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Potential Impacts of N_2-fixing *Trichodesmium* on Heterotrophic Bacterioplankton Turnover Rates and Organic Carbon Transfer Efficiency in the Subtropical Oligotrophic Ocean System

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ABSTRACT

Bacterial production (BP), primary production (PP) and N_2-fixing cyanobacteria, *Trichodesmium* spp. abundance (i.e., [Tricho#]) were measured in the N. Pacific west-boundary Kuroshio Current in summer and autumn, 2001. The warm (28 - 29°C) upper water column (0 - 30 m) in summer was low in nitrate (NO_3; 0.08 ± 0.08 μM) with *Trichodesmium* spp. (192 - 2,115 trichomes L^{-1}) observed at all sampling stations. Averaged NO_3 in the upper 30 m were higher (0.39 ± 0.27 μM) in autumn but with no *Trichodesmium* observed except 1 station with an abundance of 962 trichomes L^{-1} in surface waters. PP (21 ± 7 μg C $L^{-1}d^{-1}$) and phytoplankton turnover rate (Pμ; 0.48 ± 0.19 d^{-1}) in summer were at least 1.5-fold higher than those recorded in autumn. BP (summer, 2.5 ± 0.6 μg C $L^{-1}d^{-1}$; autumn, 2.4 ± 0.3 μg C $L^{-1}d^{-1}$) showed no seasonal difference, but bacterial turnover rate (Bμ; 0.11 ± 0.03 d^{-1}) was 57% higher in summer. The negative trend of [Tricho#] vs. NO_3 and higher transmittance in summer indicate that NO_3 depletion and better light availability might trigger the development of N_2-fixing cyanobacteria. Bμ changed positively with [Tricho#] suggesting that bacterial growth might be enhanced by the supply of "new" inorganic (i.e., NH_4) and/or dissolved organic nitrogen from N_2-fixing cyanobacterium. From the negative relationship of BP : PP ratio (7 - 21%) vs. [Tricho#], we deduce that the occurrence of high *Trichodesmium* abundance might potentially reduce the magnitude of NH_4 competition between algae and bacteria. In the open ocean, organic carbon transfer efficiency, either to higher trophic levels or to system exportation, can be

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greatly enhanced at low BP : PP ratio driven by the proliferation of N_2-fixing cyanobacterium.

(Key words: Ammonium, Bacterial production, Iron, Inorganic nutrient, Kuroshio, Primary production.)

1. INTRODUCTION

In most parts of the open ocean, phytoplankton growth and primary production are believed to be nitrogen limited (Hecky and Kilham 1988). More and more recent studies have highlighted the importance of *Trichodesmium* in fueling primary productivity in oligotrophic systems due to their unique N_2-fixing capacity (Capone et al. 1997; Karl et al. 1997). Heterotrophic bacterioplankton (bacteria) are the major organisms responsible for the decomposition of dissolved organic matter (i.e., DOM). Many researches have documented that bacteria in fact, will take up ammonium (NH_4^+) when the C : N ratio of the DOM source is higher than that of bacteria (Goldman and Dennett 1991 and citations therein). Fuhrman (1992) and Kirchman et al. (1994) showed that in marine systems, bacteria were responsible for 30 - 50% of the total uptake of ambient NH_4^+. Therefore, the supply of NH_4^+, either from N_2-fixation or regeneration processes, might control the growth of bacteria and phytoplankton concomitantly in the oligotrophic ocean (Shiah et al. 2001 and citations therein).

From the carbon cycling point of view, primary production (PP) and bacterial production (BP) could be viewed as the major CO_2 sink and source processes respectively. The changes in the BP : PP ratio might affect the efficiency of the biological pump and/or planktonic trophodynamics processes. Conan et al. (1999) suggested that a high BP : PP ratio might lead to a consequence that there may be less material available for higher trophic levels and/or for export to the deep ocean. Therefore, study on the variation and controlling mechanisms of BP : PP ratio is essential for a better understanding of aquatic microbial ecology from the perspective of carbon cycling.

In this paper we present results derived from two cruise surveys conducted in the oligotrophic Kuroshio Current in summer and autumn, 2001. Our results demonstrated that in the upper water column, phytoplankton and bacterial rate parameters (production and turnover rates) doubled in summer when *Trichodesmium* were abundant. Bacteria : algae production (and their turnover rate) ratios decreased significantly with the abundance of *Trichodesmium.* The proliferation of *Trichodesmium* in summer could be ascribed to higher magnitude of nitrate depletion and better light availability.

2. MATERIALS AND METHODS

2.1 Study Area and Sampling

The study area, with bottom depths > 100 m, is located ~5 km off the east coast of Taiwan where the northward Kuroshio Current flows. Stations A-E (Fig. 1) were visited twice in early

Sep. (summer) and late Oct. (autumn), 2001. For the later cruise, one extra station (St. K) was added. Water samples at depths of 2, 10, 30 m and 5 m above the bottom were collected by a SeaBird CTD-General Oceanic Rosette assembly with 10 L Go-Flo bottles. The depth profiles of light intensity (PAR sensor, QSP200L; Biospherical Inc.), temperature, salinity, transmittance and chlorophyll fluorescence were recorded simultaneously. All measurements described below were conducted with water samples taken from the same cast.

