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Contribution of Marine Microbes to Particulate Organic Matter in the Korea Strait

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To assess the relative contribution of bacterial and phytoplankton biomasses to particulate organic matter (POM) in the water column, microbial abundance and biomass were measured from two transects in the western channel of the Korea Strait in 1996. Bacterial abundance had a mean value of 5.9×10^5 cells/ml and chlorophyll-*a* averaged 0.14 μg/l. Bacterial abundance in the Korea Strait showed a positive relationship with chlorophyll-*a* concentration, while the distribution of POM did not covary with chlorophyll-*a*. Particulate organic carbon (POC) and nitrogen (PON) concentrations were greater in August than in October. Bacterial carbon and nitrogen biomasses were 7.29 μgC/l and 1.24 μgN/l, respectively, during the study periods. Bacterial biomass was larger in October than in August due to the autumn phytoplankton bloom. Phytoplankton biomass based on chlorophyll*a* was 7.67 μgC/l for carbon and 1.10 μgN/l for nitrogen. The ratio of bacterial carbon (BC) to phytoplankton carbon (Cp) averaged 0.95 in the Korea Strait in 1996. Bacteria may play a more significant role in the dynamics of POM than phytoplankton do in August, with BC/Cp ratio of 1.26. The ratio of BC to Cp increased with a decrease in chlorophyll-*a* concentration. Averaged over all the samples in both cruises, the contribution of microbial biomass to POC and PON was about 43% and 51%, respectively. Bacterial assemblage constituted a significant fraction of POC (21%) and PON (27%). Phytoplankton accounted for 22% of POC and 24% of PON. Microbial biomass played a more important role in the dynamics of POC and PON in October than in August due to a significant increase in microbial biomass in the southern transect (transect-B) in October by the autumn phytoplankton bloom. This study showed that marine microbes may constitute a significant part in the reservoir of POM in the Korea Strait.

Key words: particulate organic matter, bacteria, phytoplankton, Korea Strait

INTRODUCTION

Marine microbes are an important and often dominant component of the living biomass in oceanic communities, and also play a substantial role in the decomposition of organic matter (Cho and Azam, 1988), nutrient regeneration (Ducklow *et al.*, 1986), and primary and secondary production. Their distribution in the marine systems always results from the interactions of all the biotic and abiotic factors, and is constantly subjected to change (Rheinheimer, 1991).

Organic matter in the marine environment is one of the major factors that control biomass, distribution, and metabolism of microorganisms (Kogure *et al.*, 1980; Azam *et al.*, 1983). Since particulate organic matter (POM) is mostly produced by marine biological activities, the distributional aspects of marine microbes should be evaluated to study the dynamics of POM. In the ocean, substantial amounts of organic matter released or produced by phytoplankton are transformed into bacterial biomass, and then transferred to higher trophic levels (Azam *et al.*, 1983; Robarts *et al.*, 1996). It has been reported that about one half of oceanic primary production is channeled through bacteria into the planktonic food web (Linley *et al.*, 1983; Billen *et al.*, 1990; Weisse *et al.*, 1990; Robarte *et al.*, 1996).

It has been generally thought that the biomass of heterotrophic bacteria in eutrophic and mesotrophic waters is small relative to that of phytoplankton (Azam *et al.*, 1983). However, several investigations have recently found that bacterial biomass often exceeds

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that of primary producer in oligotrophic oceans (Dortch and Packard, 1989; Fuhrman *et al.*, 1989; Cho and Azam, 1990; Eppley *et al.*, 1992; Robarts *et al.*, 1996; Yoro *et al.*, 1997). The distribution of bacterial biomass is, therefore, an important factor in understanding the food-web structure, biogeochemical cycling, and sinking flux of organic matter in oligotrophic waters (Cho and Azam, 1990; Kirchman *et al.*, 1993).

The Korea Strait is a passage through which the Tsushima Current water with high temperature and high salinity is carried from the East China Sea into the East Sea. It is divided into two channels by the Tsushima Island: the eastern and the western channels. In spite of the significance of bacteria in the dynamics of organic matter, there have been few studies on bacteria in the Korea Strait (Chung and Kang, 1996). Researches on bacteria as well as phytoplankton are thus needed to better understand roles of microbes in the dynamics of POM in the Korea Strait.

In this study, the distribution of microbial abundance in the Korea Strait was investigated to assess the relative contribution of bacterial and phytoplankton biomass to POM.

