



New Production and F-ratio on the Continental Shelf of the East China Sea: Comparisons Between Nitrate Inputs From the Subsurface Kuroshio Current and the Changjiang River

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This paper reports the first results of the direct measurements of nitrate-based new production and f-ratio on the continental shelf of the East China Sea. The Kuroshio-induced upwelling off north-eastern Taiwan and river runoff from the Changjiang are two principal sources of new nitrogen on the shelf. New production ranged from 70 to 1610 mgC m⁻² d⁻¹, and values of the f-ratio were 0.17 to 0.82. Enhanced new production in the upwelling was significantly related to the ambient nitrate concentration. This implies that the nutrients brought up to the euphotic zone by the intrusion of the subsurface Kuroshio water were quickly reflected by the enhancement of new production. The prediction of f-ratio is feasible in the upwelling region from two ship-measured parameters: light intensity and surface nitrate concentration, but not feasible in the river-influenced shelf waters. New production on the riverine shelf waters, in contrast, was not related to the nitrate input from the Changjiang, but was positively ($P < 0.05$) related to water temperature. Low rates of NO₃⁻ utilization imply that factors other than nitrate (e.g. phosphate or light) could be the limiting factors determining the new production dynamics in the river mouth. © 1999 Academic Press

Keywords: new production; f-ratio; East China Sea; upwelling; Changjiang

Introduction

Primary production can be partitioned into new production and regenerated production based on the source and form of nitrogen (N) (Dugdale & Goering, 1967). This has worked well for most oceanic waters because N is often the most limiting nutrient (Vitousek & Howarth, 1991). Regenerated production is the part of production dependent upon autochthonous N, mainly ammonium (NH₄⁺) and urea, derived from the metabolic products of local biological processes. New production is the part of production dependent upon allochthonous N sources. These sources include nitrate (NO₃⁻) mixing from deep ocean reserves, NO₃⁻ and other N species transported by river runoff, and atmospheric deposition and biologically fixed N from the atmosphere. New production is considered to be the fraction of primary production that can be removed from the surface

mixed layer as fish yields or subpycnocline sedimentation without destroying the long-term integrity of a pelagic ecosystem (Vezina & Platt, 1987). Therefore, estimation of new production is essential to understand the biogeochemical process or to manage the resource balance of any oceanic ecosystem.

The East China Sea (ECS) is located on a large continental shelf bounded by the Kuroshio Current on the slope side and the coast of China on the other. It is one of the most productive areas of the world oceans. The Changjiang (Yangtze) River, which empties into the ECS at about 31°30'N latitude, ranks as the fifth largest river in the world with regard to freshwater discharge (9.24×10^{11} m³ year⁻¹) and the fourth with regard to solid discharge (4.86×10^8 tons year⁻¹) (Tian *et al.*, 1993). This discharge clearly provides large nutrient loads to the ECS shelf. Concentrations of NO₃⁻, silicate and phosphate in the Changjiang were reported to be as high as 32.9, 95 and 0.57 μM, respectively (Zhang, 1996). A net

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oceanic flux of NO_3^- was estimated to be as much as $60 \times 10^9 \text{ mol year}^{-1}$ (Edmond *et al.*, 1985). Off north-eastern Taiwan, at the southern part of the ECS, a permanent upwelling occurs when the Kuroshio Current intrudes onto the continental shelf (Chern *et al.*, 1990). Nutrients, including nitrate, phosphate and silicate (Wong *et al.*, 1991), contained within subsurface Kuroshio water are brought up to the euphotic zone at the shelf break around $25^\circ 20' \text{N}$ latitude. High phytoplankton biomass (Chen, 1992; 1994; 1995a) and primary productivity (Chen, 1995b) were reported.

The new production regime in the Changjiang estuary is likely to be far more complicated than the simple model depicted by Dugdale and Goering (1967). In their original model, nitrate from depth is the only new nitrogen source considered. Non-nitrate new nitrogen such as ammonium (NH_4^+) or organic N are supplied in significant quantities by the Changjiang river. Unlike what is observed in most oceanic environments, phosphate, not N, limits primary production near the river mouth due to high N/P in the river inflow (Harrison *et al.*, 1990), and this potentially means another definition of new production based on phosphate is required.

Although it has been well recognized that both the Changjiang river runoff and the Kuroshio upwelling are two principal sources of new N, it is still unclear how these N inputs affect the primary production and f-ratio of the ECS. The purpose of this study was to elucidate and to compare the controlling mechanisms of new production in the upwelling and the riverine shelf water regions. The authors focussed their analysis on nitrate-based production, which is likely to be the dominant portion of new production, and then compared it with the available estimates of other new N sources. Regression models also were developed to predict the nitrate-based new production in these waters.

Methods

Experiments and sampling were carried out in two water regions. The upwelling region was studied during three cruises: OR1-416 (April 15–22, 1995), OR2-124 (June 10–14, 1995) and OR1-431 (September 27–October 3, 1995), covering the same transect (stations 1–17, Figure 1). The continental shelf region influenced by runoff of the Changjiang River was studied during Cruise OR1-449 (May 2–15, 1996; stations E1–E7).

For hydrographic observations, a rosette multi-sampler with attached CTD probes (Seabird SBE

9/11) was used, and water samples were collected from 3, 10, 25, 50, 75 and 100 m. Surface water (0 m) was collected with a bucket. Water samples were filtered onboard ship using Whatman GF/F glass-fiber filters under low vacuum ($<100 \text{ mmHg}$). The filter samples were kept in darkness and frozen at -20°C until analysis. Chlorophyll *a* concentration was determined on extracted filtrate in 90% acetone for 20 h (Strickland & Parsons, 1972) using a fluorescence spectrophotometer (F3000, Hitachi Co., Tokyo, Japan). The mean of two replicates is reported below for all observations. Nitrate and phosphate concentrations were analysed by standard spectrophotometric methods (Strickland & Parsons, 1972). Surface and underwater light intensities were measured either by a quantum meter (Li-188B, Li-Cor Inc., U.S.A.) or a PAR sensor (OSP200L, Biospherical Inc., U.S.A.). The depth of the euphotic zone was defined as 0.6% of the surface light penetration. The depth of mixed layer (Z_m) was defined as the depth where the density (σ_θ) gradient exceeded 0.1 m^{-1} .

Primary production and new production measurements were conducted at selected stations (3 to 7 stations) during each cruise (Table 1). All the production stations were located on the continental shelf with water depth less than 200 m.

During the upwelling cruises, water for measurement of photosynthetic production was collected by 20-L Go-Flo bottles from the surface (100% light intensity) and from the light penetration depths (LPD) equivalent to 46, 38, 13, 2 or 0.6% of the surface irradiance. The water was immediately transferred into 2.3-L transparent polycarbonate bottles at LPD equivalents of 100, 46, 38, 13, 2 or 0.6% using neutral density screens. Two light bottles and one dark bottle were incubated at each LPD. The dark bottle was covered with four layers of black plastic sheets to ensure total darkness. The bottles were incubated on deck in transparent water tanks with flow-through of *in situ* surface seawater under natural light for 24 h. Before incubation, $\text{NaH}^{13}\text{CO}_3$ (99 atom %, Isotec, Ohio, U.S.A.) was added to the primary production bottles so that the final concentration was 0.19 mM; $\text{Na}^{15}\text{NO}_3$ was added to the new production bottles at a concentration equivalent to 10% of ambient NO_3^- concentration. The initial and the incubated water were filtered through precombusted (450°C , 4 h glass fiber filters (Whatman GF/F). The filter papers were then treated with HCl fumes for 2 h to remove carbonate and were completely dried in a vacuum desiccator. Particulate organic carbon, particulate nitrogen and the isotopic ratios of $^{13}\text{C}/^{12}\text{C}$ and $^{15}\text{N}/^{14}\text{N}$ were determined by a mass spectrometer (ANCA-MASS 20-20, Europa Scientific Ltd., Crewe, U.K.). Measurement

