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Dinoflagellate Cysts in Surface Sediments from Southern Coast of Korea

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Abstract To investigate the distributions of dinoflagellate cysts in relation to environmental conditions from southern coast of Korea, surface sediment samples collected from 11 stations in Gamak Bay, Yeoja Bay and the offshore area of Yeoja Bay were analyzed. Dinoflagellate cyst assemblages observed in the study area included many species commonly reported from other temperate regions. Among them, *Polykrikos* cysts were dominant, together with *Brigantedinium* spp. and *Spiniferites* spp. Based on cluster analysis, dinoflagellate cyst assemblages were divided into two main groups; group I, located in Yeoja Bay and group II, located in Gamak Bay and the offshore area of Yeoja Bay. Principal component analysis identified differences in salinity levels as the main environmental factors affecting the distributional characteristics of dinoflagellate cyst assemblages in the study area. Gamak Bay is a typical eutrophied area as result of extensive human activities around the bay, and heterotrophic cysts, including *Polykrikos* cysts, are remarkably abundant and likely to be a useful indicator for eutrophication in Gamak Bay.

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Introduction

Marine dinoflagellates are a major component in plankton communities and play an important role as primary producers in marine ecosystems. They are composed of autotrophic, heterotrophic, and mixotrophic species, and some of which produce during their life cycle resting cysts that can be preserved in sediments (e.g., Head 1996). The encystment of dinoflagellates is known to be affected by water temperature, nutrient availability, day length and endogenous encystment rhythms (Taylor 1987), whereas cyst distribution in sediments has been related to environmental factors such as water temperature, salinity, turbulence and the availability of nutrients (Dale 1996; Marret and Zonneveld 2003). This suggests that dinoflagellate cysts recorded from sediments can be utilized to reconstruct environmental conditions in a given study area. Many ecologists and paleontologists have tried to reconstruct the past environmental characteristics using dinoflagellate cysts, as understanding the past environmental conditions help to develop information for interpreting on environmental changes of present and future. However, in Korean coastal areas previous studies concerning dinoflagellate cysts have concentrated on only understanding their distributional characteristics (Lee and Yoo 1991; Lee and Matsuoka 1994), and there is no information available yet on the relationship between dinoflagellate cyst distribution and environmental conditions.

The relationship between dinoflagellate cysts and environmental conditions has been well documented around the world (e.g., Zonneveld 1997; Zonneveld et al. 2000; Marret and Zonneveld 2003; Radi and de Vernal 2004; Radi et al. 2007; Shin et al. 2007; Pospelova et al. 2008). In particular, paleo-environmental studies and ecological studies of eutrophied or industrial areas are increasingly being conducted with the use of dinoflagellate cysts (e.g., Sætre et al. 1997; Dale et al. 1999; Matsuoka 1999; Pospelova et al. 2002, 2005; Matsuoka et al. 2003; Dale 2009). However, the relationship between specific dinoflagellate cysts and environmental conditions has yet to be fully understood. For instance, *Lingulodinium machaerophorum* (Deflandre and Cookson) Wall (the cyst name for *Lingulodinium polyedrum*), and *Selenopemphix quanta* (Bradford) Matsuoka (the cyst name for *Protoperidinium conicum*) were regarded as species responding to cultural eutrophication in the Oslofjord of Norway (Dale et al. 1999; Dale 2001). However, these species do not occur abundantly in Tokyo Bay, Japan, which is also a heavily eutrophied area (e.g., Matsuoka 1999, 2001; Matsuoka et al. 2003). This may be due to differences in habitat preferences between geographically separated populations of the same species and/or competition with a different set of taxa (Smayda and Reynolds 2003). In other words, dinoflagellate cysts as indicators of environmental conditions may also vary in different ecosystems.

Coastal areas, including estuaries, are influenced by domestic and industrial waste waters, urban sewage, and agriculture effluents caused by anthropogenic activities, as well as freshwater runoff from rivers, and because of these, their biology and physical dynamics are often altered. Pospelova et al. (2002) reported on the relationship between dinoflagellate cyst abundance and human activity in estuarine area of Massachusetts, USA and suggested that more studies are needed to better understand such relationships as indication of eutrophication by dinoflagellate cysts varied in different areas and different eutrophication levels. Although the coastal areas of Korea, particularly the southern areas, are exposed to the open ocean, adjacent human activities cause heavily polluted surface waters. However, in Korean coastal areas, use of dinoflagellate cysts as indicators of environmental changes caused by the human activities is not well known.