MATERIALS AND METHODS

Sample collection

In the western channel of the Korea Strait, the investigations were carried out for two transects from the RV *Tamyang* in August and October 1996; transect-A (34°59'N, 129°10'E-34°51'N, 129°23'E) and transect-B (34°44'N, 128°43'E-34°29'N, 129°05'E) (Fig. 1). Maximum depth in the study area was 219 m (station A4), and the distance between each station in the transect-A and the transect-B were about 5 and 10 km, respectively. Water samples were taken at 10 stations with a CTD rosette system equipped with 2.5 1 Niskin bottles.

Microbial parameters

Water samples for total suspended matter (TSM) were filtered onto pre-combusted Whatman GF/C filter (nominal pore size, 1.2 μm). After drying filters for 2 hours at about 100°C in the laboratory, TSM was determined by the difference in the weight of GF/C filter before and after filtration of water samples.

For POC and PON measurements, seawater samples (200 ml) were filtered onto pre-combusted (450°C) GF/F filters (nominal pore size, 0.7 μm) and stored at 20°C. Before being analyzed on a Perkin Elmer CHN elemental analyser (Model 2400), the filters were fumed with HCl to remove carbonate, and then were dehydrated at 50°C for 24 hours.

Data for chlorophyll-*a* were adopted from Park *et al.* (1999) who determined chlorophyll-*a* concentra-

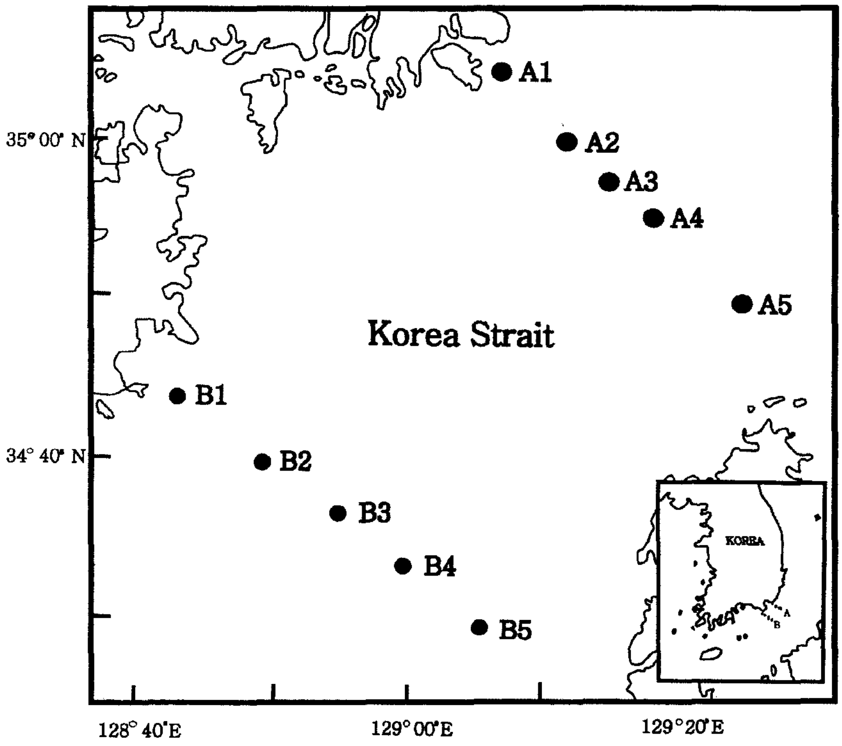

Fig. 1. Station map of the study area. Samples were taken at 10 stations along two transects, Transect-A (A1~A5) and Transect-B (B1~B5).

tion by summing chlorophyll-*a* and its degradation product, chlorophyllide-*a*. For bacteria, 20 ml of subsamples were preserved with formalin prefiltered through 0.2 μm filter (final concentration, 2%), and stored at 4°C in a dark place until the preparation for microscopic slides. Bacteria in a known volume of water were fluoro-stained with 4,6-diamidino-2-phenylindole (DAPI) (final concentration, 0.1%) for 10 min, and were filtered on Irgalan black pre-stained Nuclepore filters (0.2-μm pore size; Costar). The filters were then mounted in immersion oil on microscope slides.

Conversion factor for the estimation of bacterial biomass

To better understand the quantitative importance of microorganisms in microbial food webs are required reliable estimates of their biomass (Christian and Karl, 1994; Fukuda *et al.*, 1998). It was reported that a conversion factor on a cell-number basis, rather than a biovolume basis that results in large uncertainties associated with the estimation of the biovolume of bacteria using epifluorescence microscopy, would be more practical and accurate for biomass estimation (Lee and Fuhrman, 1987). Kroer (1994) indicated that biovolume to biomass conversion factors may be highly variable both temporally and geographically probably as a result of shifting or different bacterial species compositions. He showed that during incubations, bacterial volumes doubled from 0.070 to 0.153 μm^3 at an early stationary phase.

