

# Enhanced phytoplankton and bacterioplankton production coupled to coastal upwelling and an anticyclonic eddy in the Ulleung basin, East Sea

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**ABSTRACT:** We investigated the biomass and production rates of microorganisms associated with coastal upwelling and the anticyclonic Ulleung warm eddy (UWE) of the Ulleung basin in the East Sea. Shipboard observations revealed that depth-integrated phytoplankton biomass and production were higher in the moderately stratified ring of the UWE than in the vertically well-mixed eddy core or in the stratified region outside of the eddy in the Ulleung basin. Similarly, heterotrophic bacterial production was higher in the eddy ring than in the eddy core or outside of the eddy. Bacterial biomass in the highly productive eddy ring showed little difference compared to the bacterial biomass of the core site due to the impact of grazing by heterotrophic protozoa. Satellite imagery and diatom species composition data in conjunction with physico-chemical parameters demonstrated that wind-driven coastal upwelling in the southeast of Korea was largely responsible for the phytoplankton bloom and enhanced bacterial production along the UWE. Overall, the results indicated that the UWE entrained highly productive upwelling coastal waters and delivered enhanced microbial biomass and production into the central Ulleung basin. The results further implied that the UWE and the subsequent effect on vertical particulate carbon flux may play a significant role in stimulating benthic respiration and in sequestering organic carbon produced by coastal upwelling down into the deep Ulleung basin.

**KEY WORDS:** Bacterioplankton · Phytoplankton · Upwelling · Eddy · Ulleung basin · East Sea

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## INTRODUCTION

Planktonic microorganisms such as phytoplankton, heterotrophic prokaryotes (hereafter bacteria as a traditional ecological term), and protozoa are significant biological components that control biogeochemical C cycles in the water column and affect global environmental changes (Azam et al. 1983, Karl 1999, del Giorgio & Williams 2005). Variations in plankton community structure also determine vertical particulate C flux, thereby controlling the significance of biological pumps (Boyd & Newton 1995). Therefore, it is essential to measure microbiological parameters such as biomass, production, respiration, and community struc-

ture in order to evaluate the role of oceans in regulating global C cycles. A better understanding of the importance of microbiological components in C cycles requires detailed information on the distribution and production of microorganisms coupled to dominant physical processes.

The East Sea is an almost completely enclosed marginal sea surrounded by Korea, Japan, and Russia in the northwestern Pacific (Fig. 1), and consists of 3 major deep basins: the Japan, Yamato, and Ulleung basins. The Ulleung basin (UB) is located in the southwestern region of the East Sea (Fig. 1). The major prevailing current in the UB is the Tsushima Warm Current (TWC), a branch of the Kuroshio. The anticyclonic

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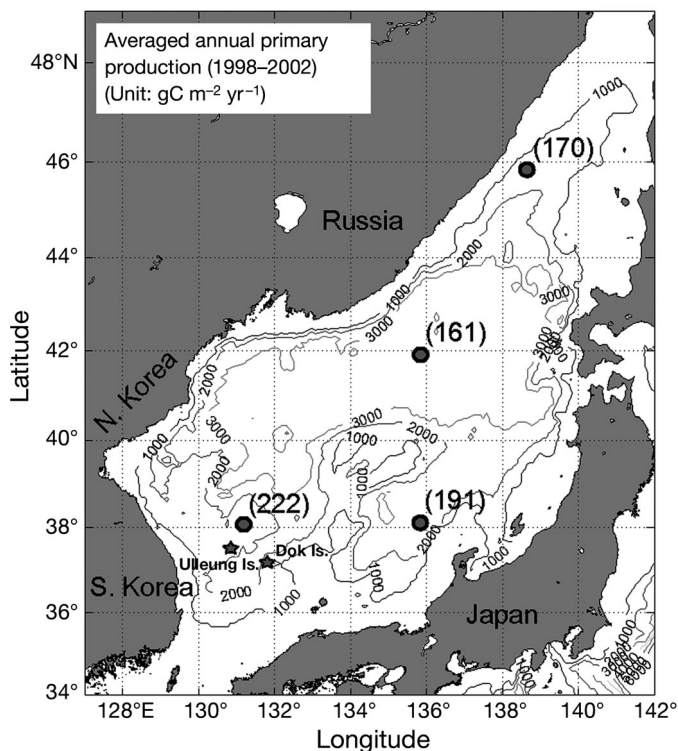


Fig. 1. East Sea surrounded by Russia, Japan, North Korea, and South Korea in the northwest Pacific. Numbers in parentheses indicate annual primary production ( $\text{g C m}^{-2} \text{yr}^{-1}$ ) averaged from 1998 to 2002 (Yamada et al. 2005). Note that the southwestern region (i.e. Ulleung Basin, UB) of the East Sea shows the highest primary production. Contour lines indicate water depth in meters

Ulleung warm eddy (UWE), originating from the East Korean Warm Current (EKWC), a northward branch of the warm and saline TWC, is a well-known physical phenomenon in the center of the southwest East Sea (i.e. the UB; Lie et al. 1995, Chang et al. 2004). Wind-driven coastal upwelling along the southeast coast of Korea is another well-defined oceanographic process in the region (Lee 1983, Lee & Na 1985). Despite the significance of coastal upwelling and eddies for microbiological parameters (Mann & Lazier 1991), little is known regarding the ecological role of the coastal upwelling and UWE in controlling microbiological parameters in the UB of the East Sea.

