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Abundance of Heterotrophic- and Photosynthetic Dinoflagellates and Factors Controlling Their Abundance and Distribution in Korean Coastal Waters During Summer, 1994

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We investigated the abundance and biomass of dinoflagellates and factors controlling their abundance in marine planktonic ecosystems in Korean coastal waters. The abundance of photosynthetic (PDNF) and heterotrophic dinoflagellates (HDNF) was in the range of 0.7×10^{0} cells/l-14.0×10^{6} cells/l and in the range of 3.0×10^{2} cells/l-6.47×10^{5} cells/l, respectively. Their biomass was 0.5×10^{-1}–2.56×10^{4} μgC/l and 2.0×10^{-1}–1.5×10^{2} μgC/l, respectively. In order to find factors controlling their abundance, stepwise regression and best subsets regression analyses were used. We found that during the summer the most important factors controlling PDNF abundance are DO, P, N and S (abiotic factors), and for HDNF, the abundance of zooplankton, ciliates and HF (biotic factors), and that high turbidity may effect the distribution of dinoflagellate species.

Keywords: Dinoflagellates, Abundance, Biomass, Controlling factors, Cluster analysis

INTRODUCTION

In diverse aquatic ecosystems, dinoflagellates have been studied because of their peculiar appearance and tendency to form massive blooms, often referred to as red tides. Dinoflagellates causing blooms are mainly phototrophs, however some heterotrophs and mixotrophs also form blooms. In addition, with the advent of an epifluorescence microscopy (e.g. Hallegraeff and Jeffrey, 1984; Lessard, 1984; Lessard and Swift, 1986) in this field, it has been revealed that many photosynthetic dinoflagellates may actually be mixotrophic forms (Gaines and Elbrächter, 1984; Schnepf and Elbrächter, 1992; Stoecker, 1999). For this reason, it is increasingly interesting to understand which factors control the abundance of heterotrophic dinoflagellates (hereafter, HDNF) and photosynthetic dinoflagellates (hereafter, PDNF).

In Korea, most previous studies on dinoflagellates were conducted in the South Sea because many dinoflagellate blooms have been observed there. A record of dinoflagellate blooms which have occurred in Korean coastal waters since 1990 has been published (Kim *et al.*, 1998). Studies on dinoflagellates forming blooms have been actively conducted by the National Fisheries Research and Development Institute, Korea (e.g., Kim *et al.*, 1993, 1998) and more recently by Red Tide Research Center, Kunsan National University (e.g., Jeong *et al.*, 1999a, b, 2001). However, little attention has been paid to the estimates of their abundance and biomass, and their role in microbial food webs.

Here, we report the estimates of the abundance and biomass of PDNF and HDNF during the summer, 1994 in coastal waters around Korea. We also measured the abundance of all plankton components and 12 abiotic factors such as dissolved oxygen, salinity, temperature, inorganic nutrients and trace metals, and used this information to understand which factors controlled the abundance and biomass of dinoflagellates during the summer.

MATERIAL AND METHODS

Study areas

Samples were collected monthly from surface water using a bucket at seven coastal sites during the summer; SokCho port (Site 1), YoungIl Bay (Site 2), JinHae Bay (Site 3), KwangYang Bay (Site 4), MokPo harbour (Site 5), KunSan

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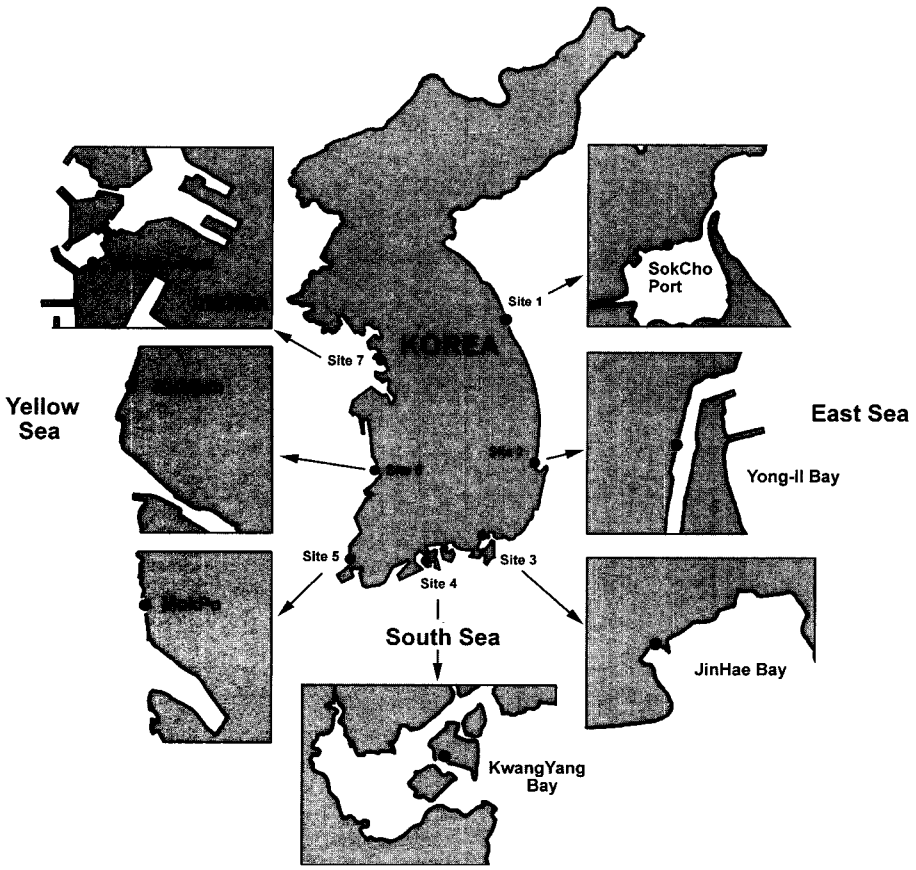

