

Temperature versus substrate limitation of heterotrophic bacterioplankton production across trophic and temperature gradients in the East China Sea

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ABSTRACT: A survey of heterotrophic bacterioplankton biomass (BB; 4 to 64 mg C m⁻³), production (BP; 0.3 to 14.7 mg C m⁻³ d⁻¹) and specific growth rates (μ ; 0.07 to 0.38 d⁻¹) as well as concentrations of nitrate (NO₃⁻; <0.1 to 15.6 μ M), particulate organic carbon (POC; 1 to 60 μ M) and chlorophyll *a* (chl; 0.1 to 4.0 mg chl m⁻³) in the euphotic zone was conducted over the continental shelf of the East China Sea during the spring seasons of 1996 and 1997. Concentrations of NO₃⁻ were high in the coastal areas and decreased offshore. In contrast, temperature (12.2 to 24.5°C) showed the opposite trend, with cool (<20°C) and warm (>20°C) waters distributed inside and outside the shelf edge, respectively. Inside the shelf edge, bacterial rate parameters (BP and μ) were positively correlated with temperature but showed no correlation with POC; values of Q₁₀ for BP and μ were 2.7 and 3.3 respectively. From the shelf edge to the adjacent open ocean, bacterial rate parameters were positively correlated with POC only. These results imply that during the spring season, mechanisms controlling the spatial patterns of bacterial rate parameters over the shelf area are system-dependent. It is concluded here that temperature plays a more dominant role than substrate supply inside the shelf edge; however, from the shelf edge to the open ocean, the situation is reversed.

KEY WORDS: Bacterial production · Bacterial growth rates · Bottom-up control · Continental shelf · Kuroshio · Q₁₀

INTRODUCTION

Heterotrophic bacterioplankton are the major organisms responsible for the decomposition of dissolved organic compounds in the sea (Fuhrman 1992 and citations therein). The study of the mechanisms controlling bacterial growth has been an important issue within the perspectives of organic carbon cycling and planktonic trophodynamics. Bottom-up control (the variation of bacterial variables is controlled by the supply rates of dissolved organic substrate) and top-down control (the variation of bacterial variables is controlled by bacterivory and viral lysis) have all been proposed as

explanations for bacterial biomass and production variations in the field (see Ducklow & Carlson 1992, Fuhrman 1992 for review). Recent studies have further demonstrated that the seasonal variations of bacterial rate parameters (production and specific growth rates) in eutrophic ecosystems (coastal, estuarine and brackish-water systems) might primarily be regulated by temperature, with substrate supply playing a lesser role (White et al. 1991, Ducklow & Shiah 1993, Hoch & Kirchman 1993, Berman et al. 1994, Griffith et al. 1994, Shiah & Ducklow 1994a,b, 1995). However, the applicability of such hypotheses to the continental shelf ecosystem (mesotrophic to oligotrophic) is a significant question that has never been fully answered (Kemp 1994 and citations therein).

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The continental shelf is affected by processes derived from land and the open ocean simultaneously (Biscaye et al. 1994). The shelf receives a large amount of inorganic nutrients from river discharge and coastal erosion processes, which results in high standing stock and production rates of organic matter (Mantoura et al. 1991) fueling bacterial growth. The heterogeneous patterns of physical, chemical and biological variables across the shelf system (see below) may create a continuous trophic gradient for bacterial growth. A detailed examination of the spatial patterns of bacterial biomass and rate parameters in the shelf system may provide some insights into bacterial growth controlling mechanisms.

During spring, water properties in the shelf of the East China Sea (ECS) may be affected by 4 end members. Two of these serve as important sources of inorganic nutrients into the shelf area (Liu et al. 1992 and citations therein). They are the cold (<15°C), low salinity (<32.000 psu) China Coastal Waters (CCW) and the cool (<20°C), high salinity Kuroshio Subsurface Waters (KSW) which outcrops at the shelf edge all year round. The other 2 oligotrophic end members are the Kuroshio Waters (KW) and the Taiwan Strait Waters (TSW). Both the KW and TSW are characterized by high temperature (22 to 25°C) and high salinity (>34.000 psu), with their main streams flowing northward on the eastern and western sides of Taiwan, respectively. Primary production and chlorophyll concentrations in areas more affected by the KSW and CCW are about 2- to 4-fold higher than those observed in the KW and the TSW (Gong et al. 1996, Shiah et al. 1996).