Several studies, mostly based on satellite image analyses, have reported annual and seasonal variations in primary production and chlorophyll *a* (chl *a*) distribution in the East Sea (Yoo & Kim 2004, Yamada et al. 2005, Kim et al. 2007). Recently, Yamada et al. (2005) reported that biomass and phytoplankton production rates were much higher in the southwestern region (i.e. the UB) compared to the other parts of the East Sea (Fig. 1). This was intriguing because the TWC introduced into the UB is characterized as a nutrient-

poor water mass with nitrate concentrations below  $3 \mu\text{M}$  throughout the year (Yoo & Kim 2004), and there is no major river input along the east coast of Korea. However, little evidence has been presented to explain the high primary production in the UB observed by Yamada et al. (2005).

The objectives of the present study are 2-fold. First, we report that the enhanced microbiological production in the UB was, to some extent, tightly coupled to coastal upwelling along the southeast coast of Korea and its subsequent entrainment into the anticyclonic UWE, which delivers the productive coastal waters into the center of the UB. Secondly, we propose that the UWE transports the enhanced biomass into the deep UB along a funnel-shaped topography, serving as a significant mechanism that stimulates benthic C mineralization and sequesters organic C produced in the highly productive coastal water column into the deep sediment.

## MATERIALS AND METHODS

**Study area.** As part of a research project designed to study the microbiological processes associated with the occurrence and fate of the spring phytoplankton bloom in the UB, shipboard observations on the physico-chemical parameters together with microbiological incubation experiments were carried out from 3 to 15 April 2006. The UB in April 2006 was characterized by 3 hydrological features: the TWC, the EKWC, and the UWE (Fig. 2). The UWE in winter and spring can generally be defined as a cold core wrapped by a warm filament (Chang et al. 2004). Water samples were collected at every  $0.5^\circ$  of longitude between  $130^\circ$  and  $132^\circ\text{E}$  along the  $37^\circ\text{N}$  latitude across the UWE (Fig. 2).

**Physico-chemical parameters.** Temperature and salinity were measured using a CTD (SBE 911 Plus, Seabird Electronics). Seawater samples for chemical and biological analyses were collected from 150, 100, 75, 50, 30, 20, 10, and 1 m depth using Niskin bottles attached to a rosette sampler. The sample bottles were first washed with 10% HCl and rinsed with Milli-Q water. Water samples for nutrient analysis were filtered through GF/F filter paper (25 mm, Whatman), placed in acid-rinsed polyethylene bottles, and frozen at  $-20^\circ\text{C}$  (Parsons et al. 1984). Concentrations of nitrate and phosphate were measured using a flow injection autoanalyzer (QuikChem AE) following standard colorimetric procedures (Strickland & Parsons 1972) and using brine standard solutions for calibrations (CSK Standard Solutions, Wako Pure Chemical Industries). Based on duplicate analyses, the precision of nitrate and phosphate measurements was 3%.

