RNA:DNA ratios of anchovy larvae for 3 larval size classes (Fig. 5). The correlations were significant ($p < 0.05$) for 7–8 mm and 8–9 mm classes.

Mean back-calculated SLs of the larvae collected from the low salinity water linearly increased with age, and could be expressed by a simple liner regression; $y = 0.63x + 1.97$ ($r^2 = 0.995$). Furthermore, the recent growth rate was calculated from the 3 outer otolith increment widths for each larva in the low salinity water. The mean recent growth rate (±SD) was 0.57 ± 0.16 mm d^{-1} (n = 123).

Fig. 6 shows the mean density of anchovy larvae in each length category (standard length) in the low salinity water at Stns D4 and D5 on Day 0 and Stns D25, D26 and D27 on Day 2. The mean length of the anchovy larvae increased from Day 0 to Day 2. Assuming that the SL of first-feeding anchovy larvae was 4 mm (Takita 1988), and the period of egg development was 1.7 d at a temperature of 20°C (Azeta 1981), then the time elapsed since spawning was estimated to be 4 to 25 d, with a mean of 8.5 d for the size frequency distribution of anchovy larvae at Day 0.

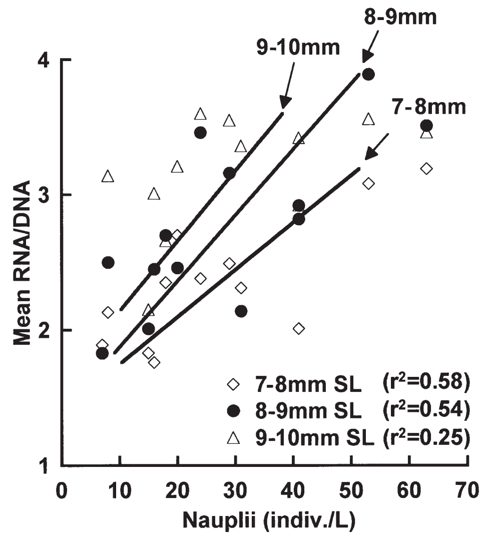

Fig. 5. Relationship between naupliar copepod abundance and mean RNA:DNA ratios of anchovy larvae for 3 size classes, measured from 18 to 22 May 1997. The mean RNA:DNA of each station was based on the data from individual larvae (1–16 ind.)

Larval mortality estimate

Larval age distributions in the low salinity water at Days 0 and 2 were obtained from the relationship between larval length and age, as described above, and the length-frequency distribution (Fig. 6). The densities of first-feeding larvae and post larvae at Day 0 (Stns D4 and D5) and Day 2 (Stns D25, D26, and D27) are shown in Table 1, together with the apparent daily mortality rates for the first feeding larvae (0.96 d^{-1}) and for the post larvae (0.18 d^{-1}). The larval survival during these 2 d were 14.5 and 70.2%, respectively.

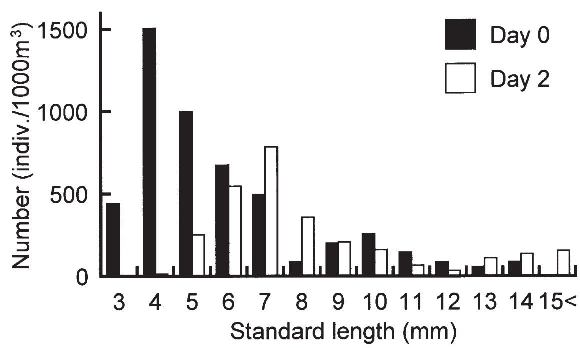

Fig. 6. Length frequency distributions of anchovy larvae collected from Stns D4 and D5 on Day 0 and Stns D25, D26 and D27 on Day 2 in the low salinity water

Table 1. Mean density of the first feeding larvae (less than 5 d old at Day 0 sampling) and the post larvae (6 to <18 d old) in the low salinity water. Apparent mortality rate (Z) and survival rate (during 2 d) of each age cohort are also demonstrated. Day 0 and Day 2 samplings include Stns D4 and D5 and Stns D25, D26 and D27, respectively

Age cohort (d) at Day 0 sampling	Larval densities (ind. 1000 m^{-3}) Day 0 sampling	Day 2 sampling	Z (d^{-1})	Survival rate (%)
<5	1810.0	263.3	0.96	14.5
6–18	3066.9	2153.6	0.18	70.2

The mortality rate estimated above could be biased by diffusion during the drifter tracking period. Assuming that time change in the width of low salinity water on the transects from Day 0 (about 15 km) to Day 2 (about 25 km) was mainly due to the diffusion in the cross-frontal direction, the diffusive loss due to this cross-frontal diffusion was approximately 40% per 2 d. Therefore, after correcting for the diffusive loss in the larval density decline, the net (biological) mortality rates for the first-feeding larvae and for the post larvae were estimated to be 0.71 and –0.08 d^{-1}, respectively.

Further, the RNA:DNA ratios of anchovy larvae in the low salinity water at Day 0 were compared with those of Day 2. As shown in Fig. 7, a significant decline in the larval RNA:DNA ratio was detected between Day 0 and Day 2 (ANCOVA, $p < 0.01$). This indicates that the larval nutritional condition at Day 2 was degraded from that at Day 0.