Physical mixing processes among these 4 water masses make the continental shelf of the ECS a system characterized by strong gradients of inorganic nutrients and organic substrate, either in terms of concentrations or supply rates. In addition, the mixing of the cold (CCW & KSW) and the warm water masses (KW & TSW) may result in a broad range (ca 10 to 25°C) of temperature change over the entire shelf area during spring. These variations provide an ideal opportunity to examine temperature and substrate supply effects on the bacterial rate parameters.

MATERIALS AND METHODS

Study area and sampling. Data were collected from 2 cruises conducted on the continental shelf of the southern ECS north of Taiwan (Fig. 1) during the spring seasons of 1996 (9 sampling stations) and 1997 (29 sampling stations). Seawater was collected from a SeaBird CTD-General Oceanic Rosette assembly with 20 l Go-Flo bottles. Light intensity was measured with a light meter (QSP200L; Biospherical), while the depth of the euphotic zone was defined as 1% of the surface light level.

Bacterial biomass, production and growth rates. Bacterial abundance was determined by using the Acridine Orange Direct Count method (Hobbie et al. 1977). Samples fixed with glutaraldehyde (final conc., 1%) were stained with acridine orange (final conc., 0.01%) for 2 min before being filtered through 0.2 µm polycarbonate filters pre-stained with an Irgalan black solution. Slides were enumerated by epifluorescence microscopy (Zeiss, Axioplan). Biomass was calculated using a carbon conversion factor of 2×10^{-14} g cell⁻¹ (Lancelot & Billen 1984). Bacterial production was estimated by the method of ³H-thymidine (Fuhrman & Azam 1982) incorporation with a conversion factor of 1.18×10^{18} cells mol thymidine⁻¹ (Cho & Azam 1988). Triplicate 30 to 40 ml aliquots of water samples were incubated with ³H-[methyl]-thymidine (S. A., 6.7 Ci mmol⁻¹; final conc., 20 nM) in clean polycarbonate tubes at *in situ* temperature. Reactions were stopped by adding formaldehyde (final conc., 1%). The killed samples including time zero controls were filtered through 0.2 µm cellulose nitrate filters. These filters were then rinsed 3 times each with ice cold 5% trichloroacetic acid and ice cold 80% ethyl alcohol sequentially. Scintillation cocktail (6 ml; Ultima Gold, Packard) was added after the dried

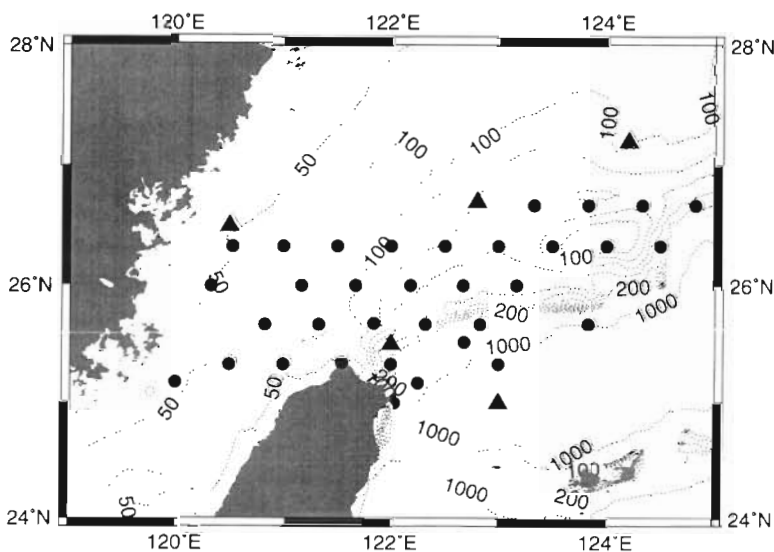


Fig. 1. Map of the southern East China Sea showing sampling stations for cruises 1996 (▲) and 1997 (●). Dashed lines indicate the bottom depths in units of meters

filters were dissolved completely in 0.5 ml of ethyl acetate. Radioactivity was determined by liquid scintillation counting (Packard 1600). Bacterial (specific) growth rates were calculated by dividing the bacterial production by the bacterial biomass.