Bacterial biomass in the ocean has been mostly estimated based on the assumption that one marine bacterial cell contains 20 fg of carbon (Lee and Fuhrman, 1987). This conversion factor has been commonly applied to marine bacterial populations. This conversion factor was, however, determined with coastal bacterial assemblages grown in filtered seawater in which bacterial physiology and taxonomic compositions of the samples change during incubation (Nagata and Watanabe, 1990). Fukuda *et al.* (1998) also indicated that the geographical and seasonal variability of bacterial carbon content is quite large, and the carbon content of oceanic samples is much lower than that of coastal ones due to differences in the physiological state of bacterial populations between oligotrophic and productive waters. Since the results estimated by 20 fgC per cell seem to differ significantly from those of natural oceanic bacteria, Kroer (1994) proposed the use of more accurate conversion factors in carbon and nitrogen budgets of marine bacteria.

Table 1 summarizes the carbon and nitrogen contents per marine bacterial cell reported in the literature. For oceanic bacterial assemblages, Christian and Karl (1994) proposed 10 fgC per cell using a least squares inverse method in the North Pacific Ocean. Fukuda *et al.* (1998) measured 12.4 fgC per bacterial cell in the Pacific Ocean. These results indicate that the use of the factor, 20 fgC/cell, may result in the overestimation of bacterial biomass in open oceans. For example, in the present study bacterial biomass estimated by the conversion factors of Lee and Fuhrman (1987) was greater about 60% for POC and 170% for PON than that using the factor by Fukuda *et al.* (1998). In this study, bacterial carbon and nitrogen biomasses were, therefore, estimated using the conversion factor obtained by Fukuda *et al.* (1998) and then compared them with phytoplankton biomasses.

Bacterial carbon biomass (BC) was estimated from bacterial abundance by assuming a per cell carbon of 12.4 fg. For bacterial nitrogen (BN), bacterial cell numbers were also converted to BN assuming 2.1 fgN per cell (Fukuda *et al.*, 1998). Though it has been known that phytoplankton carbon-to-chlorophyll-*a* weight ratios vary from 10 to 100 depending on their physiological conditions, the estimates of phytoplankton carbon (Cp) in the present study were calculated as chlorophyll-*a*×50 (Eppley *et al.*, 1977) to compare with the results of other studies. Phytoplankton nitrogen biomass (Np) was also estimated by assuming the C:N

Table 1. Mean value and standard deviation of the carbon- and nitrogen-to-cell conversion factors for marine bacteria reported in the literature.

Study Area	Carbon (fgC)	Nitrogen (fgN)	C:N (atomic ratio)	Reference
Coastal waters*	19.8±0.8	5.6±0.6	4.3±0.7	Lee and Fuhrman (1987)
″*	112.9±68.9		6.5±1.5	Kroer (1994)
″+	30.2±12.3	5.8±1.5	5.9±1.1	Fukuda *et al.* (1998)
Oceanic waters+	12.4±6.3	2.1±1.1	6.8±1.2	Fukuda *et al.* (1998)

*: cultured data. +: uncultured data

weight ratio of phytoplankton to be 6.6.

RESULTS AND DISCUSSION

Distribution of bacterial abundance

During the study periods, there was a slight variation in environmental parameters such as temperature and salinity (more evident in August). The depth of surface mixed layer varied considerably but was usually within 30 m in August and 50 m in October (Park *et al.*, 1999). Bottom cold water masses developed stronger in summer than in autumn. Surface salinity ranged from 31.4‰ to 33.6‰, with a smaller variation in October than in August.

Distinct temporal and spatial variations occurred in the distribution of marine bacteria in the Korea Strait during the study periods (Fig. 2). Average bacterial abundance was 5.3×10^5 cells/ml (ranging from 1.5 to 14.5×10^5 cells/ml) in August and 6.4×10^5 cells/ml (ranging from 0.9 to 38.3×10^5 cells/ml) in October. A peak of bacterial cell numbers was observed in October, following the autumn phytoplankton bloom. Bacterial abundance at the transect-A decreased from August to October, in contrast to a significant increase at the transect-B.