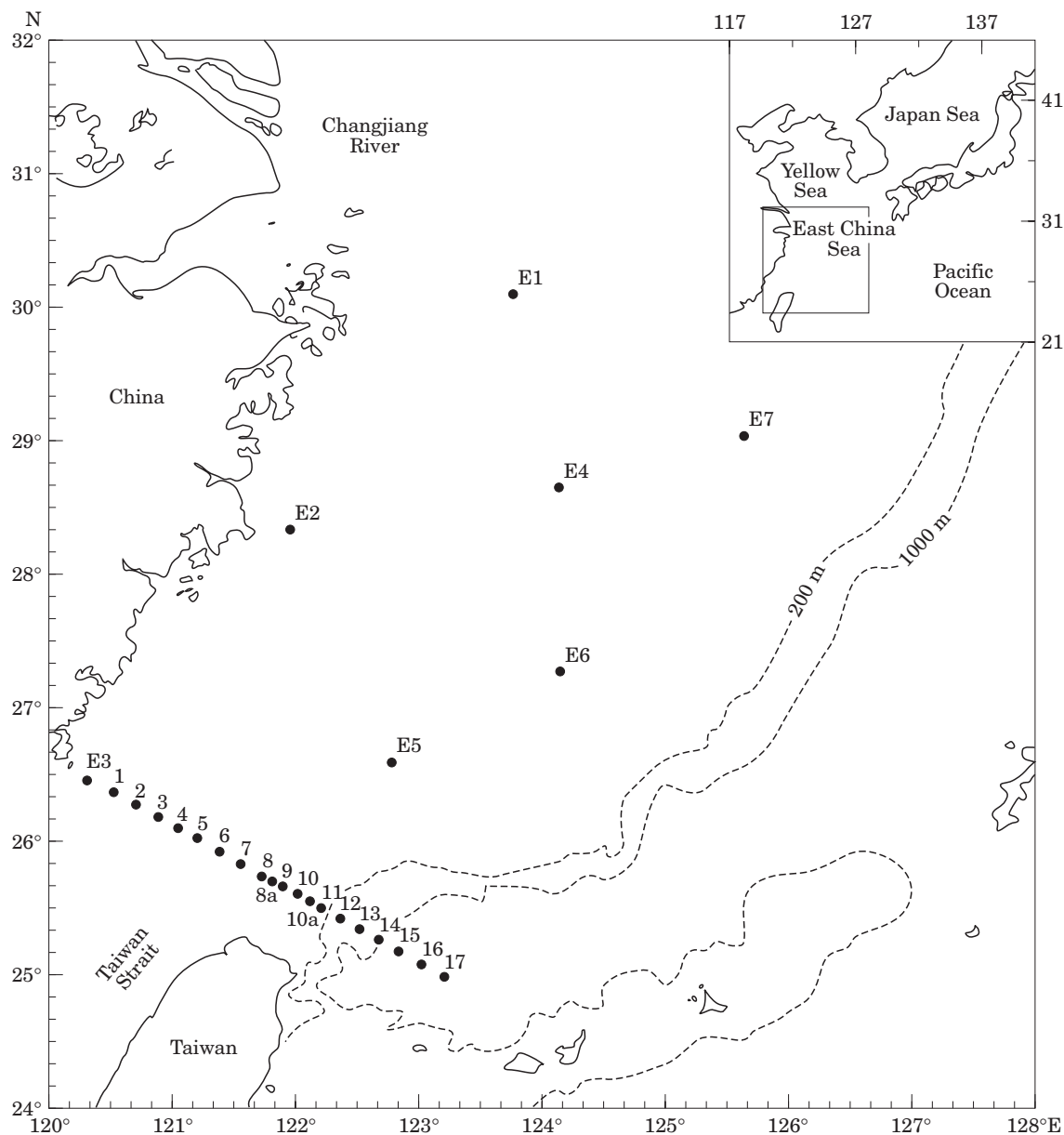


FIGURE 1. Sampling stations on the East China Sea and the Kuroshio. The transect among stations 1 to 17 were sampled during cruise 416, 124 and 431; Stations E1 to E7 were sampled during cruise 449.

of ^{13}C atom % and ^{15}N atom % were reproducible at a precision of ± 0.0002 and 0.0003% , respectively. Concentration of total inorganic carbon was determined from alkalinity (Strickland & Parsons, 1972).

Primary production measurements in the Changjiang riverine shelf water was carried out by the ^{14}C assimilation method (Parsons *et al.*, 1984). Water samples were taken before dawn. Three light and one dark 250 ml polycarbonate bottles were filled with water and inoculated with $\text{NaH}^{14}\text{CO}_3$ (final concentrations $10 \mu\text{Ci ml}^{-1}$). One light bottle was filtered

immediately as the time-zero sample. Two light and one dark bottles for each depth were tethered onto an *in situ* array. The array was anchored with a 30–50 kg weight at the bottom to position the samples at their original depths. Following retrieval of bottles after 4–5 h of incubation (from about 8:00 to noon), the water sample in each bottle was filtered through a Whatman 25 mm GF/F filter. The filters were then placed in scintillation vials with 0.5 ml of 0.5N HCl to remove residual $\text{H}^{14}\text{CO}_3^-$. Radioactivity in each vial was measured in a liquid scintillation counter (Packard 1600) after addition of 10 ml scintillation

TABLE 1. Location, bottom depth, depth of euphotic zone (0.6% of the surface light intensity) and the depth of mixed layer (Z_m , difference of $\sigma\theta$ value $<0.1 \text{ m}^{-1}$) of the sampling stations where new production and primary production were measured during various cruises

Cruise (date)	Station	Location		Bottom depth (m)	Euphotic layer depth (m)	Z_m (m)
		Longitude (E)	Latitude (N)			
416 (15–22 April 1995)	5	121°10'	26°00'	85	42	>76
	9	121°50'	25°40'	125	54	>102
	11	122°10'	25°30'	145	84	70
124 (10–14 June 1995)	8	121°40'	25°44'	117	68	77
	8a	121°44'	25°45'	123	73	70
	9	121°50'	25°40'	126	73	53
	10	122°00'	25°35'	118	30	>100
	10a	122°05'	25°30'	136	40	3
431 (27 September– 3 October 1995)	9	121°50'	25°40'	122	68	54
	10	122°00'	25°35'	116	79	38
	11	122°10'	25°30'	123	84	>102
449 (2–15 May 1996)	E1	123°48'	30°07'	60	36	10
	E2	121°59'	28°20'	50	29	10
	E3	120°16'	26°28'	45	38	5
	E4	124°08'	28°38'	80	27	40
	E5	122°46'	26°35'	106	55	20
	E6	124°08'	27°16'	100	71	30
	E7	125°37'	29°02'	100	66	60

cocktail (Ultima Gold, Packard). Nitrate uptake measurements were carried out concurrently with primary production by inoculating $^{15}\text{NO}_3$ in two 1.0 l polycarbonate bottles and incubating *in situ* for 4–5 h. $^{15}\text{NO}_3$ assimilated was determined by a mass spectrometer (VG Micro Mass 622). The uptake measured during the morning hours was multiplied by a factor of approximately three to obtain the daily assimilation rate in accordance with the local diel cycle which was previously established (unpublished results). Particulate organic nitrogen concentration was measured by a CHN analyser (Carlo-Erba EA 1400) connected to the mass spectrometer.

Two incubation schemes were used in the present study. The 24 h incubation for the upwelling area could possibly lead to underestimation of nitrate uptake because of isotope depletion during prolonged incubations. Turnover times for the observed NO_3 (observed NO_3 concentration/ NO_3 uptake rate) on the two upper incubation depths in the upwelling region were mostly in the range of <0.8 – 1.9 day. This implies that the nitrate uptake rates are probably underestimated due to substrate exhaustion. The incubation in the riverine shelf water was, by comparison, short. Underestimation of rates in riverine shelf waters was unlikely and even if underestimation were to occur this would pose no problem in our conclusion since it could occur only in the upwelling region where

nitrate uptake rates were high. In contrast, low uptake rates were observed at the Changjiang riverine shelf region. These low uptake values could not have resulted from underestimation because the incubation time was relatively short.

Primary production was calculated (Hama *et al.*, 1983) from the uptake rate of ^{13}C or ^{14}C . Hama *et al.* (1983) reported excellent agreement between the ^{14}C and ^{13}C methods. Nitrate assimilation rate was calculated following the equations (2) and (3) of Dugdale and Wilkerson (1986). From the nitrate assimilation rate and the Redfield ratio (C:N=6.6), nitrate-based new production in unit of carbon was then obtained (Dugdale *et al.*, 1989). f-Ratio was calculated as new production divided by primary production. Water column integrated production per m^2 was calculated by trapezoidal integration from 100 to 0.6 LPD to provide daily integrated primary production (IPP) and daily integrated new production (INP) per m^2 .

