

Nutrients supplied by upwelling from Shimanto Canyon to the euphotic zone of western Tosa Bay, Japan

Goro NIGI¹⁾, Izumi KINOSHITA²⁾ and Yuka SHIGETA IBARAKI^{2),3)}

Abstract: To clarify the occurrence of upwelling and its effect on primary production in Shimanto Canyon of western Tosa Bay, the vertical distributions of nutrients and chlorophyll *a* were investigated seasonally in 2010. Maximum nutrient concentrations during each survey occurred at the bottom layer in Shimanto Canyon. The vertical distribution of nutrients showed that upwelling of the nutrient-rich deep waters of the sea bottom to the upper layers occurred only in August. Simultaneously, the sharp chlorophyll *a* maximum, being the annual highest value, appeared in the subsurface layer on the rim of Shimanto Canyon when the Kuroshio Current flowed near the shore. This suggests that the upwelling occurrence in Shimanto Canyon is related to the Kuroshio Current path, which plays an important role in supplying nutrient-rich waters of the submarine canyon to the euphotic zone.

Keywords: *nutrient, upwelling, Tosa Bay, submarine canyon*

1. Introduction

Tosa Bay is an open bay facing the Pacific Ocean. A branch of the Kuroshio Current, which flows to the east on the south side of Tosa Bay, enters the bay, influencing the oceanic conditions according to the movement of the Kuroshio Current axis (FUJIMOTO, 1987). Tosa Bay plays an important role for supporting fisheries in Japan as a site for reproduction (KINOSHITA, 2006); for example, it is the only spawning ground for Japanese sardine, which is showing a decline in catch around Japan (ISHIDA, 2006). Especially in

western Tosa Bay, whales that prey on small fishes, including the Japanese sardine, appear frequently; of these, it was reported that Bryde's whale, which was previously thought to migrate, spends its entire life cycle around western Tosa Bay (KATO, 2005). Since primary production in Tosa Bay is potentially low owing to the strong influence of the oligotrophic Kuroshio Current, nutrient supply from rivers or bottom waters by upwelling is considered to be part of the mechanism that enhances primary production in the bay, which in turn offers vital support for the growth of fish and whales.

Regarding the nutrient supply from rivers to Tosa Bay, only one study to date has shown a relationship between inflow from the Shimanto River, which has the greatest discharge in the western area of the bay, and primary production in the bay (NIGI *et al.*, 2008). Although primary

1) Nishinohon Institute of Technology, 9-30, Wakamatsucho, Kochi, Kochi 780-0812, Japan

2) Usa Marine Biological Institute, Kochi University, 194 Inoshiri, Usa, Tosa, Kochi 781-1164, Japan

3) Green-Kogyo co., LTD, 5-5 Niban-cho, Chiyoda, Tokyo 102-0084, Japan

production was enhanced along the entire reach of the Shimanto River during a period of stratification in that study, the area over which influence of the river extended did not extend more than 3 km from the river mouth, suggesting that riverine nutrient inputs alone are not enough to support the biological productivity of the bay.

Generally, areas with upwellings, which are a source of nutrient supply, are well known to have high primary production and the highly productive fisheries (*e.g.*, RYTHER, 1969). Regional upwelling events have also been confirmed in the coastal waters around Japan (TSUZUKU and NAKAO, 1986). Factors impacting the upwelling include Ekman transport induced by alongshore wind (*e.g.*, PARSONS *et al.*, 1984a), eddy formation caused by current movement (*e.g.*, LEE *et al.*, 1981), eddy formation caused by the effect of coastline geometry such as an island or cape, and turbulence caused by the effect of rough sea bottom topography (*e.g.*, LAFOND and LAFOND, 1971). It has been theoretically demonstrated that submarine canyons cause upwelling (UDA and ISHINO, 1958; KISHI and SUGINOHARA, 1975), and the accelerative effect of upwelling by submarine canyons has been reported in several areas around the world (*e.g.*, ALLEN and MADRON, 2009).

Several submarine canyons run from the continental slope to the continental shelf in the south side of western Tosa Bay where whales frequently appear (Fig. 1). One of them is Ashizuri Canyon, which runs southward off Cape Ashizuri and is the largest canyon of the submarine canyons around western Tosa Bay. Among the submarine canyons around the bay, Shimanto Canyon, which is the second largest and is located on the north-northeast side, cuts to the nearest to the shore. Furthermore, there are six small canyons on the east-northeast side of Shimanto Canyon. Thus, the continental slope area throughout western Tosa Bay is character-

ized by rough and steep-sided sea bottom topography (Fig. 1). Furthermore, it can be assumed that western Tosa Bay and the adjacent area has the requisite environmental conditions for the occurrence of upwelling owing to the coastline geometry of the Ashizuri Peninsula and Cape Ashizuri and due to the onshore-offshore shifts of the Kuroshio Current axis off the cape. In the case of Tosa Bay, upwelling events have been observed only in the central region (FUKAMI and UNO, 1995; HIROTA *et al.*, 2002; ICHIKAWA and HIROTA, 2004), and it was reported that nutrients were being supplied from the bottom layer to the subsurface by intermittent upwelling events caused by changes in the Kuroshio Current's path (HIROTA *et al.*, 2002; ICHIKAWA and HIROTA, 2004). However, upwelling events have not been reported to occur around western Tosa Bay.

This study is focused on Shimanto Canyon, which is within the range of canyons and which runs from outside to inside of western Tosa Bay. To ascertain the occurrence of upwelling in Shimanto Canyon, the response of primary production in the upper euphotic zone and the relationships between the upwelling occurrence and environmental conditions such as wind and movement of the Kuroshio Current path, the vertical distributions of nutrients and chlorophyll *a* in western Tosa Bay were investigated over the course of 1 year.

