Meso-scale spatial variation in bacterial abundance and production associated with surface convergence and divergence in the NE equatorial Pacific

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ABSTRACT: To elucidate the effect of the water column structure associated with surface water convergence and divergence on bacterial parameters, we investigated the meso-scale spatial variations in bacterial abundance and production in the northeast equatorial Pacific from 5 to 12° N (longitude 131° 30' W). The area is characterized by 3 major surface currents: the South Equatorial Current (SEC), North Equatorial Counter Current (NECC), and North Equatorial Current (NEC). Surface water convergence occurred at the boundary of the westward-flowing SEC and eastward-flowing NECC, and divergence occurred at the boundary of the NECC and westward NEC. A vertically well-mixed water column observed in the SEC/NECC area appeared to be high in nutrients and chlorophyll *a* (chl *a*), whereas the strongly stratified NEC area had a relatively low trophic status, with a surface layer depleted of nitrates and chl *a*. Accordingly, bacterial abundance, production, and mean biomass turnover rates, as well as grazing by heterotrophic nanoflagellates (HNF) in the well-mixed SEC/NECC area were consistently higher than in the highly stratified NEC area. The greater bacterial production and HNF grazing in the SEC/NECC region imply that heterotrophic bacteria are a significant trophic link between dissolved organic carbon and higher trophic levels in the microbial loop of the SEC/NECC area. Our results indicate that changes in the water column structure in relation to convergence and divergence play a key role in enhancing the amount of nutrients and chl *a*, thereby stimulating bacterial abundance and production and intensifying the trophic link between heterotrophic bacteria and heterotrophic protists in the microbial food web in the study area.

KEY WORDS: Bacterial production · Convergence · Divergence · Meso-scale spatial variations · Northeast equatorial Pacific

INTRODUCTION

Heterotrophic bacteria play a significant role in the biogeochemical carbon cycle and the microbial food web. Bacteria are responsible for the rapid turnover of dissolved organic matter from various sources (Kirchman et al. 1991, Nagata 2000). Bacterial biomass in the oligotrophic open ocean is substantial among planktonic communities (Fuhrman et al. 1989, Cho & Azam 1990, Li et al. 1992, Caron et al. 1995), implying that bacteria are a major carbon-sequestering planktonic component in the open ocean. In the microbial food web, heterotrophic bacteria also serve as a significant trophic link between dissolved organic carbon (DOC) and heterotrophic nanoprotists (HNP) and small ciliates, which are then consumed by metazoan microzooplankton (Azam et al. 1983, Sherr et al. 1986).

Bacterial abundance and production, as well as the relative significance of bacterioplankton in the biogeochemical carbon cycle and microbial food web, are largely affected by water column structures that control the physical stability and nutrient conditions within a water mass (Holligan et al. 1984, Ducklow 1986, Kiørboe et al. 1990, Hyun & Kim 2003). Other

studies have also recognized that the HNP grazing that regulates bacterial biomass and production, and thereby determines the ecological role of bacteria in microbial food web processes, varied with the trophic, i.e. nutritional, conditions of water columns (Dufour & Torréton 1986, Sanders et al. 1992, Ducklow 2000). Therefore, a thorough interpretation of variations in bacterial abundance and production requires a comprehensive understanding of the water column structures controlling the physico-chemical properties of water masses.
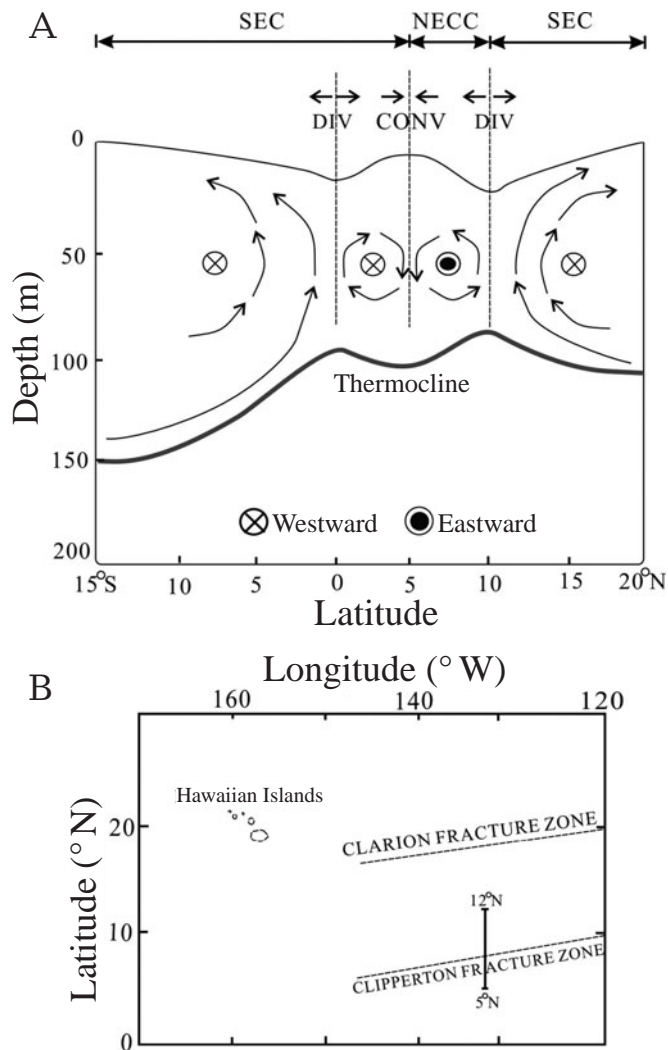

Fig. 1. (A) Schematic presentation of the surface current system in the equatorial Pacific and (B) a map showing the study area. SEC: westward-flowing South Equatorial Current; NECC: eastward-flowing North Equatorial Counter Current; NEC: westward-flowing North Equatorial Current. Surface divergence (DIV) occurs along the equator and at the boundary of the NECC and NEC, whereas surface water convergence (CONV) occurs at the boundary of the SEC and NECC

The surface waters of the northeast equatorial Pacific (5 to 20° N) are influenced by 3 major currents (Pickard & Emery 1982; Fig. 1A): the westward-flowing North Equatorial Current (NEC), the eastward-flowing North Equatorial Counter Current (NECC), and the westward-flowing South Equatorial Current (SEC). The Coriolis effect deflects the westward NEC and SEC to the north and the eastward NECC to the south. Regional surface water divergence (DIV) occurs along the boundary of the NEC and NECC, whereas surface water convergence (CONV) occurs along the boundary of the SEC and NECC. The water column structures of the DIV area are characterized by relatively lower sea level and shallower thermocline depths compared to the surrounding water masses, whereas the CONV area has a higher sea level and a deeper thermocline (Pickard & Emery 1982; Fig. 1A). The CONV and DIV events disrupt the vertical stability of the water column and add nutrient-rich subsurface waters to the nutrient-depleted surface mixed layer, thereby enhancing biological productivity (Mann & Lazier 1991) and trophic interaction between prey and predator organisms (Barange et al. 1998, Bradford-Grieve et al. 1998, James & Hall 1998).

