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Effects of ChangJiang River summer discharge on bottom-up control of coastal bacterial growth

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ABSTRACT: The East China Sea (ECS) has one of the largest shelf ecosystems in the world, and among the major external forces that affect physical and biogeochemical processes over the ECS shelf is discharge from the ChangJiang (CJ) River. This is particularly true during summer when prevailing flooding leads to the annual maxima of CJ River discharge. To explore the effects of inter-annual variations in CJ River summer discharge on bacterial growth rate (BGR), 6 cruises were conducted over the entire width of the ECS shelf in July 1998, June 2001, June and August 2003, and June and July 2004. It was found that the spatial patterns of inorganic nutrients (e.g. nitrate: <0.15 to 28 µM), chlorophyll concentrations (chl *a*: <0.20 to 16 mg m^{-3}) and BGR (<0.03 to 1.05 d^{-1}) were all negatively correlated with salinity (22.4 to 34.9 psu) during each cruise, a clear sign that river discharge had a significant effect on chemical and biological structures over the ECS shelf. Variations in BGR in the mixing zone (salinity <33 psu) and oceanic zone (salinity >33 psu) were positively correlated with chl *a*. However, the intercepts and slopes of the BGR–chl *a* relationship in the mixing zone were significantly higher than those in the oceanic zone. Noteworthy too is that on monthly and/or inter-annual scales, BGR–chl *a* coupling (i.e. the slope) in both zones changed positively with river discharge, and this coupling of the oceanic zone seems to have been more sensitive to changes in discharge. This suggests that bacterial growth in the oligotrophic zone might be more substrate-limited than that in the mixing zone. Our study is one of the few to suggest that, in summer, monthly and/or inter-annual variations in CJ River discharge might significantly alter the supply rates of inorganic nutrients and dissolved organic matter, which in turn affects the relationship between auto- and hetero-trophic processes in the ecosystem of the ECS shelf.

KEY WORDS: Bacterioplankton · Chlorophyll · East China Sea · Monthly variations · Inter-annual variations · Three Gorges Dam

INTRODUCTION

It is widely recognized that the effect of large rivers on biogeochemical transformation processes in shelf systems are extremely important on both the regional and global scale (Dagg et al. 2004). High loadings of inorganic and organic materials from large rivers are major factors that yield high biological productivity in adjacent shelf ecosystems (Wawrik & Paul 2004 and citations therein). However, on account of high bacterial activity (Smith & Hollibaugh 1993, del Giorgio et al. 1997, Duarte & Agusti 1998), many near-shore ecosystems are heterotrophic throughout most of the year. In this regard, several studies have shown that variations in river discharge on seasonal to inter-annual scales have profound effects on physical, chemical and biogeochemical processes of the coastal ecosystems (Malone 1991, Smith & Demaster 1996, Humborg et al. 1997, Milliman 1997, Lee et al. 2004).

Bacterioplankton (bacteria) are small prokaryotes responsible for the decomposition of dissolved organic carbon, which constitutes >85% of the total

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organic carbon (Hedges 1992) in many aquatic ecosystems. It has been suggested that on seasonal time scales and across different aquatic ecosystems, primary production is the crucial factor controlling bacterial production and growth (Cole et al. 1988, Conan et al. 1999 and citations therein). In fact, a coupling or a causal relationship between bacterial rate parameters and algal biomass (and/or production) has long been considered as an indication of strong bottom-up control (substrate supply) over bacterial growth (Lancelot & Billen 1984, Cole et al. 1988).

The ChangJiang (CJ) River, the world's third largest river, flows into the East China Sea (ECS) and forms the nutrient-rich ChangJiang Diluted Water (CDW) over the inner ECS shelf. The CJ River discharge exhibits a summer maxima. A 14 yr record (1962 to 1975) of monthly averaged discharge at the lower reach (Datong hydrological station) of the CJ River was always very low (<14 $m^3 s^{-1}$) from January to March, but started to increase and reach its annual maxima (>40 $m^3 s^{-1}$) from July to August (Shen et al. 1983) (Table 1). Each year in September, the discharge started to significantly decrease. As one of the major sources of inorganic nutrients and dissolved organic matter (DOM) for the ECS shelf (Liu et al. 2003a), the CDW disperses to the northeast in summer and forms strong gradients of salinity, inorganic nutrients and DOM that extend from the coast to the shelf break. The CJ River discharge, temperature and incident solar radiation all reach their annual peaks during summer. The annual cycles of the latter 2 variables do not vary much from year to year but river discharge does; thus, monthly and/or inter-annual variations in river discharge and associated delivery of nutrients are likely to lead to monthly and/or inter-annual variations in microbial biomass and productivity. Several studies have demonstrated that the activity and stocks of various plankton over the ECS shelf peak in summer, principally due to elevated nutrient-loading caused by increased discharge from the CJ River and more favorable physical conditions for the growth of plankton, i.e. warmer temperature and higher light intensity (for reviews see Chen et al. 2003, Liu et al. 2003a).