2. Data

Field observations and water sampling were carried out at three stations (Fig. 1): inside of Shimanto Canyon (Stn. A16: depth, *ca.* 300 m), the rim of the submarine canyon (Stn. A15: depth, *ca.* 200 m) and outside of the submarine canyon (Stn. A14: depth, *ca.* 100 m) on January 17, May 13, August 3 and November 29, 2010. In the field observations, water temperature, salinity and chlorophyll *a* concentration were measured at 1

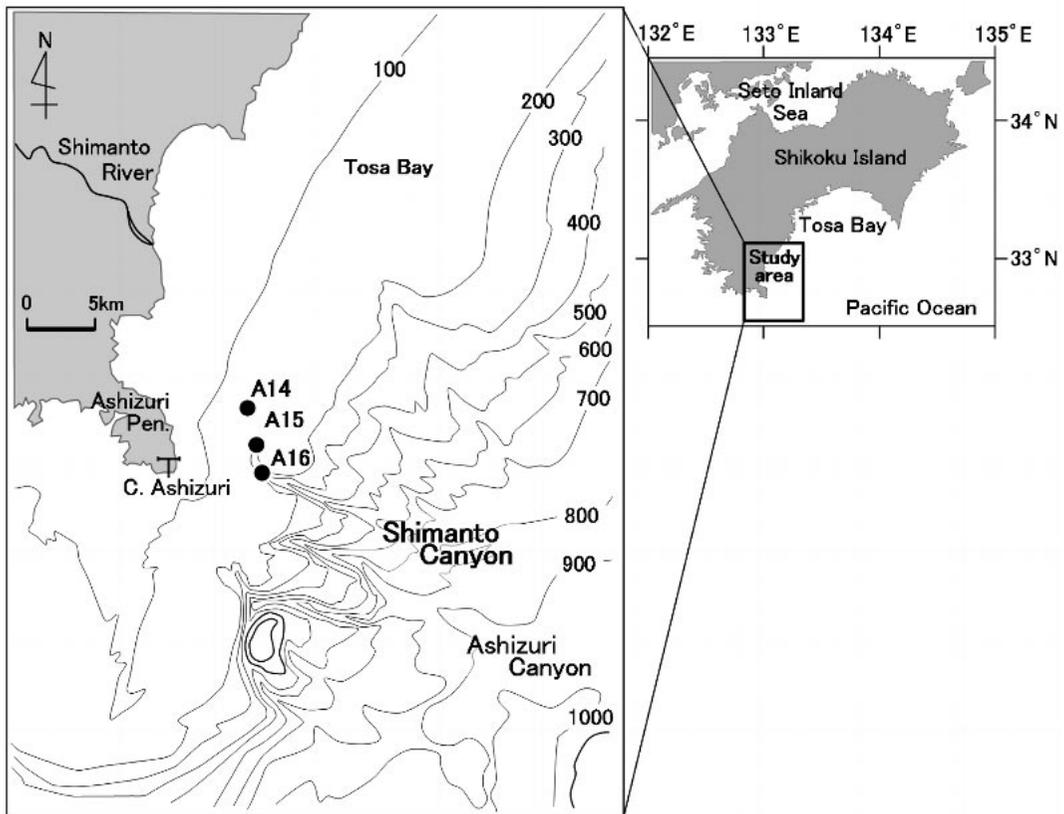


Fig. 1. Location of survey stations (Stns. A14–A16: closed circles) in western Tosa Bay with bottom topography. Inset shows the location of the main map relative to Shikoku Island and Tosa Bay. Solid lines are bathymetric contours and numbers show the depth in meters. Map symbol at C. Ashizuri denotes meteorological station.

m intervals from the surface to the bottom layer at each station using a conductivity, temperature, and depth (CTD) profiler with multiple water samplers (JFE Advantech Co., Ltd.). Water samples were collected for nutrient analysis at each station at the following depths: Stn. A14 at 0, 10, 50 and 100 m; Stn. A15 at 0, 10, 50, 100 and 200 m; and Stn. A16 at 0, 10, 50, 100, 200 and 300 m. Water samples were filtered on Whatman GF/C filters within 12 h after sampling, and the filtrate was immediately analyzed for nutrients (nitrate + nitrite, phosphate and silicate). Nutrient concentrations were determined by the colorimetric methods of PARSONS *et al.* (1984b).

To examine occurrences of upwelling, wind direction and speed data were obtained from the website of the Japan Meteorological Agency for Cape Ashizuri (<http://www.jma.go.jp/jma/index.html>), a meteorological station located near the study area (Fig. 1). In the case of waters around Izu Island (TAKAHASHI and KISHI, 1984) and in the Seto Inland Sea (YANAGI, 1985), upwelling events occurred within 5 days after a wind event during which offshore Ekman transport was likely. Based on these observations, meteorological data were collected for 4 days prior to and for the day of each survey. In addition, to understand the relationship between the upwelling occurrence