Particulate organic carbon and nitrogen concentrations. Water samples (0.5 to 1.0 l) for particulate organic carbon (POC) and nitrogen (PN) measurements were filtered through a 200 mm mesh to remove zooplankton. After filtration (25 mm GF/F filters; pumping pressure <100 mm Hg), the samples were wrapped in aluminum foil and stored at -4°C . Both the filters and aluminum foils had been pre-combusted at 550°C for 1 h before these filtration processes. POC and PN concentrations were measured by a CHN analyzer (Fisons; NA1500) after samples had been dried and acid-fumed.

Chlorophyll *a* and nitrate concentrations. Chl *a* and nitrate concentrations were measured following the methods of Parsons et al. (1984). Water samples for nutrient analyses were subsampled with clean 100 ml polypropylene bottles and frozen immediately with liquid nitrogen. Nitrate was analyzed with a self-designed flow injection analyzer (Gong et al. 1995) and was reduced to nitrite with a cadmium wire which was activated with a copper sulfate solution. For chl *a*, 1 to 2 l of seawater were filtered through 25 mm Whatman GF/F filters which were then immediately stored at -20°C . Back at the laboratory, the filters were ground in 10 ml 90% acetone followed by extraction in a 4°C shaking incubator for 2 h. After centrifugation at 1000 rpm ($200 \times g$) for 5 min, the concentrations of chlorophyll in the supernatant were measured on a Turner fluorometer (model 10-AU-005).

Data analyses. The euphotic zone integrated data set was generated by integrating measured variables over the euphotic zone by trapezoid method. Parametric methods including correlation and regression analyses were performed with the Macintosh software StatView™ II (Abacus Concepts, Inc.). The non-parametric (Spearman rank correlation) method in that software was used to double check the results derived from parametric analyses, especially for the data set with small sampling size (i.e. the $<20^{\circ}\text{C}$ data set; see below). Both methods yielded the same conclusion.

RESULTS

Data collected from the 1997 cruise (29 sampling stations) were used to describe the spatial patterns of the measured variables, while the 1996 data (9 sampling stations) were presented in the statistical analyses together with the 1997 data. The depth of the euphotic zone was about 30 to 40 m in the inner shelf but

increased to about 65 to 70 m in the outer shelf. With only a few exceptions, the euphotic zone of each station was well mixed, as judged from the homogeneously distributed temperature and salinity profiles (Fig. 2A). The average temperature of the euphotic zone changed by more than 10°C , with the cool (ca 12 to 22°C) and warm (ca 20 to 24°C) waters located at the inner shelf and outside the shelf edge, respectively (Fig. 3A). A warm water mass (TSW) with temperatures $>20^{\circ}\text{C}$ was found west of Taiwan. This northward flowing TSW mixed with the CCW and the KW thereby creating a strong temperature gradient in the middle shelf area. Salinity was positively correlated with temperature in areas of $<20^{\circ}\text{C}$ (Fig. 2A). More than half (21 out of the 38) of the sampling stations had similar salinity (~ 34.500 psu), but temperature varied from 17.0 to 24.5°C . This indicates that temperature is probably a more suitable index than salinity in exploring the magnitude of the mixing among water masses over the shelf. This is particularly true in distinguishing the upwelled KSW and the oligotrophic KW since both water masses were characterized by similar salinity but different temperature and distinct nitrate concentrations (see below).

Surface nitrate concentrations (NO_3^- ; 0.2 to $15.1 \mu\text{M}$) and euphotic zone integrated nitrate concentrations (INO; 6 to 488 mmol m^{-2} ; Fig. 3B) were high in the inner shelf region, yet decreased offshore. Two INO anomalies separated by low INO ($<100 \text{ mmol m}^{-2}$) waters were observed around the shelf edge. One was located at the upwelling area off northeastern Taiwan with INO $>250 \text{ mmol m}^{-2}$; the other (INO $>150 \text{ mmol m}^{-2}$) was situated at 26.3°N , 124.0°E . Values of INO were negatively correlated with temperature (Fig. 2B) and salinity when anomalies (7 data) derived from the upwelling areas were excluded ($p < 0.01$, $n = 31$).