Fig. 1. Map showing the sites.

port (Site 6) and YeonAn port (Site 7) (Fig. 1).

Abiotic factors

Water temperature and salinity were measured in situ with T-S Bridge (KENT). Dissolved oxygen (DO) was measured in situ with a DO meter (YSI) and trace metals such as cadmium (Cd), chromium (Cr), copper (Cu), nickel (Ni), lead (Pb) and zinc (Z) were measured by a solvent extraction using ICP-MS (Inductively Coupled Plasma Mass Spectrometry: Plasmas Quad II, VG Instruments). Total nitrogen (N), phosphate (P) and silicate (S) were analysed with duplicate samples using UV/VIS Recording Spectrophotometer (Shimadzu double beam, M/D; UV-260) according to Solozano (1969) and Parsons *et al.* (1984). An extraction method (Parsons *et al.*, 1984) was used to determine concentrations of chlorophyll *a*.

Biotic factors

Bacteria, cyanobacteria and flagellates were preserved in a final concentration of 1% formalin and quantified using epifluorescence microscopy (Zeiss Axiopot) with an UV-G excitation filter within 3 days after sampling. A few mililiters (2–5 ml) of water samples were stained with 0.5–1.0 μg/ml of DAPI (final concentration), and then filtered through on 0.22 μm black polycarbonate filters (Nuclepore). Samples for diatoms, dinoflagellates and ciliates were preserved with 1% of Lugols iodine solution (final concentration) and allowed to settle for at least 48 hrs. Subsamples (100–200 ml) settled from 1 liter were used to estimate their abundance using a Sedgwick-Rafter Chamber (McAlice, 1971) under a light microscope. Zooplankton was collected using a 150 μm zooplankton net, preserved with 5% formaldehyde (final concentration) and enumerated under a dissecting microscope.

Enumeration and biomass estimation

Cell volume was calculated assuming simple geometrical shapes (Edler, 1979). Conversion factors used to convert cell volume to carbon biomass were 19.8 fgC/cell for bacteria (Lee and Fuhrman, 1987), 294 fgC/μm^3 for cyanobacteria (Cuhel and Waterbury, 1984), 220 fgC/μm^3 for flagellates (Børsheim and

Bratbak, 1987) and 0.19 pgC/μm^3 for ciliates (Putt and Stoecker, 1989). Carbon biomass of diatoms and dinoflagellates were estimated from cell volume according to Strathman (1967).

Statistic analysis

Analysis of similarities among species composition of dinoflagellates were conducted using the statistical package PRIMER version 4.0 beta (Clarke, 1993), relying largely on cluster, a hierarchical classification technique based on the Bray-Curtis Similarity Coefficient calculated on presence/absence-transformed data. Also non-metric multidimensional scaling (MDS, Kruskal and Wish, 1978) with the PRIMER was used to compare samples from the sites by condition indices. In order to find factors controlling the abundance of dinoflagellates, we used stepwise regression, best subsets regression and direct correlation analyses in the statistical program Minitab.

RESULTS AND DISCUSSION

The results of the measurements of abiotic factors were shown in Fig. 2. Sampling sites appeared to be influenced by the inflow of freshwater and wastewater. S and Cd concentrations seemed to be derived from the inflow of freshwater because they were significantly correlated with salinity (S: $r = -0.432$, $P < 0.05$; Cd: $r = -0.567$, $P < 0.01$). Additionally, the multivariate analysis using MDS of 10 abiotic factors including DO, nutrients and trace metals, grouped roughly together the samples from each of the months (Fig. 3; stress value 0.08). Therefore it was likely that all of the sites were undergoing similar effects from the inflow of freshwater and wastewater during the same month.