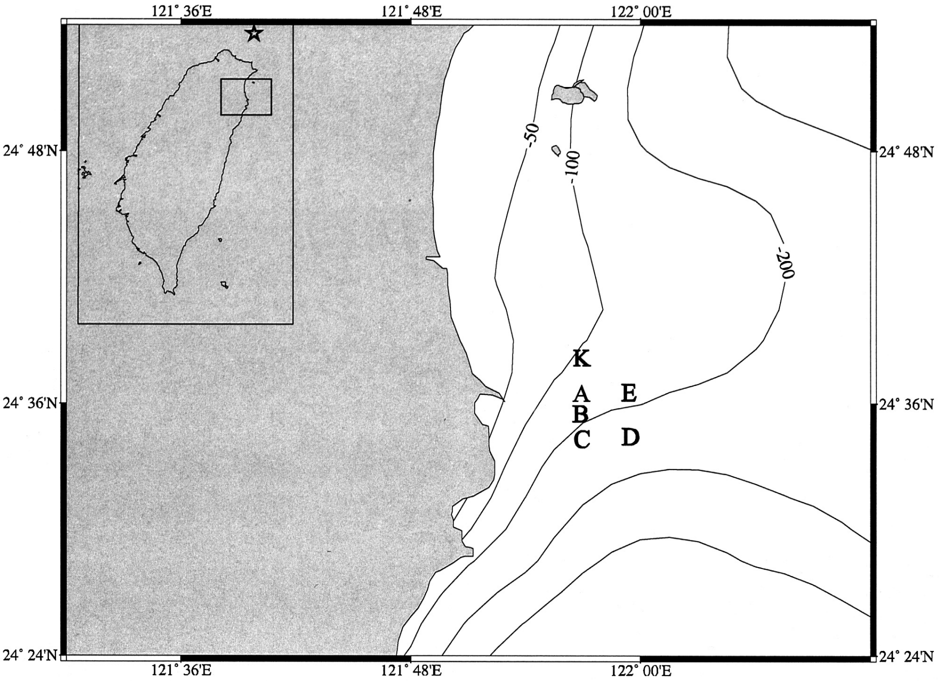

Fig. 1. Map of study area showing sampling stations. Lines with numerical values indicate bottom depth in meter. Star symbol indicates atmospheric particle collecting station.

2.1.1 Eolian Iron Flux

Atmospheric deposited particles were collected monthly at a weather station on the PengchiaYu Island (25.5°N; 122°E; Fig. 1) with Andersen acid precipitation samplers (model APS) from Aug. to Dec., 2001. Collected samples were filtered through 0.4-μm polycarbonate filters, and then subdivided into soluble and insoluble fractions. The fluxes of mineral dust were calculated from the insoluble fraction. Eolian iron fluxes were estimated from the mineral dust fluxes by multiplying a constant of 0.03 (Nishikawa et al. 2000).

2.1.2 Nitrate, Chlorophyll-a and Particulate Organic Carbon Concentrations

Nitrate (NO_3) concentrations were measured following the methods of Parsons et al. (1984) and Gong et al. (1995) with a detection limit of 0.10 μM. For chlorophyll-a (Chl-a), 2.5 L of seawater were filtered through GF/F filters which were then immediately stored at -20°C. Back at the laboratory, the filters were ground in 10ml of 90% acetone followed by extraction in a 4°C shaking incubator for 2 hrs. After centrifugation (1000 rpm, 5 mins.), Chl-a was measured by a Turner fluorometer (model 10-AU-005). The Chl-a profile was derived from the correlation ($R^2 = 0.89$, $n = 36$, $P < 0.01$) between measured values and the fluorescence readings from the CTD. Algal biomass in carbon units was derived by using a ratio of 105 gC $(\mathrm{gChl\text{-}a})^{-1}$ (Chang et al. 2002). For particulate organic carbon (POC), water samples (0.5 - 1.0 L) were filtered through a 200-μm mesh to remove zooplankton. After filtration (25-mm GF/F filters), the filters were wrapped in aluminum foil and stored at -4°C. Both the filters and aluminum foil had been pre-combusted at 550°C for 1 hr before filtration. POC concentrations were measured by a CHN analyzer (Fisons; NA1500) after samples had been dried and acid-fumed.

2.1.3 Primary Production and *Trichodesmium* spp. Microscopic Counting

The ^{14}C assimilation rate (Parsons et al. 1984) was measured by pouring surface water into duplicate 250 ml clean PC bottles. After inoculation with $H^{14}CO_3^-$ (final conc., 10 μCi ml^{-1}), samples were incubated for 3 hrs in a self-designed tank with an artificial light source. Temperature was maintained with running seawater. Incubation bottles were covered with 9 neutral density filters (LEE filters) that reduced different % of the incident light. Following retrieval, the samples were filtered through 25 mm GF/F filters. Next, 0.5 ml of 0.5 N HC1 was added to remove residual radioactivity of each filter, which then was counted in a liquid scintillation counter (Packard 1600). The Chl-a normalized productions vs. light intensity (i.e., P^B-E) curves were fitted with the Webb et al. (1974) model with R^2 (coefficient of determination) values > 0.97 (data not shown). The 0 - 30 m integrated daily PP for each station was derived with its PAR profile, Chl-a profile, the P^B-E curve and the daily light intensity collected on board. The integrated (5 A.M. - 5 P.M.) daylight intensities for summer and autumn were similar, with values ~ 50 Eins m^{-2}. Seawater samples (2.0 L) for *Trichodesmium* cell counts were collected immediately from the GO-Flo bottles and then fixed with 50 ml neutralized formalin. Identification and cell counts were made under a Nikon-TMD 300 inverted microscope at 200x or 400x.

