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Entrainment of coastal water into a frontal eddy of the Kuroshio and its biological significance

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Abstract

The Pacific coastal areas of Japanese Island are major spawning grounds of various fishes. It is considered that large amount of eggs and larvae are dragged into the Kuroshio front so that the survival of fish larvae at the front is important for their recruitment. From this viewpoint, a low-salinity water mass, which was withdrawn from the coastal area to the Kuroshio front, was investigated by drifters, in addition to fine-scale hydrographic observations and water sampling in and around the Kuroshio frontal area off Enshu-nada. The drifters were transported to the east within the low-salinity water along the Kuroshio front in the first stage, and were thereafter entrained into an eddy, which was caused by the frontal meander. They moved closely to each other along the front, but diverged in the eddy. This movement of the drifters coincided with the deformation of low-salinity water mass; the low-salinity water concentrated at the Kuroshio front surrounded by strong salinity gradients at first, while it spread out horizontally and became vague in the shallow surface layer in the frontal eddy. Comparing temperature sections across the front, the strong upwelling was detected in the eddy. Limiting factors for primary production and growth rates were calculated in six sections using the observed temperatures and concentrations of nutrients. In the frontal area of the Kuroshio, low concentration of nutrients limited the primary production shallower than 50 m. Due to the low productivity, concentration of chlorophyll *a* in the low-salinity water tended to decrease, although the initial concentration was high. Once the coastal water mass was entrained into the frontal eddy, on the contrary, the concentration recovered due to the enhanced primary production in the subsurface layer supported by the upwelling of nutrient-rich water. Fish larvae in the low-salinity water are assumed to use the new production in the eddy; otherwise, they would starve. The entrainment process, which was probably caused by offshoreward movement of the Kuroshio, holds the key to successive survival and recruitment of fish larvae in the Kuroshio system.

Keywords: Kuroshio; Frontal eddy; Upwelling; Primary production

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1. Introduction

The Enshu-nada and Kumano-nada seas located off the south coast of Japan are famous as major spawning grounds of various pelagic fishes such as sardines

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and anchovies (Fig. 1). The Kuroshio, flowing eastward in the offshore of this region, drives a cyclonic recirculation that develops westward flow in the coastal area of Enshu-nada and southwestward flow in Kumano-nada (Funakosi et al., 1979; Sugimoto, 1987). A large quantity of eggs and larvae spawned in the coastal area would be transported by the flow and entrained into the Kuroshio around Cape Shionomisaki. The eggs and larvae entrained tend to accumulate along the Kuroshio front and drift to the east (Nakata et al., 2000). High abundance of those eggs and larvae in the front suggests that their survival could greatly contribute to the sustaining fish population off the south of Japan.

It is believed that the front of the strong currents provides high biological production due to vertical motion induced by unstable meandering of the current. This phenomenon is often observed off the east of Cape Hatteras in the Gulf Stream (Hitchcock et al., 1993; Lohrenz et al., 1993) and off the east of Cape Inubozaki in the Kuroshio (Yamamoto et al., 1988; Kimura et al., 2000). In Enshu-nada and Kumano-nada, however, there is no guarantee that the production at the Kuroshio front will be high, because the Kuroshio flows rather smoothly and the frontal disturbance curvature is relatively small. It is well known that the Kuroshio takes a more stable path off the south of Japan than east of Japan, although it has a bimodal character: a straight mode and a large meandering mode (e.g., Yoshida, 1964; Taft, 1972). The production at the Kuroshio frontal area off the south of Japan, therefore, should be different from that east of Japan. It is necessary to estimate productivity in the former region, which is in the neighborhood of the spawning and nursery grounds and has implications for larval survival and recruitment.

In recent studies, on the other hand, it has been well-observed from satellite imagery and hydrographic surveys that frontal disturbance of the Gulf Stream accompanies cyclonic eddies over the southeast US outer continental shelf, which is located off the south of Cape Hatteras (e.g., Lee et al., 1981; Yoder et al., 1983). The frontal eddies are also a ubiquitous feature in Enshu-nada and Kumano-nada

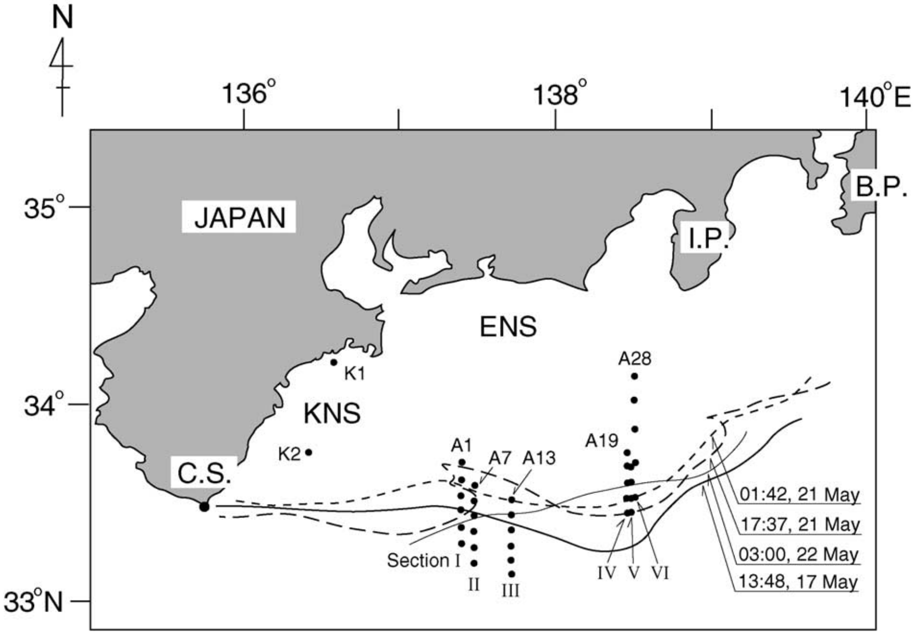


Fig. 1. Study area and location of Enshu-nada sea (ENS) and Kumano-nada sea (KNS). Solid circles indicate the hydrographic observation stations (A1–A32). K1 and K2 are CTD stations observed by the Fisheries Research Institute of Mie. The positions of the Kuroshio front detected from satellite images are indicated by solid lines that pass through the CTD observational sections. C.S., I.P. and B.P. denote Cape Shionomisaki, Izu Peninsula and Boso Peninsula, respectively.