The estimates of chlorophyll *a* concentrations and the abundance of microbes are shown in Fig. 4. The mean chlorophyll *a* concentration was 81.5±176 μg/l and was high in the sites and months which dinoflagellate blooms occurred. Bacterial abundance was mean 2.71±1.89×10^6 cells/ml, and the abundance was relatively higher in the sites 1–3 than in the sites 4–5. The mean abundances of cyanobacteria and autotrophs less than 20 μm were 3.96±8.68×10^3 cells/ml and 1.22±2.45×10^4 cells/ml, respectively. The abundance of heterotrophic flagellates (hereafter HF) excluding HDNF was mean 7.20±9.60×10^3 cells/ml and was dominated by cells less than 5 μm. The ciliate assem-

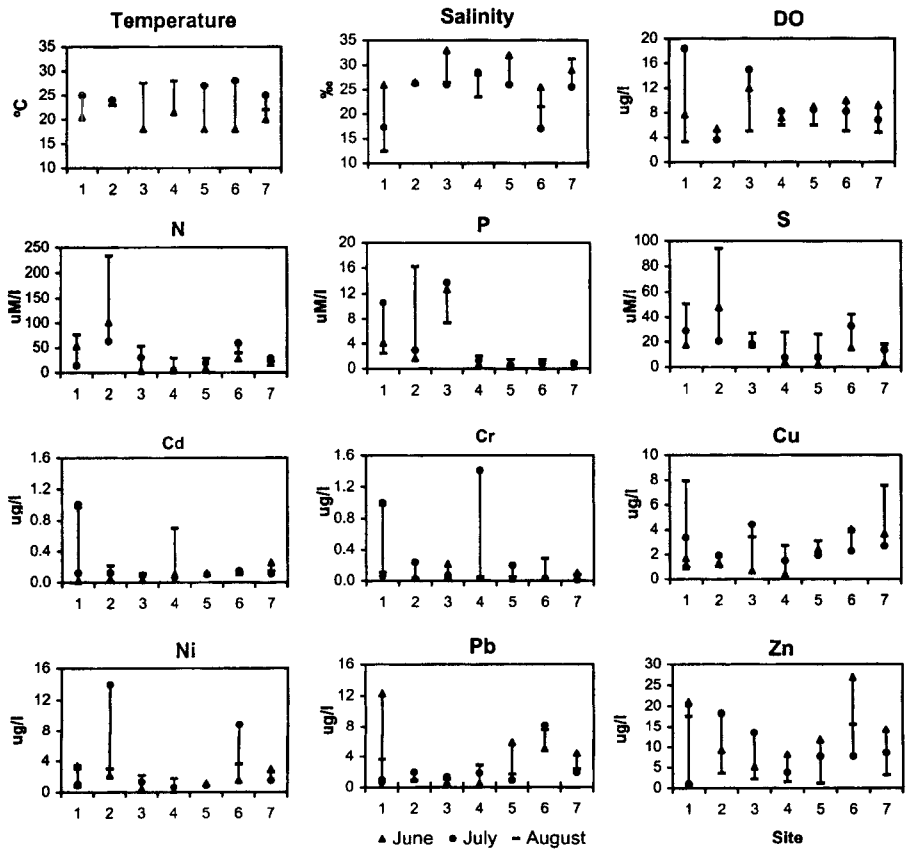

Fig. 2. Abiotic factors measured during the study.

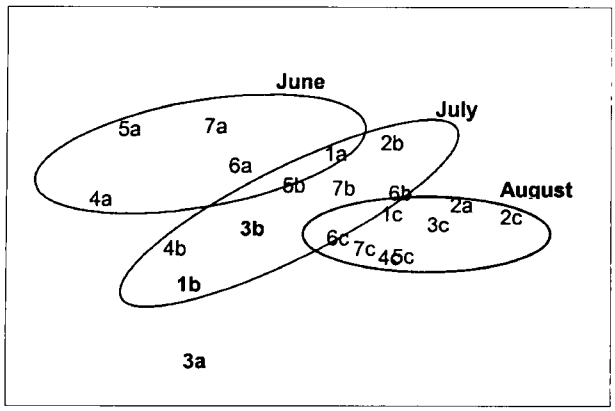

Fig. 3. MDS ordination plot of the similarity matrix of 10 condition indices (DO, nutrients and trace metals) from monthly sampling. The symbols in intalic and bold are the site and month which had a bloom. 1a represents that the sample was collected at the site 1 in June; 2b is for the sample collected at the site 2 in July, 3c is for the sample collected at the site 3 in August.

blage had a mean abundance of $9.25\pm18.7\times10^4$ cell/l and consisted mainly of small oligotrichida with a mean of 73.2% of the total ciliate abundance and tintinnids which accounted for a mean of 11.5%. The mean abundance of diatoms was $8.48\pm11.5\times10^5$ cells/l. Zooplankton consisted mainly of copepods, appendicularias, nauplii, trochophores, polychaete larvae and mulluscan larvae, and had a mean abundance of $1.53\pm4.02\times10^5$ inds./m^3. At the sites (1 and 3) where the dinoflagellate blooms occurred, the abundance of zooplankton was somewhat low (Fig. 4). At the site 1 in June there were high abundances of trochophora (mean 18.9×10^5 inds./m^3), bacteria, cyanobacteria and HF, before the bloom of *Prorocentrum* spp. in July. The multivariate analysis of 9 biotic factors using MDS (Fig. 5; stress value 0.05) grouped together the three dinoflagellate blooms from the sites 1 (July) and 3 (June and July).