Integrated bacterial number in the mixed layer at the transect-A was greater in August (63.4×10^{12} cells/m^2) than in October (52.5×10^{12} cells/m^2), whereas at the transect-B it increased from 42.4×10^{12} cells/m^2 in August to 69.4×10^{12} cells/m^2 in October. The distribution of bacteria in October showed a maximum about 15-20 km offshore (stations A3 and B3), not along the coast (stations A1 and B1). This clearly indicates that the higher bacterial numbers found are not the direct result of organic matter discharge from

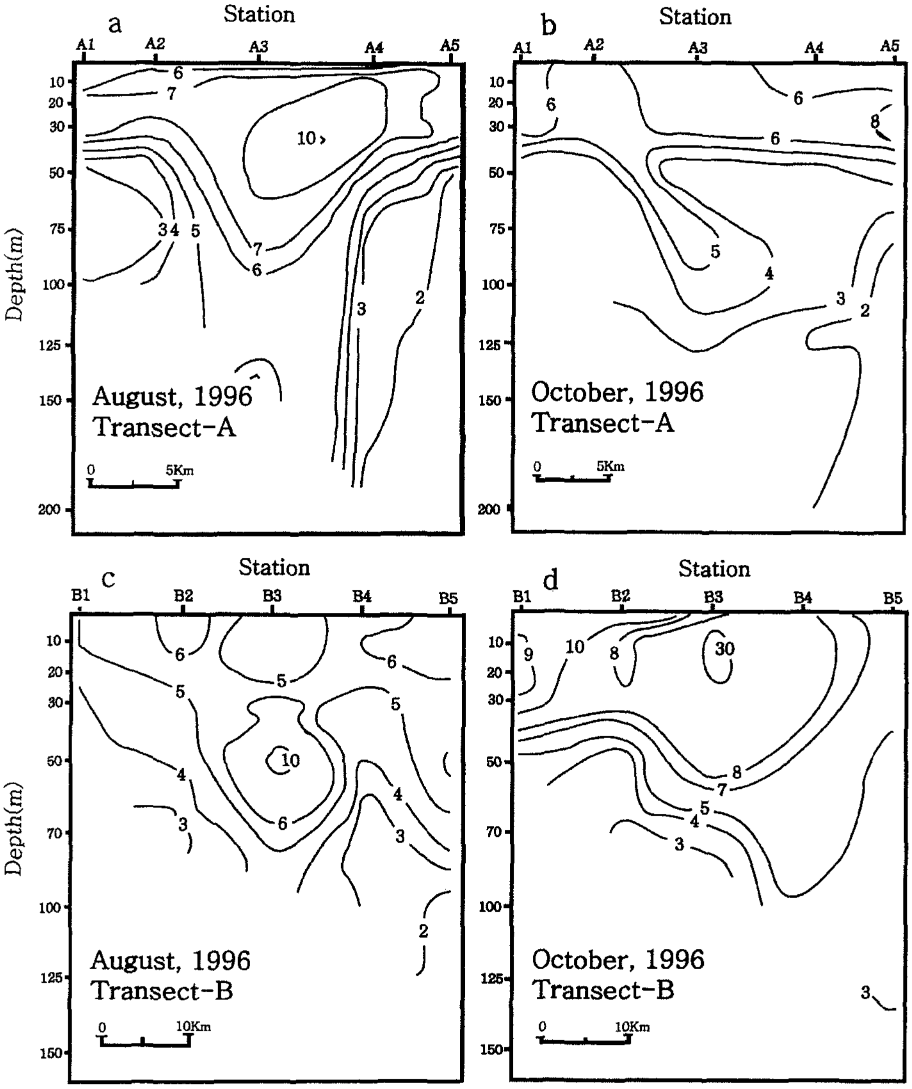

Fig. 2. Vertical distribution of bacteria in the Korea Strait, 1996.

Table 2. Mean values of particulate organic carbon (POC), particulate organic nitrogen (PON), and chlorophyll-*a* concentrations in the Korea Strait in 1996.

	POC (μg/l)	PON (μg/l)	Chlorophyll-*a* (μg/l)	C/N (atomic ratio)	C/Chlorophyll-*a*
August					
Transect-A	38.04	5.04	0.10	8.81	380.4
Transect-B	36.12	4.76	0.10	8.85	361.2
Total	37.08	4.90	0.10	8.83	370.8
October					
Transect-A	30.48	4.06	0.11	8.76	277.1
Transect-B	37.32	4.76	0.27	9.15	138.2
Total	33.72	4.34	0.18	9.06	187.3

the land, but are probably linked to the higher phytoplankton biomass (chlorophyll-*a*) produced offshore as indicated by Billen *et al.* (1990).