(Kasai et al., 1993; Kimura and Sugimoto, 1993). Their horizontal scales are 200–400 km, so that they are called mesoscale eddies. It has also been revealed from recent surveys that nutrient-rich deep water is upwelled to the euphotic zone due to the cyclonic motion in these eddies (Lee et al., 1981; Yoder et al., 1983; Sasaki et al., 1985; Tranter et al., 1986; Kimura et al., 1997). According to estimates by Lee et al. (1981) and Kimura et al. (1997), annual carbon production by the Gulf Stream and the Kuroshio frontal eddies are up to 32–64 and 40 g C m^{-2} $year^{-1}$, respectively. These results corroborate the potential significance of the frontal eddies for biological activity. It would be therefore important for eggs and larvae in the frontal region to enter the eddy water, provided that the production in the surrounding water is low. In the real ocean, however, clear evidence for entrainment of the frontal water, which contains fish eggs and larvae, has not yet been demonstrated, and thus the mechanism for fish larvae to use the enhanced production in the eddy is still uncertain.

In this study, therefore, drifters were used to examine the time evolution of physical and biological structures of the water, which was withdrawn from the coastal area of the Kumano-nada Sea and transported along the Kuroshio front. This coastal water indeed contained large amounts of anchovy eggs and larvae in addition to their food such as naupliar copepods (Okazaki et al., submitted for publication). We especially focus on the effect of the frontal eddy on the production in the coastal water. During the tracking of the drifters, physical and biological structure across the Kuroshio front accompanied by a cyclonic eddy was observed. In most of the previous studies, the observations were conducted with rather coarse horizontal scales of a few tens of kilometers or more, which were unfeasible to distinguish biological structure in the frontal eddies from that in the Kuroshio front itself. In this study, on the contrary, a fine scale (~ 10 km) survey was performed off Enshu-nada. Using the observational results, limiting factors for primary production and the growth rates were estimated. The difference between the role of the frontal eddy and that of the front itself in the biological production and successive recruitment of pelagic fish larvae is also discussed.

2. Field observations

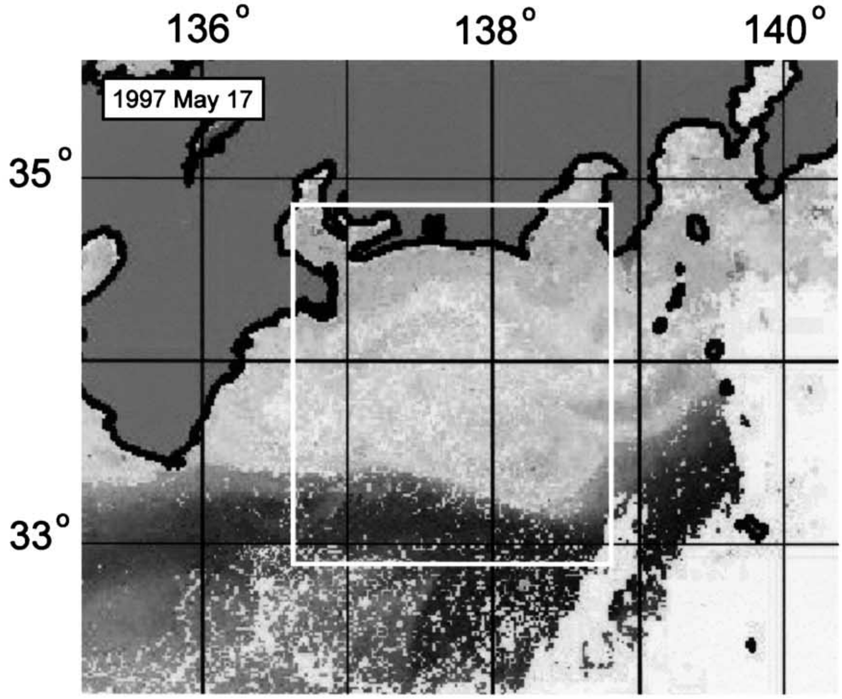
Hydrographic observation with water sampling was conducted by the R/V *Hakuho-maru* during 17–22 May 1997. Preceding the principal survey, AVHRR satellite images and expandable bathythermographs (XBTs) were used to determine the Kuroshio path and the position of the frontal eddy (Fig. 2). SST gradient larger than 0.15 °C km^{-1} demonstrates the existence of the Kuroshio front, and the frontal disturbance gave indication of a cyclonic eddy centered around 33°30′ N, 138°20′ E with 100–150 km in diameter. Cold water, which would be upwelled from the deeper ocean, showed eddy structure to the depth of 100 m (Fig. 2c). A time series of satellite images indicates that the disturbance was rather stationary and moved slightly to the east during the survey period, although the front accompanied by the eddy oscillated in the north–south direction (Fig. 1).

Drifters used in this study were composed of a surface buoy and a 2 × 5 m drogue centered at a depth of 18 m below the sea surface. The buoy was equipped with a GPS sensor and an ARGOS system, which transmitted its position to the vessel. Four drifters were released on the upstream side of the frontal eddy and tracked from 16:10, 18 May to 6:21, 21 May, for 46–54 h (Fig. 2b).

While the buoys were tracked, hydrographic observations were carried out at 32 stations along six sections as shown in Fig. 1, using a conductivity–temperature–depth profiler (CTD) from 18 to 22 May. Consequently, the water mass in which the buoys were deployed was observed repeatedly as it moved eastward by the Kuroshio. Considering the slight movement of the eddy to the east, desirable positions were selected for observing the eddy; Sections I and II were close to the western edge, Section III was in the western flank, and Sections IV, V, VI were near the center of the eddy. The latitudinal distance between the stations was designed to be about 10 km for detecting fine structures of the Kuroshio front and the associated eddy. Hydrographic results in Kumano-nada observed on 19 May by the Fisheries Research Institute of Mie were additionally used (Fig. 1).

