Temperature dependence of bacterial specific growth rates on the continental shelf of the East China Sea and its potential application in estimating bacterial production

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ABSTRACT: To decipher the relative importance of temperature and substrate supply in regulating the spatial patterns of bacterial production and specific growth rates, field surveys in the continental shelf of the East China Sea and on board substrate (dissolved free amino acids) enrichment experiments were conducted in December 1997 and March 1998. The results suggested that there was a shift from temperature dominance inside the mid-shelf to substrate supply dominance outside the mid-shelf controlling the spatial variability of bacterial growth during the cold seasons. The Q_{10} values for bacterial specific growth rates ($B\mu$) derived from the winter (Q_{10} = 3.4 ± 0.3) and the spring (Q_{10} = 3.3 ± 0.3) were very similar and comparable with the values derived from other estuarine and coastal ecosystems (Q_{10} = 3.1 to 3.4). Such a consistent relationship between temperature and $B\mu$ allows one to use sea-surface temperature (SST) and depth-integrated bacterial biomass to model depth-integrated bacterial production (IBP) inside the mid-shelf of the East China Sea. The $B\mu$ versus temperature curve, $\ln B\mu = -0.42 + 0.122 (\pm 0.02) \times$ SST, derived from a previous study in the southern East China Sea was used to simulate IBP. The total difference between the measured IBP and the simulated IBP is <20%.

KEY WORDS: Continental shelf · East China Sea · Kuroshio · Q_{10} · Heterotrophic bacterioplankton · Remote sensing · Modeling

INTRODUCTION

Heterotrophic bacterioplankton are the major organisms responsible for the decomposition of dissolved organic carbon (DOC; Fuhrman 1992 and citations therein), which constitutes >90% of the organic carbon pool in the ocean. Bacterial production and specific growth rates play a key role in determining what is actually left over or available for DOC export (Carlson et al. 1994, Carlson & Ducklow 1995, Hansell & Carlson 1998). On an areal basis, the continental shelf comprises <10% of the world ocean. These ecosystems, however, could have a very important effect on global carbon cycling (Mantoura et al. 1991, Wong et al. 2000), due to large

standing stocks of organic carbon as well as high rates of primary production. However, the actual role of these systems as sinks or sources of CO_2 is not clear (Smith & Hollibaugh 1993, Wong et al. 2000). A clear understanding of which environmental factors regulate bacterial growth and thus carbon consumption under a variety of conditions may provide insight into this issue.