Distribution of chlorophyll-a and POM

Distribution of chlorophyll-*a* was significantly different from that of POM (Table 2). Average chlorophyll-*a* was higher in August (average 0.10 μg/l) than in October (0.18 μg/l). Increase in chlorophyll-*a* in October was largely due to increase in chlorophyll-*a* at the transect-B. Integrated chlorophyll-*a* in the mixed layer increased from 9.4 (August) to 14.0 mg/m^2 (October) during the study periods due to the 10 times rise in chlorophyll-*a* at the transect-B.

POC and PON concentrations were approximately 10% greater in August than in October (Table 2). An offshore station (A4) at the transect-A showed the highest integrated POC and PON concentrations in the mixed layer, whereas at the transect-B integrated POC and PON increased from the Korean coast to the Tsushima coast.

Correlation of bacteria, phytoplankton, and POM

It has been reported that the flux of organic matter flowing through planktonic bacteria is about 60% of net primary production (Billen *et al.*, 1990) and about 20 to 60% of primary production enters the microbial food chain (Linley *et al.*, 1983; Robarts *et al.*, 1996). Bacterial abundance in August and October in the Korea Strait showed a positive relationship with chlorophyll-*a* concentration, with correlation coefficients of 0.48 and 0.77, respectively (Fig. 3). These correlations are comparable to the results reported previously (Fuhrman and Azam, 1980; Azam *et al.*, 1983; Bird and Kalff, 1984). The correlation between bac-

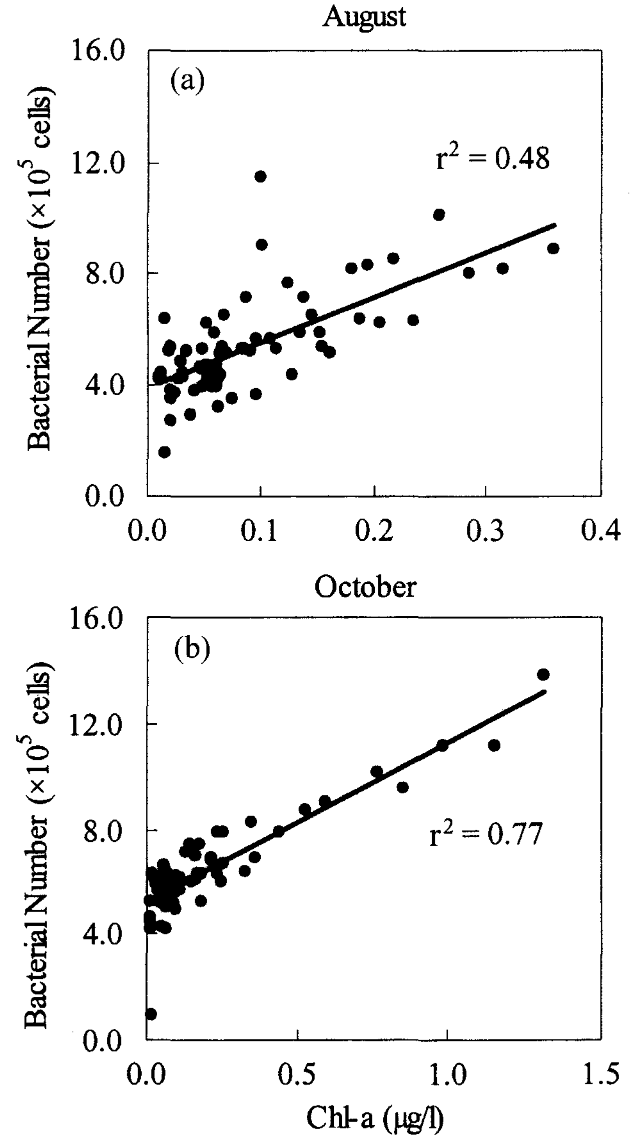

Fig. 3. Relationship between chlorophyll-*a* and bacterial abundance in (a) August and (b) October in the Korea Strait, 1996.

teria and phytoplankton may reflect the availability of biodegradable organic matter supplied by the living phytoplankton either through excretion or cell lysis (Linley *et al.*, 1983; Handa, 1992). On the other hand, relatively low correlation (r^2=0.48) observed in August compared to that in October indicates that increase in the number of bacteria does not always keep pace with increase in chlorophyll-*a*. This is probably because the distribution of bacteria is controlled by environmental conditions such as temperature, or by input of allochthonous organic matter rather than phytoplankton production (Kirchman *et al.*, 1989).