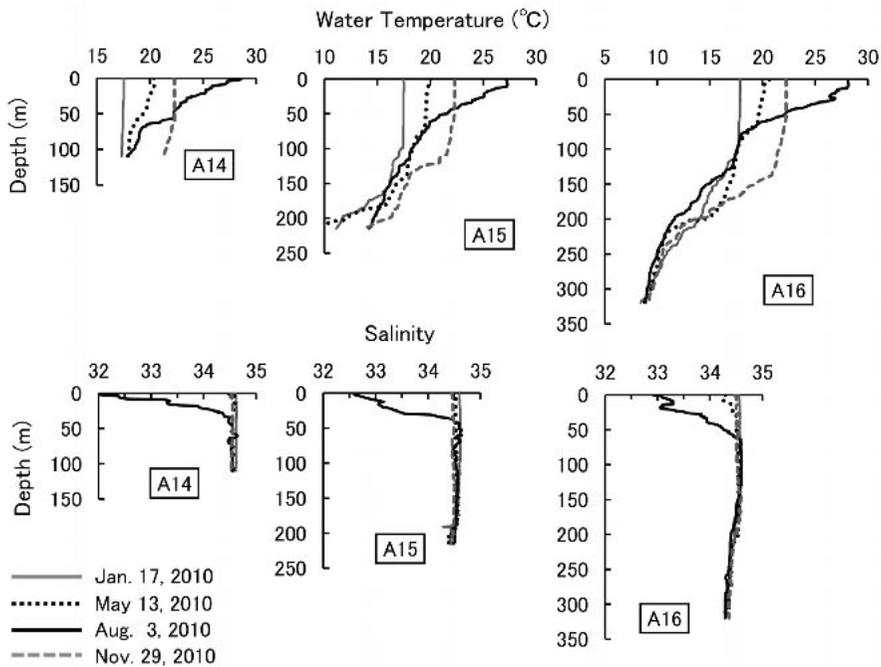


Fig. 2. Vertical distribution of water temperature (top) and salinity (bottom) at Stns. A14–A16 in western Tosa Bay in Jan., May, Aug. and Nov. 2010. Water temperature and salinity were measured at 1 m intervals from the surface to the bottom layer at each station using a CTD profiler.

and the Kuroshio Current path, the distance from Cape Ashizuri to the Kuroshio Current axis on each survey date was obtained from the “Quick Bulletin of Ocean Conditions” on the website of the 5th Regional Coast Guard Headquarters, Japan Coast Guard (<http://www1.kaiho.mlit.go.jp/jhd.html>).

3. Results

In August, water temperature at the surface (0 m depth) at each station reached 27.2–28.6 °C, which was markedly higher than at the other survey dates (Fig. 2). A thermocline was observed in the shallow water above 70 m at each station in August with a water temperature decrease of 7.5–9.3 °C from the surface (0 m) to a depth of 70 m (Fig. 2). In January, water temperature at the surface at each station was lower than at other survey dates, and the depth of

the mixed layer appeared to reach 110 m (Fig. 2). The water temperature at a depth of 300 m at Stn. A16, the deepest sample collected in this study area, was the lowest (9.0–9.6 °C) in all seasons (Fig. 2). A comparison of the water temperatures in layers deeper than 100 m for each survey date showed that the water mass below 15 °C around the bottom layer had extended to the upper layers at Stn. A16 in August (Fig. 2). Thus, the water temperatures (*ca.* 18 °C) under the thermocline at Stn. A16 in August were equal to or slightly less than those recorded in January at depths of around 80 m and deeper.

Salinity in January, May and November fluctuated around 34.5 (34.3–34.6), and no clear variation in vertical distribution was observed (Fig. 2). On the other hand, although salinity in August did not significantly differ from values for other survey dates at depths of 50–300 m, salinity

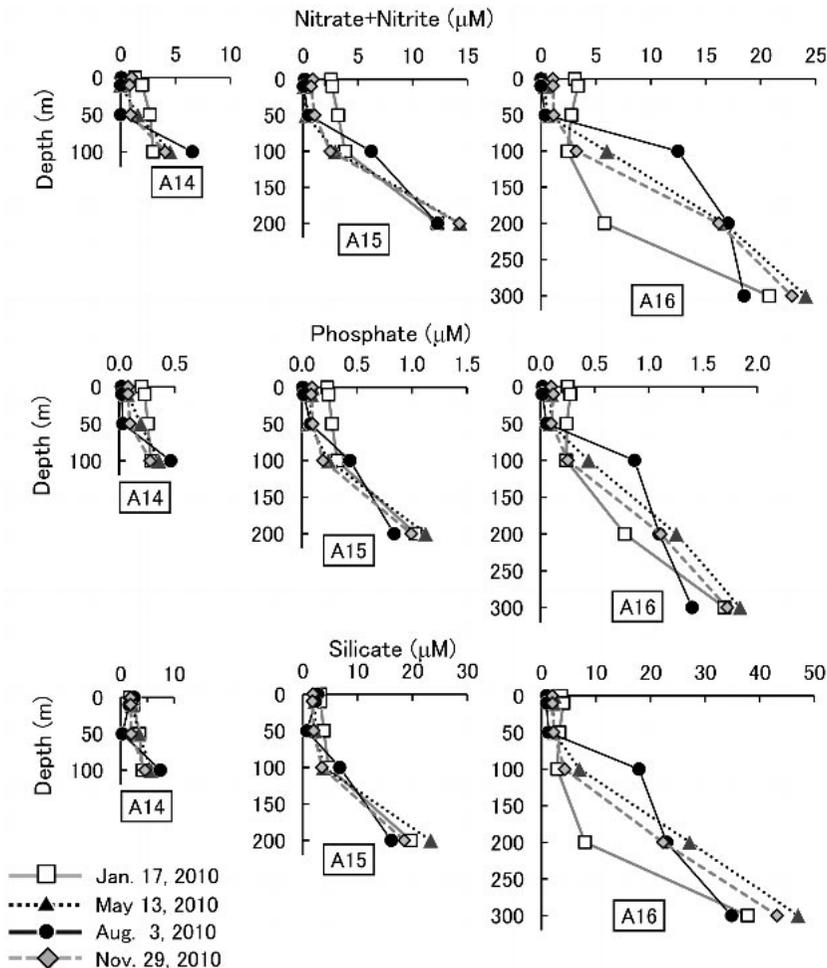


Fig. 3. Vertical distribution of nitrate + nitrite (top), phosphate (center), and silicate (bottom) concentrations at Stns. A14-A16 in western Tosa Bay in Jan., May, Aug., and Nov. 2010.

in the layers shallower than 50 m was comparatively low (31.9–34.5), and the formation of a halocline was also observed (Fig. 2).