In plume systems, the substrate supply for bacterial growth may come from autochthonous sources, including phytoplankton exudation (algal source), zooplankton sloppy feeding, excretion from other planktonic organisms, release from dead particles and virus-induced lysis (non-algal sources; for reviews see Ducklow & Carlson 1992, Fuhrman 1992). Additional inorganic nutrients and organic substrates may originate in allochthonous sources, such as riverine input and/or re-suspension processes. An increase in inorganic nutrients that coincides with seasonal peaks in water temperature and incident solar radiation may enhance primary production (Wawrik & Paul 2004), which in turn might result in an increased substrate supply from autochthonous algal and non-algal sources; DOM from allochthonous (riverine) sources may also heighten bacterial growth in the system (Malone & Ducklow 1990, Shiah et al. 2001, 2003).

It has been argued that substrate supply, not temperature, is the major regulator of the spatial pattern of bacterial growth rate (BGR) over the ECS shelf during summer (Shiah et al. 2001, 2003). The annual surface water temperature varies from <11 to >26°C in the CDW (Shiah et al. 2003). BGR values on the inner- to mid-shelf (i.e. the mixing zone) of the ECS are considerably higher than those on the oligotrophic outer-shelf (oceanic zone), similar to those found in many other shelf systems. This pattern is correlated with the rate of substrate supply (Shiah et al. 2001, 2003). However, seldom have the effects of variations in river discharge on bacterial rate parameters in this and other shelf systems on longer temporal (i.e. inter-annual) scales been explored.

As part of the 'long-term observation and research of the East China Sea' (LORECS) project, this study aimed to assess biogeochemical responses to variations in CJ River discharge (Liu et al. 2003). Using a data set from 6 summer cruises, we found that over the ECS shelf, summer BGR was highly correlated with chlorophyll *a* (chl *a*) concentrations during each cruise and, more importantly, that values of the slope of the relationship BGR vs. chl *a* in the mixing (mesotrophic) and oceanic (oligotrophic) zones exhibited differential responses to CJ River discharge. The ecological implications of our findings are discussed.

Table 1. The 14 yr record (1962–1975) of monthly averaged discharge at Datong Station (30.76° N, 117.61° E) and monthly averaged salinity at Yinshuichuan Station (31.12° N, 122.20° E). Data from Shen et al. (1983)

	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
Discharge ($m^3 s^{-1}$)	10.1	11.0	13.5	22.4	36.1	39.3	49.0	41.4	37.8	35.2	23.7	14.1
Salinity (psu)	20.6	20.9	18.7	15.7	10.8	9.8	8.8	10.4	9.4	9.3	13.3	18.5

MATERIALS AND METHODS

Study area and sampling. Six summer cruises were conducted in July 1998, July 2001, June and August 2003, June and July 2004 (Table 2) over the ECS shelf (Fig. 1A). More than 20 stations were sampled during each cruise, except for the July 2001 cruise, which only covered 9 stations along the China coastal line (Stns 4 to 7, 18 to 20 and 29 to 30). Seawater was collected with a SeaBird CTD-General Oceanic Rosette assembly with 20 l Go-Flo bottles. Samples were taken from 6 depths within the upper 50 m. To avoid potential effects from sediment re-suspension, the lowest sampling depth was at least 20 m above the bottom.