2.1.4 Bacterial Biomass and Production

Bacterial abundance was determined by using the AODC method (Hobbie et al. 1977) and epi-fluorescence microscopy (Zeiss, Axioplan). Biomass was calculated using a carbon conversion factor of 2×10^{-14} gC cell^{-1} (Ducklow and Carlson 1992). BP was estimated by the method of ^{3}H-thymidine incorporation (Fuhrman and Azam 1982) with a conversion factor of 1.18×10^{18} cells (mol thymidine)$^{-1}$ (Cho and Azam 1988). See Shiah et al. (2001) for details.

2.2 Data Analyses

Each measurement was integrated down to 30 m with the trapezoid method. The depth-weighted average was derived by dividing the integrated value with depth. Statistical analysis was performed with Macintosh software StaView™ II (Abacus Concepts, Inc.). The major reason for using the depth-weighted averages is that we were only interested in the overall responses of auto- and heterotrophic processes to the spatial and temporal variations of the N_2-fixers within the upper water column.

3. RESULTS

Physical and chemical hydrography

Surface seawater temperatures (SST) were high (> 29°C) during summer, with obvious thermoclines located at ~50 m (Fig. 2a). The SST of autumn was 2 - 4°C lower than those of summer. A higher magnitude of stratification occurred in summer as judged from the temperature profiles. At St. A, for example, temperature differences between surface and the 60 m depth in summer and autumn were 8.5 and 6.0°C, respectively. Transmittance (i.e., water column clarity index) in summer (75 - 77%) was 4% higher than that of autumn (Fig. 2b). Nitrate (NO_3) concentrations in the upper 30 m were < detection limit (0.10 μM) or very low (< 0.5 μM; Table 1) in summer. For most (4 out of 6) stations, NO_3 in the upper 20 m in autumn were non-detectable, but NO_3 at the 30-m depth were higher than those of summer (Table 1). Phosphate and silicate showed the same patterns as that of NO_3 and were not depleted in the upper 20 m in autumn (data not shown). The upper 30-m depth-weighted average of NO_3 in autumn (0.39 ± 0.27 μM) was ~3-fold higher than those of summer (0.12 ± 0.07 μM; $p < 0.01$). Summer Chl-a concentrations in the surface waters ranged 0.21 - 0.43 μgChl L^{-1}(Table 1) and then increased with depth with subsurface chlorophyll maxima (SCM; 0.8 - 1.1 μgChl L^{-1}) located at depths of 24 - 47 m (Fig. 2c). The Chl-a patterns in autumn were very similar to those of summer except that its surface Chl-a (0.41 - 0.67 μgChl L^{-1}; Table 1) and SCM concentrations (0.8 - 1.23 μgChl L^{-1}) were higher and the SCM depths (10 - 25 m; Fig. 2c) became shallower. The upper 30 m depth-weighted Chl recorded in autumn (0.62 ± 0.15 μgChl L^{-1}) was 44% higher than those in summer (0.43 ± 0.14 μgChl L^{-1}; $p < 0.05$). POC concentrations generally were high in the surface and then decreased down to depth of 30 m (Table 1). POC in summer and autumn ranged 5.2 - 12.6 and 4.0 - 13.2 μM, respectively. The depth-weighted values of POC in summer (7.5 ± 1.6 μM) were not different from those of autumn (5.9 ± 1.2 μM).

Trichodesmium abundance, eolian iron flux

In all samples, *Trichodesmium* spp. appeared as individual trichomes. Summer *Trichodesmium* spp. abundance (i.e., [Tricho#]) ranged from 192 to 2115 trichomes L^{-1}, with higher cell counts in the upper 10 m and then decreased with depth (Table 1). No *Trichodesmium* spp. was observed in autumn except at st. D, with an abundance of 962 trichomes L^{-1} in the surface waters. Note that *Trichodesmium* spp. in summer was distributed deeper, to depths of