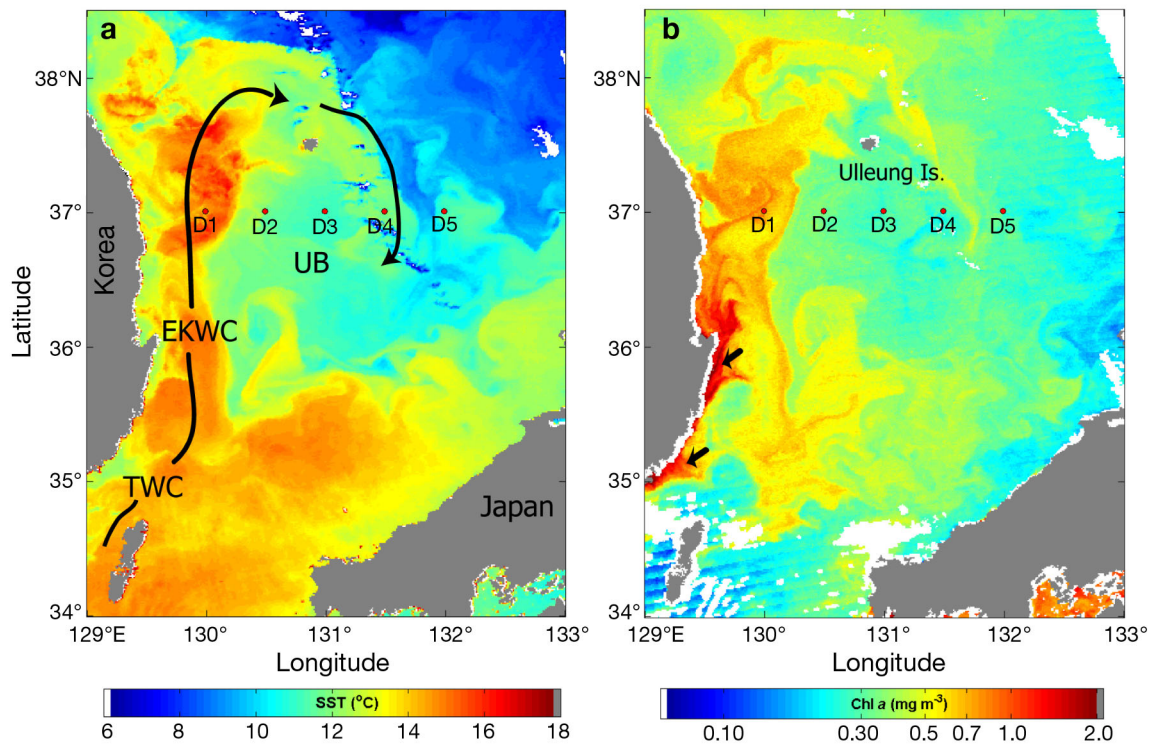


Fig. 2. Satellite images of (a) sea surface temperature (SST) and (b) chlorophyll *a* (chl *a*), showing Stns D1 to D5 in the vicinity of the anticyclonic Ulleung warm eddy (UWE) in the Ulleung basin (UB) on 3 April 2006. The UWE is formed by the northward meandering of the East Korean Warm Current (EKWC), a branch of the Tsushima Warm Current (TWC). (a) The paths of the TWC, EKWC, and UWE are shown with arrows and lines; (b) sites of upwelling are indicated by thick arrows. High-chl *a* water in (b) corresponds to cold water in (a) along the southeast coast of Korea

**Biomass estimation.** The chl *a* concentration was determined using a fluorometer (TD 700, Turner Designs) after filtration through GF/F filters (Parsons et al. 1984). Water samples for measurement of chl *a* in organisms smaller than 5  $\mu\text{m}$  (pico-size) were filtered through a 5  $\mu\text{m}$  pore-size Nucleopore polycarbonate filter, and the chl *a* in the filtrate was measured *in vivo* with an Aquafluor fluorometer (Turner Designs). Phytoplankton carbon biomass (chl-C) was estimated according to Caron et al. (1995) using a C:chl *a* ratio of 60 for depths of 0 to 30 m, a ratio of 40 for depths of 30 to 60 m, and a ratio of 30 for depths <60 m. For a quantitative estimation of major diatom species in different water masses, surface water samples were taken with Niskin bottles and preserved with 1% Lugol's solution. In the laboratory, samples were concentrated and enumerated under a light microscope (Nikon) using a Sedgwick Rafter counting chamber. Samples for bacterial abundance were preserved with glutaraldehyde at a final concentration of 1% and stored in a freezer at  $-20^{\circ}\text{C}$  (Hyun & Yang 2003). The abundance of bacteria was measured using the DAPI-staining method (Porter & Feig 1980). At least 20 microscopic fields were examined using

an epifluorescence microscope (Nikon). Bacterial carbon biomass (BCB) was estimated using a conversion factor of 15 fg C cell<sup>-1</sup> (Caron et al. 1995). Heterotrophic protozoa were enumerated microscopically by methods optimized for each group of heterotrophic nanoflagellates (HNF), heterotrophic dinoflagellates (HDF) and ciliates. To determine the abundance of HNF, 50 ml seawater samples were preserved with glutaraldehyde (final conc. 1%) and stained with proflavin (0.33%, w:v). To determine the abundance of HDF, seawater samples (200 ml) were preserved with 0.2 ml of alkaline Lugol's solution, followed by 4 ml of buffered formalin and 0.1 ml of sodium thio-sulfate (modified protocol from Sherr & Sherr 1993), and then stained with proflavin (0.33%, w:v). On board the ship, preserved samples were slowly filtered using 0.8 and 5.0  $\mu\text{m}$  black Nucleopore filter papers for HNF and HDF, respectively. During filtration, the samples were drawn down until 5 ml remained in the filtration tower. Concentrated DAPI (50 mg ml<sup>-1</sup>) was then added to the remaining sample and allowed to sit for 5 s before filtering until dry (Brown et al. 2008). HNF and HDF were enumerated under both UV and blue excitation to distinguish the

autofluorescence of chlorophyll. Each sample was counted in at least 50 random fields per slide, for a minimum of 100 cells. To determine the abundance of ciliates, 500 ml samples preserved in acid Lugol's solution (final conc. 5%) were allowed to settle in the mass cylinder for at least 48 h in the laboratory. The upper clear solution was then siphoned out, leaving 50 ml. Next, 20 to 30 ml of each sample was left to settle in sedimentation chambers before enumeration using an inverted microscope (Olympus IX 70). To estimate the carbon biomass of heterotrophic protozoa, cell volume was calculated by measuring cell dimensions with the ocular micrometer of the microscope (Edler 1979). Conversion factors and equations used to convert cell volume to carbon biomass were: 220 fg C  $\mu\text{m}^{-3}$  for HNF (Børsheim & Bratbak 1987); 0.19  $\mu\text{g C } \mu\text{m}^{-3}$  for naked ciliates (Putt & Stoecker 1989); carbon (pg) = 44.5 + 0.053 lorica volume ( $\mu\text{m}^3$ ) for loricate ciliates (Verity & Langdon 1984), and carbon (pg) = 0.216  $\times$  [volume,  $\mu\text{m}^3$ ]<sup>0.939</sup> for HDF (Menden-Deuer & Lessard 2000)

**Production rate measurements.** Primary production (PP) experiments were carried out for surface and subsurface chlorophyll maximum (SCM) layers using the <sup>14</sup>C-uptake method. Incubations were performed right after the CTD casts. Because CTDs were recovered by day and at night, photosynthesis–irradiance (P–E) curves were determined using a radial photosynthetron technique (Babin et al. 1994). Samples were taken from surface and SCM layers in ten 50 ml Falcon flasks and incubated for 1.5 h. Quantum scalar irradiance levels in the photosynthetron were determined with a Biospherical Instruments QSL-2100 4  $\pi$  sensor. Temperature was maintained at near *in situ* values using a re-circulating water bath. The P–E data were then fitted as described by Platt et al. (1980). The P–E parameters, together with depth profiles of underwater photosynthetically active radiation (PAR), and chl *a* and surface PAR throughout the day, were used to estimate daily integrated primary production. Secondary production rates of heterotrophic bacteria were estimated from the rate of <sup>3</sup>H-thymidine (<sup>3</sup>H-TdR) incorporation (Fuhrman & Azam 1980, 1982) at each water sampling depth. A conversion factor of 1.18  $\times 10^{18}$  cells mol<sup>-1</sup> (Rieman et al. 1987) was used to convert the <sup>3</sup>H-TdR measurements into bacterial production (BP).