Water samples for determining chlorophyll *a* and nutrient concentration were taken from 0, 15, 30, 50,

(a) Satellite thermal Image



(b) XBT-SST

(c) XBT-100m

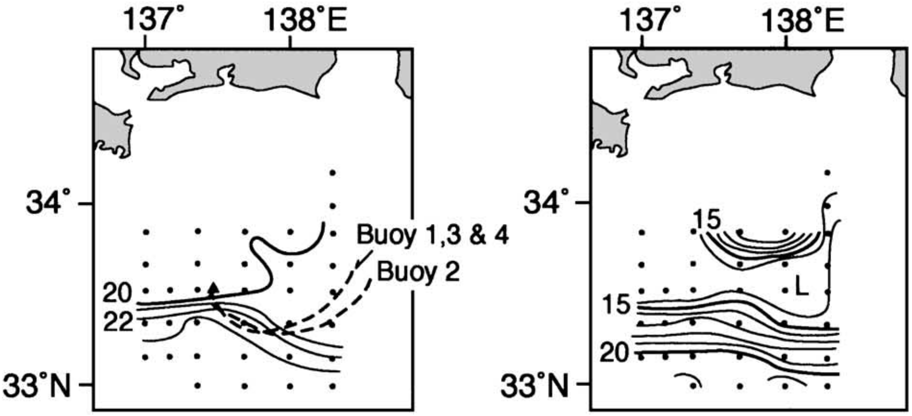


Fig. 2. (a) Satellite thermal image of the Kuroshio over Enshu-nada and Kumano-nada taken on 17 May 1997. Darker (lighter) tone indicates warmer (colder) area. White denotes cloud. (b) Distributions of sea surface temperature obtained by an XBT survey. Trajectories of drifter buoys are shown by dotted lines. A solid triangle indicates the trajectory start point. All drifters were entrained by the eddy within 38 h after release. (c) Distributions of temperature at 100 m depth obtained by an XBT survey.

75 and 100 m depths at each station with Niskin bottles mounted on a rosette sampler attached to the CTD. A 200-cm^3 quantity of each water sample was filtered onto a Whatman GF/F glass microfiber filter, then the filter was soaked in 10 ml of dimethylformamide. The chlorophyll fluorescence in the dimethylformamide

was later measured in the laboratory. The filtered water was frozen and contained nutrients were subsequently analyzed by an autoanalyzer (Technicon). Nitrate + nitrite concentration was measured as the dissolved inorganic nitrogen (DIN) concentration because no nutrients are more important than nitrogen as the potential limiting factor for phytoplankton growth in this area (Siomoto and Matsumura, 1992). Ammonium was excluded from DIN in this study because ammonium concentration is extremely low and has a minor effect on the production in our target area.

3. Results

3.1. Physical structure

Trajectories of the four drifters with positions of the Kuroshio front are shown in Fig. 3. They were deployed within 5 km from 33°30′ N, 137°25′ E, 20 km north of the front. All drifters moved southward slowly at a speed of less than 0.3 m s^{-1} for the first 8 h. Beyond 33°27′ N, they turned southeastward and moved still slowly until 33°20′ N. They then suddenly accelerated and drifted eastward until 137°50′ E. Combination of their speeds and the position of the front indicate that they were adjacent to the Kuroshio front in this stage. All drifters were within 10 km from one another until they reached Section III. However, they were trapped by the eddy as they approached the trough of the frontal disturbance (see also Fig. 2). It is worth noticing that they tended to diverge in the eddy. After the entrainment into the eddy, the drifters lost speed again and were nearly stationary in the vicinity of the eddy center (33°30–40′ N, 138°20–30′ E).

Fig. 4 shows vertical structures across the Kuroshio front observed along the six sections. The similarity between density and temperature structures in all sections shows that the density field was dominated by temperature distribution, while the salinity variations made only a minor contribution. The strong temperature gradient of more than 0.15 °C km^{-1} indicates that the Kuroshio front was located between Stn. A5 and Stn. A6 at the surface in Section I, consistent with the satellite image.

In spite of the minor contribution to the density field, the salinity distributions inform of an important feature of the front; an explicitly low-salinity water mass (<34.35 psu) existed at the northern edge of the front. A T–S diagram reveals that the upper water along Section I can be classified into three groups (Fig. 5a): the high salinity Kuroshio water ($s>34.55$ psu), moderate salinity water ($34.35<s<34.55$ psu) and the low-salinity water ($s<34.35$ psu). The water at A6 was inside of the Kuroshio and classified in the first group. The second group contains A1, A2 and A3, which were on the inshore side of the Kuroshio, and will be called OEW (off Enshu-nada water) hereafter. The shallow water at A4 and A5 was, on the contrary, explicitly distinguishable by its low

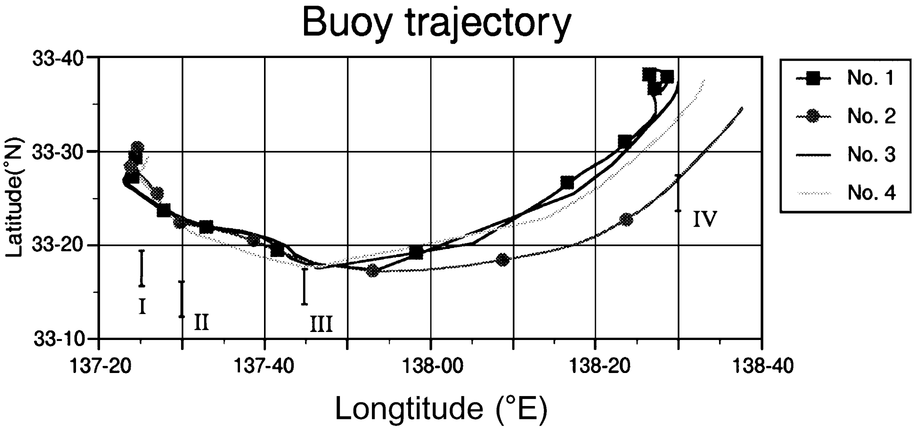


Fig. 3. Trajectories of drifters. Bars indicate the Kuroshio front estimated from the CTD survey. Marks on the trajectories are plotted every 6 h.