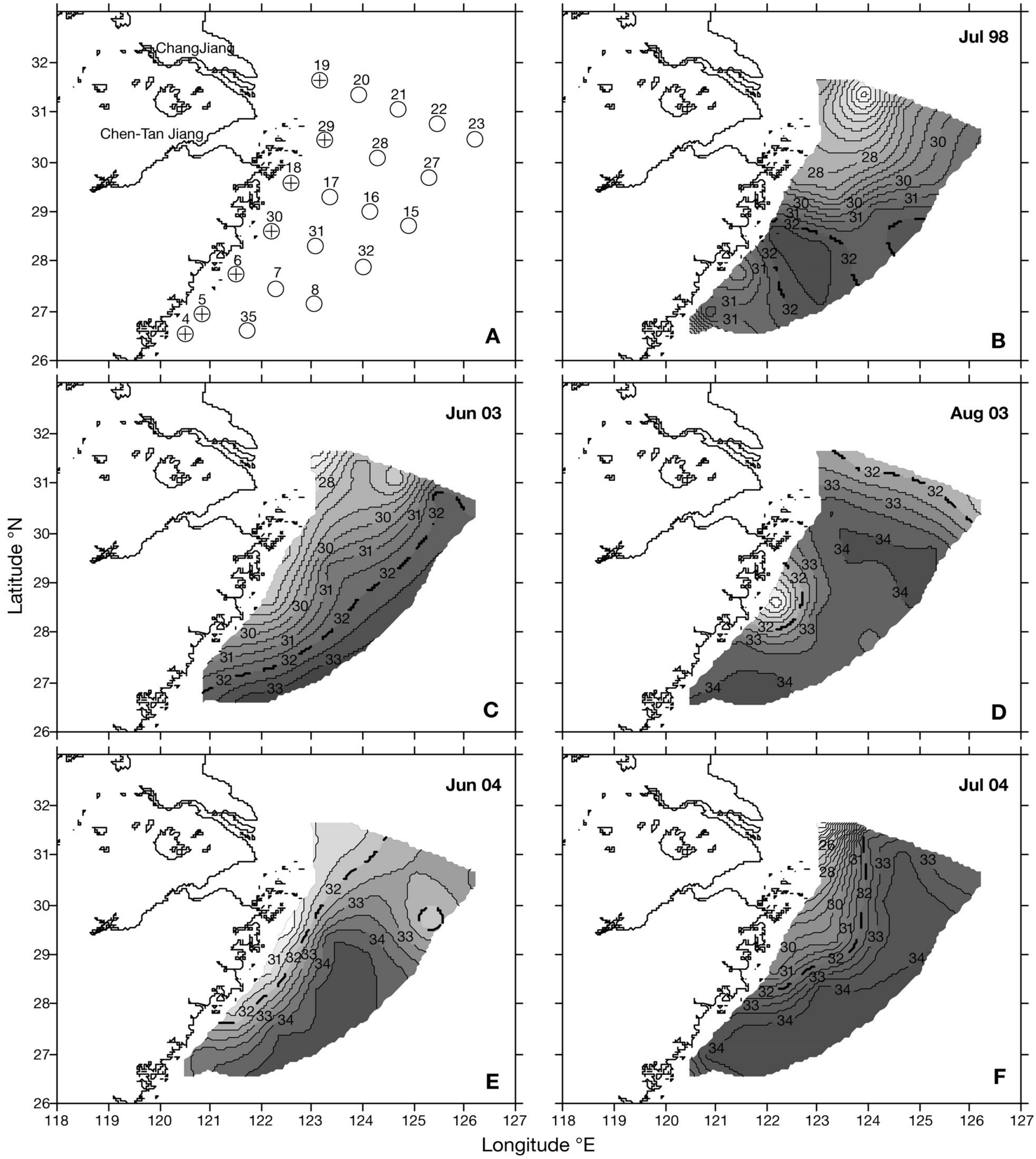

Fig. 1. East China Sea: (A) sampling stations and spatial patterns of surface salinity during cruises conducted in (B) July 1998, (C) June 2003, (D) August 2003, (E) June 2004 and (F) July 2004. ⊕: stations occupied during the July 2001 cruise