**Satellite images.** Satellite images of daily sea surface temperature (SST) and chl *a* were obtained from the Moderate Resolution Imaging Spectroradiometer (MODIS, NASA; available at modis.gsfc.nasa.gov/). The data were received and processed by the Earth Observation Research Center of the Japan Aerospace Exploration Agency (JAXA). The spatial resolution of the data was 1 km.

## RESULTS

### Physical settings

The features of the UWE that are identifiable as the cold core wrapped by a warm filament are evident from the SST image obtained on 3 April 2006 (Fig. 2). The SSTs were at least 2°C lower at the core (Stns D2 and D3) than in the surrounding warmer water branching from the EKWC (Stns D1 and D4). The eddy is also characterized by a well-mixed and vertically homogeneous water column (10 to 11°C and 34.2 to 34.4 psu) at the center (Shin et al. 2005, Shin 2006). Vertical profiles of temperature and salinity were nearly constant from the surface to a water depth of 200 m in the core of the eddy, below which water temperature and salinity decreased with depth (Fig. 3). The center of the UWE typically undergoes convective cooling during the winter, but its unique physico-chemical characteristics were preserved despite convective cooling during the previous winter (Shin et al. 2005). In contrast, the outside of the eddy (Stn D5) was characterized by stratified surface water.

Another distinct physical feature was coastal upwelling, which was identifiable on both SST and chl *a* images (Fig. 2). According to Lee (1983), upwelling in response to southwesterly wind is rapid, with a time lag of 1 to 3 d. Wind data reported from the Busan meteorological station (data not shown) indicate that strong south–southwesterly winds were continuous from 24 March to 4 April 2006, which supports the observation of wind-driven coastal upwelling along the southeast coast of the Korean peninsula during the cruise (Fig. 2).

### Nitrate and phosphate

Distributions of inorganic nutrients accurately reflected the physical setting. Like temperature and salinity, nutrient concentrations in the core of the eddy (Stns D2 and D3) were almost constant from the surface to a water depth of 200 m (Fig. 3). The absence of a seasonal thermocline inside the eddy (Stns D2 and D3) resulted in low chl *a* concentrations due to the short residence time at the surface of the water column (Sverdrup 1953). In contrast, in the moderately stratified ring of the eddy (Stns D1 and D4), nutrient concentrations were depleted in the mixed layer because of the enhanced phytoplankton biomass, but increased abruptly with water depth below the mixed layer. Consequently, depth-integrated inventories of nitrate and phosphate (Table 1) were higher in the core of the eddy (Stns D2 and D3;  $\text{NO}_3^- = 514 \pm 64 \text{ mmol m}^{-2}$ ;  $\text{PO}_4^{3-} = 37 \pm 3 \text{ mmol m}^{-2}$ ; means  $\pm$  SD) than in the ring of the eddy (Stns D1 and D4;  $\text{NO}_3^- = 317 \pm 25 \text{ mmol m}^{-2}$ ;  $\text{PO}_4^{3-} = 32 \pm 1 \text{ mmol}$