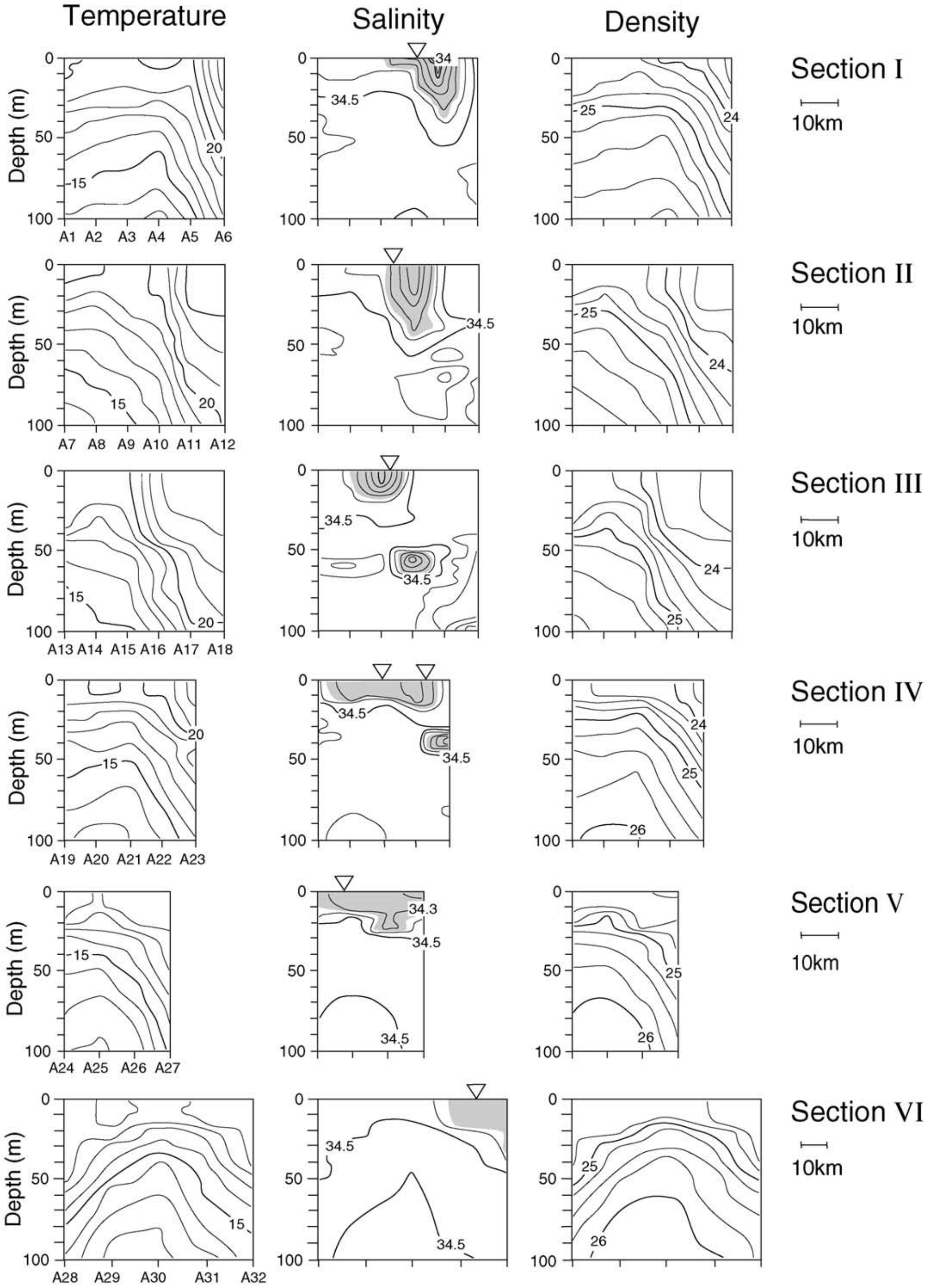


Fig. 4. Vertical distributions of temperature (°C), salinity (practical salinity units, psu) and density (σ_t) along the six sections. Shaded areas indicate the water with salinity lower than 34.35 psu. Triangles are positions of drifters.