Bacterial growth rate, nitrate and chlorophyll. Bacterial abundance was determined following the acridine orange direct count (AODC) method (Hobbie et al. 1977). Samples filtered through 0.2 µm polycarbonate filters were enumerated by epifluorescence microscopy (Zeiss, Axioplan). Bacterial biomass (BB) was calculated using a carbon conversion factor (CCF) of 2×10^{-14} g cell^{-1} (Lancelot & Billen 1984). Bacterial production (BP) was estimated following the method of ^{3}H-thymidine incorporation (Fuhrman & Azam 1982), with the CCF mentioned above and a thymidine conversion factor of 1.18×10^{18} cells mol^{-1} thymidine (Cho & Azam 1988). Triplicate 30 to 40 ml aliquots of samples were incubated with ^{3}H-[methyl]-thymidine (specific activity, 6.7 Ci mmol^{-1}; final concentration 20 nM) at *in situ* temperature for 30 to 60 min. The killed samples, including time zero (t_0) controls, were filtered through 0.2 µm cellulose nitrate filters and rinsed 3 times each with ice-cold 5% trichloroacetic acid and ice-cold 80% ethyl alcohol, sequentially. Radioactivity was determined from liquid scintillation counts (Packard 2700TR). Bacterial (specific) growth rates (BGR) were calculated as BP $\times$ BB^{-1}. For nitrate analysis (Gong et al. 1995), a custom-made flow injection analyzer with a detection limit of 0.15 µM was used. Chl *a* was collected using the filtration (25 mm GF/F) method, and was then measured with an *in vitro* fluorometer (Turner Design 10-AU-005) subsequent to acetone extraction (Parsons et al. 1984).

Data analysis. To compare the spatial (horizontal) variation in bulk properties of measured variables among the 6 summer cruises, depth-averaged values were obtained by dividing depth-integrated (trapezoidal method) values by depth. To address vertical variability, variations in the relationships among BGR, chl *a* concentrations and other measurements were analyzed using data at each depth (i.e. individual depth measurement). To derive the discharge index, we first calculated the average surface salinity of the 5 stations (Stns 17 to 20 and 29, Fig. 1) located at the mouth of the CJ River individually, and then subtracted from that average a constant of 35.0 psu. Shen et al. (1983) previously demonstrated that monthly averaged salinity recorded outside the river mouth (Yinshuichuan station) had a strong negative relationship (coefficient of determination, r^2 = 0.91) with monthly averaged discharge recorded at the Datong hydrological station (Table 1).

RESULTS

Spatial patterns and correlations among measurements

Temperatures varied more than 15°C (13.7 to 30.1°C, Table 2) among depths and cruises. Samples taken from <20°C (mostly deep water data) constituted <5% of the whole data set (data not shown). Salinity was low in the CDW (22.4 psu) but increased offshore to a value of 34.9 psu (Fig. 1B–F; only 9 stations were sampled during the July 2001 cruise; data from this cruise are not shown here). The CJ River discharge was significantly lower during the August 2003 cruise than during the other cruises, as indicated by the position of the 32.0 psu isohaline (Fig. 1D) and the lowest discharge index (Table 2).

Table 3 shows that depth-averaged nitrate concentrations were negatively correlated with salinity during all cruises. Depth-averaged chl *a* concentrations (Ichl *a*) and bacterial biomass (IBB) showed no correlation with salinity except during the 2 cruises conducted in 2004. In those cases, Ichl *a* decreased offshore, whereas IBB increased steadily from the inner- to the outer-shelf. Depth-averaged bacterial production (IBP) was positively correlated with Ichl *a* during 5 out of the 6 cruises. Half of the cases indicated that IBP was higher in the mixing zone but decreased significantly towards the oceanic zone. This was evidenced by the negative correlation between surface salinity and IBP measurements. During all 6 cruises, the depth-averaged bacterial growth rates (IBGR= IBP $\times$ IBB^{-1})

Table 2. Ranges of individual depth measurements derived from 6 summer cruises conducted over the shelf of East China Sea (ECS). *T*: temperature; S: salinity; BP: bacterial production; BB: bacterial biomass; BGR: bacterial growth rate; nd: not detected (detection limit = 0.15 µM)

Cruise	Date	No. stns per cruise	*T* (°C)	S (psu)	Mean S at river mouth[a] (psu)	NO_3 (µM)	Chl *a* (mg chl *a* m^{-3})	BP (mg C m^{-3} d^{-1})	BB (mg C m^{-3})	BGR (d^{-1})	Runoff index[b]
Jul 1998	Jun 28–Jul 06	20	14.3–28.8	23.7–34.5	27.2 ± 2.1	nd–28	0.11–9.1	0.18–16	2.9–85	0.03–0.89	7.79
Jul 2001	Jul 15–29	9	18.0–27.3	29.4–34.5	29.7 ± 0.4	nd–19	0.27–6.4	0.21–23	3.9–88	0.05–0.95	5.28
Jun 2003	Jun 18–26	20	13.7–26.0	26.3–34.8	28.8 ± 1.8	0.82–22	0.24–16	0.60–27	1.8–331	0.03–1.05	6.23
Aug 2003	Aug 13–23	22	18.9–30.1	29.2–34.6	32.9 ± 1.0	nd–14	0.10–2.6	0.60–14	8.0–214	0.04–0.33	2.08
Jun 2004	Jun 11–18	22	15.1–26.2	30.1–34.7	31.7 ± 1.6	nd–20	0.11–5.9	0.78–17	8.8–76	0.03–0.62	3.30
Jul 2004	Jul 10–19	21	17.3–28.4	22.4–34.9	28.7 ± 3.8	nd–27	0.13–7.9	1.06–52	15–122	0.06–0.87	6.35