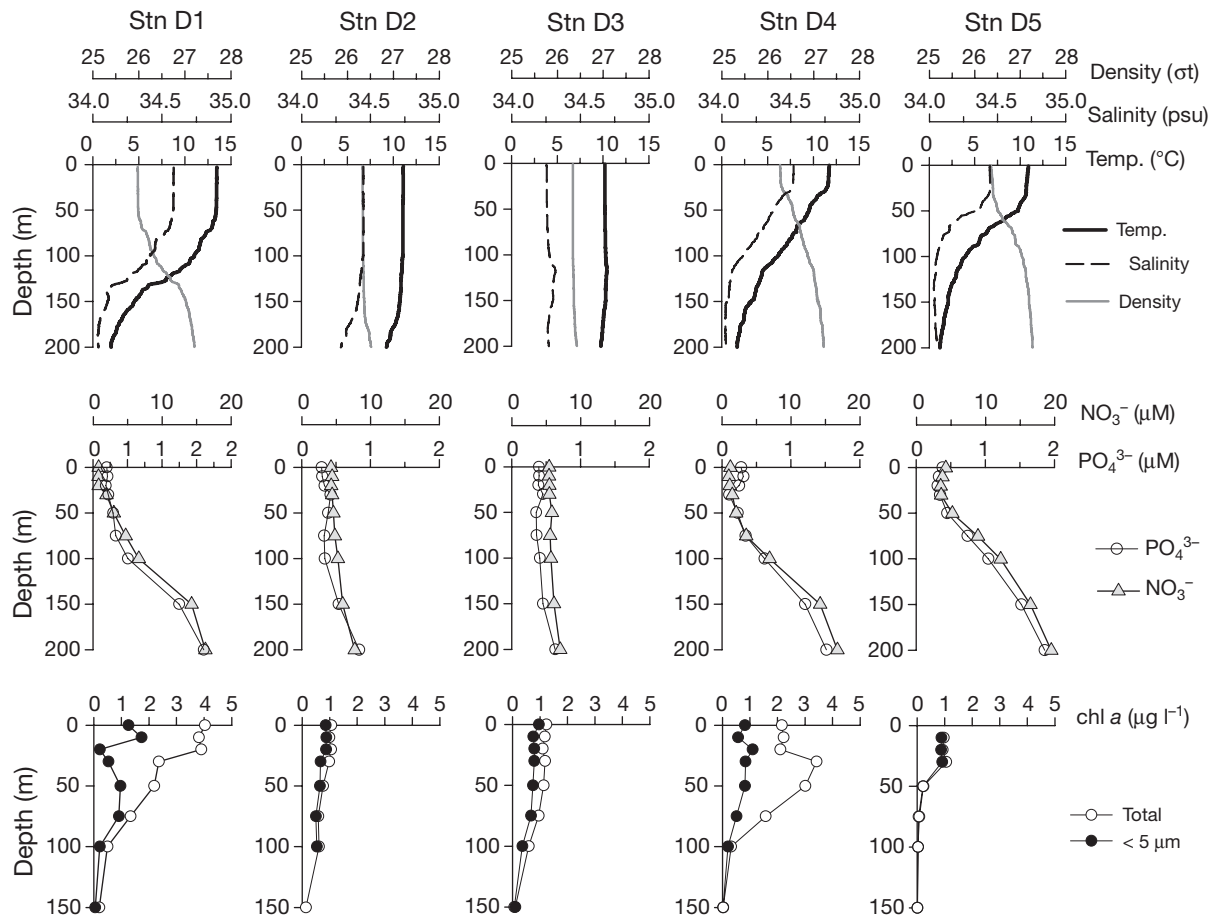


Fig. 3. Vertical profiles of physico-chemical parameters (temperature, salinity, density, and nutrients) and concentrations of chlorophyll *a* (chl *a*) at Stn D1 to D5

$\text{m}^{-2}$ ). Despite the stratified water column, a high nutrient inventory was maintained outside of the eddy (Stn D5). Inspection of a series of satellite chl *a* images indicated that a typical basin-scale spring phytoplankton bloom in the UB occurred in late April and early May 2006. As the sampling of our study was conducted before this seasonal bloom (i.e. 6 to 7 April 2006), nutrients at Stn D5 had not been fully consumed. Lower nutrient concentrations, despite low phytoplankton uptake, in the core of the eddy (Stns D2 and D3) rather than outside the eddy (Stn D5) can be explained by the fact that the nutrients in the isolated eddy core had already been consumed to some extent during the previous year as the eddy had been in the UB since the summer of 2005 (Shin 2006).

### Biomass and production of microorganisms

The biomass and production of each microbiological component were consistently higher in the ring of the UWE (Stns D1 and D4) than in the vertically well-

mixed core of the UWE (Stns D2 and D3) or at the outside of the eddy (Stn D5; Figs. 3 & 4). Daily PP at the ring sites ( $703 \pm 105 \text{ mg C m}^{-2} \text{ d}^{-1}$ ) was 4.4 times higher than at the core site ( $159 \text{ mg C m}^{-2} \text{ d}^{-1}$  at Stn D2) of the eddy (Table 1). Similarly, depth-integrated chl-C was 2.5 times higher at the ring site ( $9.82 \pm 1.44 \text{ g C m}^{-2}$ ) than in the core of the eddy ( $3.99 \pm 0.60 \text{ g C m}^{-2}$ ). PP and chl-C within the eddy core remained low because of the deep mixed layer in the core (Fig. 3). The mixed layer was much deeper than the estimated critical depth (50 to 60 m) in the region in April (Yoo & Kim 2004). Lower chl-C outside of the eddy (Stn D5) despite the high nutrient levels and stratified water column (Fig. 3) can be explained by the time lag of the spring bloom after stratification. According to Kim et al. (2007), there was a time lag of 6 to 15 d between stratification and the phytoplankton bloom in the East Sea in spring.

Spatial variation in BP was closely related to the distribution of chl *a* and PP and the abundance of heterotrophic protozoa (Fig. 4, Table 1). The BP was 1.8 times higher at the ring sites ( $157 \pm 2 \text{ mg C m}^{-2} \text{ d}^{-1}$ ) than at

Table 1. Depth-integrated (0–100 m) inventories of nutrients ( $\text{NO}_3^-$ -N and  $\text{PO}_4^{3-}$ -P), phytoplankton carbon biomass (chl-C), bacterial carbon biomass (BCB), and heterotrophic protozoa carbon biomass (PCB), and the rates of phytoplankton production (PP) and heterotrophic bacterial production (BP). ui: unidentified within 200 m of the water column; nd: no data available

Stn	Water regime	Thermocline range (m)	Mixed Layer (m)	$\text{NO}_3^-$ -N ( $\mu\text{M}$ )	$\text{PO}_4^{3-}$ -P ( $\mu\text{M}$ )	chl-C (total)	chl-C (<5 $\mu\text{m}$ )	Biomass (g C m <sup>-2</sup> ) BCB	PCB	BCB/chl-C	Production (mg C m <sup>-2</sup> d <sup>-1</sup> ) PP	BP	Sediment organic C <sup>a</sup> (% dry wt)	Sulfate reduction <sup>b</sup> (mmol m <sup>-2</sup> d <sup>-1</sup> )
D1	Eddy ring	70–130	70	335	30.79	10.84	3.59	1.33	1.03	0.12	628	158	2.9	1.85
D2	Eddy core	ui	>200	469	35.06	3.57	2.96	1.24	0.47	0.35	159	93	2.6	1.32
D3	Eddy core	ui	>200	560	39.18	4.42	3.04	1.03	0.44	0.23	nd	83	nd	nd
D4	Eddy ring	30–120	30	299	32.27	8.80	2.92	1.23	1.17	0.14	777	155	2.6	0.72
D5	Outside eddy	50–70	50	674	58.13	1.81	1.64	1.05	0.32	0.58	489	77	nd	nd