It is well known that, when other factors are not limiting, the effects of temperature (T) on many biological processes can be modeled (Day et al. 1989) using an Arrhenius expression: $y = ae^{bT}$ or $\ln y = \ln a + bT$, where $\ln a$ and b represent intercept and slope respectively. For example, the Q_{10} (the increase of rate parameter for each 10°C rise in temperature) values of phytoplankton optimal growth rate range between 1.88 and 2.30 (Eppley 1972). Bacteria are considered to have
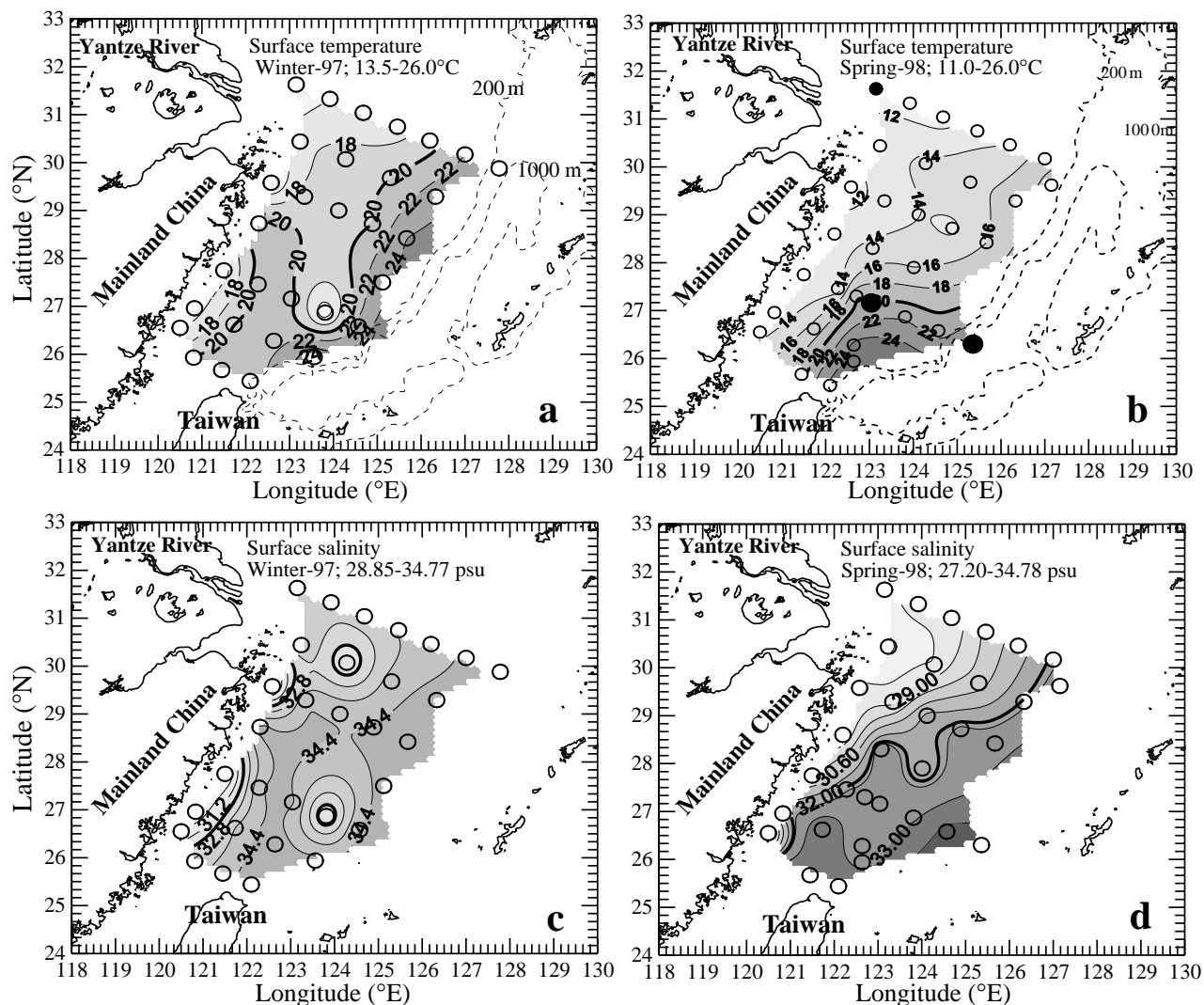
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Fig. 1. Contours for surface values of (a,b) temperature, (c,d) salinity, (e,f) nitrate concentrations and (g,h) chlorophyll concentrations showing sampling stations in the East China Sea of winter 1997 (a, c, e and g) and spring 1998 (b, d, f and h). Solid circles in (b) indicate stations where substrate enrichment experiments were performed. Bold lines in (a–d) indicate the 20°C isotherms and the 32.0 psu isohalines respectively. Dashed lines indicate bottom depth in meters

higher Q_{10} values than algae (Shiah et al. 1999, 2000 and citations therein). Recent studies (White et al. 1991, Shiah et al. 1999 and citations therein) have shown that seasonal bacterial specific growth rates followed the Arrhenius equation in neritic ecosystems with Q_{10} values > 3.0. By analyzing the correlations between bacterial rate parameters and other field variables, Shiah et al. (1999, 2000) suggested that bacterial growth on the inner shelf of the East China Sea (ECS) is not limited by substrate supply but by temperature during cold seasons, while on the outer shelf, the situation is reversed. They also suggested that the Q_{10} for bacterial specific growth rates seemed comparable over a range of temporal and spatial scales. To ascer-

tain how general these phenomena might be in the shelf ecosystem, 2 large area field surveys and 3 experiments with dissolved free amino acid mixture enrichment were conducted in the continental shelf of the ECS in winter and spring.