A step-wise multiple regression analysis procedure (Draper & Smith, 1981) was used to examine the spatial relationships of nitrate-based new production, primary production, NO_3^- concentration, water temperature and chlorophyll *a* concentration. The relationships between chlorophyll normalized uptake rates and light intensity were fitted with Michaelis-Menten equations by SigmaPlot.

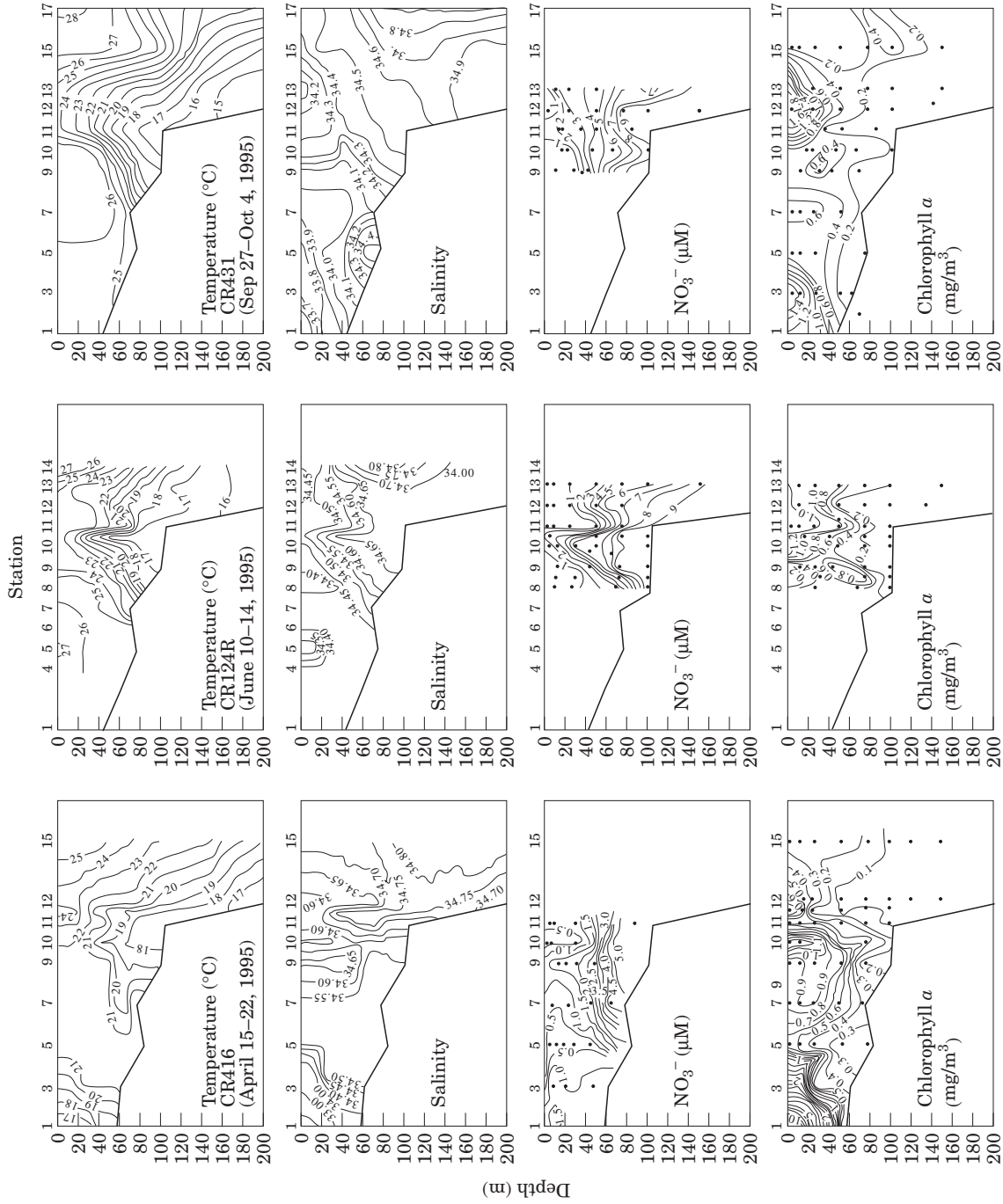


FIGURE 2. Cross-sections of temperature, salinity, nitrate concentration and chlorophyll α concentration on the transect among stations 1-17 during 3 different cruises.

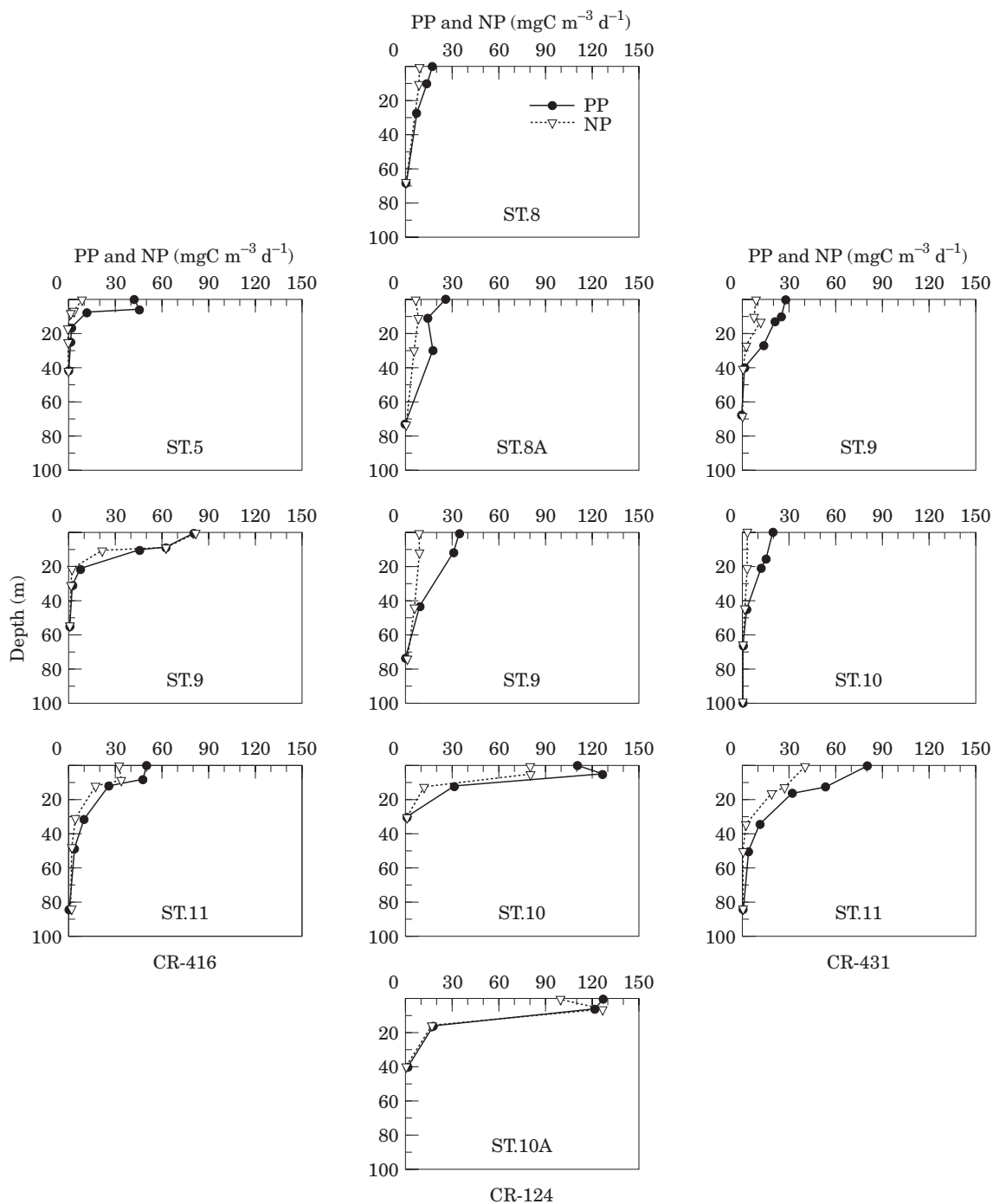


FIGURE 3. Vertical distribution of primary production (PP) and nitrate-based new production (NP) measured during three different cruises.