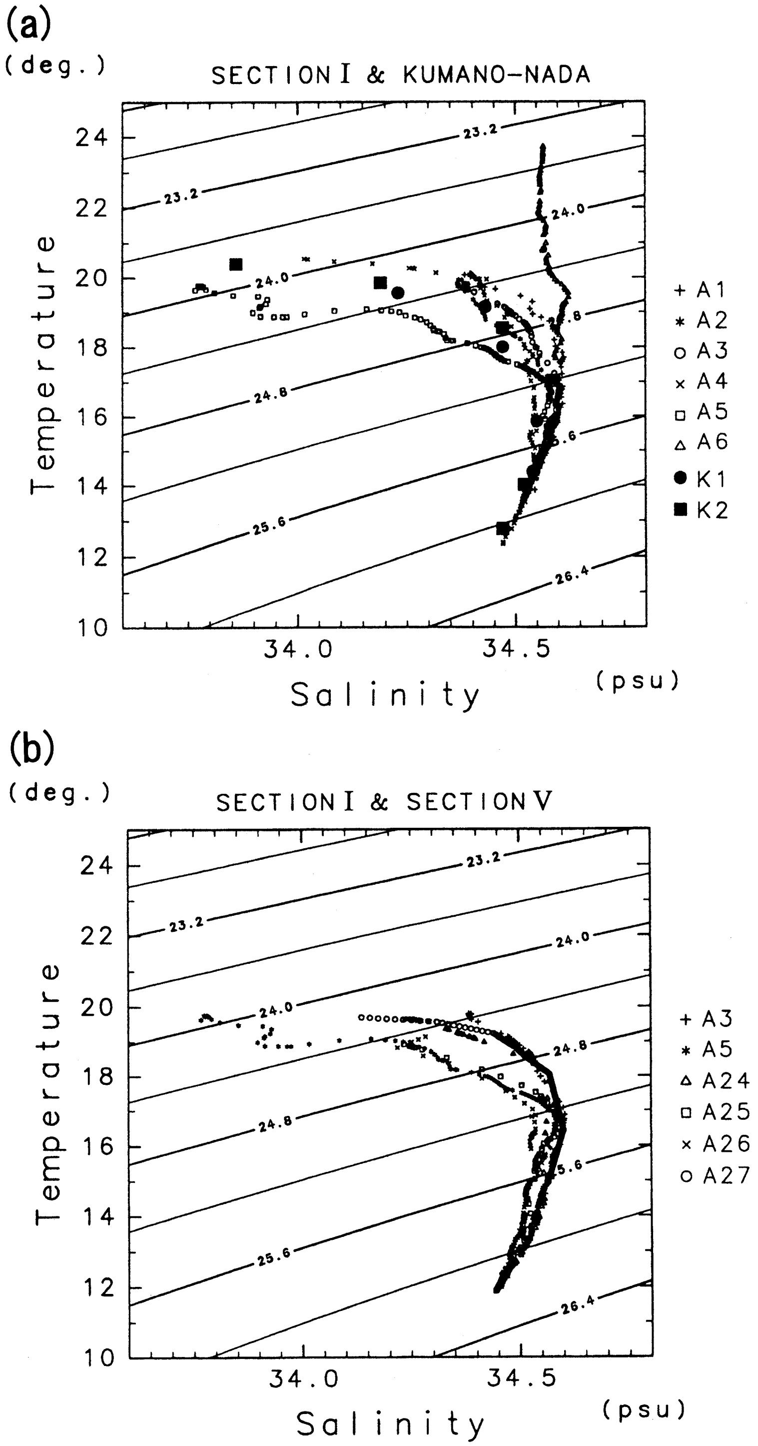


Fig. 5. Temperature–salinity diagram constructed with (a) every 1 m data from Section I and data at 0, 10, 20, 30, 50, 75 and 100 m depths from the coastal area of Kumano-nada, and (b) every 1 m data from Section I and Section V. See Fig. 1 for the location of the Kumano-nada points.

salinity from surrounding water and thus is classified in the last group. The water with salinity less than 34.35 psu, which was the lowest salinity in OEW in Section I (Fig. 5), is supposed to be the coastal water and shaded in Fig. 4. This water had similar character to the near-shore water of Kumano-nada (K1 and K2), indicating that it was withdrawn from the coastal area and transported along the Kuroshio front. Strong salinity gradients (≥ 0.1 psu km^{-1}) between the low-salinity water and the Kuroshio water (Sections I–III in Fig. 4) show that they hardly mixed with each other, when the low-salinity water was trapped by the Kuroshio front.

The positions of drifters in each section are marked with triangles in Fig. 4. Drifters were always in the low-salinity water, indicating that the trajectories of drifters represented the movements of the low-salinity water. Comparing the salinity distribution of each section, this low-salinity water was rather thick from the surface to 40 m depth at the western edge of the eddy (Sections I and II), while it changed shape as it was transported to the east. It separated into two thinner parts, one of which was still at the surface and the other was in the subsurface centered at 55 m in Section III. In contrast, in the sections across the eddy center (Sections IV–VI), the surface low-salinity water spread out horizontally from the eddy center to the front in the layer shallower than 25 m depth. This change in the distribution corresponds well with the movement of drifters, which diverged in the east of Section III (Fig. 3). The low-salinity water was explicitly distinguishable from the remainder in the former three sections, but the salinity gradient became obscure in the latter three, near the eddy center (Fig. 4). The lowest salinity increased to higher than 34.1 psu in the latter, although it kept less than 34.0 psu with a strong halocline in the former three sections. Comparing the water character of Section V with that of Section I on the T–S diagram (Fig. 5b), for example, the surface water at A27 (Section V) is positioned intermediate between those at A3 and A5 (Section I). This indicates the surface water at A27 would be a mixture of those in Section I. On the other hand, the surface water at A25 and A26 (Section V) lies in the same line as the 30–50 m depths of water at A5 on the T–S diagram, showing that the subsurface water in Section I was uplifted and composed a part of the surface water in the eddy.

Uplifted contours of temperature below the subsurface also suggest strong upwelling inside of the eddy (Fig. 4), although the weaker domed structure was recognized even at the western edge (Sections I and II). The peak of the 14 °C isotherm rose from 80 m in Section I to 40 m in Section VI, indicating that deeper water was upwelled at least 40 m due to the cyclonic motion of the eddy. A high concentration of nutrients should have been consequently lifted up to the euphotic zone in the Kuroshio region. The upwelling must contribute to primary production.

3.2. Biological structure

We pay attention to the biological structure in the low-salinity water, because it has important implication for the survival of larvae spawned in the coastal area and transported along the front within the water. Fig. 6 shows vertical profiles of chlorophyll *a*, DIN concentration, temperature and salinity at Stn. A5 (Section I) and Stn. A21 (Section IV) where the low-salinity water was observed. It is noticeable that high concentration of chlorophyll *a* was detected around a depth of 30 m at Stn. A5. In the subsurface layer, however, nutrients were depleted, indicating that there was little possibility of consequent prosperity for phytoplankton. Indeed, time change in chlorophyll *a* concentration (Fig. 7) shows that high concentration in the subsurface layer decreased as far as it was accumulated at the Kuroshio front (Section I–III). Once it was entrained into the eddy, on the other hand, chlorophyll *a* recovered in the surface layer and kept high level until the end of the observation (Section IV–VI). From the temperature and DIN profiles, nutrient-rich deeper water appears to be uplifted when it was entrained into the eddy (Figs. 4 and 6b). Comparing with the shallower layer in which large variation of chlorophyll *a* was detected, the level of chlorophyll *a* concentration was always low in deeper layer than 50 m throughout the observation (Fig. 7).

3.3. Estimate of limiting factors

To elucidate the time change in the chlorophyll *a*, the phytoplankton growth rate and limiting factors were estimated in each station based on the observed physical and biological structure. The phytoplankton