On all survey dates, nutrient concentrations at Stns. A14-A16 tended to be relatively low for depths 0–50 m, increase at 100 m, and increase sharply with depth to the bottom layer (Fig. 3). For all survey dates, the maximum concentration for each nutrient was observed at a depth of 300 m at Stn. A16 (Fig. 3): nitrate + nitrite, 18.5–24.1 μM (annual average, 21.5 μM); phosphate, 1.40–1.84 μM (annual average, 1.67 μM); and

silicate, 34.9–47.1 μM (annual average, 40.8 μM). In a comparison of nutrient concentrations among survey dates, each nutrient at depths of 0–50 m had a relatively high concentration in January (Fig. 3), and the ranges (mean at depth of 0–50 m at Stns. A14-A16) were as follows: nitrate + nitrite, 1.33–3.37 μM (2.61 μM); phosphate, 0.201–0.275 μM (0.245 μM); and silicate, 1.75–4.03 μM (3.21 μM). Average nutrient concentrations at the other survey dates throughout the year at depths of 0–50 m were as follows (Fig. 3): nitrate + nitrite, 0.49 μM ; phosphate, 0.075 μM ; and

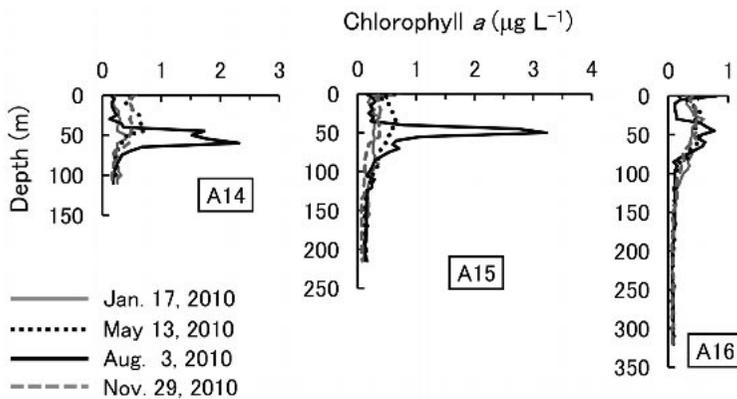


Fig. 4. Vertical distribution of chlorophyll *a* concentrations at Stns. A14–A16 in western Tosa Bay in Jan., May, Aug. and Nov., 2010. Chlorophyll *a* concentrations were measured at 1 m depth intervals from the surface to the bottom layer at each station using a CTD profiler.

silicate, $1.92 \mu\text{M}$. With regard to the nitrate + nitrite concentration in the August survey, in particular, the levels were depleted (*i.e.*, below the detection limit) at some depths at Stns. A15 and A16 (Fig. 3). At depths of 100–300 m, the vertical distribution was different for each nutrient in August compared to at other survey dates, showing that nutrient-rich deep water around the sea bottom extended to the upper layers at the August survey (Fig. 3). At a depth of 100 m at Stn. A16 in August, nutrient concentrations of nitrate + nitrite, phosphate and silicate were 2–5 times higher, 2–4 times higher and 3–6 times higher, respectively, than those at the other survey dates (Fig. 3). The distribution of nutrients higher in the water column in August corresponded with the rise of the cold water mass ($9\text{--}18^\circ\text{C}$) shown in Fig. 2.

Chlorophyll *a* concentration at each survey date tended to be low at deeper than 70–100 m (Fig. 4). Therefore, it is considered that the euphotic zone of this study area is found at depths shallower than 70–100 m. Chlorophyll *a* concentration at all stations tended to be relatively high in the subsurface layer. The maximum values in

January, May, and November were $0.6 \mu\text{g L}^{-1}$ at a depth of 30 m at Stn. A16, $0.7 \mu\text{g L}^{-1}$ at a depth of 45 m at Stn. A14, and $0.5 \mu\text{g L}^{-1}$ at a depth of 20 m at Stn. A14, respectively. Although chlorophyll *a* concentration in August showed $0.1\text{--}0.8 \mu\text{g L}^{-1}$ at depths of 0–40 m, which is equivalent to those on other survey dates, a sharp chlorophyll *a* maximum layer appeared around a depth of 50 m, which is below the thermocline, and the highest annual concentration of $3.2 \mu\text{g L}^{-1}$ was

observed at a depth of 50 m at Stn. A15.

The wind direction and speed data recorded at the Cape Ashizuri Meteorological Station (Fig. 5) showed the following prevailing wind direction and speed around this study area in different seasons: from the north at $2\text{--}4 \text{ ms}^{-1}$ in January, northeast at $2\text{--}8 \text{ ms}^{-1}$ in May, west at $2\text{--}6 \text{ ms}^{-1}$ in August, except for a period of north-northeast, and north at $1\text{--}3 \text{ ms}^{-1}$ in November.

As shown in Fig. 6, the Kuroshio Current in January, May and November was flowing far from Cape Ashizuri and was located at a distance of 30–35 nautical miles from the cape. On the other hand, the Kuroshio Current in August was flowing near the shore at a distance of 15 nautical miles from Cape Ashizuri, which is very different than the paths on the other survey dates.