Results

The upwelling region

The plume centre of the upwelling at the shelf break could be easily located by hydrography. At the plume centre, the surface water was lower in temperature

and higher in salinity, nitrate, and chlorophyll *a* concentration than the adjacent waters (Figure 2). Although the plume centre shifted slightly from cruise to cruise, it always appeared near the shelf break. These upwelling characteristics were observed repeatedly for all cruises and confirm the persistence of the

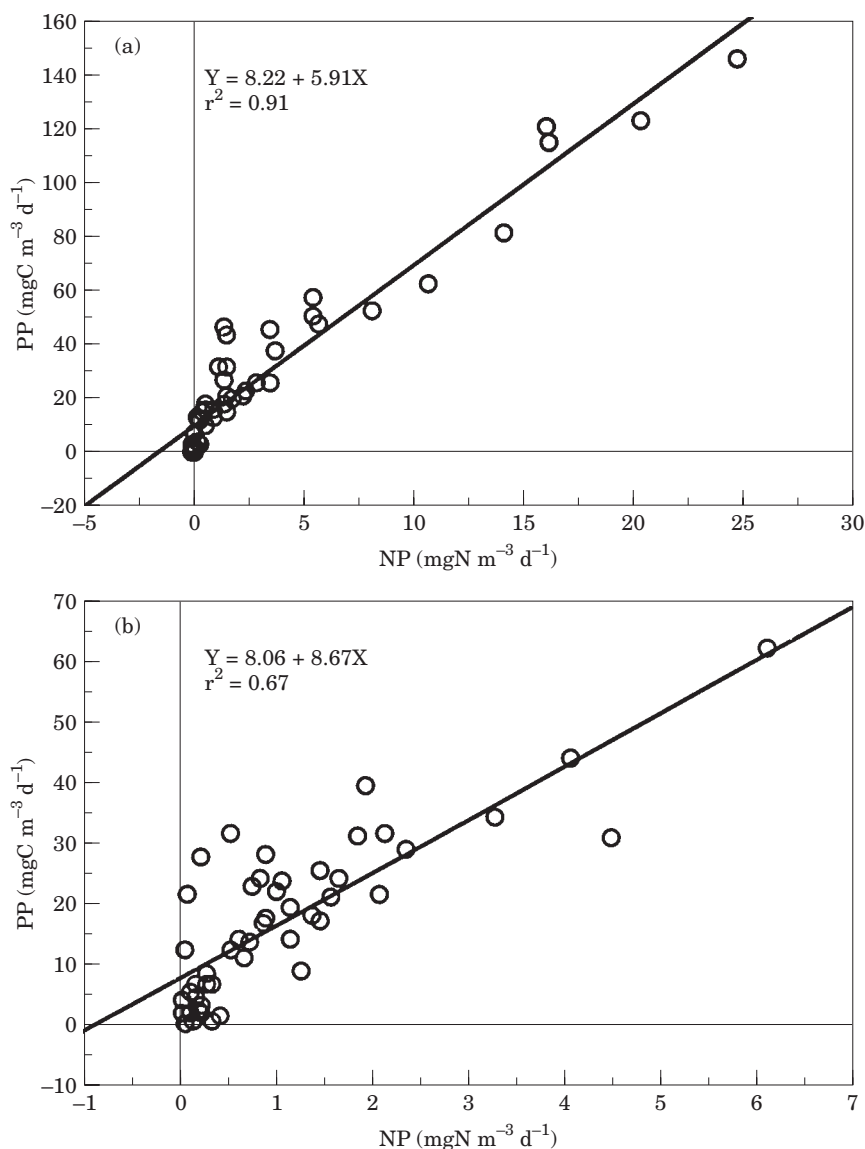


FIGURE 4. Relationship between primary production (PP) and nitrate-based new production (NP) in (a) the upwelling region and the (b) Changjiang riverine shelf region respectively.

upwelling (Chern *et al.*, 1990). Surface nitrate concentrations as high as 2 μM were observed at the location where lowest surface water temperature was measured (Figure 2). This high nitrate concentration resulted in a high chlorophyll *a* concentration in the euphotic zone (Figure 2). Shelf waters between Stations 1 and 3 near the coast of China, with the distinctive characteristic of low salinity, were also high in chlorophyll *a* concentrations.

Depth profiles of primary and nitrate-based new production in the shelf break and the adjacent shelf waters showed high values in the surface layer and decreased with depth (Figure 3). This suggests that light is possibly more important than nitrate in deter-

mining the vertical profile of production even though nitrate is usually considered a significant factor in controlling primary or new production in these subtropical waters. Vertical distributions of primary production (PP) and nitrate-based new production (NP) were also related significantly ($P < 0.01$) to *in situ* chlorophyll *a* concentration. Waters with higher chlorophyll *a* concentration ([Chl], mg m^{-3}) and average light intensity at the depth of incubation (Light, $\mu\text{E m}^{-2} \text{s}^{-1}$), i.e. shallower waters, showed a higher primary or new production than those of low-chlorophyll deep water. Correlation between PP and NP was also quite high ($r = 0.95$, Figure 4). Multiple regression analysis depicted their relationships as:

TABLE 2. Parameters of Michaelis-Menten equations describing the relationships between average light intensity (L , $\mu\text{E m}^{-2} \text{s}^{-1}$) during the incubation for various depths and nitrate uptake rate ($\rho\text{NO}_3/\text{Chl}$, $\text{mg at-N mg Chl}^{-1} \text{day}^{-1}$) or carbon uptake rate ($\rho\text{C}/\text{Chl}$, $\text{mg at-C mg Chl}^{-1} \text{day}^{-1}$). The equation fitted is $\rho_{\text{max}} \cdot L / (K_L + L)$ where ρ_{max} and K_L are the parameters

Cruise/ station	$\rho\text{NO}_3/\text{Chl}$			$\rho\text{C}/\text{Chl}$			Average surface light intensity
	ρ_{max}	K_L	R^2	ρ_{max}	K_L	R^2	
Cruise 416							
St. 5		—			—		343*
St. 9		—		20.94	1469	0.92	1322*
St. 11	2.00	1328	0.89	21.34	1466	0.94	1327*
Cruise 124							
St. 8	0.45	225.6	0.99	9.65	635.4	0.99	563*
St. 8a		—		7.02	80.43	0.96	747*
St. 9	0.29	180.5	0.83	10.1	398.1	0.84	923*
St. 10	1.61	1029	0.97	16.0	831.9	0.99	1232*
St. 10a	1.74	270.1	0.83	5.8	451.5	0.94	826*
Cruise 431							
St. 9	0.45	302.4	0.74	10.3	455.5	0.97	1068*
St. 10	0.13	100.7	0.90	8.09	329.4	0.92	472*
St. 11	0.52	497.1	0.98	4.72	72.29	0.85	1277*
Cruise 449							
St. E1	0.21	115.8	0.72		—		644†
St. E2		—		3.26	111.8	0.97	968†
St. E3	0.71	549.1	0.85	4.69	97.95	0.76	1018†
St. E4	0.37	220.9	0.97	2.66	56.21	0.98	226†
St. E5		—		3.34	159.1	0.93	579†
St. E6		—		5.09	56.41	0.87	773†
St. E7		—		4.46	90.55	0.91	1065†

—Indicates poor fitting by Michaelis-Menten equation

*data from 0 m

†data from 2 m.

$$\text{PP} = -15.39 + 56.24 [\text{Chl}] + 0.038 \text{Light} \quad (R^2=0.59);$$

$$\text{NP} = -19.36 + 55.29 [\text{Chl}] + 0.023 \text{Light} \quad (R^2=0.54)$$

The Michaelis-Menten equation was able to describe the relationships between chlorophyll normalized uptake rates and average light intensity during the incubation for each light depth at most of the stations (Table 2). Results of two representative stations are shown in Figure 5.