In this study, we document the records of dinoflagellate cyst assemblages and report their relationships with environmental characteristics in southern coastal area of Korea. We also suggest a number of dinoflagellate cyst taxa that can be considered as indicators of eutrophication in Korean coastal areas.

Study Area

The study area consists of two semi-enclosed bays, namely Gamak Bay and Yeoja Bay, and the offshore area of Yeoja Bay located on the south coast of Korea (Fig. 1). Annual precipitation in this region amounts to 150 cm, with most of this falling in summer (from July to September). The amount of freshwater entering the bay through streams and ditches ranges from 2.7×10^4 to 18.0×10^4 $m^3 day^{-1}$ (average, ~7.0×104 m^3 day^{-1}), with a large seasonal variation. Gamak Bay is oval in shape and approximately 9 km in width and 15 km in length, shallow with a mean depth of about 9 m and surrounded by the Yeosu Peninsula and Dolsan Island to the east. Surface sediments consist mainly of silty clay and clayey silt, however, slightly gravelly mud is also distributed near the channels at the bay mouth (Kim et al. 2000). Waters in this bay are exchanged mainly through the southern entrance of the bay and additionally through a narrow northeastern channel (Koo et al. 2004), and the direction of tidal flood current is shown in Fig. 1b. The bay is separated into two sub-basins (northwestern and southern basins) by a ridge that runs from east to west. The numerous oyster farms, which are densely positioned above the ridge, account for about 30% of total annual oyster production in Korea (Lee and Cho 1990), while mussel farms and fish cultures are also located throughout the bay (Fig. 1b). Filter feeders, including oysters, generally feed on diatoms, ciliates, and flagellates and their filtration activity may have an influence on local phytoplankton dynamics (Vaquer et al. 1996). Nevertheless, seasonal succession of phytoplankton assemblages in Gamak Bay has been clearly linked with nutrient dynamics (Yoon 2000). Human activity on the ridge and the dense presence of farms reduce water circulation between the northwestern and southern basins, and also between surface and bottom waters (Lee and Cho 1990; Kim et al. 2006). In particular, aquaculture wastewaters and the increase of urban sewage discharged from Yeosu City have led to eutrophic conditions since 1990 (Lee and Cho 1990; Koo et al. 2004). Anoxic conditions frequently appear in bottom waters of the northwestern area of Gamak Bay, with less than 2.0 mg/L of dissolved oxygen in the summer season (Kim et al. 2006). In addition, the frequency of harmful algal blooms has increased since 1990 (Park and Yoon 2003). Based on these facts, this bay can be considered as a typical eutrophied area.

Yeoja Bay is surrounded by Yeosu Peninsula to the east and the Goheung Peninsula to the west, and is connected to the South Sea of Korea through narrow inlets at the southern entrance of the bay. The bay is shallow with 5.4 m in average water depth, and extensive mud flats occur along the coast. Surface sediments consist mainly of silty clay with 6.0–8.7 Md φ, coarse sediments are dominant in the north and mouth of the bay (Hwang et al. 2005), and its distribution is related to a clockwise circulation of seawater during flood tides (Fig. 1b) (Lee et al. 2000). The bay is also characterized