A substantial amount of information on the spatial and temporal variations in bacterial abundance and production and the potentially limiting resources controlling bacterial production in the equatorial Pacific has been accumulated during the US JGOFS Process Study in the Equatorial Pacific (EqPac) Program (Ducklow et al. 1995, Kirchman et al. 1995, Chung et al. 1996, Landry et al. 1996, Rich et al. 1996, Landry & Kirchman 2002). To our knowledge, however, relatively few studies have focused on the meridional meso-scale spatial variation in the properties of bacteria and protozoans and the significance of the trophic linkage between bacteria and heterotrophic protists in association with water column structure in the northeast equatorial Pacific (5 to 12° N), where 3 dynamic surface currents control the physico-chemical parameters (Hyun et al. 1998, Yang et al. 2004). Thus, the objective of this study was to elucidate the spatial variations in bacterial abundance, production, and biomass turnover rates in relation to surface water CONV/DIV in the northeast equatorial Pacific. Based on the higher bacterial abundance and production together with the higher protozoan biomass and grazing impact in the well-mixed CONV/DIV area, we also discussed how variations in the water column structures were responsible for regulating the intensity of the trophic link between bacterioplankton and HNP in the microbial food web process.

MATERIALS AND METHODS

Study area. The study area is considered to be a transition zone between the classic high-nitrate, low-chlorophyll *a* (HNLC) equatorial Pacific and the oligotrophic, subtropical north Pacific gyre (SNPG) found from 15 to 35° N (Murray et al. 1995, Karl 1999). The nitrate concentration in the surface mixed layer (<1 µM) is therefore lower than in the classic HNLC environment, but higher than in the oligotrophic SNPG characterized by nitrate concentrations of <5 nM (Karl 1999). As a part of the Korea Deep Ocean Study program in 1998 (KODOS-98), we conducted water sampling at every 1° of latitude between 5 and 12° N (longitude 131.5° W) in the northeast equatorial Pacific (Fig. 1B), where interactions between 3 surface currents, the SEC, NECC, and NEC, largely determine the physico-chemical and microbiological parameters.

Environmental parameters. Water temperature and salinity were measured using a CTD meter (SBE 911 Plus, Seabird Electronics). Seawater samples were collected for chemical and microbiological analyses using Niskin bottles attached to a rosette sampler. Sampling bottles were first washed with 10% HCl and rinsed with Milli-Q water and surface seawater. Samples for the nitrate analysis were collected using acid-washed polyethylene bottles and stored at –20°C until they were processed. Nitrate was analyzed according to Parsons et al. (1984). Following acetone extraction, chlorophyll *a* (chl *a*) concentrations were measured using a spectrophotometer (Parsons et al. 1984). In addition, *in situ* chl *a* fluorescence was measured using an underwater fluorometer (SeaTech) to depict the vertically continuous distributions of chl *a*. The chl *a* concentrations were then calculated from the linear relationship between the *in situ* fluorescence (flu) and the spectrophotometrically measured concentrations of chl *a* with the following equation: chl $a = 0.2944 \times$ flu $-$ 0.2745, $r^2 = 0.83$, n = 101. Phytoplankton carbon biomass was estimated according to Caron et al. (1995) using a C:chl *a* ratio of 60 for depths of 0 to 30 m, a ratio of 40 for depths between 30 and 60 m, and a ratio of 30 for depths below 60 m.

Bacterial abundance and production. Water samples for bacterial cell counts were preserved with glutaraldehyde (final concentration 1%) and stored at –20°C until they were processed (Hyun & Yang 2003). Samples were stained with 4′,6-diamidino-2-phenyl-indole (DAPI; Porter & Feig 1980), filtered through Nuclepore filters (0.2 µm pore size, black), and mounted on slides with immersion oil (Cargille Type A). The bacteria were counted using an epifluorescence microscope (Zeiss Axioskop) equipped with a mercury lamp (HB-10101 AF), an ultraviolet (UV) excitation filter, and a BA 420 barrier filter. At least 20 microscopic fields were examined. Bacterial carbon biomass (BCB) was estimated from bacterial cell counts using a conversion factor of 12 fg C cell^{-1} (Fukuda et al. 1998).

The heterotrophic bacterial production was estimated from the incorporation rate of ^{3}H-thymidine (^{3}H-TdR; Fuhrman & Azam 1980, 1982). Duplicate 20 ml water samples were incubated with ^{3}H-TdR (final concentration 5 nM thymidine, New England Nuclear, NET 027X) at *in situ* water temperature for 30 min in disposable plastic centrifuge tubes. The samples were poured into 50% ice-cold trichloroacetic acid (TCA) solution (final concentration 5%), and TCA-insoluble macromolecules were extracted in an ice bath for 15 min. The samples were collected by vacuum filtration on 0.2 µm cellulose nitrate membrane filters (MFS) and rinsed 3 times with ice-cold 80% ethanol. The filters were placed in scintillation vials with 10 ml of scintillation cocktail (Lumagel Safe, Lumac-LSC), and the radioactivities of the TCA-insoluble macromolecules were determined using a liquid scintillation counter (LKB, RackBeta II). Samples treated with 10% TCA before the addition of ^{3}H-TdR were used as controls. To convert TdR measurements into bacterial cell production, the conversion factor of 2.15×10^{18} cells mol^{-1} was adopted from the JGOFS EqPac studies (Kirchman et al. 1995).