MATERIAL AND METHODS

Study site. Data were collected from the 2 cruises conducted on the continental shelf of the ECS north of Taiwan (Fig. 1) during December of 1997 (32 sampling stations) and early March of 1998 (34 sampling stations). Seawater was collected from a SeaBird CTD-
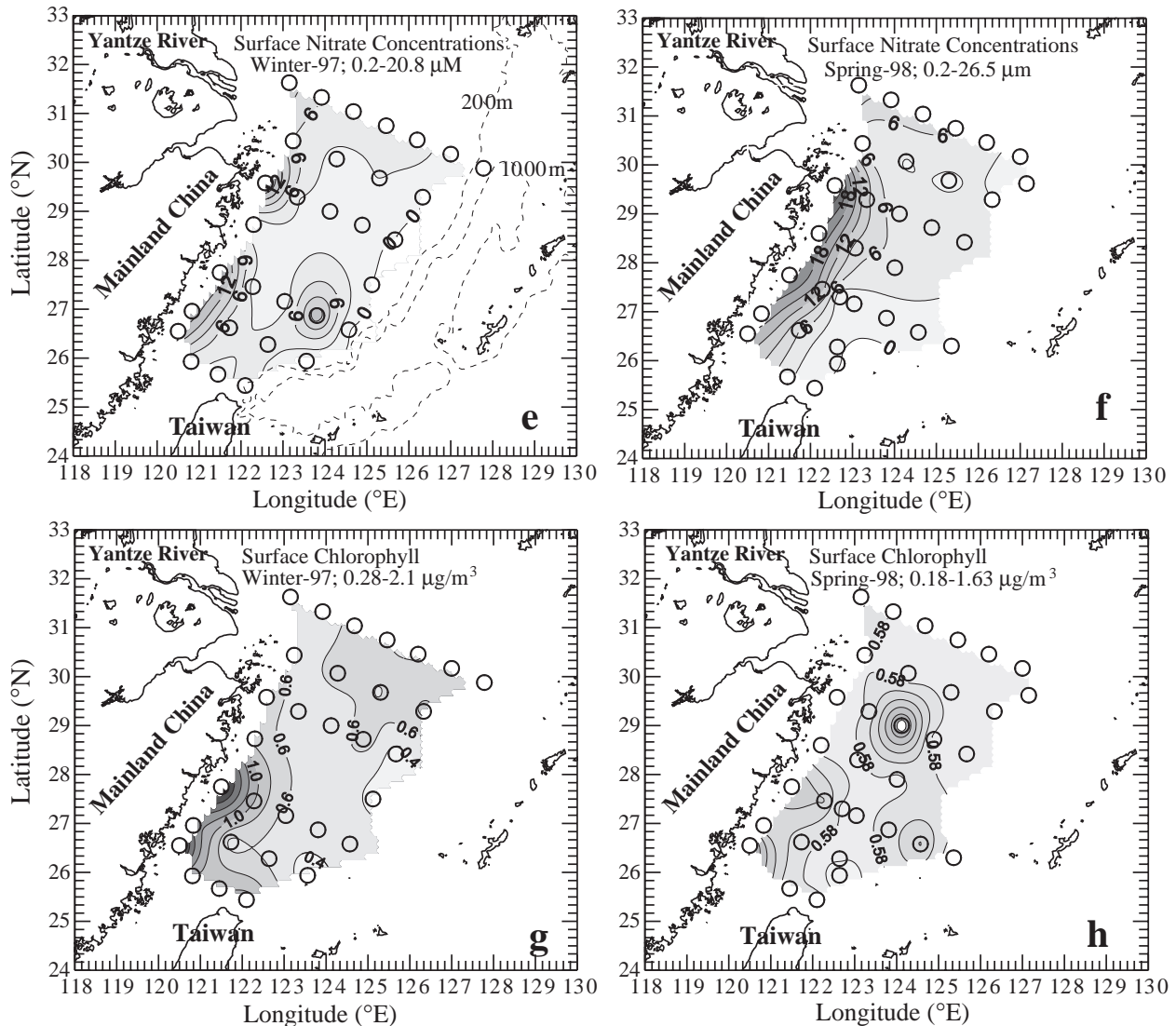
Fig. 1. (Continued)

General Oceanic Rosette assembly with 20 l Go-Flo bottles. Light intensity was measured with a light meter (QSP200L; Biospherical). The depth of the euphotic zone was defined as 1% of the surface light level, and the bottom of the mixed layer was defined as the depth where the temperature was 0.5°C lower than at the surface (Levitus 1982).