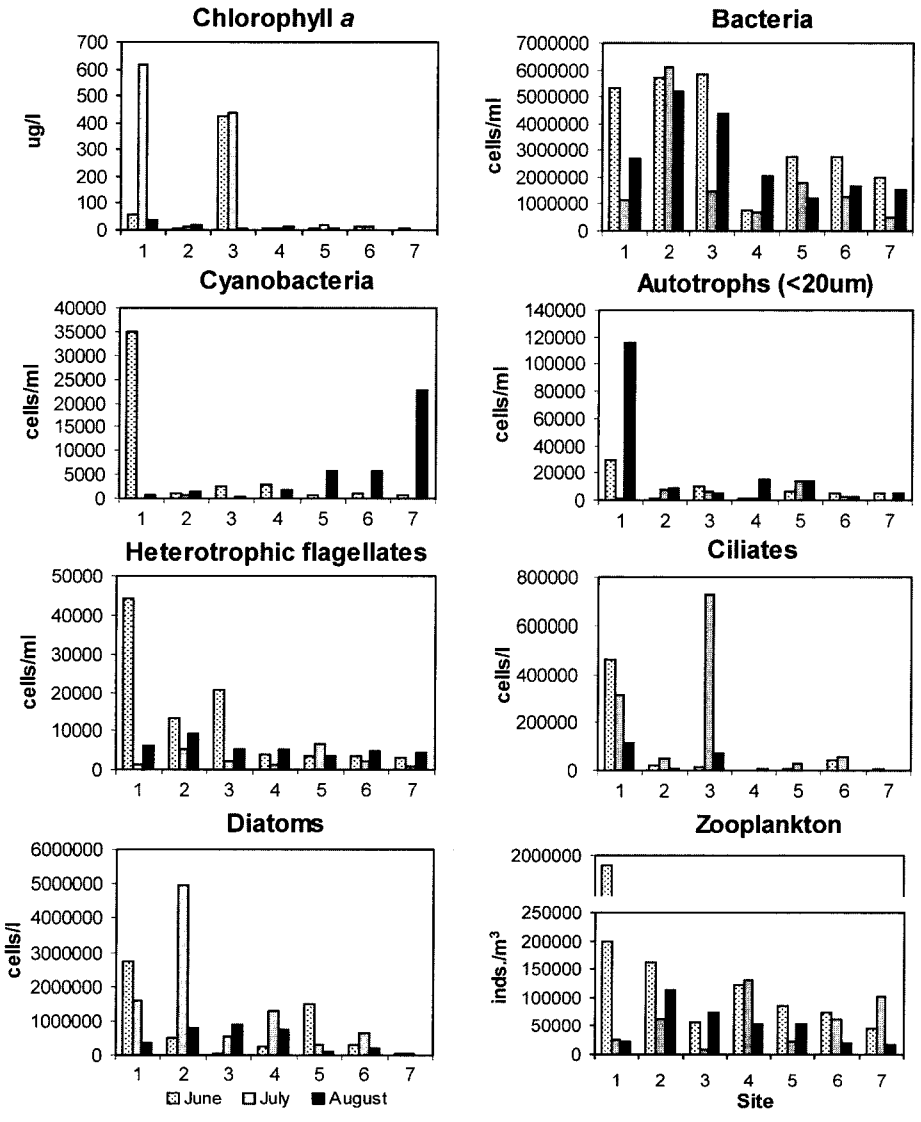

Fig. 4. Chlorophyll *a* concentrations and abundance of microbes.

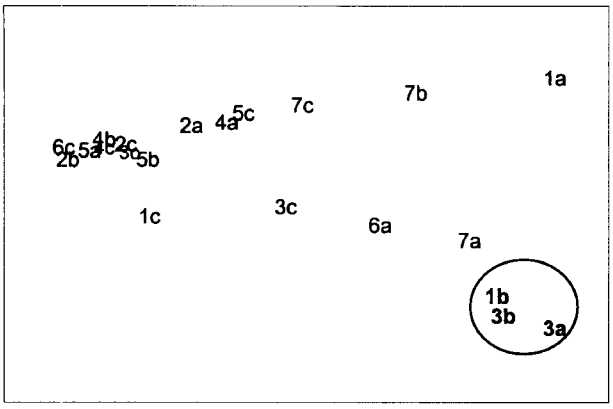

Fig. 5. MDS ordination plot of the similarity matrix of 9 condition indices (abundance of microbes) from monthly sampling. The symbols are the same as for Fig. 3.