4. Discussion

In January, nutrient concentrations were relatively high in the euphotic zone, thought to be at depths of 0–50 m, and vertical mixing was evident between depths of 0 and 100 m based on the water temperature profile, suggesting that nutrients originating in the aphotic zone were

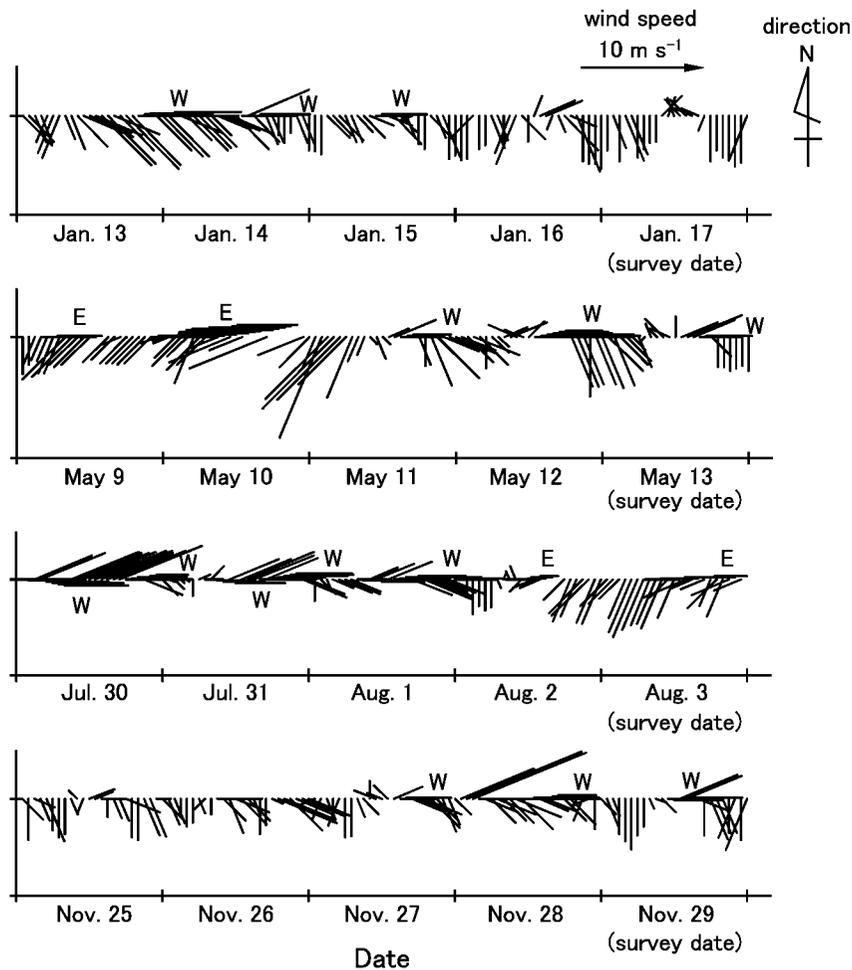


Fig. 5. Time series of hourly wind vectors observed at Cape Ashizuri for 4 days prior to and on the day of each survey. Wind direction and speed data at Cape Ashizuri was obtained from the cited website of the Japan Meteorological Agency. E and W denote easterly and westerly wind direction, respectively.

diffused to the upper layers through the winter vertical mixing. According to JUSTIC *et al.* (1995), the potential for nutrient limitation in the growth of marine diatoms is thought to occur at $1 \mu\text{M}$ of nitrate + nitrite, $0.1 \mu\text{M}$ of phosphate, and $2 \mu\text{M}$ of silicate. Since nutrient concentrations at depths of 0–50 m in January were higher than those suggested by JUSTIC *et al.* (1995), it can be concluded that the nutrient concentrations were sufficiently high to support marine diatom growth. On the other hand, most of the nutrient

concentrations at depths of 0–50 m at each station on the other survey dates were less than those suggested by JUSTIC *et al.* (1995), and oligotrophic conditions prevailed, particularly in August. The N:P:Si ratio for the average concentration of each nutrient at depths 0–50 m at Stns. A14–A16 in August was 4:1:48, suggesting that nitrogen was limiting relative to the well-known nutrient demand for it by marine diatoms (*e.g.*, JUSTIC *et al.*, 1995). However, the nutrient concentrations with an apparent nitrogen limitation at a depth of

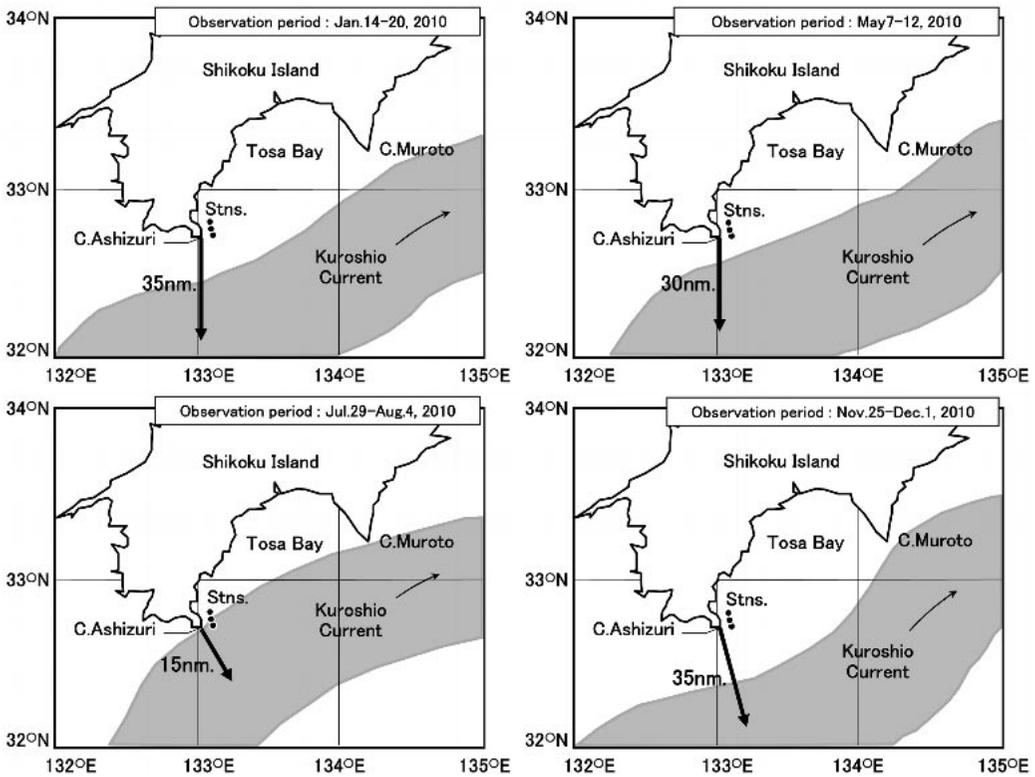


Fig. 6. The Kuroshio Current path off Shikoku Island and the distance (nautical miles abbreviated as nm.) from Cape Ashizuri to the Kuroshio Current axis around each survey. The position of the Kuroshio Current was obtained from the cited website of the 5th Regional Coast Guard Headquarters, Japan Coast Guard.