Bacterial production, abundance and specific growth rates. Bacterial production and abundance were measured by ³H-thymidine incorporation (Fuhrman & Azam 1982) and acridine orange epifluorescence microscopy (Hobbie et al. 1977) respectively (for details, see Shiah et al. 1999). For each station, duplicate samples were taken from 7 to 11 depths within the mixed layer (Z_m) or the euphotic zone (Z_e). With respect to substrate supply, the inte-

grated bacterial abundance (and production) was obtained by integrating (trapezoidal method) over Z_m or Z_e, depending on which one was deeper at the given station. Bacterial thymidine incorporation rate per cell (bacterial specific growth rate, $B\mu$) was calculated by dividing the integrated bacterial production (IBP) by the integrated bacterial abundance (IBA). For the calculation of the Q_{10} values, IBP and $B\mu$ derived from different sampling stations were natural-log transformed and a linear regression analysis was performed to calculate the slope (b) of lnIBP (and ln$B\mu$) versus sea-surface temperature (SST); the Q_{10} values were then calculated as $Q_{10} = 10^{4.3437b}$.

Substrate enrichment experiments. Experiments were performed on the spring cruise at the 3 sta-

tions (Fig. 1b) that represented the inner-, mid- and outer-shelf waters (Table 1). At each station, whole surface water samples were pre-incubated at *in situ* (Table 1) and 2 to 3 other temperatures (see Fig. 4) in sixteen, 2.0 l opaque polycarbonate bottles for 1 h, which was sufficient to allow adjustment to the new temperature. Then, a dissolved free amino acid mixture (DFAA; 15 amino acids, final conc. = 0.5 μM; Shiah & Ducklow 1994a) was added to 8 bottles (duplicates for each temperature treatment); the remaining bottles were used as controls. Bacterial production and cell abundance were sampled every 3 h for the first 12 h and then sampled every 6 h until the end of the experiment. The end of the lag period was defined as the time when bacterial production values in the DFAA treatments were significantly (p < 0.01, difference usually >20%) higher than those in the controls.

Primary production. Primary production was measured by the ^{14}C assimilation method (Parsons et al. 1984). In brief, 1 dark and 2 light 250 ml clean polycarbonate bottles (Nalgen) were filled with water samples taken from the euphotic zone. After inoculation with $H^{14}CO_3^-$ (final conc. = 10 μCi ml^{-1}), samples were incubated for 2 to 4 h in artificial light. Water temperature was maintained with running seawater. To simulate different light intensities, bottles were wrapped with neutral density filters permitting 85, 50, 25, 10 and 1% of the light to pass through. Following retrieval, the water samples were immediately filtered through Whatman GF/F 25 mm filters under low light and low pressure (<100 mm Hg). The filters were placed in scintillation vials, and 0.5 ml of 0.5 N HCl was added to remove residual $H^{14}CO_3^-$. Radioactivity was counted in a liquid scintillation counter (Packard 1600) after the addition of 10 ml scintillation cocktail (Ultima Gold, Packard) into the vials.

Chlorophyll *a* and nitrate concentrations. Chlorophyll *a* and nitrate concentrations were measured following the methods of Parsons et al. (1984). Water samples for nutrient analyses were frozen immediately with liquid nitrogen in clean 100 ml polypropylene bottles. Nitrate was analyzed with a flow injection analyzer (Gong et al. 2000) and was reduced to nitrite with a cadmium wire, which was activated with a copper sulfate solution. For chlorophyll *a*, 1 to 2 l of seawater were filtered through Whatman GF/F 25 mm 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 (~200 × *g*) rpm for 5 min, the concentrations of chlorophyll *a* in the supernatant were measured on a Turner fluorometer (model 10-AU-005).