Total dinoflagellate abundance was in the range of 4.0×10^2 cells/l–14.1×10^6 cells/l (Fig. 6). PDNF abundance significantly varied from 0.7×10^2 cells/l to 14.0×10^6 cells/l (mean 1.71×10^6 cells/l) and HDNF abundance was in the range of 3.0×10^2 cells/l–6.47×10^5 cells/l (mean 4.88×10^4 cells/l). Their biomass ranged from 0.5×10^{-1} to 2.56×10^4 μgC/l and from 2.0×10^{-1} to 1.5×10^2 μgC/l, respectively. The contributions of HDNF to the total dinoflagellate abundance and biomass were in the range of 0.2–91.7% and in the range of 0.2–96.3%, respectively. At the sites and months in which dinoflagellate blooms occurred by PDNF, the contributions were quite low. The contribution of HDNF to the total microbial carbon biomass was in the range of 0.6–21% and lower at the sites in which the blooms occurred (Fig. 7). HDNF abundance was somewhat higher than previously reported abundance range (0.4×10^2–4.5×10^4 cells/l) in marine pelagic ecosystems including polar region (Lessard, 1991 references within; Archer *et al.*, 1996; Lessard and Murrell, 1996; Levinsen *et al.*, 1999). Lessard (1991) showed that the relative contributions of HDNF to the abundance and biomass of protozoa in marine pelagic ecosystems including polar regions were 6–81% of abundance and 2–97% of biomass, and that the contributions were higher in polar region than in temperate regions. Our results were also in these ranges (5.4–82.1% to abundance,

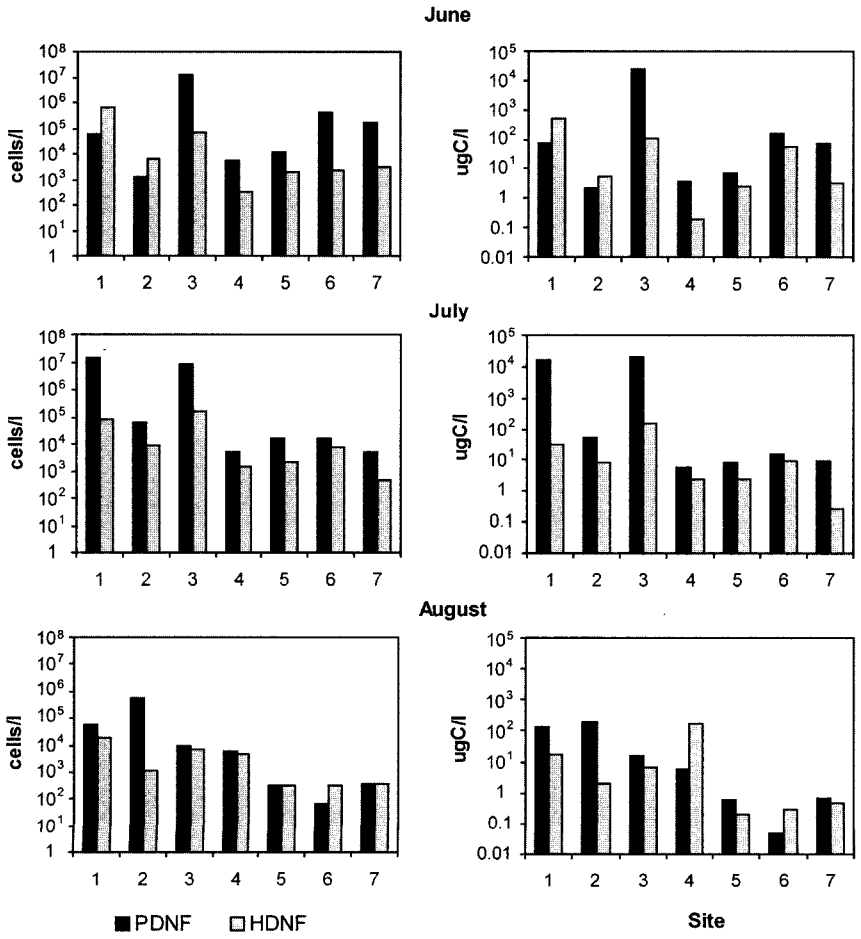

Fig. 6. Abundance and biomass of dinoflagellates.