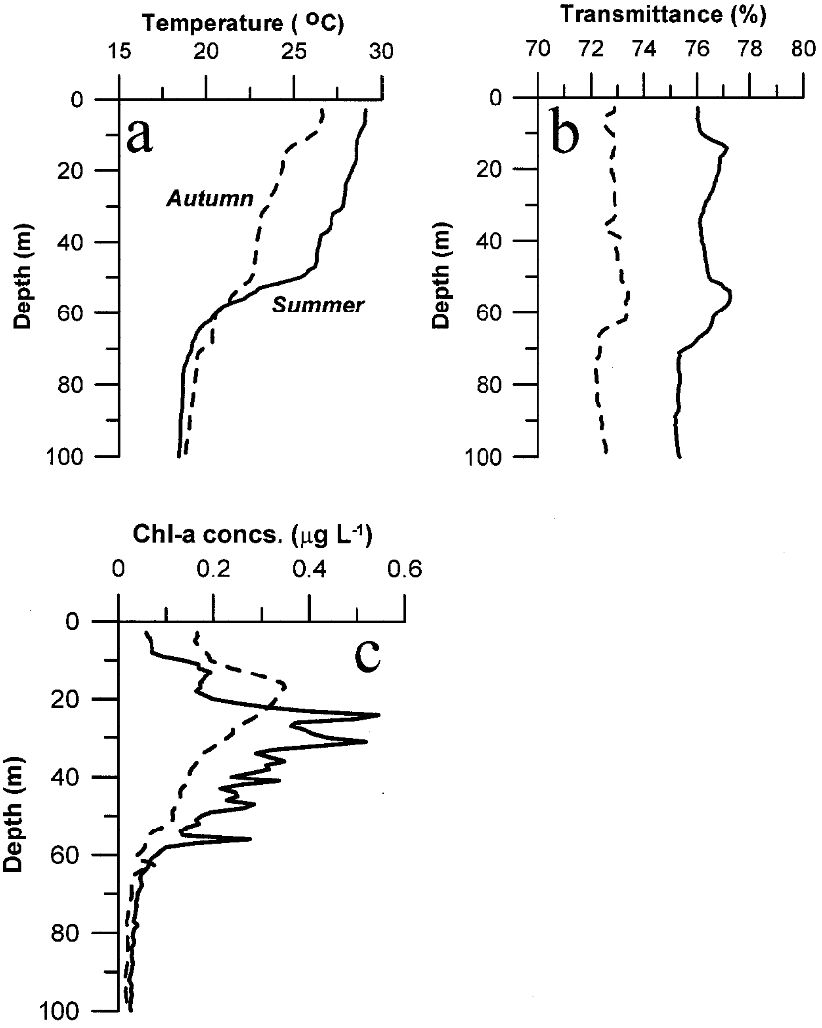

Fig. 2. Examples of (a) temperature, (b) transmittance and (c) chlorophyll profiles recorded at station A in summer (solid lines) and autumn (dashed lines), 2001. Chlorophyll profiles were derived from the correlation between measured values and the fluorescence readings from the CTD.

30 m. Values of the depth-weighted NO_3 was negatively correlated with depth-weighted [Tricho#] (Fig. 3a). Eolian iron fluxes (Fig. 4) were low in Aug. (2.5 μmol $m^{-2}d^{-1}$), and increased 7-fold in Sep., with a value of 17.6 μmol $m^{-2}d^{-1}$, and then decreased from Oct. to Dec. with values ranging 4.0 - 8.0 μmol $m^{-2}d^{-1}$. The Sep. anomaly was believed to result from the dust storm from the Mongolian desert of the Mainland China (Lin, unpublished data).

Table 1. List of variables[@] measured at different depths of the Kuroshio Current in summer and autumn, 2001. -, no data; nd, < detection limit of 0.10 μM.

		Summer							**Autumn**						
St	**Z**	**NO_3**	**POC**	**Chl-a**	**PP**	**BP**	**BB**	**Tricho#**	**NO_3**	**POC**	**Chl-a**	**PP**	**BP**	**BB**	**Tricho#**
	m	μM	μM	$\mu g\ L^{-1}$	$\mu g\ L^{-1}\ d^{-1}$	$\mu g\ L^{-1}\ d^{-1}$	$\mu g\ L^{-1}$	Trichoms L^{-1}	μM	μM	$\mu g\ L^{-1}$	$\mu g\ L^{-1}\ d^{-1}$	$\mu g\ L^{-1}\ d^{-1}$	$\mu g\ L^{-1}$	Trichoms L^{-1}
	2	nd	12.6	0.28	19.6	2.7	32	192	nd	13.2	0.67	14.4	3.0	43	0
A	10	nd	9.9	0.58		3.8	34	192	0.37	9.2	1.13		3.5	46	0
	30	0.52	9.6	0.92		3.2	33	0	1.73	4.9	0.53		1.8	38	0
	135	7.01	-	-		-	-	0	7.53	-	-		1.4	34	0
	2	nd	11.2	0.24	30.4	1.8	10	577	nd	7.8	0.61	12.8	2.2	29	0
B	10	nd	9.7	0.42		2.2	11	2115	nd	6.8	0.77		2.4	32	0
	30	nd	6.9	0.42		2.7	21	192	2.05	4.0	0.40		2.3	31	0
	175	7.89	-	-		-	-	0	8.56	-	-		1.7	30	0
	2	nd	10.3	0.43	21.0	2.6	27	192	nd	8.3	0.41	11.1	2.7	33	0
C	10	nd	8.8	0.48		3.1	30	384	nd	5.2	0.48		2.5	32	0
	30	0.43	7.8	0.75		3.5	31	0	1.00	5.0	0.64		2.3	30	0
	130	7.78	-	-		-	-	0	8.38	-	-		1.8	28	0
	2	nd	9.3	0.21	11.1	2.7	17	1154	nd	5.6	0.32	17.0	2.5	18	962
D	10	nd	6.4	0.28		2.1	13	0	nd	5.2	0.53		2.2	16	0
	30	0.51	6.5	0.34		2.4	15	0	0.20	4.3	0.45		1.7	12	0
	140	8.56	-	-		-	-	0	11.46	-	-		1.5	12	0
	2	nd	5.9	0.19	21.1	2.3	18	1346	nd	5.7	0.49	11.4	1.9	33	0
E	10	nd	5.2	0.29		1.8	14	577	nd	5.7	0.49		2.0	343	0
	30	0.32	6.5	0.32		2.0	14	384	0.70	6.0	1.04		2.5	37	0
	135	7.16	-	-		-	-	0	9.43	-	-		1.6	32	0
	2	-	-	-	-	-	-	-	nd	6.9	0.47	13.8	3.1	45	0
K	10	-	-	-		-	-	-	0.15	8.1	0.82		3.2	47	0
	30	-	-	-		-	-	-	0.54	6.6	1.03		3.1	46	0
	120	-	-	-		-	-	-	7.04	-	-		1.6	27	0

@, Z, depth; NO_3, nitrate concs.; Chl-a, chlorophyll-a concs.; PP, 0 - 30 m depth-weighted daily primary production (see text for detail); BP, bacterial production; BB, bacterial biomass and [Tricho#], abundance of *Trichodesmium* spp.