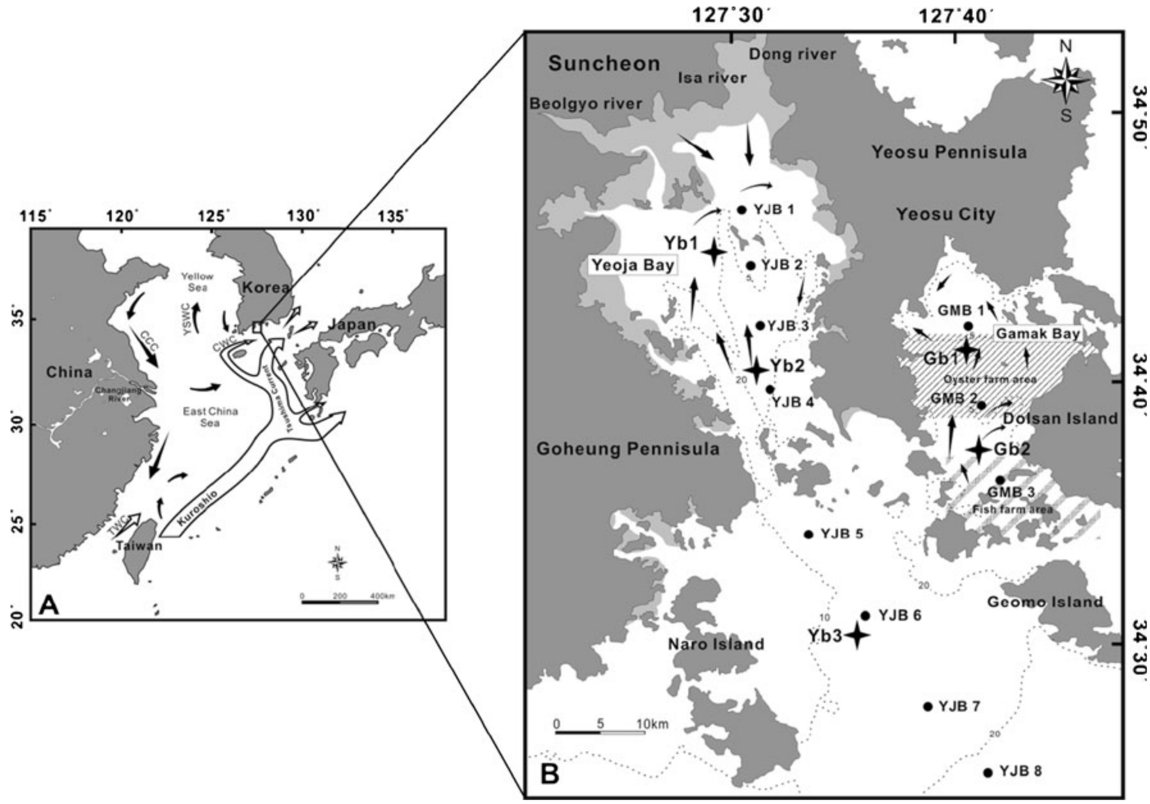


Fig. 1 Study area in the southern coast of Korea. **a** Circulation pattern of Tsushima Warm Current (*TWC*), Yellow Sea Warm Current (*YSWC*), Cheju Warm Current (*CWC*), and Chinese Coastal Current (*CCC*) suggested by Teague et al. (2003). **b** Sediment sampling stations (*dots*), observation sites of NFRDI (*stars*), and direction of tidal flood current in Gamak Bay (Lee 1992) and Yeoja Bay (Lee et al. 2000)

by an outstanding semidiurnal tide producing periodical and strong ebb tidal movements (Lee et al. 2000). Freshwater is loaded into the bay by the Beolgyo, Isa, and Dong river that flow through Suncheon City, discharging fluvial water of 0.07, 0.19, and 0.14 km^3/year, respectively. However, despite the intrusion of fresh waters with nutrients, the environmental conditions of this bay are less polluted, as indicated by chemical oxygen demand, total sulfide, and ignition loss of sediments (Hue et al. 2000; Lee and Youn 2000).

The offshore area of Yeoja Bay is strongly affected by intrusion from open seawaters such as the Tsushima Warm Current and Yangtze-River-diluted water derived from the Chinese coast (Beardsely et al. 1985; Lee 2006; Kim et al. 2007) (Fig. 1a). Although the intrusion of the Yangtze-River-diluted water, which is characterized by high temperature (>22°C), low salinity (<29 psu), and highly dissolved inorganic nitrogen (DIN) concentration, is related to the occurrence of red tides in summer, the area is relatively less eutrophicated (Kim et al. 2001). Water depth is about 20 m, while mean water temperature and salinity recorded in August were 26.2°C and 31.7 psu, respectively (Choi 2001). Salinity is similar to that of Gamak Bay (Kim 2002).

Materials and Methods

Sampling and Dinoflagellate Cyst Analysis

Surface sediment samples for dinoflagellate cyst analysis were collected from 11 stations with a gravity corer in Gamak and Yeoja Bays in May 2006 (GMB1, GMB2, and GMB3 and YJB1, YJB2, YJB3, and YJB4) and in the offshore area of Yeoja Bay in January 2007 (YJB5, YJB6, YJB7, and YJB8). The top 2 cm of core samples were sliced and all of them stored in dark and cool conditions at 4°C prior to further analysis. Sedimentation rates in Gamak Bay and Yeoja Bay were estimated using ^{210}Pb dating method, which were averaged at 2.5 and 1.1 cm/year, respectively (Shin et al. 2010a, b). Based on these results, we assumed that the top 2 cm of the sediments from the offshore area of Yeoja Bay represent less than 3 or 4 years of deposition.