Concentrations of particulate organic carbon (POC; 1.2 to $60.4 \mu\text{M}$) and the integrated POC (IPOC; 230 to 1220 mmol m^{-2}) varied respectively about 50- and 5-fold over the study area (Table 1). In 1997, most of the high IPOC values ($>400 \text{ mmol m}^{-2}$) were recorded in the middle shelf with intermediate temperatures (17 to 22°C ; Fig. 2C). Values of IPOC in the inner and middle shelf seemed to be higher ($>200 \text{ mmol m}^{-2}$) than those in the outer shelf on the 1996 cruise. Chl *a* concentrations varied 40-fold with values ranging from 0.1 to $4.0 \text{ mg chl m}^{-3}$. On both cruises, the spatial pattern of the integrated chl (Ichl; 6 to $122 \text{ mg chl m}^{-2}$) was almost identical to those of the IPOC. The correlation coefficient of Ichl versus IPOC was $>+0.90$ ($n = 38$, $p < 0.01$). IPOC was positively correlated with euphotic zone integrated particulate nitrogen (IPN; 627 to $135 \text{ mmol N m}^{-2}$; $n = 25$, $p < 0.01$); their relationship can be expressed as $\text{IPOC} = 23 + 7.1 (\pm 0.5) \times \text{IPN}$ with a R^2 (coefficient of determination) value of 0.95.