Substrate-enriched incubation experiment. To elucidate the effect of substrate enrichment on bacterial production in the SEC/NECC and NEC regions, time-course incubation experiments were designed. Surface water samples were collected at depths of 30 m at 5° N (i.e. CONV area) in the vertically well-mixed SEC/NECC area characterized by relatively high nutrient and chl *a* concentrations and at 10° N in the highly stratified NEC area with low nutrient and chl *a* concentrations. The seawater samples were first filtered through pre-combusted (400°C) GF/F filters and then mixed with ambient seawater (9:1; v/v) to minimize the grazing impact on bacterial abundance (Kirchman et al. 1991). The water samples were distributed into 2 l acid-washed polycarbonate bottles and manipulated with 2 ml of the plankton extract dissolved substrates (PEDS). The water samples were then incubated in the dark at *in situ* temperature by circulating in ambient surface seawater. Subsamples for bacterial cell counts were collected over time. The PEDS were obtained following modified methods of Cherrier et al. (1996). Natural phytoplankton and zooplankton assemblages were collected using plankton nets with a mesh size of 58 and 300 µm, respectively. The plankton samples were mixed together, placed in an incubator at 40°C for 2 h to accumulate extracellular metabolic products, and then filtered through pre-combusted (400°C) GF/F filters to remove plankton and other particles. These PEDS contain various labile substrates, such as amino

Table 1. Meridional variation of the depth-integrated (to pycnocline depth) of phytoplankton carbon biomass (chl–C), bacterial carbon biomass (BCB), and heterotrophic nanoflagellates (HNF carbon biomass), and the rates of bacterial production (BP), bacterial biomass turnover and HNF grazing. TdR: thymidine. For abbreviations of water currents, see Fig. 1. –: no data

Latitude (°N)	Water regime (m)	Pycnocline range (m)	Thermocline range (m)	NO₃-N (mmol N m⁻²)	Chl–C (mmol C m⁻²)	BCB (mmol C m⁻²)	BP (nmol TdR m⁻² h⁻¹)	BP (mmol C m⁻²)	Biomass turnover rate (d⁻¹)	HNF[a] (mmol C m⁻² d⁻¹)	HNF grazing rate on bacteria Ingestion rate (cells HNF⁻¹ h⁻¹)	Grazing rate (cells l⁻¹ h⁻¹)
5	SEC	50–120	60–120	962	118	54	541	27.9	0.51	11	6.14	2.05×10^6
6	SEC/NECC	50–150	120–150	1224	145	55	413	21.3	0.39	10	–	–
7	NECC	50–120	100–140	533	101	42	355	18.3	0.44	9	–	–
8	NECC/NEC	50–120	50–120	771	73	37	226	11.7	0.32	8	–	–
9	NEC	90–120	90–120	624	58	27	248	12.8	0.47	10	–	–
10	NEC	85–100	90–100	574	52	37	150	7.7	0.26	7	3.89	1.04×10^6
11	NEC	90–100	90–100	810	39	28	141	7.3	0.30	6	–	–

[a]Data re-calculated from Yang et al. (2004)

acids, carbohydrates, and ammonium, that stimulate bacterial growth (Münster & Chróst 1990, Sundh 1992, Cherrier et al. 1996, Strom et al. 1997, Nagata 2000).

Grazing by HNF. HNFs (2 to 5 µm in size) were chosen for bacteria ingestion experiments, as they were likely the principle predators of bacteria in the oligotrophic open ocean (Calbet & Landry 1999). Observations of HNF grazing on bacteria were made using fluorescently labeled bacteria (FLB). The FLB were prepared by staining natural bacteria samples collected 3 to 4 d before the experiments. Natural bacteria were concentrated on 0.2 µm filters following the pre-filtration of 2 l of seawater through 0.7 µm filters to remove larger size autotrophic picoplankton such as *Prochlorococcus* (0.5 to 2.0 µm) and *Synechococcus* (1.0 to 2.0 µm) (Table 1 in Sherr & Sherr 2000). As the concentration of cells by centrifugation can cause significant losses of small bacterial cells and thereby alter the original size distribution (Sherr et al. 1987), the concentrated bacteria cells were heat-killed and stained with 5-(4, 6-dichlorotriazin-2yl) aminofluorescein (DTAF), following the methods of Sherr et al. (1987). Water samples for the grazing experiments were collected at a depth of 30 m at 5 and 10° N and gently filtered through a 200 µm mesh. The FLB uptake experiments were carried out in duplicate in 300 ml bottles presoaked in 10 % HCl and rinsed well with Milli-Q water. FLB stock (1 or 2 ml) with 7 to 10 % bacterial abundance was added to the 300 ml bottles. The grazing experiment was conducted in the dark at *in situ* temperature. Subsamples of 40 ml were taken from each bottle at 0, 10, 20, 30, 45, and 60 min, preserved with a mixture of alkaline Lugol solution and borate-buffered formalin (Sherr et al. 1989), and kept refrigerated until they were examined microscopically. The subsamples were stained with DAPI (final concentration 10 µg ml⁻¹) and filtered onto 0.8 µm polycarbonate filters (black, 25 mm diameter); the filters were mounted for immediate epifluorescence microscopy. The filters were first observed under UV light at a magnification of ×1000, and, when an HNF was located, the incident light was changed to blue light, which allowed for the counting of FLB inside the HNF. The number of ingested FLB HNF⁻¹ h⁻¹ (FLB uptake rate) was calculated from the slope of ingested FLB HNF⁻¹ versus incubation time for each bottle. We calculated grazing rates on heterotrophic bacteria (cells l⁻¹ h⁻¹) and ingestion rates (cells HNF⁻¹ h⁻¹), as described by Cho et al. (2000). The coefficients of variation of the slopes from duplicate bottles were 4.7 % at 5° N and 6.4 % at 10° N.

Data analysis. The surface layers were defined based on the bottom of the pycnocline, which generally coincided with the thermocline, nitracline, and euphotic depth, i.e. approximately 100 to 150 m (Table 1, Figs. 2 & 3). Area-based inventories of nitrate,

chl *a*, and bacterial biomass and production were obtained from the integration of volume-based values at depths down to the bottom of the surface layer, i.e. the bottom of the pycnocline layer. The mean bacterial biomass turnover rates, equivalent to the mean bacterial growth rates, were estimated by dividing the depth-integrated bacterial production by the integrated bacterial biomass (Kirchman et al. 1995).