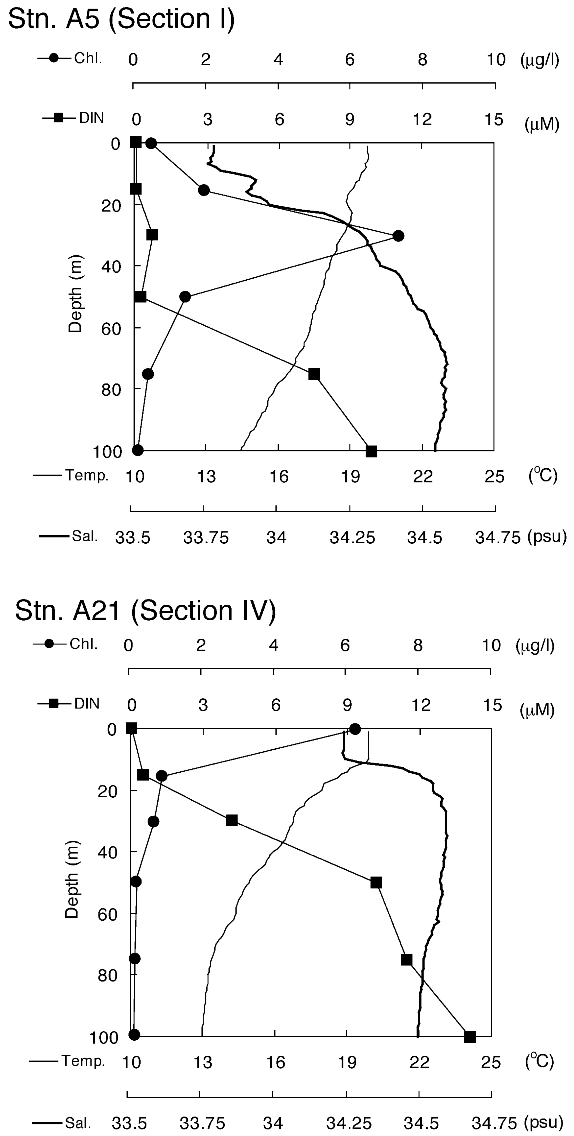


Fig. 6. Vertical profiles of temperature, salinity, chlorophyll *a* and DIN concentrations at Stn. A5 and A21.

growth rate (G) can be estimated by the multiplicative way (Yanagi et al., 1997);

$$G = G_{\max}\mu_I\mu_T\mu_N, \tag{1}$$

where $G_{\max}$ denotes the maximum photosynthetic rate of phytoplankton, and μ_I, μ_T and μ_N are light-, temperature-and nutrient-controlled growth rates of phytoplankton, respectively. This model might be simple and different from the latest models. The complicated ecosystem model would be more useful for the estimate of primary production, as presented by Kimura et al. (1997). However, the multiplicative model was applied here because it can calculate the limiting factors separately and their effects on the primary production can be clearly estimated using the observational results.

Following Steel (1962), μ_I and μ_T are estimated as

$$\mu_I = \frac{I}{I_{\text{opt}}}\exp\left(1 - \frac{I}{I_{\text{opt}}}\right) \tag{2}$$

$$\mu_T = \frac{T}{T_{\text{opt}}}\exp\left(1 - \frac{T}{T_{\text{opt}}}\right) \tag{3}$$

where I denotes the light intensity, I_{opt} the optimum light intensity, T temperature, and T_{opt} the optimum temperature for the growth of phytoplankton. The dependence of chlorophyll *a* specific rate on nutrient concentration took the form

$$\mu_N = \frac{N}{N_{\text{h}} + N} \tag{4}$$

where N is DIN concentration and N_{h} the half saturation constant for DIN.

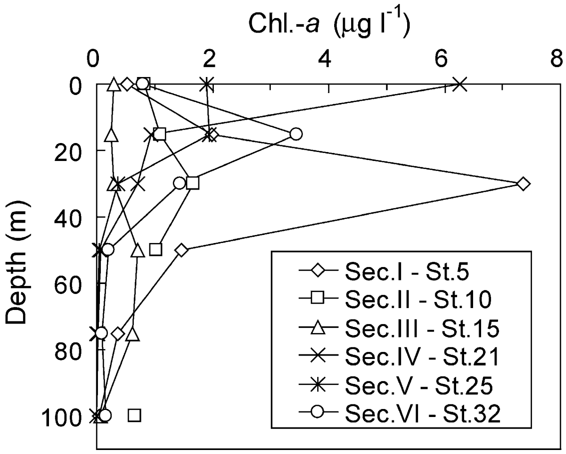


Fig. 7. Time change in vertical profiles of chlorophyll *a* concentration.

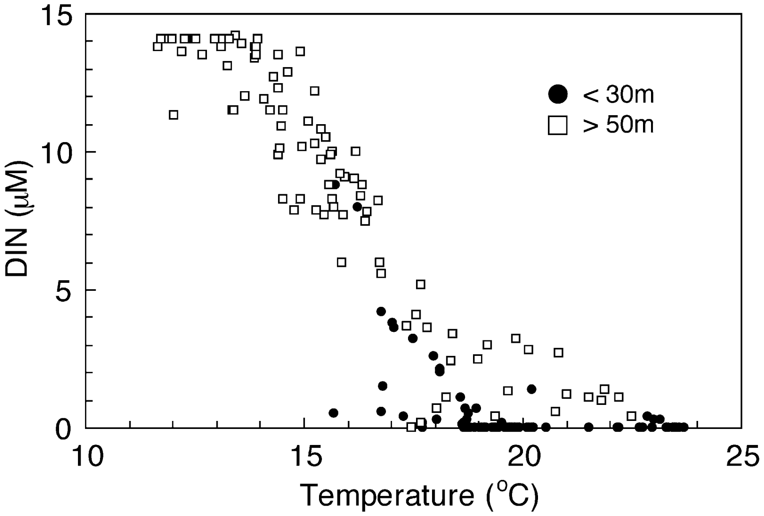


Fig. 8. Scattering diagram of DIN concentration and temperature at all stations. Circles and squares indicate data deeper than 50 m and shallower than 30 m, respectively.

Light intensity was determined by

$$I(z) = I_s \exp\left(-\int_0^z k(z)\mathrm{d}z\right) \tag{5}$$

$$k(z) = 0.04 + 0.0184C(z) \tag{6}$$

where I_s is the light intensity at the sea surface, k the extinction coefficient and z the depth (Takahashi and Parsons, 1972). Eqs. (5) and (6) represent the self-shading of phytoplankton. In Eqs. (3) and (6), observed concentrations of chlorophyll a and temperature were used for C and T, respectively. However, observed DIN concentrations might be inappropriate for the estimates of the growth rates because DIN inputs by the upwelling and/or mixing would contribute to the primary production even though the DIN in a water mass might have been consumed. Observed chlorophyll did not grow by using simultaneously observed DIN, but using pre-stage DIN. The observed DIN concentration would be the result of consumption by the growth of the observed chlorophyll, so that different from the potential DIN concentration, which should be used in the estimates. Here, the potential DIN concentration was estimated as follows. As is shown in Fig. 6, nutrient concentration is high in the deeper layer, while that in the surface is depleted. Since the upwelling of this nutrient-rich deeper water would lead to active primary production, it is impor-