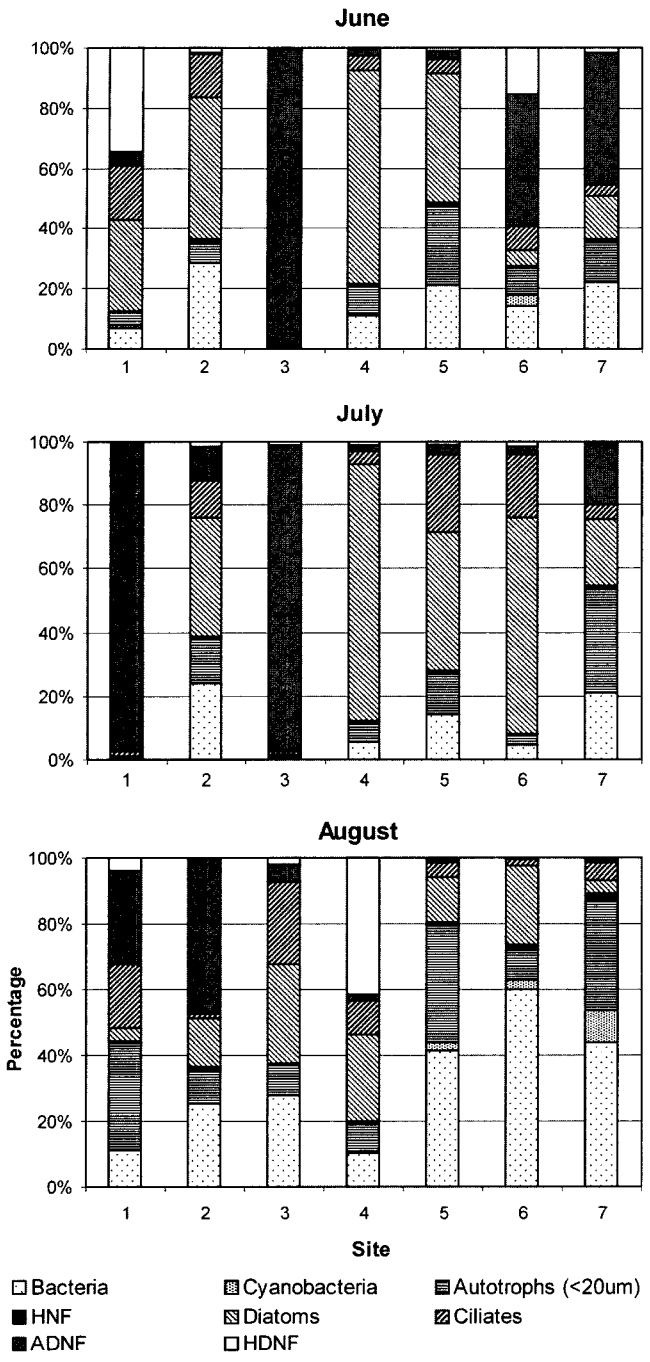

Fig. 7. Composition of the microbial carbon biomass in Korean coastal waters during summer, 1994.

3.1–80.4% to biomass) and were closer to those from temperate region. On the basis of the HDNF and PDNF contributions to the total microbial carbon biomass from this study, we conclude that HDNF and PDNF can be the major components of the microbial carbon biomass at Korean coastal sites during the summer, 1994 and that their significance in the microbial food webs may vary significantly from site to site and from month to month.

During this study, about 98 dinoflagellate species from 26 genera and 7 unidentified species were encountered (Appendix 1). The most dominant dinoflagellates belonged to the genus *Prorocentrum*. *Protoperidinium* spp were also frequently observed, but not dominant. Dinoflagellate blooms occurred with massive numbers at the sites 1 (July, *P. micans* and *P. minimum*) and 3 (June, *Akashiwo sanguinea* and *P. triestium*; July, *P. micans*) by mixotrophic dinoflagellates. These species, except for *P. micans* are known to be potentially harmful (e.g., Andersen *et al.*, 1995; Grzebyk *et al.*, 1997). However, we could not estimate the effects of the blooms on other organisms living in the sites because there were no subsequent and co-operative studies at the sites. During the blooms, these species appeared as photosynthetic forms showing a red-fluorescence under the epifluorescence microscope with BV filter and we therefore regarded these species as PDNF here. These species might have grazed inefficiently on other microbes because four abiotic factors were regarded as the most important factors controlling their abundance (see above) in this study. Grazing may be common among PDNF under certain conditions such as growth-limiting conditions (Li *et al.*, 1996; Stoecker *et al.*, 1997). It may also be an important aspect of the ecology of many dinoflagellates forming blooms because dinoflagellate blooms often develop and persist in surface waters where nutrient concentrations are low (Passsche *et al.*, 1984). Grazing in mixotrophs may give competitive benefits when the nutrient concentrations are limiting (Thingstad *et al.*, 1996). Stoecker *et al.* (1997) showed that in experiments with *Prorocentrum minimum*, addition of phosphate or nitrogen alone and low level nutrient additions sometimes was likely to stimulate feeding. In this study, there was no direct relationship between the abundance of *P. minimum* and other nutrients or N/P ratio, but the abundance was significantly correlated with DO. Otherwise, stepwise regression and best subsets regression analyses showed that the important factors controlling the abundance of *P. minimum* may be DO, S and the abundances of diatoms and ciliates (r^2=69.0%). The factors for *P. micans* were the abundance of ciliates and zooplankton, and DO (r^2=96.5%).