The average POC/chlorophyll-*a* ratio was greater in August than in October, with averages of 370.8 in August and 187.3 in October (Table 2), indicating a larger component of heterotrophs and detritus within the suspended matter in August than in October (Peña *et al.*, 1991). Kogure *et al.* (1980) and Fukami *et al.* (1983) reported a positive correlation between bacterial number and POC concentration.

The percentage of POC in TSM in the study area was less than 1%. The distribution of POM did not covary with chlorophyll-*a*, which was reflected in the lack of correlation or low correlation coefficient found for POC and PON on chlorophyll-*a* (Fig. 4). However, considerably high correlations between POC and chlorophyll-*a* at the transect-A in August (r^2=0.67) and at the transect-B in October (r^2=0.80) may imply that a substantial part of POC might originate from phytoplankton.

Bacterial and phytoplankton biomass in the Korea Strait

Average bacterial carbon biomass (BC) in the Korea Strait in 1996 was 7.29 μgC/l. BC in August ranged from 5.26 μgC/l to 9.11 μgC/l, with a total average of 6.35 μgC/l (Table 3). BC in October averaged 8.23 μgC/l, ranging from 4.76 μgC/l to 18.27 μgC/l. These are similar to those of Fukuda *et al.* (1998), who reported 3.9 to 8.5 μgC/l in oceanic waters. The maximum bacterial carbon biomass was observed in the mixed layer. Bacterial nitrogen (BN) in the study area ranged from 0.89 to 1.54 μgN/l with average of 1.07 μgN/l in August and from 0.81 to 3.09 μgN/l with average of 1.40 μgN/l in October. Total average BN in the Korea Strait in 1996 was 1.24 μgN/l.

The average of the estimated phytoplankton biomass based upon chlorophyll-*a* in August was 5.04 μgC/l for phytoplankton carbon biomass (Cp) and 0.72 μgN/l for phytoplankton nitrogen biomass (Np). Cp and Np

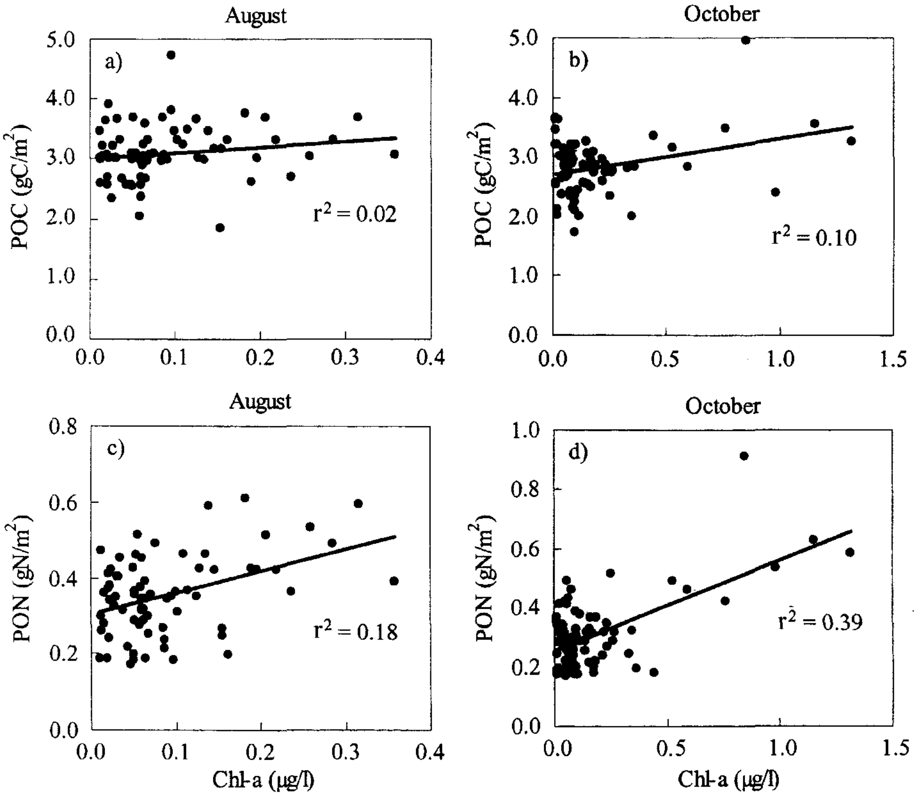

Fig. 4. Relationship between chlorophyll-*a* and POC (a, b), and chlorophyll-*a* and PON (c, d) in the Korea Strait, 1996.