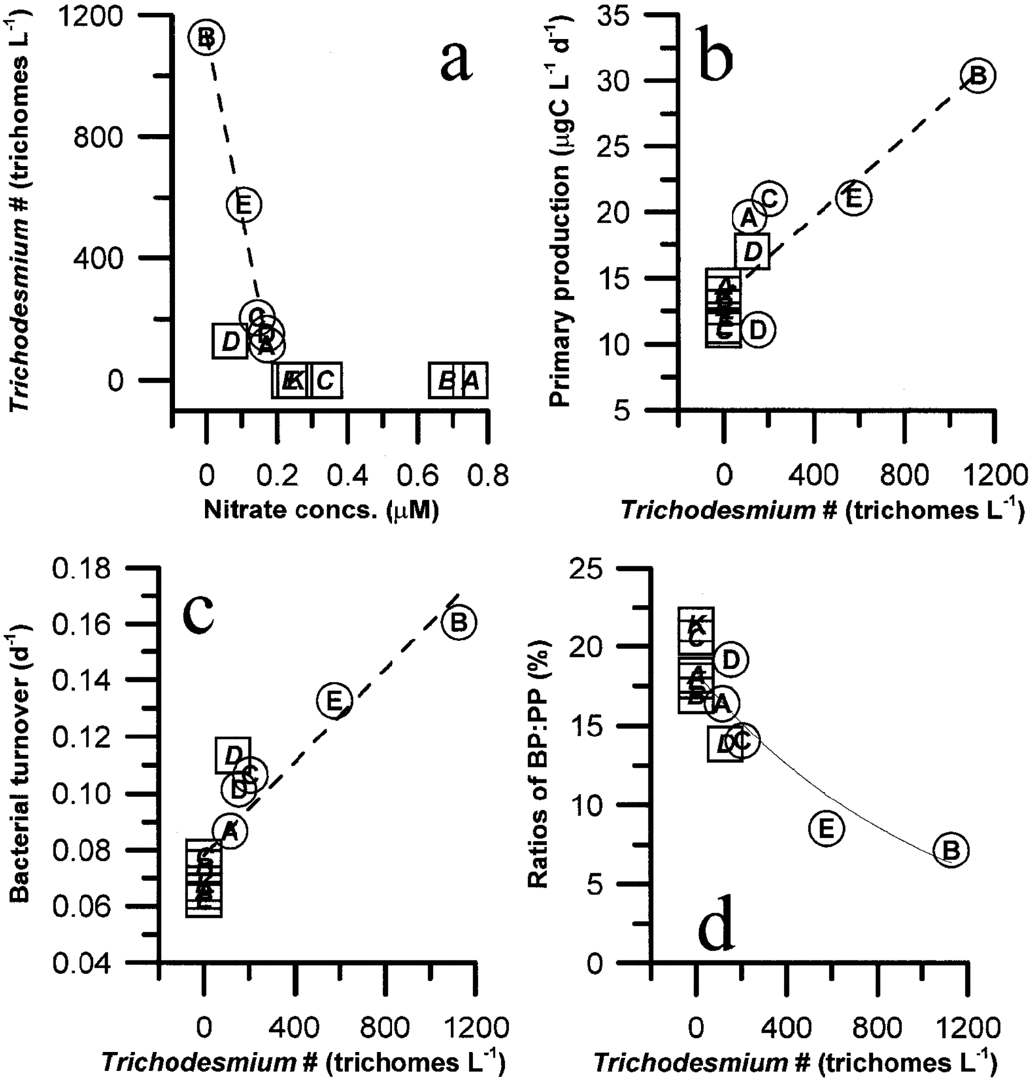

Fig. 3. Scatter plots of *Trichodesmium* spp. abundance ([Tricho#]) vs. (a) nitrate concentrations, (b) primary production, (c) bacterial turnover rates and (d) ratios of bacteria : primary production recorded in summer (circles) and autumn (squares). Alphabet within each symbol indicates sampling station. Dashed line in (a) was the linear regression ([Tricho#] = 1142 - 5960 ± 574 × NO_3, $R^2 = 0.98$, n = 5) using summer data only. See Table 2 for the regression relationships for (b), (c) and (d).

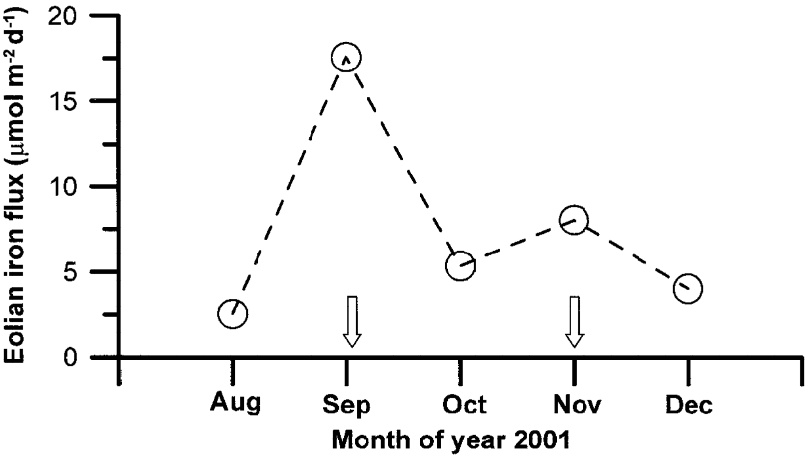

Fig. 4. Monthly eolian iron fluxes from Aug. to Dec., 2001. Arrows indicates times when cruise survey were conducted.

Primary production and bacterial production

The 0 - 30 m depth weighted daily primary production (Fig. 3b) varied ~3-fold (11 - 30 μgC $L^{-1}d^{-1}$) in summer. These values of autumn were more or less constant with the highest and lowest values at sts. D (17 μgC $L^{-1}d^{-1}$) and C (11 μgC $L^{-1}d^{-1}$), respectively. Phytoplankton depth-weighted turnover rates (Pμ) in summer (0.30 - 0.79 d^{-1}) were at least 2-fold higher than those of autumn (0.17 - 0.22 d^{-1}) except st. D, which had a Pμ of 0.37 d^{-1}. Note that depth-weighted Chl-a showed the opposite trend. Both depth-weighted PP (Fig. 3b) and Pμ (Table 2) were positively correlated with depth-weighted [Tricho#].