Stepwise regression and best subsets regression analyses showed that four factors explain the high percentage of variation in the dependant factor, PDNF abundance. These were all abiotic factors such as DO, P, N, and S which are regarded as the impor-

Table 1. Analysis of variance for the regression models

Source	DF	SS	MS	F	P
PDNF	4	3.23416E+14	8.08539E+13	46.64	<0.001
HDNF	3	4.04441E+11	1.34814E+11	1069.92	<0.001

tant factors for controlling PDNF abundance, although direct correlation analysis indicated that the relationships with N and S were negative and not significant. Ciliate abundance was excluded from the factors although its relationship with PDNF was significant in the direct correlation analysis. Many previous studies have showed that DO and nutrients are related to the abundance of PDNF or to dinoflagellate blooms (e.g., Mallin, 1994; Stoecker *et al.*, 1997; Kim *et al.*, 1998). For the abundance of HDNF, however only three biotic factors explain the maximum percentage of variation in HDNF abundance. These were the abundance of HF, ciliates and zooplankton. These had also a significant relationship with HDNF abundance in the direct correlation analysis. Some factors such as cyanobacterial abundance and Pb were excluded although they were significantly correlated in the direct correlation analysis. The models are below (Table 1):

PDNF=−4163262+522700 DO−60911 N+475359 P +104430 S (r^2=91.9%)
HDNF= −13538+0.0231 Zooplankton+0.238 Ciliates +2.51 HF (r^2=99.5%).

On the basis of the species composition of dinoflagellates from the sites (Appendix 1), we analysed the community structure using the cluster algorithm. The result is shown in Fig. 8. Two highly distinct clusters were separated at a level of 49% similarity. One of these contained only one community from the site 1. The other cluster was further subdivided into two clusters at a level of 51% similarity; one contained communities from the sites 2–4 and the other contained communities from the sites 5–7 that are located in the Yellow Sea. The numbers of dinoflagellate species encountered in the sites 2–4 were higher than those in the sites 5–7 (see Appendix 1). Turbidity is higher in the Yellow Sea than in the East China Sea and Southern coast of Korea (Choi *et al.*, 2001). High turbidity in the Yellow Sea is due to the resuspension of sediment particles by strong tidal action (Yu *et al.*, 1995b). The sprinkling of clays has been applied to remove red tide dinoflagellates (Yu *et al.*, 1995a, b; Kim *et al.*, 1998), suggesting high turbidity

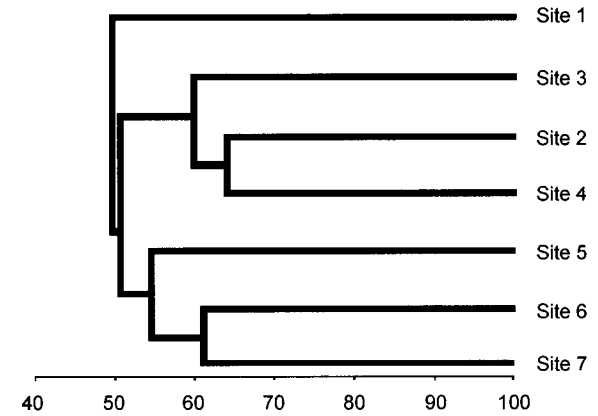

Fig. 8. Dendrogram showing the Bray-Curtis similarities (%) between the species composition of dinoflagellates from 7 sites.

may effect dinoflagellate population growth. Additionally, turbulence may inhibit the dinoflagellate population growth (e.g., Thomas and Gibson, 1990a, b; Tynan, 1993; Gibson and Thomas, 1995; Smayda, 1997; Juhl *et al.*, 2000). The strong tidal action in the Yellow Sea can cause turbulence and high turbidity, therefore possibly inhibiting the growth of dinoflagellate populations. Our Primer study (Fig. 8) suggests that these physical factors may effect the distribution of dinoflagellate species.