Primary production and new production were higher in shelf break waters than in adjacent waters. At the shelf break, primary production was usually $>1 \text{ gC m}^{-2} \text{ day}^{-1}$ with a maximum value of $1.96 \text{ gC m}^{-2} \text{ day}^{-1}$ (Table 3). In contrast, primary production in the non-upwelling shelf water ranged from $0.43 \text{ gC m}^{-2} \text{ day}^{-1}$ at Station 5 to $0.88 \text{ gC m}^{-2} \text{ day}^{-1}$ at Station 8a. New production for all stations ranged between 0.08 and $1.61 \text{ gC m}^{-2} \text{ day}^{-1}$ (Table 3). New production was generally high near the shelf break; while low values were observed at the mid-shelf stations (Stations 5, 8 and 8a). However, low new production was observed at some stations near the shelf break. For example,

new production at Stations 9 and 10 during cruise 431 were 0.27 and $0.14 \text{ gC m}^{-2} \text{ day}^{-1}$, respectively. Integrated new production (INP) was positively correlated with integrated primary production (IPP) and surface nitrate concentration ($\text{NO}_3\text{-surf}$) (Table 4). The chlorophyll normalized new production (INP/IChl , integrated new production/integrated chlorophyll a , $\text{mgC mgChl}^{-1} \text{ day}^{-1}$) was also significantly and positively correlated to chlorophyll normalized primary production (IPP/IChl) and the surface nitrate concentration (Table 4). The combined regression equation is:

$$\text{INP}/\text{IChl} = -0.9801 + 0.693 \text{IPP}/\text{IChl} + 6.31 \text{NO}_3\text{-surf} \quad (R^2=0.89)$$

Integrated f-ratio (INP/IPP) was significantly related to the average on-deck light intensity during incubation (Light , $\mu\text{E m}^{-2} \text{ s}^{-1}$) and the surface nitrate concentration (Table 4). The combined equation is:

$$\text{f-Ratio} = 0.127 + 0.0002427 \text{Light} + 0.176 \text{NO}_3\text{-surf} \quad (R^2=0.72)$$

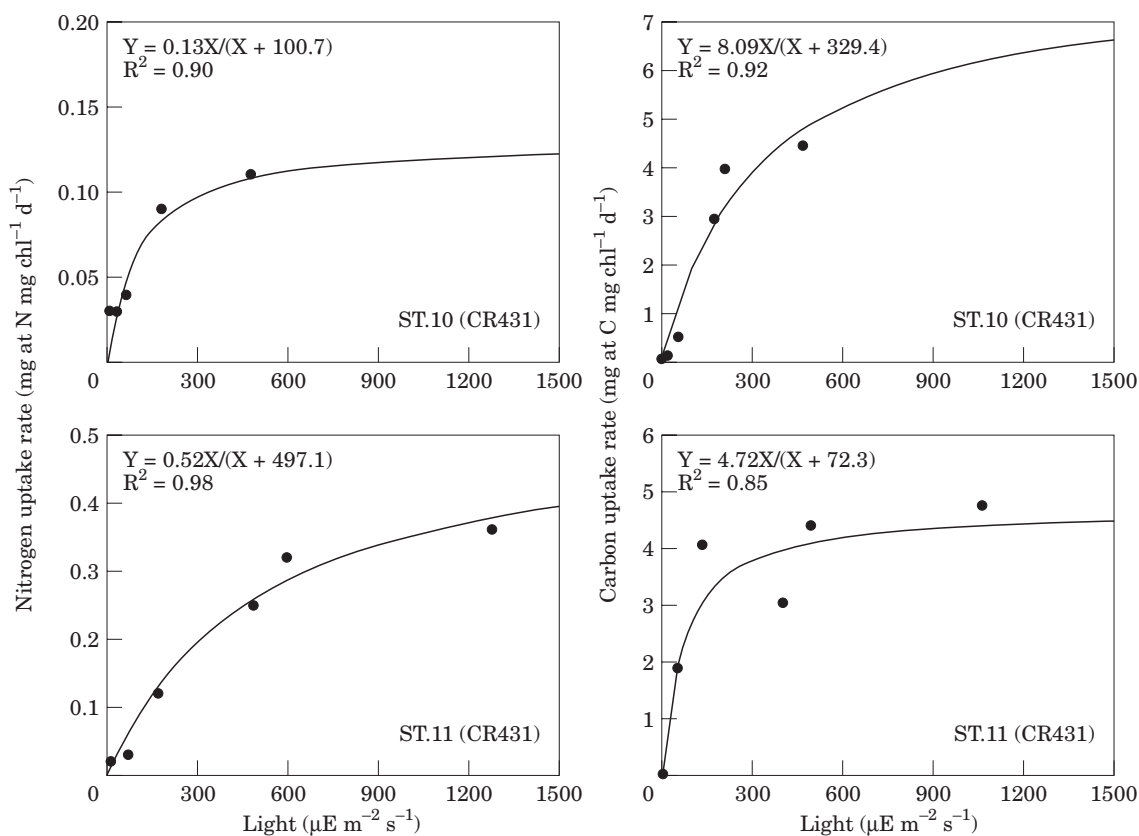


FIGURE 5. Effects of the average light intensity ($\mu\text{E m}^{-2} \text{s}^{-1}$) during the incubation on nitrate ($\text{mg at-N mg Chl}^{-1} \text{day}^{-1}$) and carbon uptake rate ($\text{mg at-C mg Chl}^{-1} \text{day}^{-1}$) at respective light depth in Station 10 (a shelf station) and Station 11 (an upwelling station) investigated during cruise 431.

Thus the prediction of f-ratio in this region is feasible from ship-measured parameters which are often readily available.

The Changjiang riverine shelf region

Primary production and nitrate-based new production measured in river-influenced shelf waters generally decreased with increasing depth, similar to what was observed in the upwelling region (Figure 6). Correlation between PP and NP was also high ($r=0.82$, Figure 4). The magnitude of primary production and new production also related significantly ($P<0.01$) to chlorophyll *a* concentration. Multiple regression analysis examining the effects of light availability and chlorophyll *a* concentration revealed the following relationships:

$$\text{PP} = 0.645 + 17.80 [\text{Chl}] + 0.021 \text{ Light} \quad (R^2 = 0.72)$$

$$\text{NP} = -1.092 + 8.205 [\text{Chl}] + 0.008 \text{ Light} \quad (R^2 = 0.48);$$

Both riverine shelf water and upwelling water showed a similar pattern with maximum chlorophyll-

specific production occurring in or near the surface layer, implying that their vertical distributions were light-dependent rather than nutrient-dependent. There were, however, observations at several stations that did not follow the trend that production decreased with depth. Light-dependence parameters obtained in this region are listed in Table 2. An example is shown for Station E2 where a significant relationship was not established (Figure 7).

Nitrate-based new production measured during cruise 449 ranged from 0.07 to $0.34 \text{ gC m}^{-2} \text{day}^{-1}$ and primary production from 0.25 to $0.75 \text{ gC m}^{-2} \text{day}^{-1}$. In contrast to what was observed in the upwelling region, the variation of integrated new production was related to neither surface nitrate concentration, primary production, chlorophyll *a* concentration, nor incubation light intensity (Table 5). However, both f-ratio and the integrated chlorophyll-specific new production was significantly and positively related to the surface water temperature over the range 15 – 21 °C for all stations (Table 5). There was no significant relationship

TABLE 3. Water column integrated primary production ($\text{gC m}^{-2} \text{day}^{-1}$), integrated new production ($\text{gC m}^{-2} \text{day}^{-1}$) and f-ratio obtained at seven sampling stations during three different cruises

Cruise	Station						
	5	8	8a	9	10	10a	11
Primary production							
416	0.43			1.00			1.03
124		0.71	0.88	1.32	1.22	1.96	
431				0.66	0.60		1.43
New production							
416	0.08			0.77			0.66
124		0.30	0.32	0.36	0.80	1.61	
431				0.27	0.14		0.72
f-ratio							
416	0.19			0.77			0.64
124		0.42	0.36	0.27	0.66	0.82	
431				0.41	0.23		0.50

TABLE 4. Matrix of correlation coefficients (r) for the variables f-ratio (INP/IPP), integrated new production (INP), integrated primary production (IPP), chlorophyll a normalized integrated new production (INP/Ichl), chlorophyll a normalized integrated primary production (IPP/Ichl), integrated chlorophyll a concentration (Ichl), integrated nitrate concentration (INO_3), surface nitrate concentration ($\text{NO}_3\text{-surf}$), surface temperature (Temp-surf) and average surface light intensity (Light) obtained in the upwelling region northeast Taiwan

Variables	f-ratio	INP	IPP	INP/Ichl	IPP/Ichl	Ichl	INO_3	$\text{NO}_3\text{-surf}$	Temp-surf
INP	0.88**								
IPP	0.67*	0.89**							
INP/Ichl	0.87**	0.99**	0.87**						
IPP/Ichl	0.64*	0.87**	0.96**	0.90**					
Ichl	0.52	0.50	0.59	0.37	0.34				
INO_3	-0.16	-0.06	0.16	-0.07	0.12	0.20			
$\text{NO}_3\text{-surf}$	0.77**	0.86**	0.73*	0.82**	0.68*	0.50	0.02		
Temp-surf	-0.34	-0.32	-0.26	-0.24	-0.12	-0.45	0.49	-0.53	
Light	0.68*	0.46	0.46	0.45	0.42	0.50	0.19	0.48	-0.22

* $P < 0.05$, ** $P < 0.01$.

between the new production and the surface nitrate concentration (Table 5).