50 m in August corresponded to a chlorophyll *a* maximum at the same depth, suggesting that nitrate + nitrite had been largely depleted by its significant uptake by marine diatoms.

The chlorophyll *a* maximum of $3.2 \mu\text{g L}^{-1}$ in this study was observed at the subsurface (depth of 50 m) of Stn. A15 in August, which is a much higher value than the chlorophyll *a* concentrations ($0.2\text{--}0.4 \mu\text{g L}^{-1}$) recorded off Cape Ashizuri observed by TAKAHASHI *et al.* (1985). In addition, with regard to the chlorophyll *a* in the surface layer at a site near the mouth of the Shimanto River during the period of stratification (from May to October) investigated by NIGI *et al.* (2008), a maximum chlorophyll *a* concentration of $1.4 \mu\text{g L}^{-1}$ with increasing nutrient concentration

was observed when the influence of the Shimanto River was strongest (salinity 30.4). Thus, the maximum chlorophyll *a* concentration in August in this study was more than double of that near the Shimanto River mouth (NIGI *et al.*, 2008), about 8 times that off Cape Ashizuri (TAKAHASHI *et al.*, 1985) and higher than those in previous research in western Tosa Bay and around the adjacent sea. As discussed above, nutrient and chlorophyll *a* concentrations at the surface at the August survey in this study were mostly lower than those at the other survey dates, making it difficult to consider that nutrient supply from a river such as the Shimanto River supported the increase in chlorophyll *a* concentration at the subsurface layer. On the other hand, nutrient

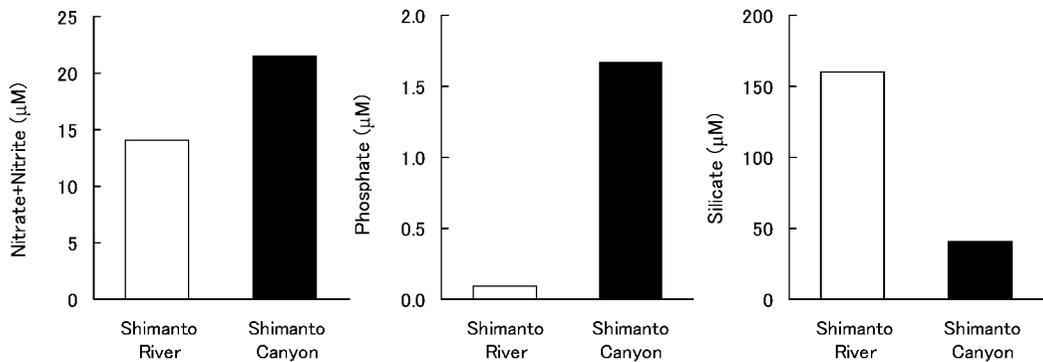


Fig. 7. Comparison of annual average of nutrient concentrations between Shimanto Canyon at a depth of 300 m and the lower reaches of the Shimanto River. Nutrient concentrations at the lower Shimanto River were investigated monthly in 2005 (NIGI *et al.*, 2008).

concentrations at 100 m at the August survey were similar to those at 300 m and were higher than those at the other survey dates. As can be seen from Fig. 2, water temperatures (9.0–16.5 °C) at depths of 130–300 m at the August survey date were lower than those at the other survey dates, and water temperatures (16.5–18.0 °C) at depths of 80–130 m were relatively low, approximately equal to that in January. The temperature of 18 °C at the depth of 80 m was equal to that observed at the subsurface when upwelling occurred in the central region of Tosa Bay in summer (ICHIKAWA and HIROTA, 2004). Therefore, it is thought that upwelling occurred in August and that nutrients were supplied from the sea bottom to the euphotic zone.

The ratio of the annual average nutrient concentrations in the bottom layer of Shimanto Canyon (*i.e.*, 300 m depth at Stn. A16), which had high nutrient concentrations, was N:P:Si = 13:1:24. Since this ratio is similar to the well-known cellular chemical composition of marine diatoms (REDFIELD *et al.*, 1963; LIBES, 1992), the origin of the nutrients in Shimanto Canyon is thought to be from the decomposition of diatoms. A comparison of the annual average concentration of nutrients at a depth of 300 m in Shimanto Canyon and the

average concentrations in the lower reaches of the Shimanto River (NIGI *et al.*, 2008), which supplies most of the freshwater discharge to western Tosa Bay, indicated that the nutrients other than silicate were present in the submarine canyon in higher quantities than in the river (Fig. 7). That is, the nitrate + nitrite concentration, which was thought to be the limiting nutrient in this study area, was approximately 1.5 times higher and the phosphate concentration was 19 times higher than those in the lower Shimanto River by NIGI *et al.* (2008). This indicates that upwelling from the submarine canyon is an important source of nutrients for enhancing primary production in Tosa Bay.