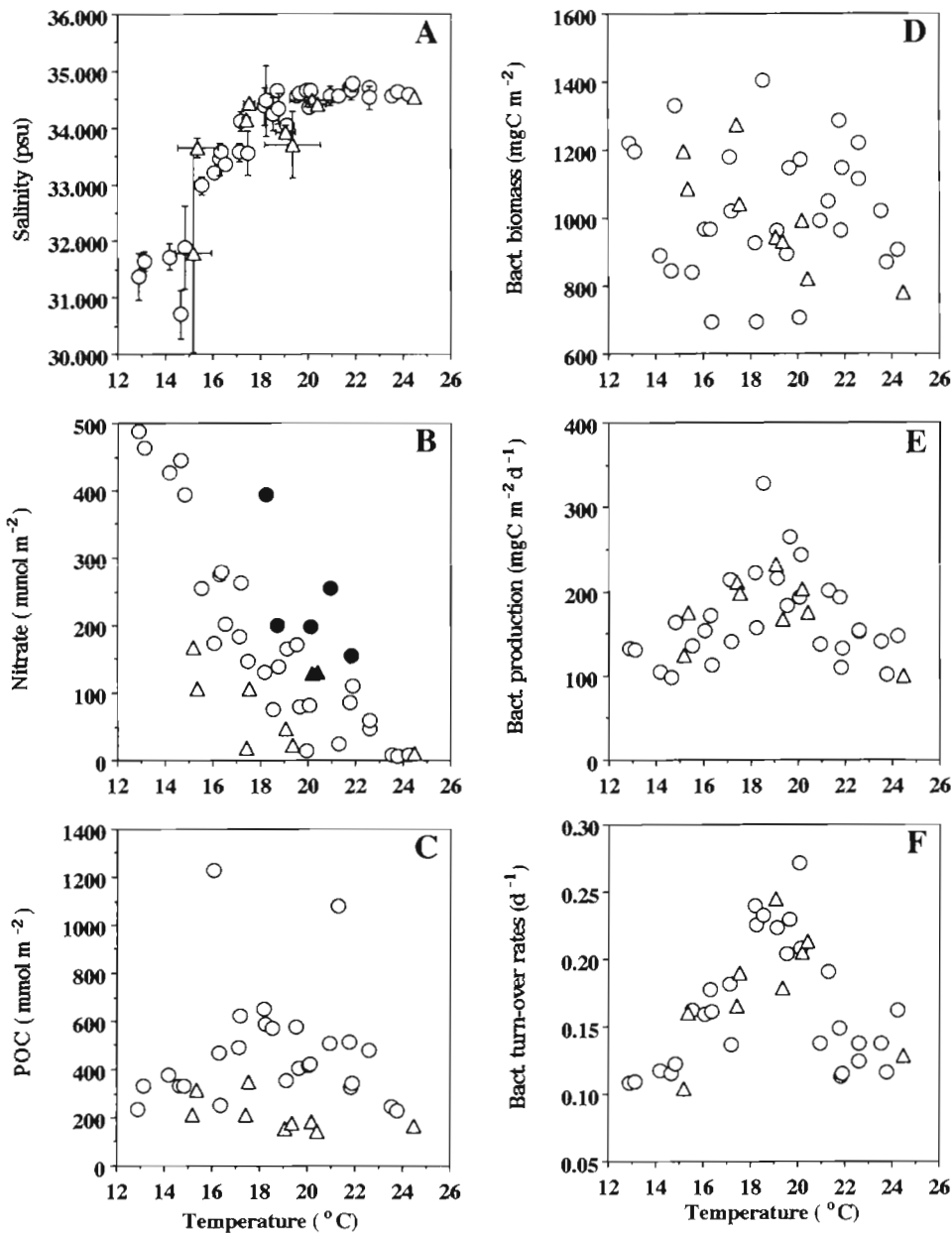


Fig. 2. Scatter plots of the euphotic zone averaged temperature versus averaged salinity (A) and averaged temperature versus other euphotic-zone integrated variables (B–F). Horizontal or vertical bars in (A) indicate standard deviation. (Δ) 1996 data; (\circ) 1997 data. Solid symbols in (B) indicate upwelling stations

Bacterial biomass (BB; 4 to 64 mg C m⁻³) varied 16-fold over the study area. Bacterial production (BP) and individual growth rates (μ ; BP/BB; Table 1) varied >40-fold (0.3 to 14.7 mg C m⁻³ d⁻¹) and >5-fold (0.07 to 0.37 d⁻¹), respectively. The integrated values of BB and BP (IBB and IBP) as well as the averaged growth rates (μ_{ze} ; IBB/IBP), were in the ranges of 694 to 1406 mg C m⁻², 98 to 328 mg C m⁻² d⁻¹ and 0.11 to 0.27 d⁻¹, respectively. In 1997, no clear spatial pattern for IBB existed in areas inside the shelf edge. However, in warm water areas (>20°C), IBB tended to decrease from the shelf edge to the open ocean (Fig. 2D). On the 1996 cruise, IBB decreased from the inner to outer shelf, as indicated by the negative trend between IBB and temperature (Fig. 2D).

On both cruises, in terms of their relationships with temperature, bacterial rate parameters (IBP and μ_{ze}) showed similar patterns over the shelf (Fig. 2E–F). In areas with temperatures <20°C, IBP and μ_{ze} increased with rising temperature; above 20°C, these parameters showed no significant trend relative to temperature (see below). The use of the averaged value (μ_{ze}) to represent bacterial individual growth rates at different depths (i.e. μ) seems reasonable since the values of μ did not vary much within the euphotic zone at any given station. For almost all of the sampling stations, the standard deviations of μ were quite small, while the coefficients of variation (CV = standard deviation \times 100/average) seldom exceeded 20%. The correlation

coefficient (i.e. r) of μ versus μ_{ze} was significant ($r = 0.92$, $n = 38$, $p < 0.01$).

The relationship of temperature versus IBP (and μ_{ze}) was examined with a polynomial curve fitting method, which justified that the apex of that best-fitted curve was located at 20°C ($n = 38$, $R^2 = 0.67$, $p < 0.01$). After this, the multiple regression of natural log transformed IBP ($\ln \text{IBP}$) and μ_{ze} ($\ln \mu_{ze}$) on temperature and IPOC (independent variables) in the ranges of $<20^\circ\text{C}$ and $>20^\circ\text{C}$ was performed. Inside the shelf edge ($<20^\circ\text{C}$), more than 50% of the variations ($R^2 = 0.48$ to 0.77 ; $p < 0.01$) of IBP and μ_{ze} could be explained by temperature alone (Table 2); in fact, the slopes of $\ln \text{IBP}$ on temperature for the 1996 (0.10 ± 0.04) and 1997 (0.10 ± 0.02) cruises were almost identical (ANCOVA; $p > 0.05$). Analysis of $\ln \mu_{ze}$ versus temperature showed the same trend with slope values of 0.12 ± 0.05 and 0.12 ± 0.01 , respectively. The estimated Q_{10} (the increase in the growth rate for each 10°C increase in temperature) values of IBP and μ_{ze} for the pooled data set were 2.7 and 3.3, respectively. Neither temperature nor IPOC correlated with IBB.