<sup>a</sup>Organic C content in the surface sediment (0–2 cm; from Lee et al. 2008)

<sup>b</sup>Depth integrated (0–15 cm) rate of sulfate reduction (from Lee et al. 2008)

the core sites ( $88 \pm 7 \text{ mg C m}^{-2} \text{ d}^{-1}$ ). Relatively little difference in BCB between the core ( $1.14 \pm 0.15 \text{ g C m}^{-2}$ ) and ring area ( $1.28 \pm 0.07 \text{ g C m}^{-2}$ ) was observed, whereas PCB was 2.8 times higher in the eddy ring ( $1.10 \pm 0.10 \text{ g C m}^{-2}$ ) than in the core of the UWE ( $0.46 \pm 0.02 \text{ g C m}^{-2}$ ).

## DISCUSSION

Because of the typical oceanic characteristics of temperature and salinity that generate a unique thermohaline circulation similar to 'the Great Ocean Conveyor Belt' (Broecker 1991), in the East Sea, it has often been referred to as a miniature ocean (Kim & Kim 1996, Kim et al. 1996). In addition, based on the recent warming of seawater below 500 m depth (from 0.08 to 0.24°C at 1000 m depth) during the period from 1969 to 1999 (Kim et al. 2001), comparable to a temperature increase of ca. 0.3°C during the last 5 decades in the world ocean (Levitus et al. 2000), the East Sea has drawn attention as a natural laboratory for investigating and predicting the variations in major oceanographic processes such as the Great Conveyor Belt System with a view toward global climate change (Kim et al. 2001). Microbiological components respond to the variations in the physico-chemical conditions of water regimes associated with global-scale biogeochemical carbon cycles and climatic changes (Karl 1999). Therefore, it becomes important to understand the response of microbial components to the variations in the water regime in the East Sea.

### Enhanced biomass and production coupled to coastal upwelling and UWE

Several lines of evidence based on direct shipboard observations of the physico-chemical and microbiological parameters coupled to satellite image analysis indicated that the higher primary production in the southwestern part (i.e. UB) of the East Sea (Yamada et al. 2005) was uniquely coupled to a combination of coastal upwelling and its entrainment by the UWE that flows into the center of the UB. First, the distribution of size-fractionated chl *a* and diatoms (Tables 1 & 2) shows a pattern related to the entrainment of coastal water by a convergent eddy. The continuous decrease in the gradient of chl *a* concentration from the hotspots in the coastal upwelling region (indicated by arrows in Fig. 2) away to the basin indicates that the source of high chl *a* in the eddy ring (Stn D4) was the upwelled water on the coast. Supporting evidence for this interpretation includes a high fraction of chl *a* in organisms > 5  $\mu\text{m}$  (Table 1, Fig. 3) and the composition and quan-