Depth distribution of bacterial production (BP; summer 1.8 - 3.8; autumn 1.7 - 3.5 μgC $L^{-1}d^{-1}$) and biomass (BB; summer 10 - 34; autumn 12 - 47 μgC $L^{-1}d^{-1}$) in the upper 30 m varied 2 - 4 fold (Table 1). Depth weighted BP was positively correlated with depth-weighted POC ($r = +0.70$; $p < 0.01$; $n = 11$) but showed no correlation with depth-weighted [Tricho#]. Depth weighted BB showed no relationship with depth-weighted [Tricho#] (Table 2). Autumn depth-weighted bacterial turnover rates (Bμ) were < 0.08 d^{-1} except st. D, which had a value of 0.11 d^{-1} (Fig. 3c). Summer Bμ were higher ranging 0.09 - 0.16 d^{-1}. Bμ changed positively with depth-weighted [Tricho#] (Fig. 3c and Table 2), and was also positively correlated with depth-weighted PP and Pμ with correlation coefficients (i.e., r) of +0.84 and +0.98 ($n = 11$), respectively. Since BP is a product of Bμ and BB (i.e., BP = Bμ × BB), the insignificant correlation between depth-weighted BP and depth-weighted [Tricho#] was due to the lack of correlation between depth-weighted BB and depth-weighted [Tricho#]. The ratios of BP : PP ranged from 14 to 21% in samples with low or no *Trichodesmium* spp. and then decreased exponentially down to ~7% as depth-weighted [Tricho#] increased (Fig. 3d). Bμ : Pμ ratios (20 - 38%) also showed a negative trend with depth-weighted [Tricho#] (Table 2).

Table 2. Linear regression analysis of depth-weighted average of *Trichodesmium* spp. abundance vs. depth-weighted averages of bacterial and phytoplankton measurements (dependent variables). ns, not significant at p = 0.01 level. R^2, coefficient of determination. All sampling size =11.

Items[@]	Unit	Intercept	Slope[#]	R^2
PP	$\mu g\ C\ L^{-1}\ d^{-1}$	14	+0.015 (±0.003)	0.78
Pμ	d^{-1}	0.23	+0.53 (±0.05) $\times 10^{-3}$	0.93
Bμ	d^{-1}	0.08	+0.08 (±0.01) $\times 10^{-3}$	0.84
L_n (BP:PP)	-	2.9	-0.09 (±0.01) $\times 10^{-3}$	0.86
L_n (Bμ:Pμ)	-	3.5	-0.05 (±0.01) $\times 10^{-3}$	0.74
PB	$\mu g\ C\ L^{-1}$	ns	ns	ns
BP	$\mu g\ C\ L^{-1}\ d^{-1}$	ns	ns	ns
BB	$\mu g\ C\ L^{-1}$	ns	ns	ns

@, PB, phytoplankton biomass in C unit, assuming a C : Chl ratio of 105 (see text); P*μ* and B*μ* represents phytoplankton and bacterial turnover rates, respectively. Note that the ratios of BP : PP and B*μ* : P*μ* were natural log transformed.

#, numbers in the parentheses indicate standard deviations.

4. DISCUSSIONS

Our summer and autumn results showed great contrast. The summer warm water column was characterized by low NO_3 and BP : PP (and B*μ* : P*μ*) ratios but with higher values of depth-weighted [Tricho#], PP, P*μ* and B*μ*. While in autumn, with the exception of st. D, all these variables or parameters showed the opposite trend, with rate and ratio readings ~50% lower than those of summer. In comparison, our depth-weighted PP (11 - 30 $\mu gC\ L^{-1}d^{-1}$), BP (1.8 - 3.2 $\mu gC\ L^{-1}d^{-1}$) and B*μ* (0.06 - 0.16 d^{-1}) were within ranges that have been reported in the Kuroshio Current (i.e., KC). The annual range of PP in the KC varied from < 20 to 70 $\mu gC\ L^{-1}d^{-1}$ (Gong et al. 2000; Chen-Lee 2000). Shiah et al. (2000a, 2000b) showed that the upper ends of the ranges of BP and B*μ* in the KC were 2.5 $\mu gC\ L^{-1}d^{-1}$ and 0.12 d^{-1}, respectively.

Several environmental factors including temperature, water column stability (i.e., turbulence), grazing, light and nutrient (NO_3 and iron) availability, have been considered important in regulating *Trichodesmium* abundance (and growth rate) in the field (Orcutt et al., 2001 and citations therein). The minimal temperature for *Trichodesmium* to survive is ~20°C (Marumo and Nagasawa 1976, Carpenter 1983). In the KC north of 25°N, Chang et al. (2000) observed *Trichodesmium* at 24°C, which is lower than the autumn temperatures (Fig. 2a) of this study. It is suggested that temperature variation might not be the crucial factor in determining the absence or occurrence of *Trichodesmium* during the study period. On the other hand, we did observe higher values of depth-weighted PP and Bμ (Figs. 3b, c) in summer. Intuitively, one may ascribe these to warmer temperature. Note that in an oligotrophic environment (e.g., the KC) where planktons' growth is limited by bottom-up control processes, increasing temperature alone can hardly stimulate their growth or production since organisms feed on materials (organic or inorganic) but not temperature. However, we could not deny the possibility that during summer, when substrate supplies were more copious due to the proliferation of *Trichodesmium* (see more details below), higher temperatures might help lead to higher PP and Bμ.