DISCUSSION

Larvae originating from coastal water have been collected in the Kuroshio front (Hattori 1970, Kuroda 1986), suggesting that entrainment of coastal larvae frequently occurs in the Kuroshio region. The low salinity water discharged from estuaries along the coast moves through the coastal region of the Kuroshio with a speed of about 5 to 10 cm s^{-1} (Imasato & Qio 1987). Assuming that the distance from the coast to the Kuroshio front was 50 to 100 km, the low salinity water could take 6 to 23 d to get to the Kuroshio front, which is consistent with the age range (4 to 25 d old) estimated for the anchovy larvae collected in the low salinity water. Therefore, these anchovy larvae were likely transported together with coastal water from their spawning grounds to the Kuroshio frontal region.

Although high naupliar abundance and copepod RNA:DNA ratios were obtained in the low salinity water at Day 0, both decreased in the subsequent transects (Lines 3 and 4). According to Kasai et al. (2002), nutrients were already depleted in the low salinity water at Day 0, suggesting that primary productivity rapidly declined in the surface water. This could lower secondary production. Furthermore, the RNA:DNA ratios of the anchovy larvae in the low salinity water also decreased in the latter transects. The significant positive correlation between RNA:DNA ratios of anchovy larvae and naupliar abundance was consistent with several other recent studies, e.g. Canino et al. (1991), Bailey et al. (1995) and Chícharo et al. (1998). The results of our study mentioned above indicate that biological production in the Kuroshio frontal region could not be sustained or accelerated by the coastal water entrainment. Instead, the frontal eddy, as was shown in Lines 3 and 4, may play an important role in the biological production and larval survival in the Kuroshio frontal region.

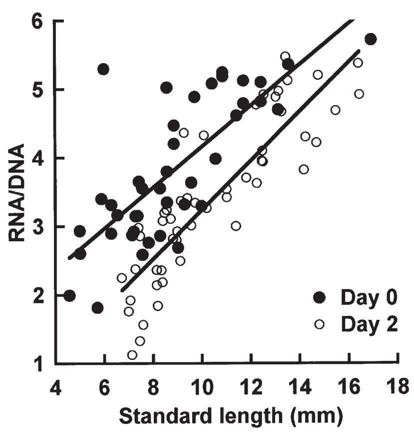

Fig. 7. Scattergrams and least squares regressions of standard length (SL) and RNA:DNA ratios for anchovy larvae in the low salinity water on Days 0 and 2

Although there has been no information on the mortality rate of Japanese anchovy larvae in the Kuroshio region, that of northern anchovy larvae in the California Current region was reported to range from 0.13 to 0.23 d^{-1}, over a period of yolk-sac absorption through to ca. 25 to 30 d old (Hewitt & Methot 1982). In the southern Brazilian Bight, the mortality rate of larval anchovy was 0.064 d^{-1} from 15 to 35 d (Kitahara & Matsuura 1995). Castro & Hernandez (2000) reported the mortality rates of the Peruvian anchovy *Engraulis ringens* off central Chile to be 0.05 and 0.07 d^{-1} for the first 35 d. Our estimate of the biological mortality rate (0.71 d^{-1}) of first-feeding larvae is appreciably high compared to the mortality rates reported previously for *Engraulis* spp. The mortality rate of post larvae, after correcting for diffusive loss, was negative, suggesting that it could be distorted by the immigration of larger larvae from the outside and that the biological mortality must be much smaller than that of the first-feeding larvae. In general, mortality of marine fish is a sizespecific phenomenon (McGurk 1986, Houde 1997); thus relatively small larvae (less than 7 mm SL) have higher mortality rates. Kitahara & Matsuura (1995) reported that the mortality rate of southwest Atlantic anchovy larvae smaller than 12 mm SL was higher than the rate of larger larvae. Mitani (1990) demonstrated that Japanese anchovy larvae up to 8 mm total length after hatching have no fin-lay, and therefore poor ability of swimming. Hence, first-feeding stage of anchovy larvae were more vulnerable to starvation or predation.

Along the last transect, anchovy larvae were most abundant in the outer edge of a frontal eddy in association with the entrainment of the low salinity water into the eddy (Fig. 4). Bakun (1996) mentioned that as cyclonic curvature develops, divergence and upwelling occur on the concave side of the eddy, while convergence occurs on the convex side. This convergence of the surface water may have implications for the larval aggregation on the eddy edge. The frontal eddy could have a function of enhancing primary production due to upwelling (Lee et al. 1981, Shiomoto & Matsumura 1992, Kimura et al. 1997, 2000). Nakata et al. (2000) further indicated that naupliar copepod abundance in the frontal eddy approximately doubled in 2 d, indicating that the encounter with the frontal eddy could improve larval feeding conditions.

In conclusion, declines in the copepod RNA:DNA ratio, naupliar abundance, and the RNA:DNA ratio of anchovy larvae in the low salinity water indicate that food availability of anchovy larvae gradually decreased in the water entrained into the Kuroshio front. The most probable reason for larval abundance decline during the drifter tracking, especially for first-feeding stage larvae, could be poor nutritional condition or starvation due to low prey abundance. This result suggests that the offshore entrainment of fish larvae originating from coastal water could be unfavorable for their survival. The encounter with a frontal eddy would enhance the food production and the subsequent survival of anchovy larvae in the frontal region; otherwise they may perish due to low food availability.

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