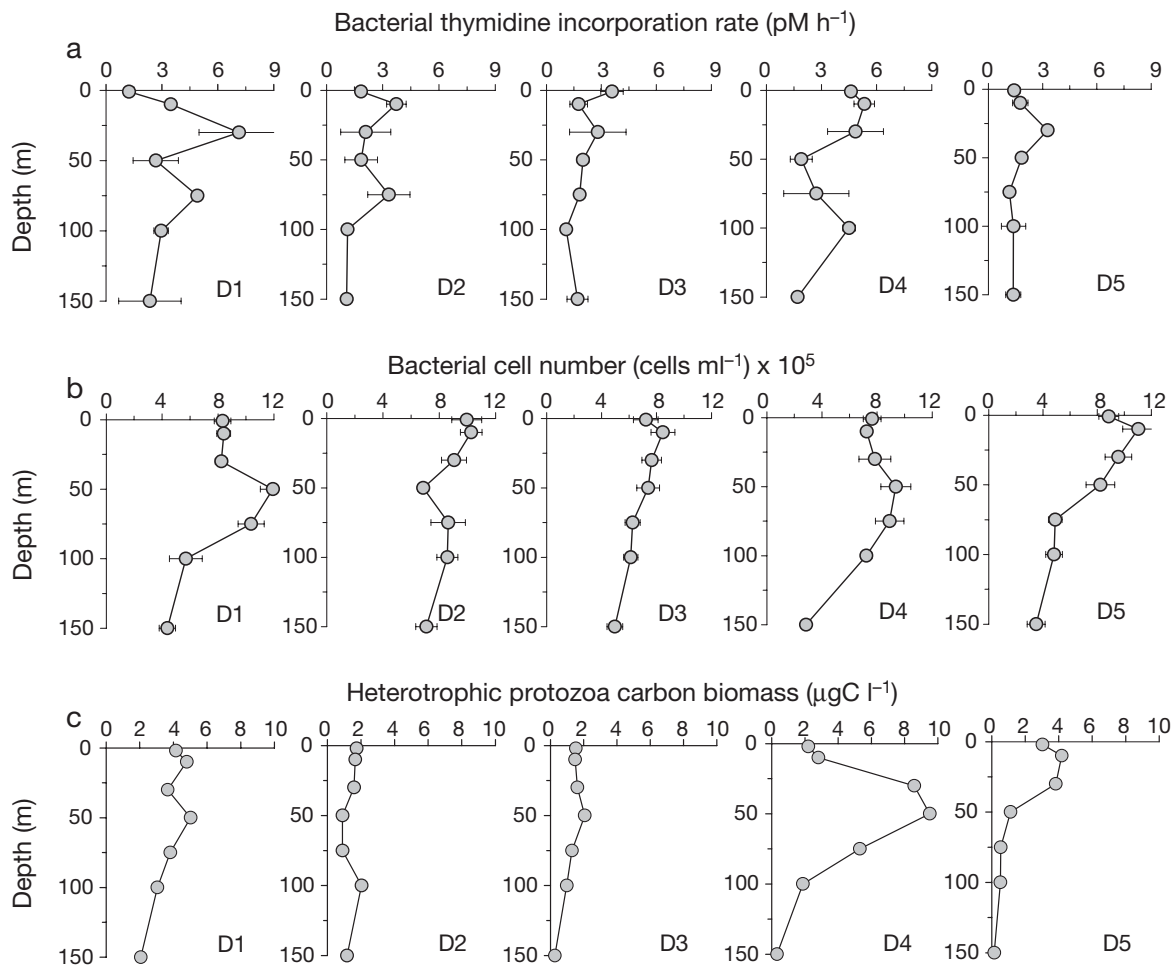


Fig. 4. Vertical profiles of (a) heterotrophic bacterial production (BP) and (b) bacterial abundance, and (c) heterotrophic protozoa carbon biomass (PCB) at Stn D1 to D5

titative distribution of large diatoms (Table 2). Generally, larger diatoms are more common in new production-dominated conditions such as an upwelling system (Smetacek 1985). Therefore, if the high nutrient upwelled water was entrained by the EKWC (i.e. UWE) and transported to the eddy core in the UB along the eddy ring, we would expect a distribution of chl *a* in organisms  $> 5 \mu\text{m}$  and of diatoms in the order of  $D1$  and  $D4 > D2$  and  $D3 > D5$ . Stn D5 would show the lowest value, as UWE is a convergent eddy. Such a pattern is clearly recognizable in Tables 1 & 2. The species composition of diatoms (Table 2) renders further evidence to support this idea. Of the 16 diatom species at Stn D1, 8 species were observed at Stn D4, whereas only 1 or 2 species occurred in the eddy core (Stns D2 and D3) and none of the species occurred outside of the eddy (Stn D5). The UWE during the cruise was approximately 500 km in circumference (C. W. Shin unpubl. data), and the typical velocity of the UWE is  $40 \text{ cm s}^{-1}$  (Lie et al. 1995). Thus, it takes approximately

7 d for the diatoms at Stn D1 to travel to Stn D4 (i.e. half of the circumference) along the ring of the UWE.

Secondly, it has been shown that the biomass structure as partitioned between phytoplankton and heterotrophic bacteria accurately reflects the trophic status of the water column (Cho & Azam 1990). Generally, a higher ratio of BCB:chl-C appears under conditions with low chlorophyll concentrations (Cho & Azam 1990, Hyun & Yang 2005). In fact, the ratio of BCB:chl-C showed distinct clustering according to each condition (Table 1); the ratio was lower in the highly productive eddy ring (0.12 at Stn D1, 0.14 at Stn D4) than in the eddy center (0.35 at Stn D2, 0.23 at Stn D3), and the highest ratio was at the outside of the eddy (0.58 at Stn D5) with the lowest chl *a* concentration. The lower BCB:chl-C ratio in the highly productive eddy ring is associated with an enhanced phytoplankton biomass, especially the larger diatoms (Tables 1 & 2) and abundance of heterotrophic protozoa that effectively control the biomass of fast-growing bacterial populations

Table 2. Spatial distribution of diatoms (cells l<sup>-1</sup>) at the eddy ring (Stns D1 and D4), eddy core (Stns D2 and D3), and outside the eddy (Stn D5)

	Stn D1	Stn D2	Stn D3	Stn D4	Stn D5
<i>Cerataulina pelagica</i>				480	
<i>Chaetoceros</i> sp.	1 719 000			286 000	
<i>Coscinodiscus</i> sp.			240		
<i>Dactyliosolen pukenensis</i>	120				
<i>Detonula pumila</i>	22 560			2520	
<i>Eucampia cornuta</i>	120				
<i>Eucampia zodiacus</i>	2400				
<i>Guinardia flaccida</i>	1890				
<i>Lichmophora</i> sp.	240				
<i>Nitzschia longissima</i>	18 570	120		4300	
<i>Nitzschia</i> sp.	360			4320	
<i>Pleurosigma</i> sp.	240			120	
<i>Pseudonitzschia pungens</i>	4640			6240	
<i>Rhizosolenia setigera</i>	360				
<i>Rhizosolenia shrubsolei</i>	120			120	
<i>Skeletonema costatum</i>				1920	
<i>Stephanophyxis palmeliana</i>	240				
<i>Thalassionema flauenfeldii</i>	120			120	
<i>Thalassionema nitzschioides</i>	120		120		
<i>Thalassiosira</i> sp. 1		120	12 670		120
<i>Thalassiosira</i> sp. 2			4200	360	
Total	1 771 100	240	17 230	306 500	120

(Sherr et al. 1992). In the northeast equatorial Pacific, Hyun & Yang (2005) reported that high phytoplankton biomass and intense heterotrophic nanoplankton grazing on actively growing bacterial biomass result in low BCB:chl-C in a high nutrient convergent region caused by the southern equatorial current and the northern equatorial counter current. A similar pattern of BCB and chl-C at Stn D1 compared to Stn D4, approximately 150 km away from Stn D1 (Fig. 2), provided further evidence that the highly productive coastal upwelling water mass is delivered into the UB via the UWE.