RESULTS

Hydrography

The study area was characterized by strong gradients of temperature (Fig. 1a,b; 11 to 26°C), salinity (Fig. 1c,d; 27.20 to 34.78 psu), nutrients (Fig. 1e,f; surface nitrate, <0.2 to 26.5 μM) and high phytoplankton standing crops (Fig. 1g,h; surface chlorophyll ≈ 0.2 to 2.1 mg m^{-3}). Three water masses (Gong et al. 2000 and citations therein) could be identified in the ECS shelf (Table 1). They were the China Coastal Waters (the CCW; cold, eutrophic to mesotrophic with low salinity), the Kuroshio Waters (the KW; warm and oligotrophic with high salinity) and the mid-shelf Mixed Waters (the MW; a mixture of the CCW and KW). Note that during spring, about half of the study area was covered by low salinity (<32 psu; Fig. 1d) waters, which indicated a strong influence from freshwater discharges. For both cruises, the mixed layer (Z_m) depth inside the mid-shelf was deeper than or similar to those of the euphotic zone (Z_e). Depths of Z_e were usually <20 m in the CCW and ~50 m in the MW. In the outer shelf area (the KW), Z_e extended down to ~100 m with a Z_m of ~60 m.

SST was used in our analysis for 2 reasons. SST reflected the spatial location of sampling stations (Fig. 1a,b), that is, the SST increased offshore. In addition, SST was identical to the average mixed layer temperature. Note that in areas adjacent to the Yangtze River, the temperatures in spring 1998 were 2 to 3°C lower than in winter 1997 (Fig. 1b).

Table 1. *In situ* values of measured variables for samples used in substrate enrichment experiments in spring 1998

Variable	Units	China Coastal Waters	Mid-shelf Mixed Waters	Kuroshio Waters
Temperature	°C	11	20	25
Salinity	psu	32.20	34.29	34.78
Nitrate	μM	11.0	0.4	0.25
Chlorophyll	mg m^{-3}	0.87	0.52	0.39
Bacterial TdR incorporation rate	pM h^{-1}	1.67	2.07	1.17
Bacterial abundance	× 10^9 cell l^{-1}	0.79	0.28	0.25
Bacterial turnover rates	× 10^{-21} mol TdR cell^{-1} h^{-1}	0.06	0.21	0.13

Table 2. Intercepts, slopes and Q_{10} values for natural-log transformed depth-integrated bacterial production (lnIBP) and bacterial turnover rates (ln$B\mu$) versus temperature for the <20°C data collected from the 2 cold-season cruises. All equations are significant at the p = 0.01 level

Cruise	Variable	Intercept	Slope (±SE)	Q_{10}	Sample size	R^2
Winter	lnIBP	+2.57[a]	0.10[b] (±0.02)	2.46	20	0.65
1997	ln$B\mu$	−0.48	0.12 (±0.01)	3.41	20	0.83
Spring	lnIBP	+3.69[a]	0.05[b] (±0.01)	1.68	23	0.67
1998	ln$B\mu$	−0.45	0.12 (±0.01)	3.32	23	0.86

[a,b]Different from each other at p = 0.05 level by analysis of covariance

Spatial patterns of bacterial measurements

Depth-integrated bacterial production (IBP) during winter (37 to 91 × 10^{-9} mol TdR m^{-2} h^{-1}) and spring (44 to 104 × 10^{-9} mol TdR m^{-2} h^{-1}) was low in cold (5 to 10°C; inner shelf) and warm (>22°C; outer shelf) water areas (Fig. 2a). Below the 20°C isotherm (areas inside the mid-shelf; Fig. 1b), IBP was higher in spring than in winter. On the outer-shelf, IBP of both cruises decreased with increasing temperature and was positively correlated with the euphotic zone integrated primary production (IPP) in the outer-shelf areas (Fig. 3; r = 0.85, n = 13, p < 0.001). This suggested that substrate supply could be more crucial in controlling bacterial

growth outside the mid-shelf. For the areas with a temperature <20°C, IBP was correlated with temperature (Table 2) but not with IPP (Fig. 3; p > 0.05, n = 46), which indicated that local substrate supply might not be the major controlling factor in regulating the spatial variability of IBP inside the mid-shelf (see also the results of the DFAA enrichment experiments).