RESULTS

Hydrographic conditions

The water temperature and salinity ranged from 11.20 to 28.51°C and from 33.81 to 35.02 psu, respectively. The vertical profiles of water temperature, salinity, and density (Fig. 2) indicated that water temperature was the major factor determining water column density in the study area. The most pronounced physical features that appeared in the upper 200 m were: (1) a weak, broad, seasonal thermocline between 5 and 8°N and (2) a highly stratified water column with a sharp thermocline between 9 and 12°N. A weak seasonal thermocline within 200 m depth in the stations located from 5 to 8°N suggested that the

water mass was vertically well mixed. This vertical mixing was associated with a surface water convergence resulting from the shear between the westward-flowing SEC and the eastward-flowing NECC (Johnson 1996, Archer et al. 1997). The deepest thermocline (approximately 150 m) appeared at 6°N, where CONV occurred at the boundary of SEC and NECC. On the other hand, DIV resulted in a shallow seasonal thermocline at 8°N, where the westward-flowing NECC meets the eastward-flowing NEC (Pickard & Emery 1982). The vertical profiles of water temperature and density in the study area in July 1998 indicated that the water columns could be divided into 2 categories: a well-mixed water mass resulting from surface water convergence between 5 and 7°N (SEC/NECC area) and a highly stratified water column between 9 and 12°N (NEC area; Fig. 2).

Nitrate and chl *a*

NO_3^- levels in the surface waters of the stratified NEC area were depleted by biological uptake and by the deep seasonal thermocline, which ultimately blocks the supply of limiting nutrients from below (Fig. 3). In contrast, a relative abundance of NO_3^- was
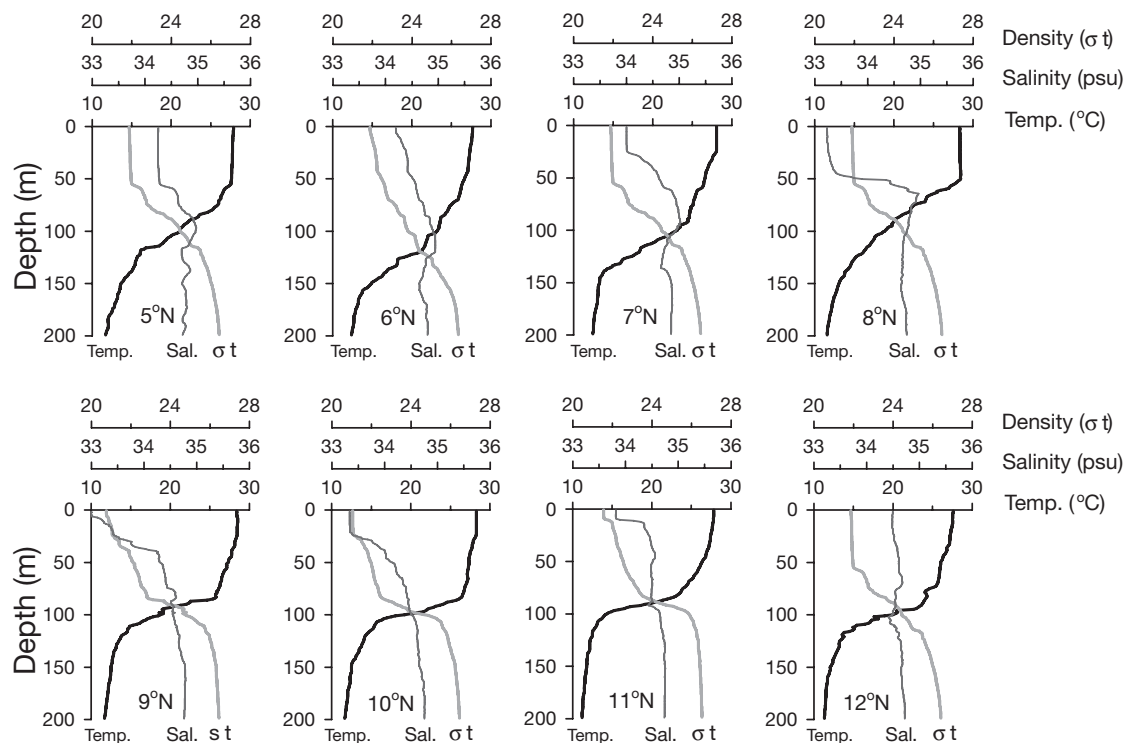

Fig. 2. Vertical distributions of temperature, salinity, and density. Surface water convergence is evident from the weak vertical density gradient in the SEC/NECC area from 5 to 7°N, whereas the NEC area is characterized by a strong vertical density gradient from 9 to 12°N. A divergence center with a shallow thermocline depth appears at 8°N
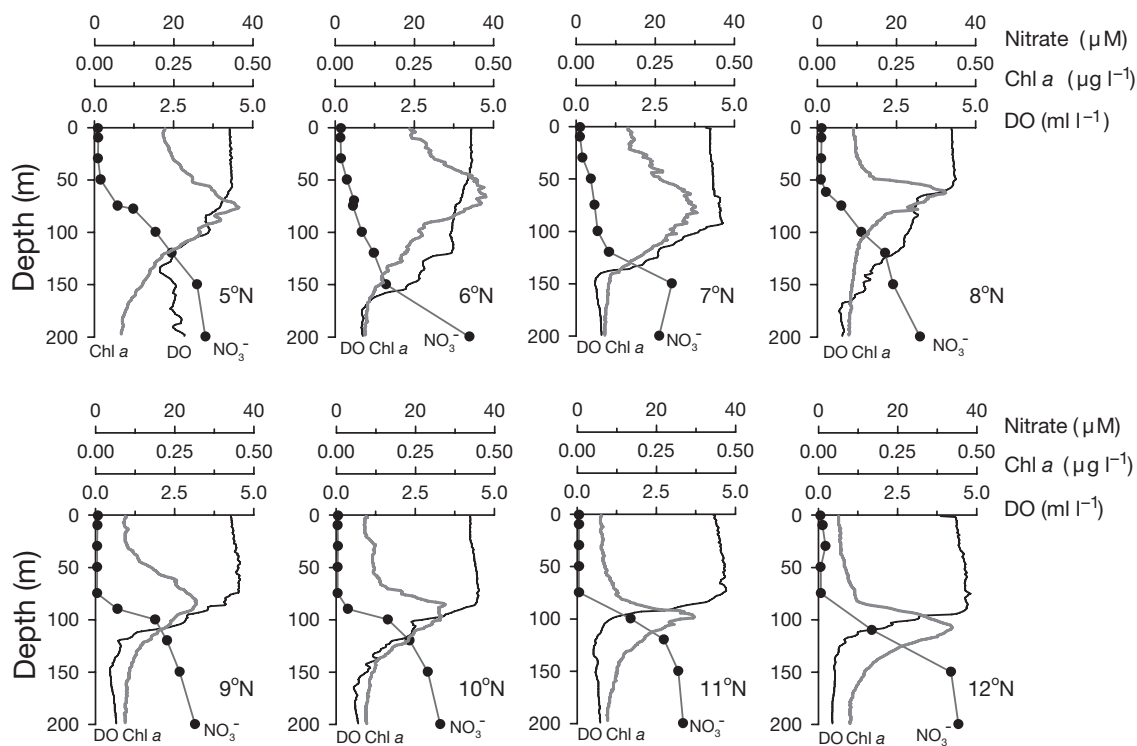
Fig. 3. Vertical distributions of nitrate (NO_3^-), chlorophyll a (chl a), and dissolved oxygen (DO)