Light intensity seemed not to be crucial in affecting the spatial variation of integrated new production on the continental shelf off the Changjiang. There was no significant relationship between integrated new production and the average on-deck light intensity during incubation. There was a subsurface maxima of new production at Station E2 (Figure 7) where the surface nitrate concentration was high and the integrated new production was low. Maximum new production was located at 10–15 m (four times greater than that at 2 m) in the euphotic zone where nitrate was abundant and uniformly distributed. Similarly high, subsurface new production was also observed at Stations E1, E7 and E6.

Water column f-ratio ranged between 0.17 (Station E2) and 0.51 (Station E6) (Table 6). Its variation was positively related to surface water temperature (Table 5), but not to light intensity, surface nitrate concentration, and integrated nitrate concentration (Table 5).

Discussion

Data review, NP and PP

The present study reports the first values of nitrate-based new production on the continental shelf of the East China Sea. Rates ranged from 80 to $1610 \text{ mgC m}^{-2} \text{day}^{-1}$ in the upwelling region and from 70 to $340 \text{ mgC m}^{-2} \text{day}^{-1}$ in the broad shelf

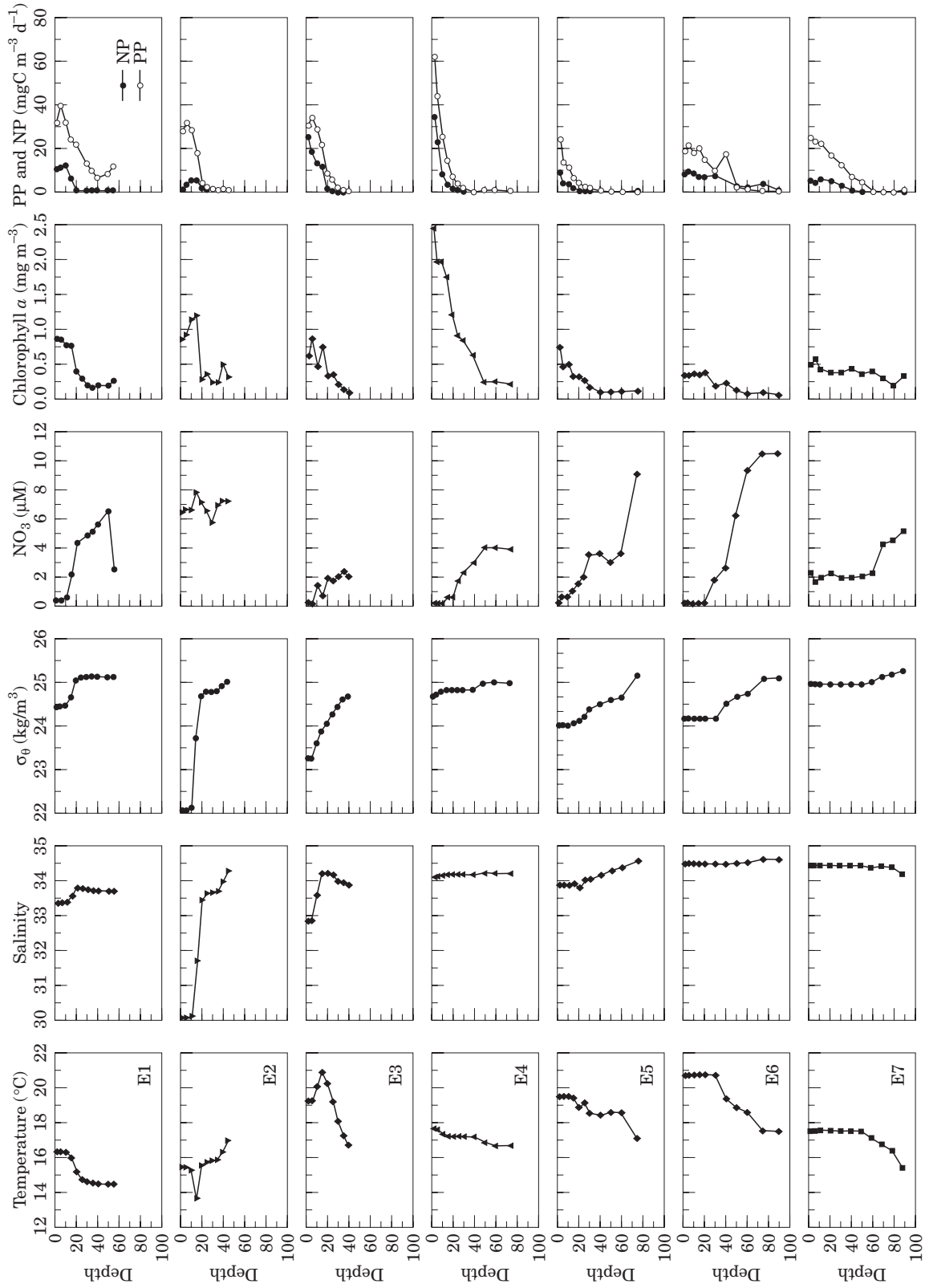


FIGURE 6. Vertical distribution of temperature, salinity (σ_t), nitrate concentration (NO_3), chlorophyll a concentration (Chlorophyll a), primary productivity (PP) and new productivity (NP) measured at seven stations during cruise 4449.

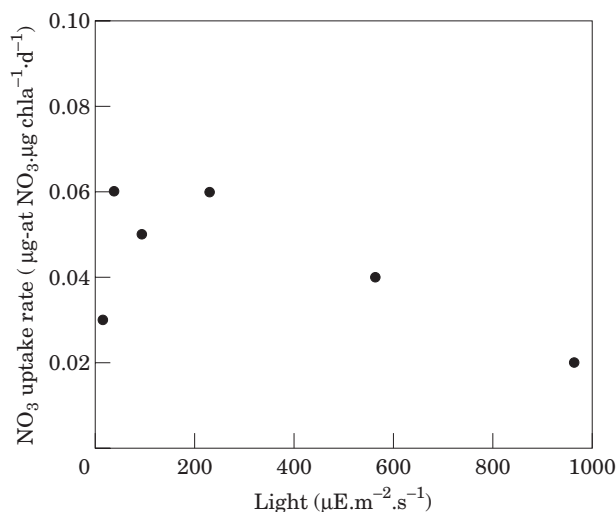


FIGURE 7. Relationship between light intensity ($\mu\text{E m}^{-2} \text{S}^{-1}$) and nitrate uptake rate ($\mu\text{g at-N } \mu\text{g Chl}^{-1} \text{day}^{-1}$) at Station E2.

area including the Changjiang-influenced waters. These values are much higher than previously calculated estimates of $80 \text{ mgC m}^{-2} \text{day}^{-1}$ by Li (1995) and $73 \pm 22 \text{ mgC m}^{-2} \text{day}^{-1}$ by Chen (1996). Similarly, much higher f-ratios were obtained from our direct measurements (0.17–0.82) than those estimated by Chen (0.15) and by Li (<0.16). Average f-ratio was 0.48 for the upwelling region and 0.34 for the Changjiang continental shelf region. These average values were computed by placing equal weight on each of the stations, regardless of their uneven distribution and sampling frequency. For comparison, f-ratios as low as 0.05 were reported for oligotrophic central oceans and as high as 0.5 in a productive coastal-upwelling regions (Harrison *et al.*, 1987).

Primary production observed in this study ranged from 430 to $1960 \text{ mgC m}^{-2} \text{day}^{-1}$ in the upwelling region (Table 3). The data are consistent with previous observations in a similar area (Chen, 1995b). The values ranged from 250 to $750 \text{ mgC m}^{-2} \text{day}^{-1}$ in the shelf region off Changjiang (Table 6), and also comparable with, but slightly lower than, the value obtained by Hama *et al.* (1997), who reported the average primary productivity of $750 \text{ mgC m}^{-2} \text{day}^{-1}$ for the shelf area close to this study. High productivity in the ECS, especially at the upwelling plume was confirmed in this study.