In winter, depth-integrated bacterial abundance (IBA; 9 to 15 × 10^{12} cells m^{-2}) showed no pattern with SST (Fig. 2b), salinity or IPP (data not shown). In contrast, spring IBA (10 to 33 × 10^{12} cells m^{-2}) varied more than 3-fold, with higher values observed on the inner-shelf. It decreased offshore with increasing SST (r = −0.88, n = 33, p < 0.01) and salinity (r = −0.67, n = 33, p < 0.01), and then remained more or less constant outside the mid-shelf. No significant relationship was observed between IBA and IPP inside the mid-shelf during spring; however, IBA was positively correlated with IPP (r = 0.63, n = 13, p < 0.001) on the outer-shelf.
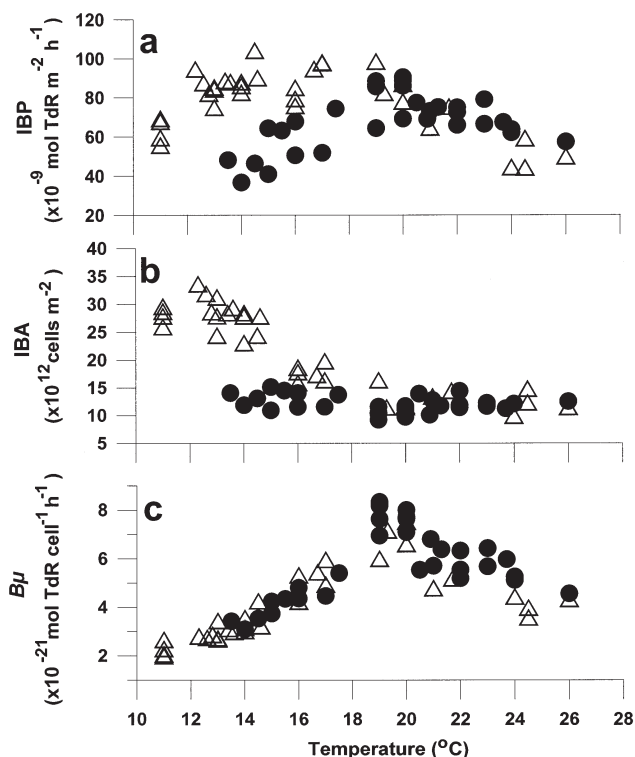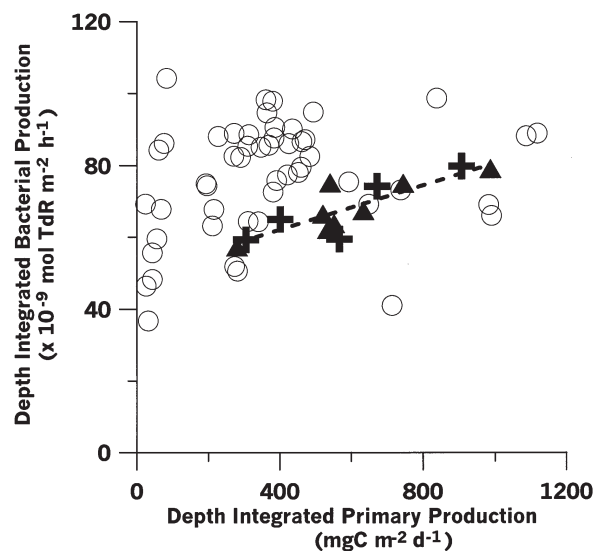

Fig. 2. Depth-integrated (a) bacterial production (IBP) and (b) abundance (IBA) and (c) specific growth rates ($B\mu$) along the temperature gradient in winter 1997 (●) and spring 1998 (△)

Fig. 3. Depth-integrated bacterial production (IBP) versus depth-integrated primary production (IPP). Outer-shelf data (T > 21°C, S > 34.500 psu) are shown for winter 1997 (+) and spring 1998 (▲). The relationship is IBP = 49 + 0.032 (± 0.006) × IPP (R^2 = 0.72, n = 13, p < 0.001)

Bacterial specific growth rates ($B\mu$ = IBP/IBA; 2.0 to 8.3×10^{-21} mol TdR cell^{-1} h^{-1}) of the 2 cruises showed similar patterns with SST (Fig. 2c). Values of $B\mu$ were low (2 to 3×10^{-21} mol TdR cell^{-1} h^{-1}) on the inner-shelf, they peaked at the mid-shelf (7 to 8×10^{-21} mol TdR cell^{-1} h^{-1}) along the 20°C isotherm, and then they decreased to values ca 3 to 4×10^{-21} mol TdR cell^{-1} h^{-1} in the outer-shelf area. For both cruises, no significant relationship was observed between $B\mu$ and IPP inside the mid-shelf. However, $B\mu$ was positively correlated with IPP (r = 0.60, n = 13, p < 0.001) on the outer-shelf.