observed in the well-mixed SEC/NECC area. The northern part of the study area (9 to 12° N) had nitrate concentrations <1 µM, somewhat different from the typical HNLC environment of the equatorial Pacific (Murray et al. 1995). Inventories of NO_3^- integrated down to the surface layer depth ranged from 574 to 1224 mol N m^{-2} (mean: 785 mol N m^{-2}). Inventories of NO_3^- at the well-mixed SEC/NECC area (mean: 906 mol N m^{-2}) were higher than at the highly stratified NEC area (mean: 669 mol N m^{-2}; Table 1).

Concentrations of chl a ranged from 0.09 to 0.48 µg l^{-1} and appeared to be influenced by the physico-chemical conditions of the water column (Fig. 3). Depth-integrated phytoplankton carbon biomass (chl–C) ranged from 39 to 145 mmol C m^{-2} (mean: 83.7 mmol C m^{-2}). Chl–C in the well-mixed SEC/NECC area was higher (mean: 121.3 mmol C m^{-2}) than in the highly stratified NEC area (mean: 49.7 mmol C m^{-2}; Table 1), which was associated with the relative abundance of nutrients supplied through the weak seasonal thermocline (Figs. 2 & 3). The subsurface chl a maximum (SCM) layer, which forms at depths where both light and nutrient conditions are suitable for phytoplankton growth, generally occurred at the thermocline depth. The SCM layers in the NEC stations were observed at depths between 90 and 110 m, with a sharp vertical gradient in chl a concentrations, while the SCM layers in the mixed

stations appeared to be broader, in agreement with the broad formation of the seasonal thermocline and nitracline (Figs. 2 & 3). Overall, the distribution of physico-chemical and biological parameters was closely associated with water column structures. The mixed SEC/NECC area appeared to be high in nutrients and chl a, whereas the strongly stratified NEC area showed relatively lower trophic status, with a surface layer deplete of nitrates and chl a (Fig. 3).

Bacterial abundance and production

The bacterial cell numbers in the surface water columns ranged from 4.20×10^7 to 6.26×10^8 cells l^{-1} (mean: 2.85×10^8 cells l^{-1}), and bacterial production ranged from 0.14 to 4.89 pM TdR h^{-1} (mean: 1.95 pM TdR h^{-1}; Fig. 4). The distribution of bacterial abundance and production appeared to be controlled by the physico-chemical properties in the water column (Figs. 2 & 3), with higher values in the well-mixed SEC/NECC area. Depth-integrated BCB within the surface layer ranged from 27 to 55 mmol C m^{-2} (mean: 40.0 mmol C m^{-2}; Table 1). Bacterial biomass in the well-mixed SEC/NECC region (mean: 50.3 mmol C m^{-2}) was higher than that in the stratified NEC region (mean: 30.7 mmol C m^{-2}).

Bacterial cell number ((cells l^{-1}) x10^8)

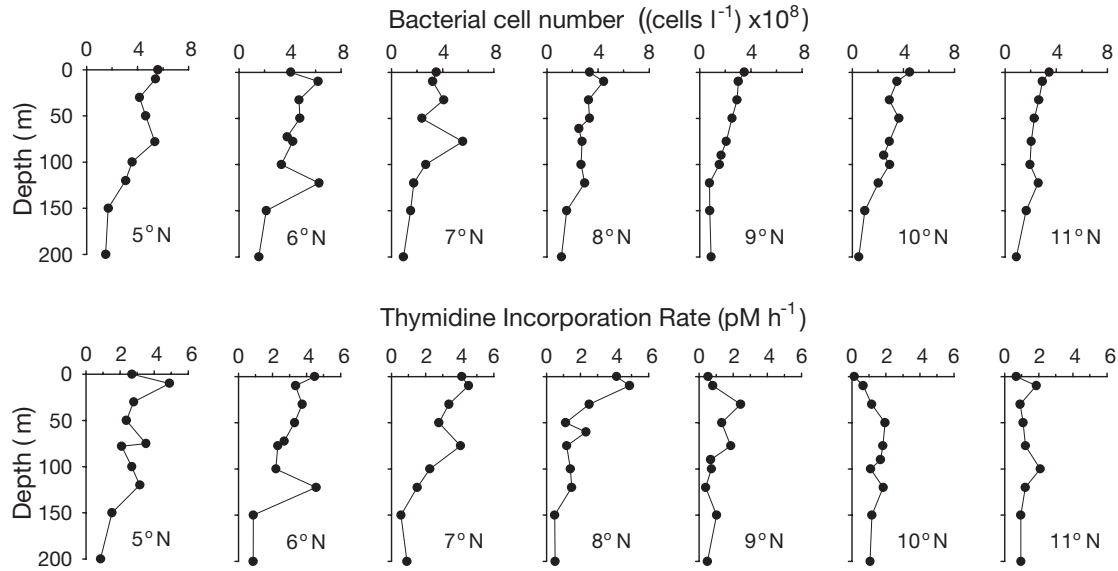Thymidine Incorporation Rate (pM h^{-1})

Fig. 4. Vertical distributions of total prokaryotic cell number and heterotrophic bacterial production

Depth-integrated bacterial production ranged from 141 to 541 nmol TdR m^{-2} h^{-1} (mean: 296 nmol TdR m^{-2} h^{-1}), and was also higher in the SEC/NECC region (mean: 436 nmol TdR m^{-2} h^{-1}) than in the stratified NEC region (mean: 180 nmol TdR m^{-2} h^{-1}). The bacterial biomass turnover rates, estimated by dividing bacterial production by bacterial biomass, ranged from 0.26 to 0.51 d^{-1} (mean: 0.38 d^{-1}), and were higher in the SEC/NECC region (mean: 0.45 d^{-1}) than in the stratified NEC region (mean: 0.34 d^{-1}; Table 1). Higher turnover rates in the SEC/NECC area were a result of the relatively higher bacterial production.