Effect of upwelling on NP

Both new production and primary production in the upwelling region are under strong control of nutrient

supply via upwelling. N is generally considered to be a limiting element in the dynamics of new production. This is clearly shown in the upwelling region of the present study (Figure 8). The upwelling INP and IPP were related to NO_3 -surf, but not to INO_3 . This implies that INP and IPP are responding to a factor to which NO_3 -surf is related, not necessarily to NO_3^- concentration itself. NO_3 -surf likely represents ‘strength’ of the upwelling or the rate of supply of deep water and N to the photic zone. The present upwelling had a maximum surface nitrate concentration of $2 \mu\text{M}$ and f-ratios of 0.23–0.82. In contrast, the Peruvian upwelling has f-ratios of 0.10–0.84 and a maximum surface nitrate concentration of $>20 \mu\text{M}$ (Wilkinson & Dugdale, 1987). Nitrate supply from the subsurface Kuroshio waters to these subtropical waters appears to contribute in a similar manner to primary production as in the Peruvian upwelling. The high f-ratio and correlation of INP and NO_3 -surf in this study indicate that phytoplankton response to the upwelling is faster than in the Peruvian upwelling system, where time-lags of phytoplankton growth are often observed.

The distribution of high new production and f-ratio matched the distribution of low temperature and high nitrate concentration at the centre of the upwelling water. The chain reaction from physical effect (upwelling) to chemical change (high nitrate) to the biological response (high INP) was clearly demonstrated. The behaviour of the Kuroshio Current therefore is an important force in determining the dynamics of new production in these shelf waters.

Control of the Changjiang NP: (1) Temperature

Unlike the Kuroshio Current, the nitrate-rich Changjiang runoff did not bring similarly high, nitrate-based new production to its immediate shelf water. Station E2 with a surface nitrate concentration as high as $6.4 \mu\text{M}$, higher than the maximum surface concentration of $2 \mu\text{M}$ observed in the upwelling, had the lowest new production ($70 \text{ mgC m}^{-2} \text{day}^{-1}$) and f-ratio (0.17) of all stations (Figure 8). The subsurface Kuroshio water is warm and salty in contrast to the cold and less saline turbid Changjiang plume. Water temperature was positively related to new production off the Changjiang continental shelf region. The Changjiang-influenced water was both low in surface temperature and new production. Positive correlation between water temperature and nitrate uptake rate has been previously reported (Slawyk, 1979; Le Bouteillier, 1986) where factors such as light intensity and nutrient concentration were relatively uniform. There are conflicting reports depicting the linkage

TABLE 5. Matrix of correlation coefficients (r) for the variables f-ratio (INP/IPP), integrated new production (INP), integrated primary production (IPP), chlorophyll *a* normalized integrated new production (INP/Ichl), chlorophyll *a* normalized integrated primary production (IPP/Ichl), integrated chlorophyll *a* concentration (Ichl), integrated nitrate concentration (INO₃), surface nitrate concentration (NO₃-surf), surface temperature (Temp-surf) and average surface light intensity (Light) obtained in the continental shelf region off the Changjiang

Variables	f-ratio	INP	IPP	INP/Ichl	IPP/Ichl	Ichl	INO ₃	NO ₃ -surf	Temp-surf
INP	0.79*								
IPP	-0.14	0.47							
INP/Ichl	0.73	0.88**	0.34						
IPP/Ichl	0.10	0.54	0.72	0.73					
Ichl	-0.02	0.01	0.09	-0.47	-0.57				
INO ₃	-0.21	0.01	0.12	0.28	0.41	-0.53			
NO ₃ -surf	-0.67	-0.57	-0.14	-0.49	-0.26	0.03	0.46		
Temp-surf	0.87*	0.67	-0.13	0.76*	0.25	-0.34	0.08	-0.68	
Light	-0.34	-0.14	0.17	0.10	0.32	-0.48	0.41	0.60	-0.22

* $P < 0.05$, ** $P < 0.01$.

TABLE 6. Spatial variation of water column integrated primary production (gC m⁻² day⁻¹), integrated new production (gC m⁻² day⁻¹) and f-ratio obtained in the continental shelf off the Changjiang during cruise 449

	Station						
	E1	E2	E3	E4	E5	E6	E7
Primary production	0.75	0.43	0.52	0.50	0.25	0.66	0.71
New Production	0.16	0.07	0.25	0.21	0.09	0.34	0.16
f-ratio	0.21	0.17	0.48	0.43	0.36	0.51	0.23

between surface temperature and new production. Kamykowski and Zentara (1986) found that surface temperature of water in an upwelling system was low whilst concentration of nitrate was high; new production was high in upwelled water despite the low surface temperature. However temperature effect in this study could also be a surrogate of the effects linking to the water mass rather than its direct physiological influence on phytoplankton cells.

Control of the Changjiang NP:(2) PO₄

Although the upwelling and the Changjiang-influenced waters were both rich in nitrate, there were differences in other nutrient concentrations. Our study showed that *in situ* measurements of N:P ratios ([NO₃⁻]/[PO₄³⁻]) in the water column of the euphotic zone were mostly below the Redfield ratio of 16:1 (Table 7), with the exception of Station E2. This indicates that most of the water on the shelf was potentially more insufficient in nitrate than in phosphate. On the contrary, N:P ratios as high as 213:3 were observed in the surface water of Station E2, and

its phosphate concentration was at the limit of detection (0.03 μM). Phosphate concentration was undetectable in the upper 20 m of Station E4. This implies that within the river-influenced water, such as Station E2, the limitation on production was probably from phosphate instead of N. There were other reasons for supporting the differences in N:P ratio between these two nitrate-rich waters. Chen (1996) reported that the nutrient flux from the Kuroshio water to the shelf was 14.3:1 which is close to the 16:1 Redfield ratio, whereas N (nitrate+ammonium):P ratio from the Changjiang river fluxes was 126:1. A steep gradient of nitrate (65–15 μM), phosphate (0.7–0 μM) and N:P ratio (90–150) was found over the salinity gradient from the river mouth to the open sea (Harrison *et al.*, 1990). Mesocosm experiments off the coast of mainland China indicated that phytoplankton growth was limited by phosphorus rather than by N (Harrison *et al.*, 1990). Station E2 had a surface salinity of 30.04 and was within the range of 0 to 32 in the phosphate-limiting region described by Harrison *et al.* (1990). It is, thus, very likely that the water at this station was phosphate-limited rather

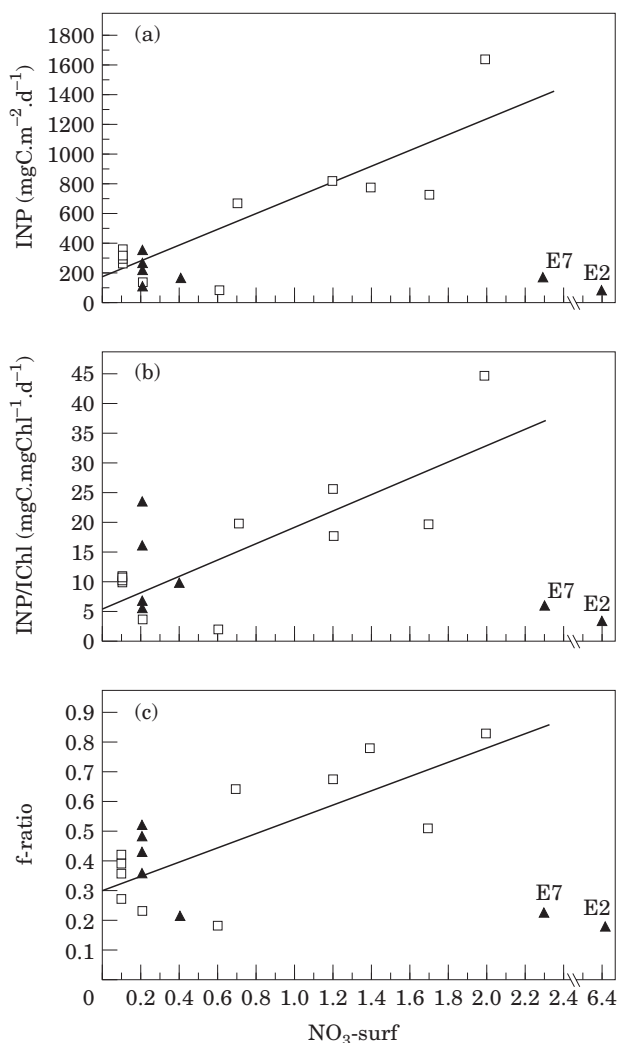


FIGURE 8. Relationships between surface nitrate concentration and integrated new production (a), chlorophyll *a* normalized integrated new production (b), and *f*-ratio (c), measured in the upwelling region (\square) and in the continental shelf off the Changjiang (\blacktriangle). Regression line was calculated based on the data in the upwelling region during three cruises.

than N-limited, as has been reported seasonally for other river-influenced regions such as Chesapeake Bay (e.g. Fisher *et al.*, 1992).