The maximum chlorophyll *a* concentration in this study was observed at the subsurface not at Stn. A16, where water temperatures were relatively low (11.6–18.0 °C) at depths of 80 m and deeper, but at Stn. A15, where water temperatures were 14.7–19.2 °C were higher at depths of 80–200 m. In the case of coastal waters around the Izu Islands (TAKAHASHI *et al.*, 1980), while a water mass with upwelling was characterized by low water temperature, high nutrient concentrations and low chlorophyll *a* concentration, water slightly away from that area contained

a high chlorophyll *a* concentration with water temperatures almost equal to those in surrounding waters. It is thought that the water mass with high chlorophyll *a* was previously upwelled and that phytoplankton then multiplied in the water mass over time. Generally, phytoplankton biomass requires at least more than one day to double (PARSONS *et al.*, 1984a), and the formation of a phytoplankton bloom at 3 days after the upwelling event around Izu Island was reported in FURUYA *et al.* (1986). Thus, there is a possibility that the water mass containing high chlorophyll *a* observed at Stn. A15 had upwelled a few days in advance and shifted.

The effects of wind and topography are well known to induce occurrences of upwelling, and regional upwellings characterized by the effects of both wind and topography have been reported in the coastal waters around Japan (*e.g.*, TSUZUKU and NAKAO, 1986). Due to the presence of Cape Ashizuri and submarine canyons including Shimanto Canyon in this study area, the conditions seem to be conducive for upwelling. However, because upwelling was not observed on all survey dates in this study, it is considered that upwelling occurs only when environmental conditions, such as wind or ocean currents, are favorable for producing the phenomenon in combination with the topography effect. The coastline of the Ashizuri Peninsula side of Tosa Bay is aligned approximately in the N-S direction (Fig. 1), and the wind direction that can produce upwelling due to Ekman transport (*i.e.*, transport of the surface layer to the east) is thought to be from a southerly direction. However, the wind direction and speed data at the Cape Ashizuri Meteorological Station showed that the prevailing wind around this study area for the 4 days prior and on the August survey date, when upwelling occurred, was not from the south (Fig. 5). Thus, it is thought that the upwelling

observed in August was unlikely to have occurred due to a wind-driven effect.

An association between upwelling events in Tosa Bay and adjacent coastal areas and the movement of the Kuroshio Current path has been reported in the past. For example, a counterclockwise flow developed in the central region of the bay when the Kuroshio Current path flowed near the shore (ICHIKAWA and HIROTA, 2004), intrusion of bottom waters on the continental slope was associated with movement of the Kuroshio Current path to the shore in the Bungo Channel (KANEDA *et al.*, 1996), and inflow of bottom waters on the continental slope was associated with offshore movement of the Kuroshio Current path in the Kii Channel (KASAI *et al.*, 2001). As shown in Fig. 6, the Kuroshio Current axis was only flowing near the shore at a distance of 15 nautical miles from Cape Ashizuri in August when upwelling occurred.

Although only one occurrence of upwelling (in August) was confirmed in this study, this analysis suggests that movement of the Kuroshio Current path is related to upwelling in Shimanto Canyon and that it occurs when the Kuroshio Current flows onshore. Taken together, the following are thought to be mechanisms for the occurrence of upwelling in this study area.

- i) Strong flow passing over the rough continental slope, where Shimanto Canyon is located, creates turbulence and vertical motion of the water mass when the Kuroshio flows near the shore.
- ii) The bottom waters in Shimanto Canyon are forced to rise along the steep-sided slope coinciding with the movement of the Kuroshio Current to the shore.
- iii) The strong flow to the east around Cape Ashizuri produces an eddy in the lee side of the cape, where Shimanto Canyon is located on the sea bottom, as the Kuroshio Current

flows near the shore.

Thus, it is thought that a combination of the movement of the Kuroshio Current path along with the bottom topography of Shimanto Canyon in the case of mechanisms i) and ii), or with the coastline geometry of Cape Ashizuri in the case of iii) promoted the upwelling occurrence, and these factors play an important role in supplying nutrient-rich waters from the submarine canyon to the euphotic zone.

With a close relationship between the presence of submarine canyons and upwelling occurrence, it is possible that a large quantity of nutrients was supplied from the sea bottom to the euphotic zone during this study due to the shift in the route of the Kuroshio Current to flow near the shore and over the submarine canyons during this study. Because Ashizuri Canyon is the largest submarine canyon and is located to the south-southwest of Shimanto Canyon (*i.e.*, upstream of Shimanto Canyon on the route of the Kuroshio Current), it is possible that the maximum chlorophyll *a* observed at the rim of Shimanto Canyon (Stn. A15) was caused not by nutrients supply from Shimanto Canyon, but by the movement of nutrient-rich waters that were upwelled at Ashizuri Canyon toward Shimanto Canyon by the strong Kuroshio Current.

However, because there was only one upwelling occurrence in August, further examination of additional upwelling occurrences in not only Shimanto Canyon, but also in the neighboring submarine canyons is necessary to elucidate the relationship between the onshore-offshore movement of the Kuroshio Current path and upwelling. In addition, to distinguish between the effects of sea bottom topography and coastline geometry, we plan to investigate and compare the slope of the areas inside and outside of submarine canyon in future studies. If the mechanism of upwelling in this study area can be clarified, and

the frequency and duration of its occurrences can be estimated, it will be possible to clarify the biological production structure specific to western Tosa Bay. Understanding the factors affecting primary production will also provide insights into the population structures of large mammals, such as the breeding habits of Bryde's whale.

Acknowledgements

We wish to express our thanks to the late Dr. S. FUKUDOME and I. FUKUDOME, President of Nishinohon Institute of Technology, for their supporting in this study. We also thank Dr. M. IFUKU, Professor Emeritus of Ehime University, for his valuable advice. The staff of Laboratory for early life history of fishes, Usa Marine Biological Institute, are thanked for their assistance in the field.