Only *Trichodesmium* in colonial form are fragile to turbulence caused by strong mixing but *Trichodesmium* spp collected in this study were all free trichomes. Zooplankton in particular, the harpacoid copepods may exert strong impact on *Trichodesmium* abundance (O'Neil and Roman 1994). On both cruises, no harpacoid copepods were observed (data not shown). *Trichodesmium* growth is sensitive to light intensity. Higher transmittance (light availability) in summer (Fig. 2b) might offer a better physical condition for the development of *Trichodesmium*. Table 1 also showed that *Trichodesmium* spp. was observed only in the surface sample during autumn while those in summer distributed down to a depth of 30 m. Finally, a higher magnitude of NO_3 depletion during summer (Fig. 3a) might trigger the progress of *Trichodesmium* since they can synthesize nitrogenous nutrient for growth via N_2-fixation processes.

Iron limitation on *Trichodesmium* has been reported by many studies (Orcutt et al. 2001 and citations therein), but seems to be unlikely for this study since the sampling site is located in an area with a high annual iron deposition rate (Duce and Tindale 1991). The coupling of high iron anomaly and high [Tricho#] in Sep. might just be a coincidence. As one may note that the lowest eolian iron flux (2.5 μmol $m^{-2}d^{-1}$) recorded in this study is at least 3 times higher than that of the Sargasso Sea (0.2 - 0.8 μmol $m^{-2}d^{-1}$; Duce and Tindale 1991) where *Trichodesmium* have been frequently observed. Many studies have demonstrated that algal (i. e., diatom, flagellate) and bacterial growth also can be limited by iron availability (DiTullio et al. 1993, Pakulski et al. 1996 and citations therein). As argued above, this will not be the case due to high eolian iron inputs.

Unlike *Trichodesmium* that have N_2-fixation ability, the growth of eukaryotic algae and bacteria could be limited by nitrogenous nutrients when iron is surplus (Fig. 4) and NO_3 is depleted (Fig. 3a). The "new" nitrogenous inorganic nutrient (i.e., NH_4^+) and/or organic substrate from *Trichodesmium* spp. might intuitively impinge on algal and bacterial rate parameters (Table 2). It is well known that when facing different forms of nitrogenous nutrients, phytoplankton have a preference for taking up NH_4^+ which is in the most reduced status when compared with NO_3^- and NO_2^-. To incorporate NH_4^+ will cost phytoplankton the least energy, and thus make them grow most efficiently. As one may note that Pμ can be viewed as an index for photosynthesis efficiency. The positive relationship of Pμ vs. depth-weighted [Tricho#] (Table 2) implies that phytoplankton growth and thus, the release of photosynthetic exudates could be greatly enhanced by N_2-fixing cyanobacteria (see also below).

Depth-weighted BP was positively correlated with depth-weighted POC (r = +0.70), while Bμ was positively correlated with depth-weighted PP (r = +0.84), Pμ (r = +0.98) and [Tricho#]

(Fig. 3c). These seem to indicate that in the KC, the standing stock of organic substrate (i.e., POC) settles the upper-limit (i.e., carrying capacity) of bacterial production, while supply of organic substrate (and/or inorganic nutrient) determines the variation of bacterial turnover rates. In the open ocean, DOM released from algal exudation processes has been considered an important source for bacterial growth (Ducklow and Carlson 1992, Fuhrman 1992 and citations therein). However, algal exudates are primarily composed of carbohydrate with low mineral nutrient content (Myklestad 1974), and that bacteria growth on these C-enriched exudates requires additional uptake of mineral nutrients (Bratbak and Thingstad 1985; Obernosterer & Herndl 1995). Therefore, the "*Trichodesmium* → phytoplankton exudates → Bμ" scenario seems to be less applicable in explaining the positive relationship between Bμ and PP (r = +0.84) in the KC where bacterial growth has been proven to be N-limited (Shiah 1999, Shiah et al. 2001, more discussion below). Another better nitrogenous source for bacteria may come from the release of dissolved organic nitrogen (i.e., DON) from *Trichodesmium* (Glibert and Bronk 1994), although its importance has not been clearly identified.

On average, recorded PP was about 6-fold of that of BP. This implies that proportionally, the contribution of N_2-fixation to algae might be much less than that to bacteria. A simple calculation may clarify this. To estimate N_2-fixation rate, a constant of 5.6 pmol N Tichome^{-1}d^{-1} was adopted (Chang et al. 2000). The C : N molar ratios of 6.6 (Redfield et al. 1963) and 4.0 (Lancelot and Billen 1985) were used respectively to transform PP and BP to an equivalents in N units. The maximal estimated N_2-fixation rate (12 nMNd^{-1}) constituted 5% and 23% of PP and BP, respectively. Assuming that NH_4^+ and DON release rates are equal to that of N_2-fixation and bacteria take both up, about half of bacterial N requirement could be satisfied by *Trichodesmium*. We proposed that bacteria might respond quicker and more directly than algae to the increase of N_2-fixing activity. This is not unreasonable since bacteria are more competitive for NH_4^+ uptake due to their much smaller size (Bratbak and Thingstad 1985). The increase of PP (and or Pμ) at high [Tricho#] might be due to what we called the "secondary or left-over effect" and that is discussed below.