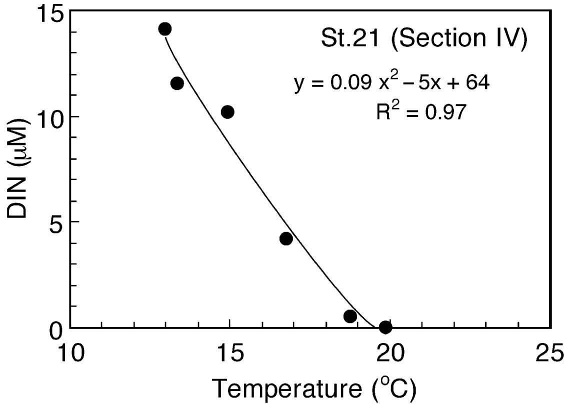


Fig. 9. Relation between DIN concentration and temperature at Stn. 21 (Section IV).

Table 1
Parameters used in the estimates

Symbol	Definition	Value	Reference
I_s	daily-averaged surface irradiance	80.0 (W m^{-2})	Kimura et al. (1997)
I_{opt}	optimal irradiance	70.0 (W m^{-2})	McAllister et al. (1964)
T_{opt}	optimal temperature	25.0 (°C)	Yamaguchi (1991)
N_h	half saturation constant for DIN	0.5 (μM)	Eppley et al. (1969)

tant to estimate the upwelled DIN to the euphotic layer. Fig. 8 shows a scattering diagram of temperature and DIN concentration. Water temperature has a strong negative correlation with DIN concentration below 50 m ($r^2 = 0.85$), while that in the shallow layer does not. This indicates that the upwelled low-temperature water originally contained enough DIN for phytoplankton growth in the lower layer and that the DIN was used in the shallow layer. Using the correlation in Fig. 8, the input of potential DIN concentration can be estimated by monitoring of water temperature. The water mass nearest to the buoy in each line is supposed to be the one that had the same temperature at the nearest station to the buoy in the

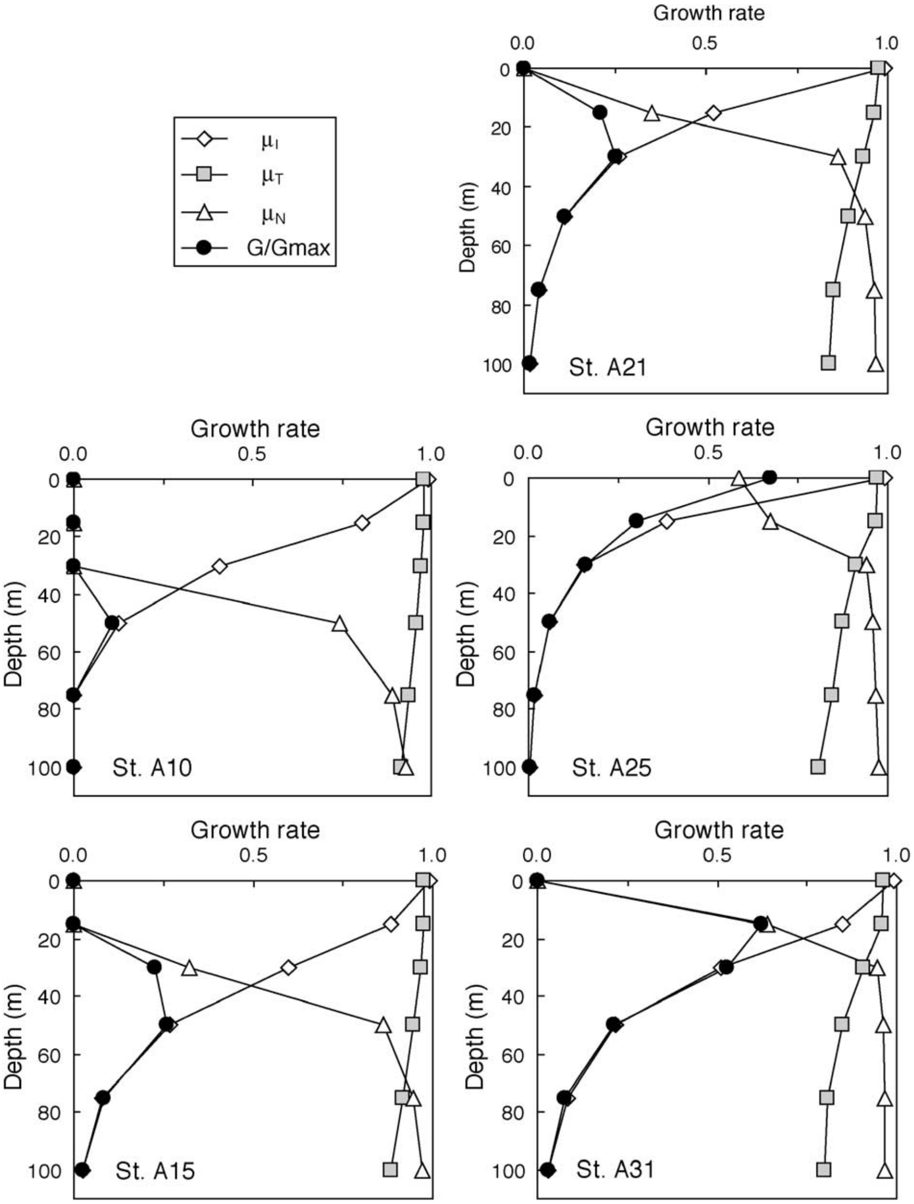


Fig. 10. Vertical profiles of estimated limiting factors and growth rates.

previous line. On this assumption, the potential DIN concentration in the water mass can be estimated from the temperature–DIN relation in the previous line. For example, Fig. 9 illustrates the temperature–DIN relation at Stn. A21, which was the nearest point to the buoy in Line IV. Using this well-correlated relation between the DIN concentration and temperature, the potential DIN concentration at Stn. A25, which was the nearest point to the buoy in Line V, was calculated. Since DIN and temperature were strongly correlated in all lines, potential DIN concentration at any depth in the low-salinity water can be determined. Parameters used in the estimates are listed in Table 1.