PEDS enrichment experiment

The enrichment incubation experiment investigated the response of bacterial populations to the addition of resources directly extracted from natural plankton assemblages. Under the minimized grazing conditions, bacterial cell numbers in both PEDS-amended and unamended samples increased with time at both stations (Fig. 5). In unamended samples, the bacterial cell increase rate was 2 times higher at the 5°N station (5349 cells ml^{-1} h^{-1}) in the well-mixed SEC/NECC than at the nutrient-depleted 10°N station (2923 cells ml^{-1} h^{-1}) in the stratified NEC area. In contrast, the increase rate in bacterial cell numbers in PEDS-amended samples was 2 times higher at the 10°N station (22 938 cells ml^{-1} h^{-1}) than at the 5°N station (12 500 cells ml^{-1} h^{-1}). The results indicated that bacterial production was more resource-limited in the highly stratified NEC area (10°N) than in the well-mixed SEC/NECC area with higher chl a concentrations.

Biomass structure

The ratio of BCB to chl–C ranged from 0.19 to 0.96 (mean: 0.48), and increased with decreasing chl a and nutrient concentrations (Fig. 6A). This general relationship between BCB/chl–C and the trophic condi-
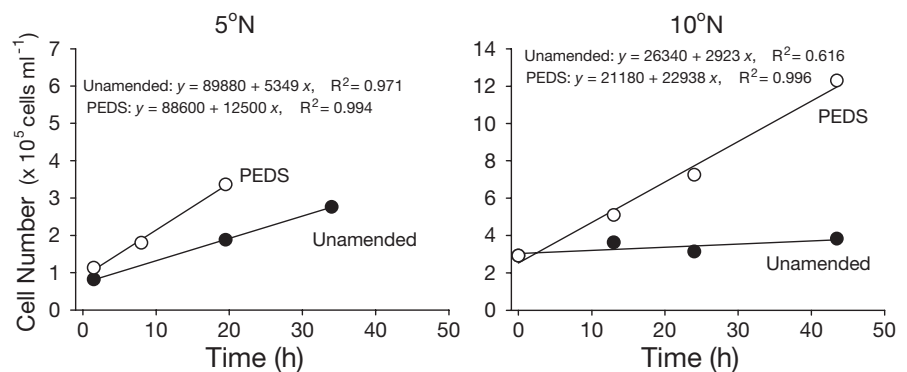

Fig. 5. Variations in bacterial abundance in the plankton extract dissolved substrate (PEDS)-amended incubation experiment in the well-mixed SEC/NECC area at 5°N and the highly stratified NEC area at 10°N
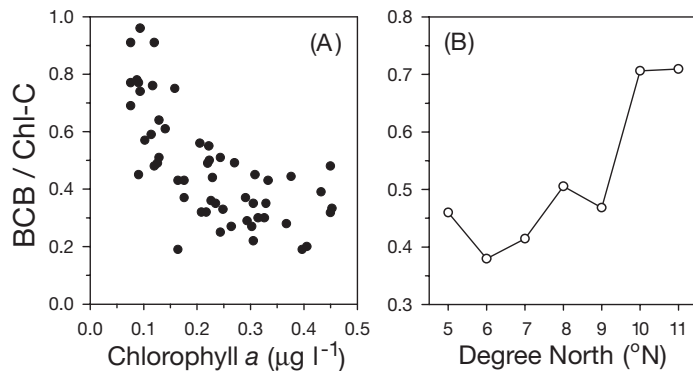
Fig. 6. Relationship between bacteria carbon biomass (BCB) and phytoplankton carbon biomass (chl–C). (A) Variations in BCB/chl–C with chl *a* concentrations and (B) meridional variations in BCB/chl–C

tions of the water column was clearer when the depth-integrated BCB/chl–C ratio was plotted against sampling stations (Fig. 6B). The ratio ranged from 0.38 to 0.71 (mean: 0.52), and was higher in the NEC region (mean: 0.63), with relatively high chl *a* and nutrient concentrations, than in the SEC/NECC area (mean: 0.42).

Ingestion and grazing rates of HNF

The ingestion rates of HNF on bacteria were 3.89 cells HNF^{-1} h^{-1} at 10° N and 6.14 cells HNF^{-1} h^{-1} at 5° N (Table 1). The grazing rates of the HNF population were 1.04×10^6 cells l^{-1} h^{-1} at 5° N and 2.05×10^6 cells l^{-1} h^{-1} at 10° N. The rates were consistently higher in the mixed SEC/NECC areas, where bacteria and HNF abundance were higher, than in the stratified NEC areas. Despite the different ingestion and

grazing rates in the SEC/NECC and NEC regions, estimated HNF bacterivory appeared to be similar; HNF ingested 31.4 and 38.4% of the bacterial production at 5° N (SEC/NECC region) and 10° N (NEC region), respectively (Table 2). The removal rates in this study were higher than those reported in the Antarctic (Becquevort 1997) and Arctic regions (Sherr et al. 1997), but were within the range reported for other oligotrophic open ocean areas (Christaki et al. 1999, 2001, Cho et al. 2000). The results implied that HNF are an important trophic link between bacteria and microzooplankton in the northeast equatorial Pacific (Yang et al. 2004).

DISCUSSION

The major findings from the meso-scale spatial investigation of the physico-chemical and microbiological parameters were that: (1) the water column structures in the study area were clearly categorized as a well-mixed water mass, resulting from surface water convergence between 5 and 7° N (SEC/NECC area) and a highly stratified water column between 9 and 12° N (NEC area) (Fig. 2); (2) the well-mixed SEC/NECC area appeared to be high in nutrients and chl *a*, whereas the strongly stratified NEC area had a relatively low trophic status, with a surface layer depleted of nitrates and chl *a* (Fig. 3); and consequently (3) the bacterial parameters (i.e. abundance, production, and biomass structure) and intensity of HNF grazing differed between the well-mixed SEC/NECC area and the highly stratified NEC area (Table 1, Figs. 3, 4 & 6).