[a]Average surface salinity at Stns 17–20 and 29 (Fig. 1A); [b]Residual values of 35 psu minus the mean salinity of the CJ River mouth

Table 3. Correlation matrix for depth-averaged values and surface salinity (S) measured during 6 summer cruises over the shelf of the ECS. Correlation coefficients are significant at $p < 0.05$. INO_3, Ichl *a*, IBP, IBB: depth-averaged nitrate, chl *a*, bacterial production and bacterial biomass, respectively. IBGR: IBP × IBB^{-1}

	Jul 1998		Jun 2001		Jun 2003		Aug 2003		Jun 2004		Jul 2004		Pooled data	
	S	Ichl *a*	S	Ichl *a*	S	Ichl *a*	S	Ichl *a*	S	Ichl *a*	S	Ichl *a*	S	Ichl *a*
INO_3	−0.51		−0.85		−0.71		−0.68		−0.75		−0.66		−0.60	
Ichl *a*									−0.45		−0.50		−0.35	
IBP		+0.59		+0.80	−0.51		−0.64	+0.50	−0.69	+0.73		+0.54	−0.26	+0.20
IBB				+0.65					+0.63	−0.59		−0.55		−0.22
IBGR		+0.89	−0.63	+0.50	−0.71	+0.62	−0.62	+0.68	−0.71	+0.81	−0.75	+0.76	−0.57	+0.67

were positively correlated with Ichl *a*; during 5 out of the 6 cruises, IBGR values were negatively correlated with surface salinity. For the pooled data set, all measurements except those for IBB showed negative correlations with surface salinity, and the bacterial rate parameters (IBP and IBGR) were positively correlated with Ichl *a*. There were neither correlations between surface temperature and IBP nor between surface temperature and IBGR during any of the 6 cruises. For vertical variability, the correlation between individual depth BGR and individual depth temperature was also insignificant (data not shown).

Chl *a* and salinity effects on the BGR

During all 6 cruises, values of individual depth BGR were positively correlated with individual depth chl *a* concentrations (Table 3). The slopes (0.049 to 0.110) of the BGR–chl *a* relationship (i.e. $slope_{BGR-chl\ a}$) varied as much as 2-fold throughout the investigative period. However, the scatter plots of BGR vs. chl *a* (Fig. 2) suggest that BGR–chl *a* relationships fell into 2 categories, with a salinity of 33.0 psu being the cut-off point. When we divided the data at that cut-off point, we were able to define the mixing and oceanic water types as salinity <33.0 and >33.0 psu areas, respectively. It then became obvious that the BGR per unit chl *a* in the mixing zone was consistently higher, and that BGR here increased more rapidly with increasing chl *a* than in the oceanic zone. Consistent with this, Table 4 indicates that values of the intercepts and slopes for the BGR–chl *a* relationship in the mixing zone (intercepts: 0.111 ± 0.073; slopes: 0.091 ± 0.014) were all higher than their counterparts in the oceanic zone (intercepts: 0.036 ± 0.025; slopes: 0.062 ± 0.023; *t*-test, n = 6, $p < 0.01$). Note that the only exception to this is the data for July 2001, when the intercept in the mixing zone (−0.004) was much lower than that of the oceanic zone (0.012).

The values of $slope_{BGR-chl\ a}$ derived from the mixing and oceanic zones increased significantly as the discharge index increased (Fig. 3). In addition, the slope value of $slope_{BGR-chl\ a}$ vs. discharge index in the oceanic zone (0.009 ± 0.002) was significantly higher (~30%) than that in the mixing zone (0.007 ± 0.001, analysis of co-variance [ANCOVA], $p < 0.05$).