The samples were processed according to the palynological method of Matsuoka and Fukuyo (2000) as follows: Approximately 2 g of each sample was placed into an acid-resistant 100-ml beaker and then treated to remove calcium carbonate and silicate materials with 10% HCl and 47% HF at room temperature, respectively. The residues were rinsed with distilled water, sonicated for about 30 s, and sieved with stainless steel screens of 125- and 20-μm opening mesh size. The residues on the 20-μm mesh were made up to a 10-ml aliquots by adding distilled water. Identification of dinoflagellate cysts was carried out on a 1-ml subsample of the 10-ml aliquot under an Olympus IX 70 interference optical microscope. *Alexandrium*-type cysts were identified with the Primuline-staining direct count method of Yamaguchi et al. (1995) because primuline stains cysts after the treatment with acids (Shin et al. 2010b).

For measurement of water content, a part of each sample was weighed wet and then dried in an oven under 70°C for 24 h. In this study, cyst concentrations are shown as the number of cysts per gram of dry weight sediment (cysts g^{-1} dry weight).

Statistical Treatments and Environmental Data

Cluster analysis was conducted with the PRIMER software, which contains the Bray-Curtis similarity coefficient, using the components of cyst concentration and the number of species in order to clarifying the characteristics of dinoflagellate cyst assemblages.

The mud content was measured with a laser particle size analyzer (SALD-3100, Shimadzu), and defined less than 63 μm as the proportion of sediments. Mean surface water temperature, salinity, DIN and chlorophyll *a* concentration in February and August from 2005 to 2006 were obtained from five sites of National Fisheries Research and Development Institute (Table 1; Fig. 1b). According to de Vernal et al. (1994) and Radi et al. (2001), the environmental data for the coldest and warmest months provide information on the annual hydrographical cycle, which seems to be more of a determinant for the dinoflagellate cysts distribution that seasonal or annual means. Consequently we selected the environmental data obtained made in February and August. In order to identify the environmental characteristics of our study area, principal component analysis (PCA) was performed on the obtained environmental parameters using SPSS version 10.0 for windows. Results are summarized in Table 2.

Table 1 Mean surface water temperature, salinity, dissolved inorganic nitrogen (DIN) and chlorophyll *a* concentration of 2005 and 2006 obtained from NFRDI (http://www.nfrdi.re.kr)

Station	Tem (°C)	Sal (psu)	DIN (mg l^{-1})	Chl *a* (μg l^{-1})
August				
Gb1	27.9	30.8	0.031	2.6
Gb2	25.9	31.1	0.038	3.7
Yb1	30.0	28.0	0.095	3.2
Yb2	27.4	29.6	0.065	2.1
Yb3	24.8	31.3	0.082	2.5
February				
Gb1	6.00	33.7	0.041	1.8
Gb2	7.30	33.8	0.064	2.1
Yb1	4.30	32.8	0.070	3.9
Yb2	5.65	33.3	0.056	4.7
Yb3	6.20	33.7	0.048	1.8

NFRDI National Fisheries Research and Development Institute, *Tem* water temperature, *Sal* salinity, *DIN* dissolved inorganic nitrogen, *Chl a* chlorophyll *a* concentration

Results

Dinoflagellate Cyst Assemblages

A total of 35 dinoflagellate cyst taxa were identified from the 11 studied stations (Tables 3 and 4), some of which are shown in Fig. 2. Concentrations of the most abundant taxa at each station are shown in Fig. 3. Cysts produced by *Protoperidinium* (*Brigantedinium* spp.) and *Gonyaulax* (*Spiniferites* spp.) were dominant, while *Brigantedinium* spp. were particularly abundant in the offshore area of Yeoja Bay and Gamak Bay. *Spiniferites* spp. mainly composed of *Spiniferites bulloideus* (Deflandre and Cookson) Sarjeant (the cyst name for *Gonyaulax scrippsiae*) were only abundant at YJB6 and YJB8. Cysts of *Polykrikos kofoidii* Chatton and *Polykrikos schwartzii* Bütschli were abundant at YJB6, YJB8, and GMB3. Cysts of *Alexandrium affine* (Inoue and Fukuyo) Balech type and *Alexandrium catenella* (Whedon and Kofoid) Balech/*tamarense* (Lebour) Balech type were abundant in the offshore area of Yeoja Bay and Gamak Bay. *L. machaerophorum* (Deflandre and Cookson) Wall and *S. quanta* (Bradford) Matsuoka appeared to be relatively low in abundance.