In the northeast equatorial Pacific, the range and location of each current system, which determine the scale and location of divergence and convergence, vary both temporally and spatially (Pickard & Emery 1982). In the summer, the NECC in the northeast equatorial Pacific is normally observed from 3 to 8° N. During the EqPac cruise, the oceanic convergent front line was observed around 3° N at 140° W (Yoder et al. 1994, Johnson 1996, Archer et al. 1997). During the present cruise (131° 30′ W), despite the similar longitude to the EqPac cruise, the convergence event appeared at 5 to 6° N. This large-scale spatial variation in hydrographic conditions is unusual, and may be associated with El Niño and La Niña events, which prevailed from 1997 to 1999 (http://topex-www.jpl.nasa.gov). In fact, an

Table 2. Percentage of bacterial production removed by heterotrophic nanoflagellates (HNF) in various ocean environments

Study area	Bacterial production ingested by HNF (%)	Source
Northeast equatorial Pacific	31.4 (5° N, 30 m) 38.4 (10° N, 30 m)	Present study
East Sea	33–98 (epipelagic) 22–79 (mesopelagic)	Cho et al. (2000)
Antarctic	3.6 (avg. at polar frontal zone, 20 m) 6.9 (avg. at intermediate water zone, 20 m) 4.1 (avg. at marginal ice zone, 20 m)	Becquevort (1997)
Arctic	4.5–31.7 (10 m)	Sherr et al. (1997)
Mediterranean Sea	40 (epipelagic, Mar) ~100 (epipelagic, Sep)	Christaki et al. (1999)
Mediterranean Sea	45–87 (epipelagic, Jun)	Christaki et al. (2001)

exceptionally deep seasonal thermocline (approximately 100 m) was observed at 10° N (Fig. 2), which was 30 to 40 m deeper than the thermocline depth during the previous 3 yr (approximately 65 m; unpubl. data).

The difference in physical stability of water column structures between the well-mixed SEC/NECC area and the stratified NEC area (Fig. 2) influenced the distribution of chl *a* in the surface water column (Fig. 3), and consequently determined bacterial properties (Figs. 4 & 5). Higher bacterial biomass and production (Fig. 4), but lower increase in bacterial abundance during the PEDS enrichment incubation experiments (Fig. 5) in the SEC/NECC region also indicated that resources available for bacterial growth were more abundant than in the stratified NEC area. Chl *a* provides the resources that stimulate bacterial production in open ocean environments (Bjørnsen 1988, Cole et al. 1988). Protozoa also release substantial amounts of DOC, which is directly available for bacterial growth (Nagata & Kirchman 1992, Nagata 2000).

The ratio of bacteria to phytoplankton biomass generally increased from higher (i.e. the SEC/NECC region) to lower trophic states (i.e. the NEC area) (Fig. 6). The lower values for BCB/chl−C in the well-mixed SEC/NECC area (Fig. 6) seem to be a result of the abundant distribution of large diatoms, resulting in higher chl−C in the convergent area (Yoder et al. 1994, J.-H. Noh unpubl. data), and abundant HNF, which effectively control the biomass of fast-growing bacterial populations (Table 1). Previous analyses of microbial biomass structure have consistently revealed that nutrient conditions largely determine the biomass structures of bacterioplankton and phytoplankton. Cho & Azam (1990) found that the ratio of bacterial to phytoplankton biomass was >1 for chl *a* concentrations <0.2 mg m^{-3}. Herndl (1991) reported small-scale (approximately 100 m) differences in biomass structures in which the ratio of bacteria to phytoplankton biomass generally increased from eutrophic to oligotrophic environments. BCB to chl−C ratios plotted with the trophic (chl *a*) gradient in the water column (Fig. 6B) also confirmed the generalization that the biomass structures of planktonic communities vary with the trophic state of the water column. Although the absolute ratio of BCB to chl−C depends on the conversion factors for the carbon content of chl *a* (Vedernikov et al. 1977, Li et al. 1992, Christian & Karl 1994, Caron et al. 1995) and bacterial cells (Lee & Fuhrman 1987, Fukuda et al. 1998), the general relationship between BCB/chl−C and trophic status remains valid regardless of the conversion factors.

Our results also revealed that the variation in the water column structure regulating the physico-chemical conditions was responsible for regulating the inten-sity of the trophic link between bacteria and HNP. Daily HNF ingestion and grazing rates were approximately 2 times higher in the well-mixed SEC/NECC region at 5° N than at the highly stratified station at 10° N (Table 1). HNP (including heterotrophic nanoflagellates and heterotrophic dinoflagellates) are the major consumers of bacterial production in this study area (Yang et al. 2004, Table 1), and are themselves preyed upon by larger microzooplankton in the pelagic microbial food web (Sieburth et al. 1978, Sherr et al. 1986, Stoecker & Capuzzo 1990). Therefore, the ecological implication of the higher biomass and ingestion rate of HNP in the SEC/NECC region is that the trophic link between bacterioplankton and heterotrophic protists is tighter in the well-mixed, high-nutrient SEC/NECC region, resulting from convergence and divergence. These results are consistent with the generalization that the impact of grazing on bacterial abundance increases in productive regions where bacteria are metabolically active and fast growing (Sanders et al. 1992, Dufour & Torréton 1996, Ducklow 2000).

The bacterial abundance in this study (Fig. 4) was represented by prokaryotic cells, because the phototrophic prokaryotes, such as *Prochlorococcus*, are not easily distinguished from heterotrophic bacteria in the epifluorescent microscopic enumeration of DAPI-stained samples (Sieracki et al. 1995). Given that the abundance of *Prochlorococcus* accounts for approximately 15 to 20% of the total prokaryotic cell count in the study area (Landry et al. 1996, Landry & Kirchman 2002, Noh et al. 2004), the heterotrophic bacterial abundance in this study may overestimate the actual heterotrophic bacterial abundance by approximately 20%. Despite this uncertainty, the results of bacterial cell counts in the PEDS-amended incubation experiment (Fig. 5) and grazing experiment (Table 1) are not likely to be affected by the existence of *Prochlorococcus*, because the incubations for the time-course experiments were conducted in the dark. In those experiments, we also pre-filtered natural seawater at the beginning of the experiment using 0.7 µm filters and GF/F filters for the HNF grazing experiment and PEDS-amended incubation experiment, respectively.