The relationships between IBP and SST for the <20°C data were significant (Table 2). However, the Q_{10} value for the spring IBP ($Q_{10} = 1.68$) was only 68% of that of the winter IBP ($Q_{10} = 2.46$). This could be ascribed to the different IBA during winter and spring (Fig. 2b; see 'Discussion and conclusions'). In contrast, the Q_{10} values of $B\mu$ for the winter ($Q_{10} = 3.41$) and spring ($Q_{10} = 3.32$) were quite consistent.

Substrate enrichment experiments

Fig. 4 shows that when incubated at *in situ* temperatures (Table 1) the addition of DFAA does not enhance $B\mu$ (or bacterial production) within 21 h in the samples taken from the inner-shelf. On the other hand, $B\mu$ of the samples taken from the mid- and outer-shelf increased rapidly (<3 to 5 h) after the addition of DFAA. Note also that changing incubation temperature had a very similar effect on $B\mu$ in all 3 experiments; the lag periods required for bacteria to respond to DFAA enrichment were negatively correlated with incubation temperatures (p < 0.01).
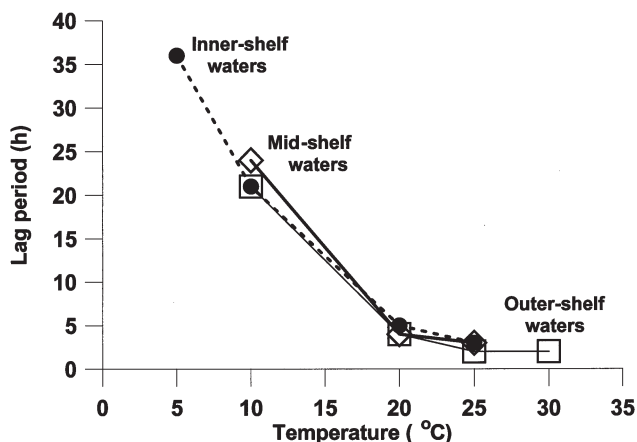

Fig. 4. Temperature effects on the lag period required for bacteria to respond to an enrichment of dissolved free amino acids. (●) Inner-shelf waters; (◇) mid-shelf mixed waters (3 treatments only); and (□) outer-shelf waters

DISCUSSION AND CONCLUSIONS

Several previous studies explicitly addressing spatial (Shiah et al. 1999, 2000), temporal (Shiah & Ducklow 1994b, 1995) and cross-system (White et al. 1991) variation of $B\mu$ showed that the Q_{10} for $B\mu$ varied within a narrow range of 3.13 to 3.42 in neritic ecosystems. All this evidence suggests that temperature dependency of $B\mu$ might be comparable across different temporal and spatial scales. A significant correlation of $B\mu$ with temperature indicates that during the cold seasons temperature, instead of substrate supply, probably was the major limiting factor for $B\mu$ inside the mid-shelf. In the outer-shelf region, the situation might be reversed. Values of IPP (r = −0.88, n = 13, p < 0.05), IBP and $B\mu$ decreased with increasing temperature outside the mid-shelf (Fig. 2a,c), and this implies that as the system becomes more oligotrophic (Fig. 1e,f), substrate control of bacterial growth becomes more significant (Figs. 3 & 4; White et al. 1991, Shiah et al. 1999).

Different IBA values observed within the inner-shelf on the 2 cruises might be related to the different magnitude of interactions (mixing) between the KW and the CCW in the ECS shelf. During winter, the intrusion of the oligotrophic KW (Gong et al. 1996) into the ECS shelf and the low discharge rate of the Yantze River (Fig. 1c) might result in low IBA. During spring, the KW withdrew from the shelf and river discharge rates started to increase as indicated by a larger plume of cold, low salinity water along the coast of mainland China during spring 1998 (Fig. 1b,d), this might lead to more riverine bacteria in the inner-shelf area. Different strengths of removal processes (bacterivory and viral lysis) during these 2 cruises might also have resulted in distinct IBA. However, no conclusion could be made due to the lack of protozoan and viral data. Interestingly, although the values of spring IBP and IBA observed in the inner shelf (Fig. 2a,b; <14°C) were at least 2 times higher than those of the winter, $B\mu$ of the 2 cruises behaved almost exactly the same with changing temperature (Fig. 2c). This once again indicates that the temperature response of $B\mu$ seems to be constant over the seasons.