Control of the Changjiang NP:(3) Light

As well as ambient nitrate concentration light intensity is another important factor (Kanda *et al.*, 1989) in affecting nitrate uptake. The waters of the Changjiang carry a high concentration of suspended matter (Tian *et al.*, 1993). These river-borne particulates are maintained in suspension in the surface layer to salinities >20 , and their concentrations vary between 20 and

1000 mg l^{-1} and decrease to 10 mg l^{-1} with higher salinity (Edmond *et al.*, 1985). Light availability increases as the suspended particulate matter settles (Ning *et al.*, 1988). The nitrate uptake rate, integrated over the water column, measured in the Changjiang continental shelf water, however, did not show any significant relationship with the light intensity in the present study. The water which was most likely to be affected by the riverine input (Station E2) showed a rather deep euphotic depth (29 m, Table 1) and high incubation light intensity ($1383 \mu\text{E m}^{-2} \text{S}^{-1}$) when compared with the same parameters at station E4 (27 m and $332 \mu\text{E m}^{-2} \text{S}^{-1}$), with double the amount of new productivity. Density ($\sigma\theta$) profiles showed that Station E2 was highly stratified and its mixing depth was shallow (Figure 6) compared to the euphotic zone depth. This suggested that the slow uptake of nitrate in the upper water column of the station was not due to limitation by light intensity. The observation that incubation light intensity was not significantly correlated with specific nitrate uptake rate at that station (Figure 7) provides further direct evidence. Low INP (161.55), low *f*-ratio (0.23) as well as high surface nitrate concentration ($2.3 \mu\text{M}$, Figure 8) was also observed at Station E7. Limitation due to light intensity seems to be unlikely due to the relatively high light intensity ($1243 \mu\text{E m}^{-2} \text{S}^{-1}$) and low light extinction coefficient (0.077) during the incubation. However, the low uptake rates of nitrate at Station E7 could be attributed to lack of vertical stratification in the water column. The mixed layer of Station E7 was 60 m (Figure 6), and deep mixing reduces average light intensity available for phytoplankton, which then become light-limited instead of nutrient-limited. Stratification is considered important to stimulate the onset of spring phytoplankton growth in many coastal waters such as Chesapeake Bay and Delaware Bay (Pennock & Sharp, 1990; Glibert *et al.*, 1995). Phosphate limitation was also unlikely because the surface phosphate concentration of $0.21 \mu\text{M}$ was relatively moderate. The influence of river discharge on Station E7 was minimal because its surface salinity was 34.45.

Contribution of other new N to the ECS new production

The new production and *f*-ratio in our study would be even higher if N fixation from *Trichodesmium* sp. and *Richelia intracellularis*, a symbiont within diatoms *Rhizosolenia* spp. and *Hemiaulus* spp., were also included in the measurement of new production. *Trichodesmium* sp. is abundant in the Kuroshio Current and the water where the Kuroshio Current encounters the coastal water (Marumo & Asaoka,

TABLE 7. Nitrate and phosphate concentrations as well as nitrate/phosphate (N/P) ratios measured at various sampling stations in the upwelling region (Cruises 416, 124 and 431) and the continental shelf region off the Changjiang estuary (Cruise 449)

Station	Depth (m)	NO ₃ (μM)	PO ₄ (μM)	N/P	Station	Depth (m)	NO ₃ (μM)	PO ₄ (μM)	N/P
Cruise 416					Cruise 449				
5	0	1.09	0.58	1.9	E1	2	0.40	0.05	8.0
	50	0.51	0.54	0.9		20	4.10	0.21	19.5
	75	1.00	0.52	1.9		40	5.34	0.24	22.3
11	0	0.49	0.43	1.1	E2	50	6.29	0.31	20.3
	50	2.90	0.72	4.0		2	6.40	0.03	213.3
	100	6.20	0.57	10.9		10	6.41	0.06	106.8
Cruise 124						15	7.50	0.20	37.5
8	0	0.00	0.48	0.0		25	6.34	0.25	25.4
	50	1.68	0.67	2.5		40	6.94	0.27	25.7
	100	10.23	1.16	8.8	E3	2	0.20	0.24	0.8
8a	0	0.11	0.50	0.2		10	1.17	0.10	11.7
	50	2.73	0.70	3.9		19	1.61	0.10	16.1
	100	9.81	1.11	8.8	40	1.77	0.17	10.4	
9	0	0.15	0.54	0.3	E4	2	0.20	<0.03	>6.7
	50	4.66	0.74	6.3		10	0.16	<0.03	>5.3
	100	6.92	0.95	7.3		20	0.50	<0.03	>16.7
10	0	0.20	0.59	0.3		24	1.63	0.05	32.6
	50	6.60	0.80	8.3		60	3.82	0.24	15.9
	100	9.63	1.03	9.4	E5	2	0.20	0.11	1.8
10a	0	0.05	0.56	0.1		9	0.55	0.14	3.9
	50	5.48	0.89	6.2		20	1.39	0.19	7.3
	100	10.56	1.20	8.8	40	3.19	0.21	15.2	
Cruise 431						75	8.97	0.67	13.4
9	0	0.00	0.08	0.0	E6	2	0.20	0.07	2.9
	40	2.89	0.34	8.5		20	0.12	0.10	1.2
	68	8.52	0.45	18.9		40	2.04	0.22	9.3
10	0	0.16	0.05	3.2		60	9.23	0.62	14.9
	45	4.78	0.43	11.1	E7	2	2.30	0.21	11.0
	100	8.71	0.72	12.1		10	1.83	0.23	8.0
11	0	1.74	0.14	12.4		30	1.97	0.23	8.6
	50	4.48	0.46	9.7	50	2.03	0.22	9.2	
	84	10.40	0.89	11.7	69	4.32	0.28	15.4	

1974). *Trichodesmium* is capable of very high rates of N fixation ($14.0 \text{ ngN } \mu\text{g algal N}^{-1} \text{ h}^{-1}$; Saino & Hattori, 1978). Moreover its density could reach 10^2 – 10^3 filaments per liter in summer (Marumo & Nagasawa, 1976). However, the effects of *Trichodesmium* spp. and *Richelia* containing diatoms were not studied intensively enough in our research to enable the estimation of this portion of new production. The summertime N fixation by *T. thiebautii* was estimated to be $8 \times 10^{10} \text{ gN}$ in the south-eastern East China Sea and accounted for approximately 6% of the N requirements for primary productivity (Saino & Hattori, 1980). In addition, a relatively high concentration of ammonium ($14.6 \text{ } \mu\text{M}$) was also reported in the Changjiang water (Zhang, 1996). This corresponds to about half of the average concentration of nitrate in the run-off (Zhang, 1996). Urea and other DON

should also be accounted for, but the available data are scarce. The contribution to primary production from these N sources was a part of the new production, at least in those areas influenced by the river runoff, such as Stations E1 and E2. Therefore the real f-ratio would be higher than that obtained in our measurements, which were based solely on nitrate uptake. By simple calculation from the quantity of nitrate flux, Chen (1996) estimated the contribution from the Kuroshio upwelling to be many times greater than the inputs from the Changjiang and the Yellow River combined. With our findings that nitrate contributed more to new production in the upwelling waters than in the riverine waters, the importance of the input from the Kuroshio compared with the Changjiang river is further emphasized. However, the contribution of ammonium and DON in river water

may be significant and hence the river contribution could be larger. Additional studies on a larger scale dealing with seasonal variations and the spatial extent of both the river plume and upwelling are warranted to understand the relative importance of the two N sources in the dynamics of new production in the East China Sea.

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