As mentioned earlier, BP : PP ratio can be viewed as an index for the magnitude of organic carbon utilization by higher trophic levels or exportation out of the system (Conan et al. 1999). In a review paper, Ducklow (1998) claimed that the global average for the BP : PP ratio should not exceed 25%. The summer and autumn BP : PP ratios on the outer-shelf of the East China Sea (ECS) ranged from 10 to 30% with higher values (> 20%) in the oligotrophic KC, and a negative relationship of BP : PP ratio vs. PP was observed (Shiah et al. 2001). Such a pattern had been recorded previously in the cold Southern Ocean where *Trichodesmium* has never been reported (Lochte et al. 1997) with several possible explanations. These included extremely low exudation rate, low bacterial uptake or conversion of DOM, repression of bacterial metabolism by low temperatures or high grazing pressure.

Shiah et al. (2001) proposed that NH_4^+ availability is the most probable factor in regulating the spatial variations of BP, PP and BP : PP ratio on the ECS outer-shelf. They argued that as the system became more oligotrophic, both BP and PP decreased due to reducing "regenerated" NH_4^+ availability. This might lead to a higher BP : PP ratio in lower PP areas (i.e., the KC system) since bacteria are more competitive for NH_4^+ uptake. The negative relationship of BP : PP (and Bμ : Pμ) ratio vs. depth-weighted [Tricho#] suggests that the increase of

NH_4^+ (and/or DON) supply rate due to the proliferation of N_2-fixing cyanobacteria might potentially reduce the magnitude of NH_4^+ competition between algae and bacteria. More specifically, we suggested that most (if not all) of bacterial N-demand could be satisfied by the increasing "new" NH_4^+ (and/or DON) supply from *Trichodesmium.* And that this might in turn leave more "regenerated" NH_4^+ for algal uptake and result in elevated $P\mu$ and PP at high [Tricho#].

The relationship of BP : PP ratio vs. depth-weighted [Tricho#] shown above suggests that N_2-fixation might insert profound effects on carbon cycling in the open ocean by enhancing organic carbon transfer efficiency. An extra line of evidence comes from community respiration (CR) data (Wu and Shiah, in preparation). The PP/CR (or P/R) ratio is used commonly as an index to evaluate whether the system is in autotrophic or heterotrophic status. In the upper water column of the KC, CR ranged from 1.4 to 2.6 $\mu MO_2 d^{-1}$. The ratio of PP/CR was consistently low (0.7 - 0.8; assuming $O_2 : N = 138 : 16$) when *Trichodesmium* spp. was absent, and then rose up to 1.5 as [Tricho#] increased (Fig. 5). This indicates that as the abundance of N_2-

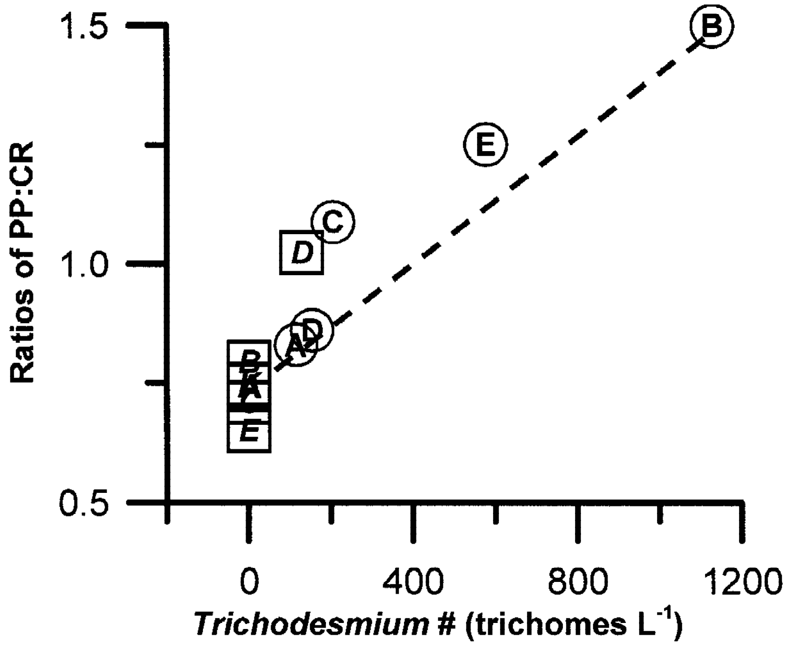

Fig. 5. Scatter plot of the ratio of primary production:community respiration rate vs. Trichodesmium spp. abundance ([Tricho#]) in summer (circles) and autumn (squares). Dashed line was the linear regression of all data, $PP/CR = 0.8 + 0.7\ (\pm 0.1) \times 10^{-3}$ [Tricho#], $R^2 = 0.87$, $n = 11$, $p < 0.01$. CR was measured by the change of O_2 concentrations via dark incubation, and see details in Lai (2004).

fixing cyanobacteria increased, the system switches more toward an autotrophic status. This supports the deduction based on the BP : PP ratio data.

5. CONCLUSIONS

This report is perhaps one of the few studies offering evidence to show that N_2-fixing cyanobacteria may act as an important agent in regulating the variations in algal and bacterial rate parameters, especially their rates ratios in a subtropical open ocean system. Extreme depletion of NO_3 and higher light availability in summer seem to be the major factors triggering the development of N_2-fixing cyanobacteria in the Kuroshio Current. The proliferation of *Trichodesmium* spp. may boost up bacterial growth rates by offering extra "new" inorganic and organic nitrogen, and potentially reduce tension over NH_4^+ competition between algae and bacteria. In terms of planktonic tropho-dynamics and/or biological pumping, the prevalence of N_2-fixers in the open ocean may increase organic carbon transfer efficiency by lowering the bacteria to primary production ratio.

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