Dinoflagellate Cyst Distribution

Cyst concentration ranged from 173 to 1,276 cysts g^{-1} (Fig. 3), and the highest cyst concentration was recorded at YJB6 and the lowest at YJB5. Cyst concentration in the offshore area of Yeoja Bay was relatively higher than in Gamak and Yeoja Bays. Heterotrophic cysts accounted for more than 50% of total assemblages in all samples (Fig. 3). The highest proportion of heterotrophic cysts was recorded at GMB1 (74.2%) and the lowest at YJB4 (51.6%). The proportion in Gamak Bay was generally higher than in Yeoja Bay and the offshore area of Yeoja Bay.

Based on cluster analysis, dinoflagellate cyst assemblages of the study area were divided into two main groups at a level of 71 Bray-Curtis similarity coefficient; Group I consisted of the assemblages in Yeoja Bay (YJB1, YJB2, YJB3, YJB4, and YJB5) characterized by low cyst

Table 2 Principal component analysis results (eigenvalues, eigenvectors, and scores) from environmental parameters

Parameters	August		February		Station	Score	
	PCA1	PCA2	PCA1	PCA2		PCA1	PCA2
Tem (°C)	−0.730	0.531	0.983	−0.048	Gb1	0.342	0.206
Sal (psu)	0.886	−0.189	0.960	−0.218	Gb2	1.221	0.966
DIN (mg l^{-1})	−0.752	−0.492	−0.116	0.962	Yb1	−1.506	0.909
Chl *a* (μg l^{-1})	−0.130	0.856	−0.143	0.104	Yb2	−0.278	−1.162
					Yb3	0.222	−0.920
Eigenvalues	4.33	2.05					
Variations (%)	54.1	25.7					

concentration with relatively low proportion of heterotrophic cysts and group II consisted of the assemblages in Gamak Bay and the offshore area of Yeoja Bay (YJB6, YJB7, and YJB8 and GMB1, GMB2, and GMB3) characterized by relatively high cyst concentration, with high proportion of heterotrophic cysts (Fig. 4). *Protoperidinium* cysts were abundant in stations of group II. However, *Selenopemphix nephroides* Benedeck (the cyst name for *Protoperidinium subnerme*) and cysts of *Protoperidinium americanum* (Gran and Braarud) Balech were abundant in group I, and *P. americanum* cysts are also observed in inner part of Gamak Bay (Fig. 3).

Environmental Analysis

PCA produced two important components, PCA 1 and PCA 2, which explains together 79% of total variation of the selected environmental parameters (Table 2). The eigenvectors for environmental parameters showed that PCA 1 is positively correlated with salinity, and has a negative correlation with water temperature and DIN in August. PCA 2 is positively correlated with DIN in winter and chlorophyll *a* concentration in August. Sample scores of the two components show distribution of the stations according to differences in salinity and seasonal variations of DIN (Fig. 5). Gb1, Gb2, and Yb3, which had a positive correlation with PCA 1, are located in the outer part of Gamak Bay and the offshore area of Yeoja Bay, where are strongly affected by open seawaters. However, Yb1 and Yb2, which had a negative correlation with PCA 1, are located in Yeoja Bay, where are easily affected by intrusion of freshwater. In addition, Gb1, Gb2, and Yb1, which has a positive correlation with PCA 2, are characterized by high DIN in February and chlorophyll *a* concentration in August. Salinity level in Gamak Bay (Gb1 and Gb2) and offshore area of Yeoja Bay (Yb3) was relatively higher than Yeoja Bay (Yb1 and Yb2).

The mud content is more that 90% at all stations (Table 4), which suggests a very similar hydrodynamic system across sites.