The substrate enrichment experiments (Fig. 4) and the relationship of IPP versus IBP (Fig. 3) support the deduction of the transition of temperature control inside the mid-shelf to substrate control outside the mid-shelf. These findings also support the conclusion of several previous studies (Hollibaugh 1979, Wiebe et al. 1992, 1993), which suggested that the substrate effects on bacterial growth were temperature dependent. In addition, strong temperature regulation on $B\mu$ occurred only when substrate supply was high (Berman et al. 1994, Shiah & Ducklow 1994a).

Satellite remote sensing has become very promising in estimating primary productivity, although quite a few obstacles are still to be overcome. One intriguing question concerns whether SST, derived from either satellite or cruise measurement, can be used to estimate bacterial production for coastal environments within a limited temperature range and seasons. The distinct temperature response of IBP of the 2 cruises (Table 2) rules out the possibility of using SST to estimate IBP directly. However, the constancy of the Q_{10} value of $B\mu$ may allow us to model IBP based on the measurements of SST and IBA, which can be quickly acquired by flow cytometry (Sieracki & Viles 1990, Li et al. 1993). The $B\mu$ versus temperature ($\ln B\mu = -0.42 + 0.122 \pm [0.02] \times$ SST, n = 22, $R^2 = 0.78$, p < 0.01) relationship derived previously (Shiah et al. 1999) for the southern ECS was adopted to simulate IBP in this study. The modeled IBP and the measured IBP agree very well (Fig. 5), with slope and R^2 values of 0.87 ± 0.08 and 73%, respectively. The total difference {[($\sum$ measured IBP $-\sum$ modeled IBP)/$\sum$ measured IBP] × 100%} between them was 19%.

There are 2 major limitations to this approach. It can be applied only to areas of the mid-shelf during cold seasons, and measurements of bacterial biomass or abundance are still required. However, for some modelers who do not have access to and some scientists who are not familiar with the use of (or not allowed to use) radioisotopes (i.e. ^{3}H-thymidine and ^{3}H-leucine) to estimate bacterial production, this approach may offer an alternative means of deriving IBP with an accuracy no less than ca 80% (Fig. 5).
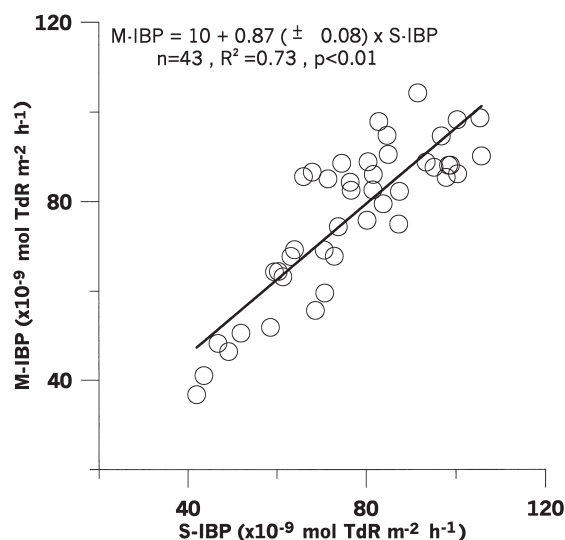
Overall, this study systematically demonstrated a well-known but not fully developed theory which indicates that the temperature dependency of bacterial specific growth rates in high productivity ecosystems is comparable over different temporal and spatial scales during seasons (and areas) in which substrate supply is not limiting. With bacterial biomass data and reliable relationships of $B\mu$ with temperature, the depth-integrated bacterial production can be quickly and easily calculated, although limitations to this application are noted.

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Fig. 5. Measured depth-integrated bacterial production (M-IBP) versus the simulated values (S-IBP). The $B\mu$ versus SST curve ($\ln B\mu = -0.40 + 0.122 [\pm 0.02] \times$ SST) was adopted from Shiah et al. (1999)

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