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Appendix 1. List of species encountered during this study

Species	Site 1	Site 2	Site 3	Site 4	Site 5	Site 6	Site 7
Akashiwo sanguinea		*	*	*			*
Alexandrium sp.				*	*	*	
Amphidinium crassum			*				
Amylax triacantha		*			*	*	
Ceratium arietinum		*					
Ceratium furca		*	*	*	*		
Ceratium fusus	*	*	*	*	*	*	*
Ceratium horridum			*				*
Ceratium kofoidii		*	*	*	*	*	*
Ceratium lineatum	*		*	*		*	*
Ceratium tripos				*			
Dinophysis acuminata	*	*	*	*	*		*
Dinophysis caudata			*				
Dinophysis fortii	*	*	*		*		*
Dinophysis infundibulus							*
Dinophysis lenticula	*	*	*	*			*
Dinophysis rotundata	*	*		*	*		*
Dinophysis rudgei		*	*				
Diplopsalis lenticula		*	*				
Diplopsalopsis asymmetrica		*	*				
Diplopsalopsis globula		*					
Diplopsalopsis lebourae		*		*			
Diplopsalopsis minor	*	*	*	*		*	*
Diplopsalopsis orbicularis	*		*	*	*		
Gonyaulax digitale				*	*		
Gonyaulax polygramma		*	*	*		*	*
Gonyaulax scrippsae					*	*	
Gonyaulax spinifera			*	*	*	*	*
Gonyaulax turbynei		*		*			
Gonyaulax verior			*	*			*
Gymnodinium mikimotoi			*				*
Gymnodinium situla		*	*	*			
Gymnodinium viridescens		*					
Heterocapsa triquetra	*	*	*	*			*
Lingulodinium polyedrum		*		*		*	
Mesocena polymorpha var. *bioctonaria*				*	*		
Noctiluca scintillans	*		*	*		*	*
Oblea rotundata	*	*	*			*	*
Oxyphysis oxytoxoides		*	*	*	*		
Oxyrrhis marina	*	*		*			
Peridinium bipes			*				
Peridinium penardiforme			*				
Peridinium quinquecorne			*	*			
Peridinium volzii				*			
Polykrikos kofoidii	*			*			
Prorocentrum dentatum			*		*		
Prorocentrum micans	*	*	*	*	*	*	*
Prorocentrum minimum	*	*	*		*		*

Appendix 1. continued

Species	Site 1	Site 2	Site 3	Site 4	Site 5	Site 6	Site 7
Prorocentrum triestinum		*	*				
Protoperidinium acutum					*		*
Protoperidinium angustum		*		*			
Protoperidinium bipes	*	*	*		*	*	
Protoperidinium bipes forma *occulatum*				*			
Protoperidinium breve	*	*	*	*			
Protoperidinium brevipes		*	*	*	*	*	
Protoperidinium brochii				*			
Protoperidinium cerasus	*	*	*			*	*
Protoperidinium claudicans		*	*	*		*	
Protoperidinium clavus	*	*					
Protoperidinium conicoides	*	*	*	*	*	*	*
Protoperidinium conicum		*		*		*	*
Protoperidinium consimilis			*				
Protoperidinium crassipes							*
Protoperidinium curvipes	*	*			*	*	*
Protoperidinium depressum		*					
Protoperidinium diabolus	*						
Protoperidinium divergens	*	*	*				
Protoperidinium excentricum		*		*	*	*	*
Protoperidinium granii	*	*	*	*		*	
Protoperidinium hemisphericum				*			
Protoperidinium hirobis	*	*	*	*	*	*	*
Protoperidinium hyalinium	*						
Protoperidinium leonis	*	*	*	*			
Protoperidinium minutum				*			
Protoperidinium mite		*					
Protoperidinium monospinum		*		*	*		
Protoperidinium oblongum		*	*	*		*	
Protoperidinium oceanicum		*		*		*	
Protoperidinium ovatum				*			
Protoperidinium pallidum		*	*	*	*	*	*
Protoperidinium parvum							*
Protoperidinium paulseni				*	*	*	*
Protoperidinium pellucidum	*	*	*	*	*	*	*
Protoperidinium pentagonum		*	*	*			*
Protoperidinium pentagonum var. *latissmum*			*	*			
Protoperidinium petersi					*		
Protoperidinium punctulatum			*				
Protoperidinium pyriforme	*	*	*	*	*	*	*
Protoperidinium quarnerense		*					
Protoperidinium roseum		*	*		*		*
Protoperidinium spinulosum		*	*	*			
Protoperidinium steinii		*		*			
Protoperidinium subinerme			*			*	
Protoperidinium thorianum						*	*
Protoperidinium sp.1	*		*				
Protoperidinium sp.2		*					

Appendix 1. continued

Species	Site 1	Site 2	Site 3	Site 4	Site 5	Site 6	Site 7
Protoperidinium sp.3		*					
Protoperidinium sp.4		*					
Protoperidinium sp.5		*		*			
Protoperidinium sp.6			*				
Pyrocystis lunula		*		*		*	*
Pyrophacus horologium							*
Scrippsiella trichoidea	*	*	*	*	*	*	*
Spiraulax jolliffei				*			
Triadinium orientale				*			