Calculation of limiting factors shows that phytoplankton growth was mainly restricted by light in the deeper layer, while the nutrients were the main limitation in the upper layer (Fig. 10). Temperature plays minor contribution to the limitation of phytoplankton growth, because it was near the optimum temperature in the region. This tendency of different limiting factor between the layers was prevalent throughout the observations. The light-controlled growth rate was severer in the eddy because of high chlorophyll concentration than at the front. In the former lines, depletion of nutrients reduced the growth rate in the shallow layer. The consequent production would be low when the low-salinity water was trapped at the Kuroshio front. This low productivity in the low-salinity water indicates that fish larvae staying in the water at the front will starve after they exhaust the transported plankton, which was initially produced in the coastal area of Enshu-nada and/or Kumano-nada.

However, once it was entrained into the eddy and mixed with OEW water, as indicated previously by the salinity distribution and buoy trajectories, nutrients were supplied to the euphotic zone by the upwelling. The consequent growth rate and production recovered in the latter three sections. It is worth noticing that the production would be high in the subsurface, while the high phytoplankton biomass was observed at the surface. This indicates that the produced biomass is uplifted in the eddy.

4. Discussion

Using drifter tracking in conjunction with intensive transect survey, the entrainment process of coastal water into the frontal eddy and the enhancement of the production in the eddy were demonstrated in this study. It has been suggested by a number of works that new production due to upwelling of nutrient-rich deep water in frontal eddies and subsequent secondary production would benefit the fish larvae (Lee et al., 1981; Kimura et al., 1997; Nakata et al., 2000). This concept has led to the misunderstanding that the entire frontal region provides high production. However, the present study revealed that the production in the front itself remains low by the nutrient depression, while the nutrient-rich upwelled water leads to new production in the frontal eddy. The time evolution of observed chlorophyll concentration supports this idea. The average of chlorophyll concentration in the low-salinity water ($s < 34.35$ psu) enriched from 1.3 μg l^{-1} (Sections II and III) to 2.4 μg l^{-1} (Sections IV, V and VI). Therefore, entrainment into the eddy from the frontal region seems to hold the key to the survival of fish larvae.

Since the eggs and larvae have little swimming ability, their position is mainly determined by the movement of the ambient water mass. Recent observations have shown that water parcels undergo large horizontal excursions as they enter and leave the strong currents. Onshore–offshore oscillation of the front, probably caused by the movement of the Kuroshio axis, would be one of the plausible mechanisms causing rectangular movements of the water mass in the region. This process was demonstrated by Awaji et al. (1991), using a particle tracking method in the numerically reproduced velocity field. In the model, particles originally released along the Kuroshio front were transported eastward smoothly and never separated from the front when the Kuroshio took a stable path. A large amount of the particles at the front, however, started to be entrained into the cyclonic eddy in association with offshoreward movement of the Kuroshio. The following onshoreward movement of the Kuroshio brought no additional entrainment of the frontal water into the eddy, although subsequent mixture of the frontal and shoreside waters was induced. Their numerical results are consistent with our results. In the present case, the series of satellite images shows that the front moved onshoreward from 17 to 21 May (Fig. 1). The ocean color image (not shown here) shows that no frontal water was entrained into the eddy in this period. The following sudden offshore-

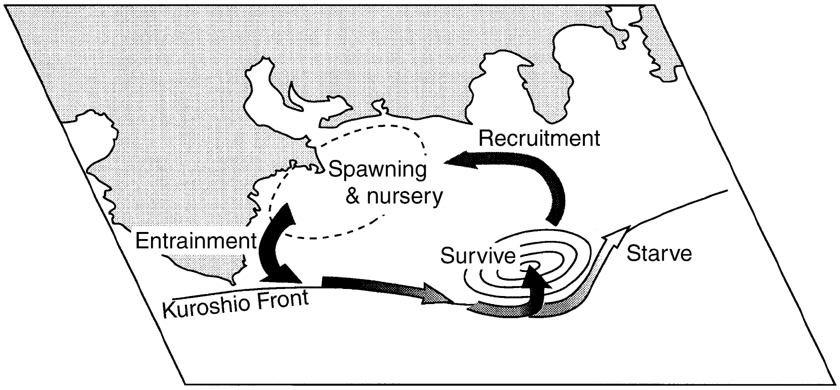


Fig. 11. Schematic view of the flow of fish larvae in the Kuroshio system south of Japan. Black and white arrows indicate good and poor survival conditions, respectively.

ward movement of 20 km within 16 h occurred on 21 May (Fig. 1). This would be sufficient for the mixture of the low-salinity water and OEW, because in the model by Awaji et al. (1991), movement of the front over a distance of 30 km yielded effective water exchange, equivalent to 20% of the water volume of the shelf and coastal region.

The entrainment process is also important for fish recruitment in the sense that they can remain in the coastal nursery area (Fig. 11). As shown in the buoy trajectories (Fig. 3), water masses at the Kuroshio front are transported to the east at a speed of over 1 m s^{-1}. This indicates that it takes only 3 days to pass through Enshu-nada, and fish larvae would be flushed toward further east and lost to the Japanese coastal nurseries. On the other hand, once they are entrained into the eddy, their speed slows down. In addition, the cyclonic recirculation of Enshu-nada tends to transport the eddy into the coastal area. This means the reentry of fish larvae to Enshu-nada. It is well known that the Kuroshio has a bimodal character off the south of Japan. Entrainment of the eddies and the frontal water to the coastal area are more frequently observed with a period of several tens of days when the Kuroshio takes the large meandering path than the straight path (Kasai et al., 1993). In the Enshu-nada and Kumano-nada system, therefore, this mechanism would contribute to better recruitment of pelagic fishes (Watanabe, 1982).

The present analysis is mainly focused on the effect of the eddy on primary production, but some other studies have extended their investigation to secondary and/or tertiary production. From a time series survey of chlorophyll *a*, copepod and anchovy larvae, Nakata et al. (2000) indicated that copepod production in a frontal eddy would be sustained by upwelling, which subsequently enhanced foods for the larvae. Okazaki et al. (submitted for publication) also concluded the entrainment of anchovy larvae into an eddy could enhance their survival in the Kuroshio frontal region, based on the estimates of naupliar copepod abundance and copepod production. These studies strongly suggest the importance for fish larvae of encountering the frontal eddy.

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