Table 3. Average microbial carbon (μgC/l) and nitrogen (μgN/l), and the ratio of bacterial carbon (BC) to phytoplankton carbon (Cp) in the Korea Strait in 1996.

Month	Station	Bacteria		Phytoplankton		BC/Cp
		BC	BN	Cp	Np	
August	A1	6.01	1.02	7.39	1.06	0.81
	A2	6.51	1.10	4.26	0.61	1.53
	A3	9.11	1.54	6.84	0.98	1.33
	A4	7.03	1.19	2.77	0.40	2.54
	A5	5.62	0.95	3.62	0.52	1.55
	B1	5.34	0.90	7.67	1.10	0.70
	B2	6.21	1.05	4.14	0.59	1.50
	B3	6.94	1.18	3.52	0.50	1.97
	B4	5.46	0.92	4.64	0.66	1.18
	B5	5.26	0.89	5.59	0.80	0.94
	Total	6.35	1.07	5.04	0.72	1.26
October	A1	5.55	1.04	3.95	0.56	1.41
	A2	5.31	0.90	4.24	0.61	1.25
	A3	6.41	1.09	4.62	0.66	1.39
	A4	4.76	0.81	7.11	1.02	0.67
	A5	6.36	1.08	7.10	1.00	0.90
	B1	10.82	1.83	37.27	5.32	0.29
	B2	10.17	1.72	9.81	1.39	1.04
	B3	18.27	3.09	19.14	2.74	0.95
	B4	8.30	1.41	5.89	0.84	1.41
	B5	6.36	1.07	3.74	0.53	1.70
	Total	8.23	1.40	10.29	1.47	0.80
Total Average		7.29	1.24	7.67	1.10	0.95

* All data were shown as mean values for the whole water column. BN=Bacterial nitrogen; Np=Phytoplankton nitrogen.

in October varied between 3.74 and 37.27 μgC/l with an average of 10.29 μgC/l and between 0.53 and 5.32 μgN/l with an average of 1.47 μgN/l, respectively. Total average Cp and Np in the Korea Strait in 1996 were 7.67 μgC/l and 1.10 μgN/l, respectively.

The average ratio of BC to Cp was 0.95 in the Korea Strait in 1996, with mean values of 1.26 in August and 0.80 in October (Table 3). This result implies that bacteria may play a more significant role in the dynamics of particulate organic matter than phytoplankton in August as indicated by Linley *et al.* (1983). Even though it was assumed that only a half of marine bacteria were expected to be retained on GF/F filters (Lee and Fuhrman, 1987), BC collected on the filters was almost equal to Cp. Several investigators have recently proposed a greater biomass of bacteria than that of phytoplankton. Eppley *et al.* (1992) showed that the standing stock of bacterial C and N in the equatorial Pacific Ocean exceeded that of phytoplankton. Cho and Azam (1990) also reported that in oligotrophic waters bacterial biomass was commonly 2 to 3 times greater than that of phytoplankton.

The ratio of bacterial to phytoplankton carbon biomass (BC:Cp) increased with a decrease in chlorophyll-*a* concentration (Fig. 5). Log transformed plot between BC and Cp showed a relationship of:

$$\log BC\ (\mu gC/l)=0.373 \log Cp\ (\mu gC/l)+0.56$$
$$r^2=0.66,\ n=148,\ p<0.001$$

For chlorophyll-$a \leq 0.2$ μg/l, 82% (August) and 92% (October) of BC were greater than Cp, which is similar to the result estimated by Cho and Azam (1990). Dortch and Packard (1989) noted that food webs in eutrophic waters are dominated by primary producer biomass whereas in oligotrophic waters are dominated by decomposer biomass. Cho and Azam (1990) reported that bacteria:phytoplankton biomass ratios are close to 1 when chlorophyll-*a* is about 0.5 μg/l.

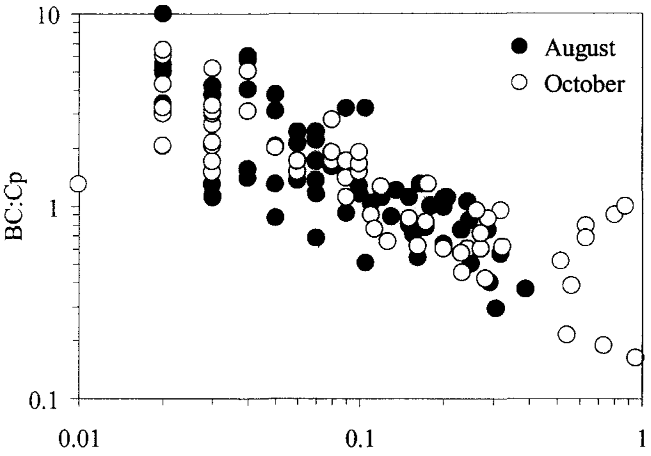

Fig. 5. Plot of ratio of bacterial carbon to phytoplankton carbon vs chlorophyll-*a* in the Korea Strait in 1996.