DISCUSSION AND CONCLUSIONS

Similar to observations in many other large plume systems, such as the Mississippi River (Wawrik & Paul 2004) and Chesapeake Bay (Malone & Ducklow 1990), the ECS shelf is a system with strong physical (Fig. 1B–F), chemical and biological gradients (Table 3, Fig. 2) during summer, owing to CJ River discharge (Shiah et al. 2001, 2003). However, one important

Table 4. Intercept and slope values ± SD of linear regressions of individual depth BGR vs. individual depth chl *a* concentrations. Mixing and oceanic zone data were taken from samples of salinity <33.0 and >33.0 psu, respectively

Cruise	All data				Mixing zone				Oceanic zone			
	Intercept	Slope	n	r^2	Intercept	Slope	n	r^2	Intercept	Slope	n	r^2
Jul 1998	0.057 ± 0.009	0.097 ± 0.004	124	0.83	0.093 ± 0.008	0.107 ± 0.004	71	0.92	0.011 ± 0.007	0.083 ± 0.003	53	0.94
Jul 2001	−0.025 ± 0.009	0.084 ± 0.005	51	0.88	−0.004 ± 0.027	0.091 ± 0.008	10	0.94	0.012 ± 0.004	0.046 ± 0.003	41	0.85
Jun 2003	0.143 ± 0.019	0.110 ± 0.005	101	0.85	0.222 ± 0.026	0.103 ± 0.005	67	0.86	0.049 ± 0.009	0.076 ± 0.012	34	0.55
Aug 2003	0.060 ± 0.006	0.049 ± 0.008	103	0.29	0.111 ± 0.012	0.066 ± 0.011	17	0.71	0.062 ± 0.004	0.027 ± 0.005	86	0.28
Jun 2004	0.031 ± 0.008	0.085 ± 0.005	107	0.71	0.103 ± 0.009	0.086 ± 0.005	33	0.92	0.019 ± 0.004	0.056 ± 0.003	74	0.81
Jul 2004	0.063 ± 0.007	0.110 ± 0.004	106	0.87	0.143 ± 0.020	0.093 ± 0.007	30	0.87	0.063 ± 0.007	0.081 ± 0.009	76	0.52
Average	0.071 ± 0.042	0.089 ± 0.023			0.111 ± 0.073	0.091 ± 0.014			0.036 ± 0.025	0.062 ± 0.023		