Discussion

Characteristics of Dinoflagellate Cyst Assemblages

Marret and Zonneveld (2003) summarized the global distribution of extant dinoflagellate cysts from recent sediments and their relationship with environmental conditions based on integrative data from the literature. In comparison with their results, the species composition of dinoflagellate cysts in this study generally resembled that of surface sediments in other temperate regions (e.g., Cho and Matsuoka 2001; Pospelova et al. 2002; Matsuoka et al. 2003; Wang et al. 2004; Shin et al. 2007), and dominant species such as *Brigantedinium* spp., *Spiniferites* spp. and *Polykrikos* cysts were cosmopolitan. Of them, *S. bulloideus* has been reported to be abundant in Asian coastal areas such as the southern coastal areas of Korea (Lee and Matsuoka 1994; Shin et al. 2007), and southern Japanese waters (Matsuoka 1985) which is characterized by high salinity. Matsuoka (1985) reported that the abundant occurrence of *S. bulloideus* with *Spiniferites* spp. along coasts of western Japan may be due to the effect of Tsushima Warm Current. Ellipsoidal *Alexandrium* cysts are also abundant in those areas together with East China Sea and Chinese coasts (e.g., Cho and Matsuoka 2001; Wang et al. 2004). According to Marret and Zonneveld (2003), high relative abundances of *S. bulloideus* and ellipsoidal *Alexandrium* cysts are related to high salinity. These species are abundantly found along offshore areas of Yeoja Bay and Gamak Bay, which may be related to the effect of open seawaters.

Distribution of Dinoflagellate Cyst Assemblages and Environmental Characteristics

Tidal dynamics can control gradients of bottom sediment texture, and consequently distribution of dinoflagellate cysts (Marret and Scourse 2002). As such, the presence of strong tidal currents may lead to the transport of dinoflagellate cysts from places where they were originally

Table 3 List of identified dinoflagellate cysts from surface sediments

Dinoflagellate vegetative stage (biological name)	Dinoflagellate cyst (paleontological name)
Gonyaulax digitalis	*Spiniferites bentorii*
Gonyaulax scrippsiae	*Spiniferites bulloideus*
Gonuaulax elongata	*Spiniferites elongatus*
G. spinifera complex	*Spiniferites hyperacanthus*
Gonyaulax membranacea	*Spiniferites membranaceus*
G. spinifera complex	*Spiniferites mirabilis*
G. spinifera complex	*Spiniferites* spp.
Alexandrium affine	Cyst of *Alexandrium affine* type
Alexandrium catenella/tamarense	Cyst of *A. catenella/tamarense* type
Lingulodinium polyedrum	*Lingulodinium machaerophorum*
Protoceratium reticulatum	*Operculodinium centrocarpum*
Pyrophacus steinii	*Tuberculodinium vancampoae*
Scrippsiella spp.	*Scrippsiella* spp.
Gymnodinium catenatum	Cyst of *G. catenatum*
Pheopolykrikos hartmannii	Cyst of *P. hartmannii*
Cochlodinium spp.	*Cochlodinium* spp.
Protoperidinium denticulatum	*Brigantedinium irregulare*
Protoperidinium sp.	*Brigantedinium asymmetricum*
Protoperidinium avellanum	*Brigantedinium cariacoense*
Protoperidinium conicoides	*Brigantedinium simplex*
Protoperidinium spp.	*Brigantedinium* spp.
Protoperidinium sp.	*Echinidinium aculeatum*
Protoperidinium leonis	*Quinquescuspis concreta*
Protoperidinium subinerme	*Selenopemphix nephroides*
Protoperidinium conicum	*Selenopemphix quanta*
Protoperidinium compressum	*Stelladinium reidii*
Protoperidinium stellatum	Cyst of *P. stellatum*
Protoperidinium pentagonum	*Trinovantedinium applanatum*
Protoperidinium sp.	*Trinovantedinium pallidfulvum*
Protoperidinium oblongum	*Votadinium calvum*
Protoperidinium claudicans	*Votadinium spinosum*
Protoperidinium americanum	Cyst of *P. americanum*
Protoperidinium divaricatum	*Xandarodinium xanthum*
Protoperidinium cf. *minutum*	Cyst of *Protoperidinium* cf. *minutum*
Protoperidinium latissimum	Cyst of *P. latissimum*
Oblea acanthocysta	Cyst of *Oblea acanthocysta*
Protoperidinium meunieri	*Dubridinium caperatum*
Polykrikos kofoidii	Cyst of *P. kofoidii*
Polykrikos schwartzii	Cyst of *P. schwartzii*