References

- ALLEN, S. E. and X. D. MADRON (2009): A review of the role of submarine canyons in deep-ocean exchange with the shelf. *Ocean Sci.*, **5**, 607–620.
- FUJIMOTO, M. (1987): On the flow types and current stability in Tosa Bay and adjacent seas. *Sea and Sky*, **62**(4), 127–140. (in Japanese)
- FUKAMI, K. and K. UNO (1995): Distribution and fluctuation of bacteria and bacterivorous nanoflagellates in the front area of Tosa Bay and Kuroshio Current. *Bull. Coast. Oceanogr.*, **33**(1), 29–38. (in Japanese)
- FURUYA, K., M. TAKAHASHI and T. NEMOTO (1986): Summer phytoplankton community structure and growth in a regional upwelling area off Hachijo Island, Japan. *J. Exp. Mar. Biol. Ecol.*, **96**(1), 43–55.
- HIROTA, Y., T. ICHIKAWA, H. MORIMOTO and H. SAKAMOTO (2002): Temporal increase phytoplankton in summer in Tosa Bay. *Fish. Biol. Oceanogr. Kuroshio*, **3**, 35–46. (in Japanese)
- ICHIKAWA, T. and Y. HIROTA (2004): Seasonal changes of primary productivity in Tosa Bay, Japan. *Oceanogr. Japan*, **13**(3), 259–269. (in Japanese)

- ISHIDA, M. (2006): Rapid decrease of egg production of Pacific stock of Japanese sardine, *Sardinops melanostictus*, and characteristics of persistent spawning ground in Tosa Bay, southwestern Japan. Bull. Jpn. Soc. Fish. Oceanogr., **70** (3), 170-175. (in Japanese)
- JUSTIC, D., N. N. RABALAIS, R. E. TURNER and Q. DDORTCH (1995): Changes in nutrient structure of river-dominated coastal waters: stoichiometric nutrient balance and its consequences. Estuar. Coast. Shelf Sci., **40**, 339-356.
- KANEDA, A., H. TAKEOKA and Y. KOIZUMI (1996): Decrease of water temperature in the Bungo Channel in summer 1993. Bull. Coast. Oceanogr., **34**(1), 71-78. (in Japanese)
- KASAI, A., T. FUJIWARA and M. TADA (2001): Flow structure and nutrient transport in the Kii Channel. Proc. Coast. Eng., JSCE, **48**, 436-440. (in Japanese)
- KATO, H. (2005): "Kujira-damari", Richly whale aggregate waters in Tosa bay. Aquabiology, **27** (6), 627-631. (in Japanese)
- KINOSHITA, I. (2006): Significance of the research of shirasu fishery grounds for resource and ecological study of pelagic fishes. Fish. Biol. Oceanogr. Kuroshio, **7**, 3-12. (in Japanese)
- KISHI, M. J. and N. SUGIYOHARA (1975): Effects of longshore variation of coastline geometry and bottom topography on coastal upwelling in a two-layer model. J. Oceanogr. Soc. Jpn., **31**, 48-50.
- LAFOND, E. C. and K. G. LAFOND (1971): Oceanography and its relation to marine organic production. In Fertility of the sea, volume I. COSTLOW, J. D. (ed.), Gordon and Breach Science, New York, p.241-265.
- LEE, T. N., L. P. ATKINSON and R. LEHECKIS (1981): Observations of a Gulf Stream frontal eddy on the Georgia continental shelf, April 1977. Deep Sea Res., **28**(4), 347-378.
- LIBES, S. M. (1992): An introduction to marine biogeochemistry. John Wiley and Sons, New York, 734pp.
- NIGI, G., I. KINOSHITA and K. FUKAMI (2008): Effects of Nutrients Supplied by the Shimanto River on Seasonal Changes of Nutrient Distributions and Primary Production in the Western Tosa Bay, Japan. Oceanogr. Japan, **17** (5), 357-369. (in Japanese)
- PARSONS, T. R., Y. MAITA and C. M. LALLI (1984b): A manual of chemical and biological methods for seawater analysis. Pergamon Press, Oxford, 173pp.
- PARSONS, T. R., M. TAKAHASHI and B. HARGRAVE (1984 a): Biological Oceanographic Processes, Third Edition. Pergamon Press, Oxford, 344pp.
- REDFIELD, A. C., B. H. KECTCHUM and F. A. RICHARDS (1963): The influence of organisms on the composition of seawater. In The sea, Vol.2. HILL, M. N. (ed.), Wiley Interscience, New York, p.26-77.
- RYTHER, J. H. (1969): Photosynthesis and fish production in the sea. Science, **166**, 72-76.
- TAKAHASHI, M. and I. KOIKE, T. ISHIMARU, T. SAINO, K. FURUYA, Y. FUJITA, A. HATTORI and S. ICHIMURA (1980): Upwelling plumes in Sagami Bay and adjacent water around the Izu Islands, Japan. J. Oceanogr. Soc. Japan, **36**, 209-216.
- TAKAHASHI, M. and M. J. KISHI (1984): Phytoplankton growth response to wind induced regional upwelling occurring around the Izu Islands off Japan. J. Oceanogr. Soc. Japan, **40**, 221-229.
- TAKAHASHI, M., T. NAKAI, T. ISHIMARU, H. HASUMOTO and Y. FUJITA (1985): Distribution of the surface chlorophyll maximum and its nutrient-light environment in and around the Kuroshio off Japan. J. Oceanogr. Soc. Japan, **41**, 73-80.
- TSUZUKU, T. and T. NAKAO (1986): Reviews of the characteristics of oceanographical environments of the natural upwelling area. Fish. Eng., **22** (2), 41-58. (in Japanese)
- UDA, M. and M. ISHINO (1958): Enrichment pattern resulting from eddy systems in relation to fishing grounds. J. Tokyo Univ. Fish., **44**, 105-129.
- YANAGI, T. (1985): Coastal upwelling and downwelling events in the Seto Inland Sea. J. Oceanogr. Soc. Japan, **41**, 435-440.

Received: October 6, 2016

Accepted: November 14, 2016