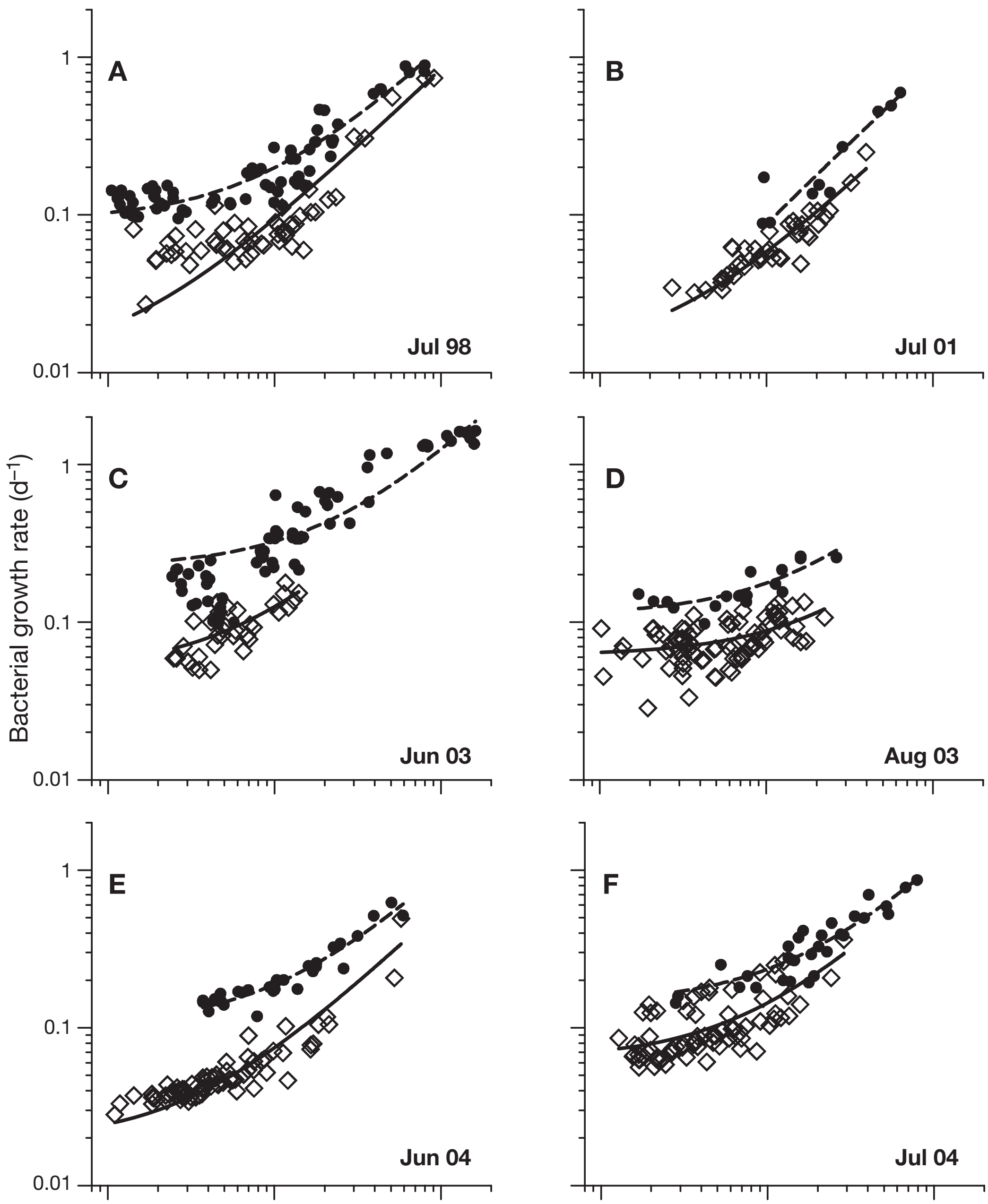

Fig. 2. Individual depth bacterial growth rates (BGR) vs. individual depth chl *a* concentrations; (A) July 1998, (B) July 2001, (C) June 2003, (D) August 2003, (E) June 2004 and (F) July 2004. ●, – – – –: mixing zone, ◇, ———: oceanic zone. Lines indicate linear regression. NB: *x*- and *y*-axes are in log scales for better presentation

difference among these systems must be noted: in the Mississippi River and Chesapeake Bay systems, annual cycles of flow are characterized by spring peaks; in contrast, the CJ River peaks during summer. This means that, in the former 2 systems, the annual cycle of nutrient delivery is out of phase with the annual cycles of solar radiation and temperature. Gong (2004) showed that the optical absorption coefficient (i.e. an index of concentration) of colored DOM in the study area decreased with increasing salinity. Dissolved organic carbon (DOC) concentrations during the July 1998 cruise ranged from 120 µM over the inner shelf to 75 µM over the outer shelf (Hung et al. 2003). Table 4 shows that the intercepts in the mixing zone (0.111 ± 0.073) were about 3 times as great as those in the oceanic zone (0.036 ± 0.025, ANCOVA,

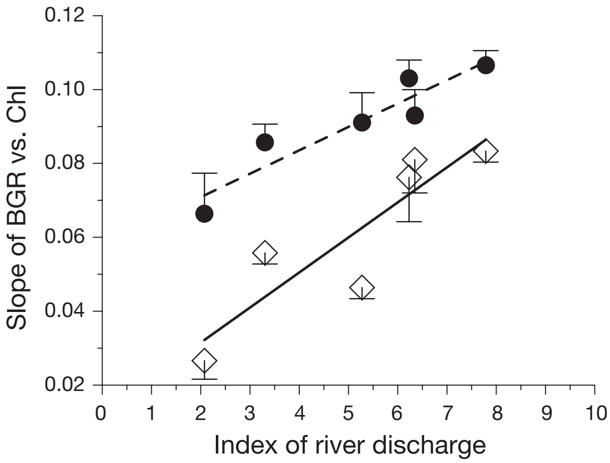

Fig. 3. Relationship between slopes of BGR vs. chl *a* concentrations and the discharge index. ●: mixing zone, ◇: oceanic zone data. Lines indicate linear regression, vertical bars = SD

$n = 6$, $p < 0.05$). This suggests that a fraction of riverine DOC might have been labile and fuelled a portion of bacterial growth (i.e. higher intercept and/or slope values) in the mixing zone. Thus, it should not be particularly surprising that during every cruise, higher BGR values on a per chl *a* basis were recorded in the mixing zone (Fig. 2).