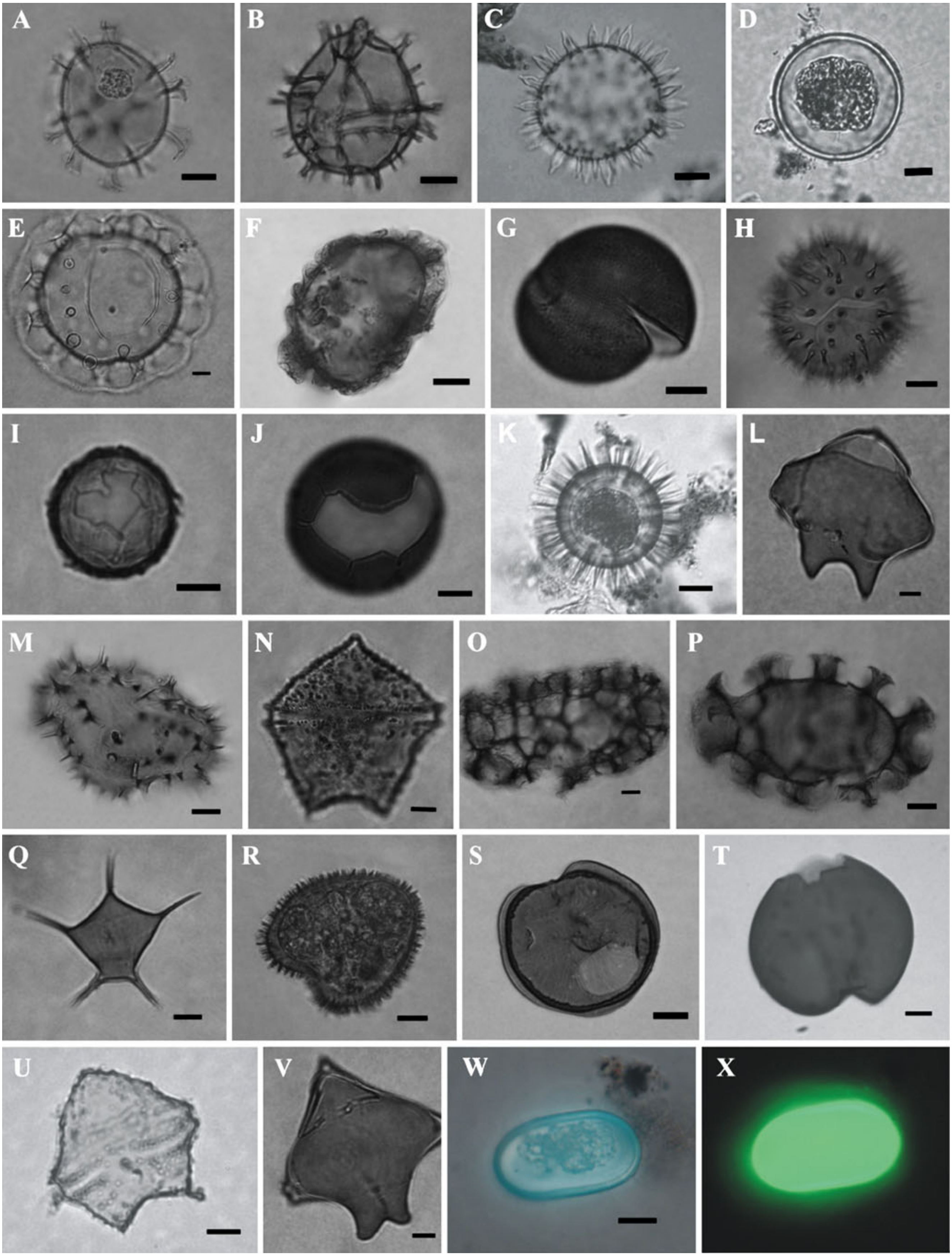
produced. However, since mud content was very high in all stations of study area (>90%) and Gamak Bay and Yeoja Bay characterized by low water depth are enclosed by several small islands located in the southern and northeastern channels, there is no expectation of significant transport of produced organic particles, including dinoflagellate cysts.