Table 4. The percentage of microbial biomass to particulate organic carbon (POC) and particulate organic nitrogen (PON) in the Korea Strait in 1996. Bacterial carbon (BC) and phytoplankton carbon (Cp) were represented as a percentage of POC, and bacterial nitrogen (BN) and phytoplankton nitrogen (Np) as that of PON.

	Carbon		Nitrogen	
	BC (%)	Cp(%)	BN(%)	Np(%)
August				
Transect-A	18	13	23	14
Transect-B	16	14	21	15
Total	17	14	22	15
October				
Transect-A	19	18	24	19
Transect-B	29	41	38	45
Total	24	31	32	34
Total average	21	22	27	24

Contribution of microbial biomass to POM

In August, the microbial biomass calculated as the sum of bacterial and phytoplankton biomasses in this study was nearly twice that in October. During the study periods, the microbial biomass constituted 31% (August) and 55% (October) of POC, and 37% (August) and 66% (October) of PON (Table 4).

Microbial carbon in the two cruises contributed 43% of POC. This value was similar to the result of Eppley *et al.* (1983) who showed that the living plankton usually accounted for less than half of the POC collected in the ocean. Caron *et al.* (1995) indicated that microorganisms in the open ocean play a major role as repositories for carbon. BC accounted for 21% of POC, comparable to the report of Yoro *et al.* (1997). Cp in this study averaged 22% of POC. Microbial nitrogen accounted for 51% of PON in the Korea Strait, with 27% of PON by BN and 24% by Np.

The transect-A did not show much variation in the fractions of microbial carbon in POC and microbial nitrogen in PON from August to October. The fraction of microbial carbon in POC at the transect-B, however, increased from 30% in August to 70% in October, and that of microbial nitrogen in PON from 36% in August to 84% in October (Table 4). It suggests a more significant role of microorganisms to the dynamics of POC and PON in October in the transect-B.

The ratio of integrated BC to integrated POC and that of integrated Cp to integrated POC increased from 0.20 to 0.30 and from 0.16 to 0.42, respectively, from August to October (Table 5). Integrated BC was greater than integrated Cp in August, whereas integrated Cp exceeded integrated BC in October due to a prominent increase in chlorophyll-*a* as presented in Park *et al.* (1999). There was a more variation in the contribution of integrated BC to POM in the

Table 5. The ratio of integrated microbial biomass to particulate organic matter (POM) in the mixed layer of the Korea Strait in 1996 (mean±SD).

Month	Station	BC:POC	Cp:POC	BN:PON	Np:PON
August	Transect-A	0.23±0.08	0.18±0.09	0.27±0.11	0.19±0.10
	Transect-B	0.17±0.02	0.14±0.06	0.18±0.02	0.14±0.07
	Total	0.20±0.06	0.16±0.05	0.23±0.09	0.16±0.08
October	Transect-A	0.25±0.04	0.31±0.13	0.32±0.05	0.35±0.15
	Transect-B	0.36±0.21	0.53±0.34	0.45±0.25	0.68±0.57
	Total	0.30±0.15	0.42±0.18	0.38±0.19	0.51±0.43

*BC=Bacterial carbon; Cp=Phytoplankton carbon; BN=Bacterial nitrogen; Np=Phytoplankton nitrogen; POC=Particulate organic carbon; PON=Particulate organic nitrogen.

mixed layer at the transect-B than at the transect-A. Integrated BN and Np showed the same pattern as the integrated BC and Cp.

CONCLUSIONS

Microbial biomass contributed 43% of POC and 51% of PON in the Korea Strait during the study periods. It played a more significant role in the dynamics of POC and PON in October than in August because microbial biomass in the southern transect (transect-B) in October significantly increased due to the autumn phytoplankton bloom. These results indicate that marine microbes may constitute a significant part in the reservoir of POM in the Korea Strait. The average ratio of bacterial carbon to phytoplankton carbon was 1.95 in the Korea Strait in 1996, implying that bacteria play a more significant role in the dynamics of POM than phytoplankton does.

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