As for temporal variations, the CJ River discharge index varied more than 11 units throughout the investigative period (Table 2). It is worth noting that, in 1998, the most serious countrywide summer flooding occurred, breaking the previous CJ River flooding record set in 1954 (www.hydroinfo.gov.cn/gb/sqnb.asp). Also of significance was that the reservoir-filling processes of the Three Gorges Dam were completed by June 11, 2003. These 2 events were reflected in our findings, which show that in August 2003, the values of the discharge index, chl *a* (Table 2), BGR (Fig. 2D) and $slope_{BGR-chl\ a}$ (Fig. 3) were substantially reduced (to less than one-half) when compared with those recorded in higher discharge years (i.e. July 1998 and June 2003). We propose that the reservoir-filling processes must have been one, if not the most, likely cause of the significant reduction in CJ River discharge in August 2003. Gong et al. (2006) recently suggested that the much lower chl *a* concentration (and primary production) recorded in August 2003 might have been caused by a reduced supply of silicic acid from the CJ River. Decreased river discharge may have also led to lower loadings of DOM. These very 2 factors, in turn, might have created conditions under which the auto- and allochthonous substrate supply rates were greatly reduced. Further, this could very well have led to the lower BGR and BP values in August 2003.

Another particularly interesting phenomenon, seldom addressed in other studies, is readily observed in our data. This concerns the differential biological coupling ($slope_{BGR-chl\ a}$) that is induced by monthly and/or inter-annual variations in river discharge in the mixing and oceanic zones. Fig. 3 indicates that variations in discharge seem to have had a greater effect on $slope_{BGR-chl\ a}$ values in the oceanic zone than in the mixing zone, which strongly suggests that the relationship between bacterioplankton and phytoplankton in the oligotrophic environment was more sensitive to the changes in the CJ River discharge. We hypothesize that, in the study area, growth conditions for bacteria can be considered to be 'feast or famine'. That is, in terms of growth phase, bacteria in the oceanic zone might be in the lag phase and/or in the lower part of the exponential phase, whereas bacteria in the mixing zone might be in the upper part of the exponential phase and/or in the stationary phase. It would therefore follow that, in the mixing zone, increases in river discharge and the associated substrate and nutrient fluxes push the BGR into the saturation portion of the growth curve, whereas increases in fluxes in the oceanic zone push the BGR up into the exponential portion of the curve. This may lead to BGR increasing at a greater rate in the oceanic zone than in the mixing zone as river discharge elevates.

It is also worth noting that in shelf systems, the substrate for bacterial growth might come from many sources. In addition to the direct effects from organic and inorganic loadings mentioned above, other discharge-associated processes might to some extent, or even substantially, shape the BGR–chl *a* relationship. For example, top-down control processes including bacterivory (Fuhrman & McManus 1984, Sherr et al. 1987) and viral lysis (Proctor & Fuhrman 1991, Hwang & Cho 2002) could affect BB and, at the same time, release organic substrates (Fuhrman 1992, Nagata & Kirchman 1992) to support more bacterial growth. The observed BGR–chl *a* pattern could have occurred if the strength of these top-down control processes were discharge-associated. Nonetheless, we are only able to point out their potential importance here: related studies on bacterivory and viral-lysis processes in the ECS shelf system were not performed during these cruises, which makes further discussion very difficult. We noted that BB varied by more than 2 orders of magnitude (Table 2) within this study. However, correlations of IBB vs. S and IBB vs. Ichl *a* (Table 3) varied among cruises. Without bacterivory and vial lysis measurements, it is difficult to offer any explanations for such a huge variation in BB.

In summary, the summer season is a critical period for biogeochemical processes over the ECS shelf, because it is at this time that physical conditions such as temperature, light intensity and CJ River discharge reach their maxima. Hence, biological activity must play a stronger role in determining the characteristics of the system (e.g. source or sink of carbon) in summer than in other seasons. The fact that there are such significantly strong co-variations in the BGR–chl *a* relationship with the alteration of coastal discharge suggests that the ECS shelf system responds almost immediately to changes in CJ River discharge, but that the shelf system has a low buffering capacity when it encounters sudden changes in external forces. This study also argues that the relationship between BGR and chl *a* (i.e. $slope_{BGR-chl\ a}$) in the oceanic zone seems to be more sensitive to monthly and/or inter-annual variations in river discharge than that in the mixing zone. Our 'feast or famine' hypothesis, which accounts for differential bottom-up control on bacterial growth in meso- and oligo-trophic environments, nevertheless calls for more detailed comparisons in future studies.

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