Conversely, IBP, μ_{ze} and IBB values recorded outside the shelf edge were positively correlated with IPOC, with R^2 values of 0.37 to 0.78 ($n = 11$, $p < 0.01$). For the $<20^\circ\text{C}$ data, the addition of IPOC as an extra independent variable only slightly increased the R^2 values of IBP and μ_{ze} (Table 2). On the other hand, IPOC was the predominant factor in explaining the variance of IBP, μ_{ze} and IBB in the warm water areas.

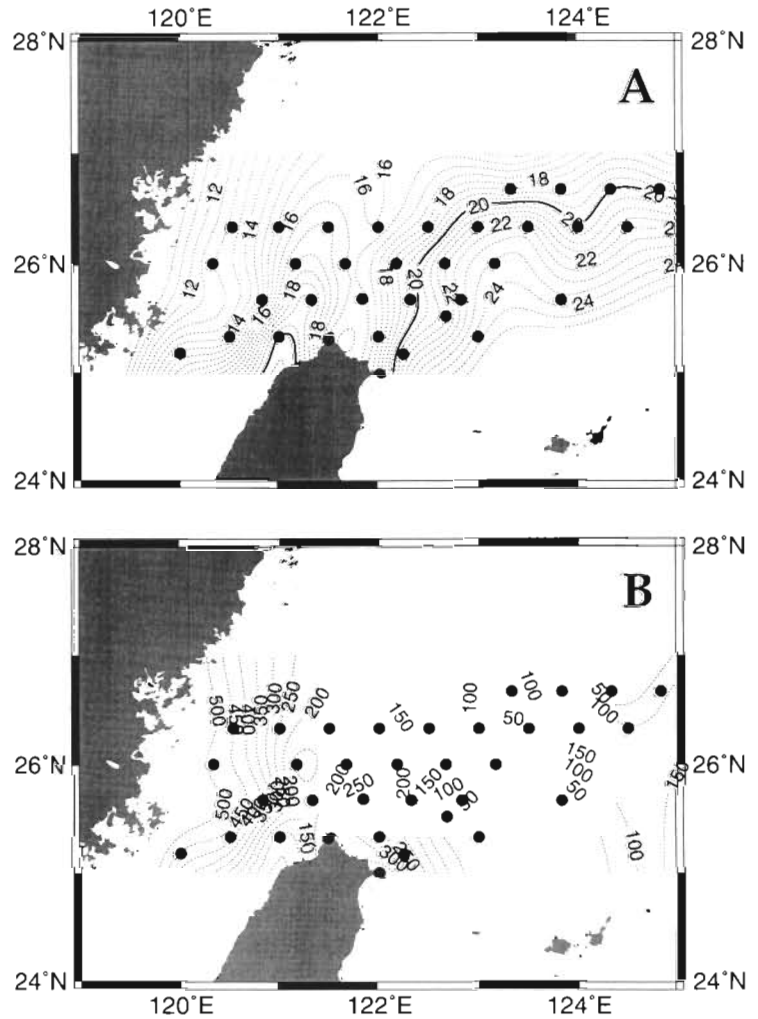


Fig. 3 Contours of the euphotic-zone averaged temperature (A: °C) and the euphotic-zone integrated nitrate concentrations (B: mmol m^{-2})

DISCUSSION

The spatial patterns of temperature over the shelf give rise to 2 important implications in this study. Physiologically, temperature may directly affect bacterial growth rates and thus production, which peaked at 20°C (Fig. 2E–F). This confirms many studies (Shiah & Ducklow 1995 and citations therein) which have indicated that in temperate and subtropical areas, the optimal temperature for bacterial growth was in the range of 20 to 25°C. From a hydrographic point of view, the 20°C isotherm (Fig. 3A) located at the shelf edge served as a mark separating the study area into 2 systems with distinct temperature (cold vs warm) and trophic (mesotrophic vs oligotrophic) characteristics. Temperature

Table 1. Ranges of measured variables collected from the euphotic zone in the continental shelf of the southern East China Sea during the spring seasons of 1996 and 1997

Variables	Symbol	Unit	1996	1997
Temperature	T	°C	13.6/24.5	12.2/24.3
Salinity	S	psu	30.043/34.497	30.012/35.700
Nitrate	NO_3^-	μM	$<0.2^a/9.6$	$<0.2/15.6$
Particulate organic carbon	POC	μM	1.2/52.2	3.2/60.4
Chlorophyll	Chl	mg chl m^{-3}	0.2/2.4	0.2/4.0
Bacterial biomass	BB	mg C m^{-3}	4/64	14/35
Bacterial production	BP	$\text{mg C m}^{-3} \text{d}^{-1}$	0.3/14.7	1.3/11.5
Bacterial turn-over ^b	μ	d^{-1}	0.07/0.31	0.07/0.38