To our knowledge, this is the first report regarding the response of low trophic level organisms (i.e. phytoplankton, heterotrophic bacteria and protozoa) to the prevailing physical forces associated with coastal upwelling and the anticyclonic warm eddy in the UB. Similar nutrient dynamics and response of phytoplankton in relation to the eddy process have been reported in the Gulf of Alaska, where an eddy evolving from nutrient-rich coastal water carries nutrients to nutrient-poor offshore waters (Crawford et al. 2005, Peterson et al. 2005). In the East Sea, however, the TWC that contributes to the UWE is considered a low-nutrient water regime with nitrate and phosphate concentrations below 3 and 0.2  $\mu\text{M}$ , respectively, throughout the year (Yoo & Kim 2004). In addition, along the east coast of Korea, there are no major rivers that would serve as a source of nutrients for sustaining high microbiological biomass and productivity along the ring of the UWE. Therefore, the enhanced biological biomass and

production around the ring of the UWE (Stns D1 and D4; Tables 1 & 2) must have been sustained by nutrients supplied via coastal upwelling.

#### Bacterial parameters associated with the phytoplankton

From the depth-integrated phytoplankton and bacterial parameters (Table 1), the amount of carbon from BP corresponded to 20 to 25% (eddy ring) and 58% (eddy center) of PP, and BP was significantly correlated with the phytoplankton biomass ( $r^2 = 0.8497$ ,  $p = 0.0259$ ). These results indicated that heterotrophic BP is closely coupled to organic substrates produced by phytoplankton (Cole et al. 1988), and heterotrophic bacteria are a significant component in channeling photosynthetically fixed C in the UB affected by the combination of upwelling and the UWE. Less bacterial biomass in the productive eddy ring, despite the enhanced BP (Stns D1 and D4; Table 1) indicated that the heterotrophic protozoa effectively control the bacterial biomass in the eddy ring. The biomass of heterotrophic bacteria in highly productive regions is predominantly controlled by the grazing of heterotrophic protozoa, whereas heterotrophic BP in the open ocean is largely dependent on the availability of dissolved substrates that are released from phytoplankton and protozoa (Ducklow 2000, Hyun & Yang 2005).



### Implications of the high vertical flux in the UB

Downward flux of the biological production in the surface water column represents an important mechanism for C sequestration in the ocean. The community structure of plankton by size and species composition associated with a trophic gradient largely determines the downward flux of particulate organic C (Karl 1999, Cotner & Biddanda 2002). In biologically productive regions where inorganic nutrient concentrations are high, increased phytoplankton size and particle concentrations shift the planktonic community from domination by osmotrophic heterotrophic microbes to domination by phagotrophic zooplankton, which consequently increases vertical sinking fluxes (Cotner & Biddanda 2002). Large diatoms are particularly significant in mediating vertical flux during bloom periods and in upwelling systems (Boyd & Newton 1995).

The anticyclonic eddy process (Figs. 2 & 3), together with the occurrence of large diatoms along the eddy ring (Tables 1 & 2), implied that the highly productive coastal waters entrained by the UWE are ultimately transported to the UB along a funnel-shaped topography. This is a significant mechanism that stimulates benthic respiration and sequestration of organic matter produced in the highly productive coastal water column into the deep UB. Indeed, Lee et al. (2008) recently reported that the organic C content in the surface sediment of the UB was strikingly high (2.6 to 2.9% dry wt, Table 1), and that the organic C accumulation rates in the UB also showed high values, exceeding  $2 \text{ g C m}^{-2} \text{ yr}^{-1}$  (Lee et al. 2008); such a value has rarely been found for deep-sea sediments below 2000 m, except in regions of intense upwelling (Calvert & Price 1983, Böning et al. 2004). Since the UB is not influenced by any large river discharges (Hong et al. 1997), this exceptionally high organic C content was ascribed to high biological production in the water column. Actually, the C:N ratio of 6.98 measured in the sediment is close to the Redfield ratio (6.63), indicating that the organic matter deposited in the UB is predominantly of marine origin (Lee et al. 2008). This high organic C content together with high organic C accumulation rates are associated with the remarkably high level of C mineralization by sulfate reduction in the sediments of the UB (0.72 to  $1.85 \text{ mmol m}^{-2} \text{ d}^{-1}$  in Lee et al. 2008). Our results based on the spatial distribution of biomass and production of the microbial communities associated with the coastal upwelling and the anticyclonic warm eddy (Tables 1 & 2), together with the distinctly high sedimentary organic C contents and C mineralization by sulfate reduction (Lee et al. 2008), strongly indicated that benthic metabolism in the UB in spring was closely coupled to the enhanced biological production triggered by coastal upwelling and subse-

quent transport into the deep basin by the UWE. Direct estimation of the vertical fluxes to evaluate the coupling of benthic mineralization to microbiological production in the water column is necessary for a more comprehensive understanding of the biogeochemical C cycles in the UB.

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