The major ecological role of heterotrophic bacteria in the marine environment depends on whether bacteria act as a trophic link between photosynthetically fixed organic carbon and higher trophic levels, i.e. HNP and metazoan microzooplankton (Azam et al. 1983, Sherr et al. 1986), or as a carbon sink respiring most of the primary production (Ducklow 1986, del Giorgio et al. 1997). Spatially variable bacterial biomass turnover rates (Table 1) and biomass structure (Fig. 6) implied that the ecological roles of bacteria in the well-mixed SEC/NECC area and the highly strati-

fied NEC area were different. First, intense HNP grazing in the SEC/NECC region (Table 1) indicated that the bacterivores preferentially remove dividing cells (Sherr et al. 1992) and metabolically active cells (del Giorgio et al. 1996) in the high nutrient and chl *a* environment, and implied that actively growing bacterial carbon was transferred to higher trophic levels. Therefore, as a result of the combined effects of a sufficient resource supply, i.e. DOC from phytoplankton and protozoans (Nagata 2000), and tight grazing control on the actively growing bacterial cells, heterotrophic bacteria in the SEC/NECC area functioned as a trophic link between DOC and higher trophic levels (Table 3). On the other hand, the lower bacterial biomass turnover rates (Table 1) and the highly enhanced bacterial cell numbers in the PEDS enrichment experiment in the NEC area (Fig. 6B) suggested that bacterial production was primarily resource limited. The combined effects of the low availability of DOC and other bio-limiting nutrients in the oligotrophic open ocean create a stressful environment for bacteria, making the maintenance of active transport systems and production of extracellular enzymes difficult, and thus induce low bacterial growth efficiency (del Giorgio & Cole 1998, 2000, Ducklow 2000). Consequently, in energy-limited environments, bacteria use much of the organic carbon in their surrounding environment for respiration (del Giorgio et al. 1997). Bacteria in the stratified NEC region were therefore likely a relative carbon sink for photosynthetically fixed organic carbon (Table 3).

In the nutrient-depleted stratified environment, relatively faster growing picoautotrophic prokaryotes, e.g. cyanobacteria or *Prochlorococcus* rather than heterotrophic bacteria, may be more important as a trophic link to heterotrophic nanoflagellates. For example, in the oligotrophic Mediterranean Sea, where picoautotrophic cyanobacteria are dominant primary producers, consumption of cyanobacteria by protozoa plays a pivotal role in mediating organic fluxes from primary producers to heterotrophic bacteria (Hagström et al. 1988). In turn, a substantial fraction of protozoan carbon is released through excretion and cell lysis and can be used by heterotrophic bacterioplankton. Hagström et al. (1988) further concluded that about 86% of the autotrophic production was balanced with respiration by heterotrophic bacteria and protozoa, suggesting that a significant fraction of the photosynthetically fixed carbon would be remineralized within the microbial loop, thus rendering it an energy-sink. In association with the relative significance of autotrophic picoplankton in oligotrophic environments, Hyun et al. (1998) found higher picoplanktonic chl *a* (65% of total chl *a*) at oligotrophic stations at 10° N than in the diverging region (40% of total chl *a*). On the same cruise, Yang et al. (2004) repeatedly observed that pico-sized (<3 μm) chl *a* constituted 85.2% of the total chl–C in the stratified NEC region, whereas the nano-sized (3 to 20 μm) fraction made up only 8.7%. Similarly, Landry et al. (1996) found a higher fraction of *Prochlorococcus* in the total bacterial populations at their northern (oligotrophic) stations, between 7 and 12° N at a longitude of 140° W.

Table 3. Summary of the variation in physico-chemical parameters, microbiological properties and the ecological role of heterotrophic bacteria in the SEC/NECC and NEC regions of the northeast equatorial Pacific. HNP: heterotrophic nanoprotists; BCB: bacterial carbon biomass; PEDS: plankton extract dissolved substrates

	SEC/NECC region	NEC region	Evidence
Physico-chemical properties	Vertically well-mixed water mass with a weak seasonal thermocline →Abundant nutrients in the mixed layer →High chl *a* concentration	Highly stratified water column with a strong seasonal thermocline →Nutrient depletion in the surface layer →Low chl *a* concentration	Figs. 2 & 3, Table 1
Bacterial parameters	High abundance and production →High mean biomass turnover rate	Low abundance and production →Low mean biomass turnover rate	Fig. 4, Table 1
Time-course experiment	Low increase in cell numbers in the PEDS-amended samples →Relatively abundant resources available for supporting high bacterial growth	High increase in cell numbers in the PEDS-amended samples →Relative lack of substrate for supporting bacterial growth	Fig. 5, Table 1, Yang et al. (2004)
HNP grazing and biomass structure (BCB/chl–C)	High phytoplankton biomass and intense HNP grazing on the actively growing bacterial biomass →Low BCB/chl–C	Low phytoplankton biomass and HNP grazing on the slowly growing bacterial biomass →High BCB/chl–C	Fig. 6, Table 1, Hyun et al. (1998)
Ecological role of heterotrophic bacteria	Actively growing bacterial biomass is transferred to HNP (i.e. it is a significant trophic link in microbial food web)	Bacteria respire most organic carbon to yield metabolic energy (i.e. they act as a biogeochemical carbon sink for photosynthetically fixed organic carbon)	

In conclusion, our results indicate that the bacterial abundance and production and the environmental conditions controlling bacterial parameters in the SEC/NECC region were intrinsically different from those in the stratified NEC area (Table 3). The variation in the water column structures associated with surface convergence and divergence resulting from the surface current system were mainly responsible for the observed differences in trophic conditions (i.e. nutrients and chl *a*) of the water column and the subsequent spatial variation in the bacterial parameters and HNF grazing. The SEC/NECC area in the equatorial convergent region is a well-established area of the open-ocean fishery (Mann & Lazier 1991), and the variability in microbial food web processes associated with physical forcing could profoundly affect the species composition and biological productivity at higher trophic levels. Further investigation of the relationships between bacterial respiration and growth efficiency and trophic conditions is needed to provide more quantitative information on the different ecological and biogeochemical roles of heterotrophic bacteria in these 2 water columns in the northeast equatorial Pacific.

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