^aDetection limit
^bCalculated as BP/BB

Table 2. Coefficient of determination (R^2) (all significant at $p < 0.01$ level) for multiple regression analyses of temperature (T) and the euphotic-zone integrated particulate organic carbon concentrations (IPOC) versus bacterial measurements (the euphotic-zone integrated bacterial production [IBP], bacterial biomass [IBB] and averaged growth rates [μ_{ze} : IBP/IBB] after natural log transformation). T, IPOC: independent variables. n: sampling size

Category	n	R^2 for T only	R^2 for IPOC only	R^2 for T + IPOC
<20°C				
ln IBP	27	0.48	–	0.48
ln μ_{ze}	27	0.77	–	0.79
ln IBB	27	–	–	–
>20°C				
ln IBP	11	–	0.78	0.79
ln μ_{ze}	11	–	0.37	0.37
ln IBB	11	–	0.52	0.53

was an indication of the inorganic nutrient supply (Figs. 2B & 3B) which, in turn, affected algal biomass, activity (i.e. primary production) and, hence, the potential supply rates of substrate (IPOC; see below) required for bacterial growth. This might be particularly true for bacteria outside the shelf edge in warm and oligotrophic waters (Fig. 2C). Since bacterial rate parameters peaked at 20°C and the 20°C isotherm roughly separated the study area into 2 different trophic systems, we chose the temperature of 20°C as the cut-off point in statistical analyses.

Primary production and dissolved organic carbon concentration data were not available in this study. IPOC was used as the index of substrate supply since they were positively correlated with Ichl. In fact, IPOC might be more indicative than Ichl since all biological components (except most bacteria and viruses), dead or alive, are included.

The results here suggest that the controlling mechanisms of bacterial growth might be quite different inside and outside the shelf edge, as judged from their distinct relationships with temperature and IPOC in different temperature ranges (<20°C and >20°C; Fig. 2F, Table 2). More specifically, it is hypothesized here that during the spring season, bacterial growth inside and outside the shelf edge are primarily controlled by temperature and substrate supply, respectively.

Substrate supply has long been recognized as a dominant factor in regulating bacterial growth rates in aquatic ecosystems (Cole et al. 1988, see also Ducklow & Carlson 1992, Fuhrman 1992 for review). However, several recent studies have suggested that the strength of bottom-up control might be system dependent and might also change temporally within a system. Duck-

low & Shiah (1993) first proposed that bacterial growth in estuaries might be temperature limited, with the substrate supply playing a less important role. This hypothesis has been confirmed by experiments performed in Delaware Bay (Hoch & Kirchman 1993), Chesapeake Bay (Shiah & Ducklow 1994b, 1995) and Kiel Fjord (Berman et al. 1994). These findings are of little surprise because many estuaries are eutrophic, showing large amounts of external inputs, either in terms of inorganic nutrients or organic substrate. Under such conditions, bacterial growth might actually be saturated by high substrate supply rates during most seasons of the year.

The data in this study lend support to the fact that the temperature dominance hypotheses could also be applied in explaining the spatial pattern of bacterial growth rates in a mesotrophic environment. As argued by Ducklow & Shiah (1993) and others, if bacterial growth is primarily controlled by factors other than temperature, then a strong relationship between bacterial growth rates and temperature is less likely to occur. That is, bacteria simply cannot grow without the proper amount of substrate supply, even when growth temperature is optimal (see also below). More importantly, the Q_{10} value derived from this study (3.3) was very similar to the ones reported by Shiah & Ducklow (1994a, 1995) in their seasonal studies in Chesapeake Bay (averaged $Q_{10} = 3.2$) and in a salt marsh tidal creek (overall $Q_{10} = 3.2$). White et al. (1991) reported an average Q_{10} value of 3.3 for bacterial growth rates based on data collected from 57 studies conducted in fresh, marine and estuarine/coastal waters. Interestingly, those 3 studies addressed the temperature effects on bacterial temporal variability within eutrophic systems, whereas the present one emphasized spatial variability in mesotrophic environment (i.e. areas inside the shelf break). This indicates that the temperature dependence of bacterial growth rates (Q_{10}) might be comparable in both systems and over both temporal and spatial scales.

In warm water areas, a strong correlation between bacterial growth rates and IPOC (Table 2) was observed. This indicates that substrate supply rates rather than temperature might be the major factor in regulating bacterial growth rates in areas outside the shelf edge. The following scenario is proposed as an explanation. In areas next to the oligotrophic environment (the KW), temperature (20.0 to 24.5°C) itself was probably optimal for bacterial growth (Shiah & Ducklow 1994a,b, 1995). However, as temperature increased, the system became more oligotrophic (Fig. 2B) which resulted in the reduction of substrate supply and thus bacterial growth rates. This implies that as the system became more of an oligotrophic condition, the more significant substrate control of bacter-

ial growth might become. Outside the shelf edge, IBB was positively correlated with IPOC with an R^2 value of 0.52. This observation supported the conclusion of Sanders et al. (1992) who suggested that bottom-up (substrate supply) control dominated in regulating bacterial biomass in oligotrophic environments.

In addition to temperature and substrate supply rate, other factors, such as bacterivory and viral lysis (top-down control; see Ducklow & Carlson 1992, Fuhrman 1992 for review) also play significant roles in regulating bacterial biomass and production. Bacterial biomass inside the shelf edge showed no distinct relationships with any other environmental variables. It is very possible that the spatial pattern of bacterial biomass inside the inner shelf was more affected by these 2 processes. However, no tangible conclusion regarding this can be made due to the lack of bacterivory and viral lysis data.

The outcrop of the nutrient-enriched Kuroshio Sub-surface Waters (KSW) caused by the change of bottom topography definitely has a strong influence on the hydrography and thus, the spatial patterns of biological phenomena. The most recent study (Liu et al. 1999) showed that for the continental shelf of the ECS, nutrient (nitrate as example) flux derived from the KSW (5.5 to 7.1 kmol N s⁻¹) at the shelf edge adjacent northern Taiwan (i.e. the first INO anomaly in Fig. 3B) was at least 2-fold higher than that from coastal input (i.e. river runoffs; 2.1 kmol N s⁻¹; Zhang 1996). Our observation suggests that there might be other upwellings (i.e. the second INO anomaly in Fig. 3B) along the shelf edge. Their occurrence frequency (persistent or episodic) and possible contribution in importing nutrients into the continental shelf of the ECS and the oligotrophic Kuroshio waters merit further investigation.

Another interesting phenomenon which is worthy of further study is that the values of IPOC were also more or less peaked at the boundary of the inner and outer shelf regions (ca 16 to 20°C; Fig. 2C). The high correlation observed between Ichl and IPOC (see above) indicated that the biomass (and perhaps activities) of algae and other planktoners within this 'transition zone' were high. In comparison to this area, nutrient-rich waters in the inner shelf (see also below) were colder and more turbid, which were not favorable for the development of high Ichl and IPOC (Shiah et al. 1996). More interestingly, the nitrogen to phosphate ratios (N/P ratios) from the river runoffs were in the range of 46 to 84 (Edmond et al. 1985, Zhang 1996), while the N/P ratios of the KSW (14.0 to 15.4; Liu et al. 1999) were slightly lower than the Redfield ratio of 16. Wong et al. (1998) deduced that such serious N/P imbalance probably was the major factor in limiting algal biomass (and productivity) in the inner shelf areas. Finally, differential grazing pressure from zooplankton might be an important reason but needs to be verified in the future.

During spring, the spatial variation of bacterial growth rates and production in the continental shelf of the East China Sea were interactively regulated by both temperature and substrate supply. However, the relative strength of these 2 controlling factors varied, with temperature and substrate supply dominating inside and outside the shelf edge, respectively. The strong relationship observed between bacterial growth rates and temperature implies that during spring, bacterial growth in the shelf system might not be limited by substrate supply. In view of other published results derived from the eutrophic environment, it seems feasible that in both mesotrophic and eutrophic ecosystems, temperature plays a more dominant role than substrate supply in regulating bacterial growth rates, at least during certain seasons (e.g. spring) of the year. In addition, similar Q_{10} values derived from this and other studies further suggest that temperature dependence of bacterial growth and production might be comparable in these ecosystems.

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