Nevertheless, cyst concentrations within Yeoja Bay were relatively low in comparison with those of Gamak Bay and the offshore area of Yeoja Bay. High abundance of dinoflagellate cysts can be explained by high dinoflagellate production, and since high nitrate loading into the water column enhances occurrence and number of dinoflagellate species, dinoflagellate productivity is directly influenced by nitrate concentration (Lopes et al. 2007). Nitrogen loading into Yeoja bay is related to the intrusion of freshwaters derived from rivers located in the northern part of the bay. DIN in the inner area of Yeoja Bay (Yb1) is relatively

Table 4 Species composition and abundances (cysts g^{-1} dry weight) of dinoflagellate cysts collected from the surface sediments and mud contents in each station

Dinoflagellate cysts	Station										
	YJB1	YJB2	YJB3	YJB4	YJB5	YJB6	YJB7	YJB8	GMB1	GMB2	GMB3
Spiniferites bentorii	0	0	0	0	2	0	0	0	0	3	16
Spiniferites bulloideus	16	18	13	8	8	72	16	95	28	6	28
Spiniferites elongatus	0	0	0	0	0	0	3	0	0	0	0
Spiniferites hypercanthus	29	26	11	21	0	0	0	0	0	3	0
Spiniferites mirabilis	0	0	0	3	0	4	0	0	0	0	0
Spiniferites membranaceus	0	0	0	0	0	0	3	11	0	0	0
Spiniferites spp.	73	62	67	61	19	160	68	246	55	64	81
Cyst of *Alexandrium affine* type cyst	10	39	33	40	12	175	26	46	52	19	65
Cyst of *Alexandrium catenella/tamarense* type cyst	8	21	29	45	10	56	55	84	55	19	84
Lingulodinium machaerophorum	3	5	11	5	2	20	16	25	12	10	16
Operculodinium centrocarpum	0	3	2	3	2	44	6	11	3	16	9
Tuberculodinium vancampoae	0	8	7	8	4	12	0	11	0	3	9
Scrippsiella spp.	0	0	0	0	0	0	3	0	0	0	0
Cyst of *Gymnodinium catenatum*	0	0	0	3	6	0	3	7	0	0	3
Cyst of *Pheopolykrikos hartmanii*	0	0	2	0	0	0	3	7	3	0	3
Cochlodinium spp.	0	0	0	0	0	4	3	7	0	0	0
Brigantedinium asymmetricum	5	0	0	5	0	8	3	0	34	0	12
Brigantedinium cariacoense	0	0	2	0	2	4	10	7	0	38	12
Brigantedinium irregulare	0	3	0	3	2	4	3	11	3	0	6
Brigantedinium simplex	0	0	0	0	0	0	10	18	18	0	19
Brigantedinium spp.	86	82	81	74	54	259	126	222	259	79	221
Selenopemphix nephroides	16	31	29	11	8	24	6	21	3	6	12
Selenopemphix quanta	8	21	16	3	8	32	16	49	31	3	9
Cyst of *Protoperidinium stellatum*	0	0	0	0	0	8	3	4	15	13	3
Stelladinium reidii	3	0	0	0	0	8	0	0	3	16	0
Trinovantedinium applenatum	3	0	7	11	4	12	0	11	3	6	3
Trinovantedinium pallidifurvum	8	10	7	3	0	8	0	7	0	0	3
Quinquescuspis concreta	0	13	11	5	0	8	0	21	12	6	12
Votadinium calvum	8	5	9	16	8	16	13	35	18	13	22
Votadinium spinosum	0	3	2	3	0	12	3	0	46	10	12
Cyst of *Protoperidinium americanum*	26	15	9	8	2	40	6	7	37	38	3
Cyst of *Protoperidinium latissinum*	0	0	0	0	0	0	0	7	0	0	0
Echinidinium aculeatum	0	3	0	0	0	0	10	4	6	0	3
Xandarodinium xanthium	0	0	0	0	0	0	0	4	0	0	0
Cyst of *Protoperidinium* cf. *minutum*	0	15	0	0	6	84	29	56	64	32	19
Cyst of *Oblea acanthocysta*	8	21	11	13	2	36	13	32	21	25	9
Dubridinium caperatum	5	0	9	5	0	28	23	14	6	3	6
Cyst of *Polykrikos kofoidii*	16	31	40	42	12	108	29	109	12	10	165
Cyst of *Polykrikos schwartzii*	3	0	4	8	2	32	16	39	6	3	22
Total	331	434	413	404	173	1,276	528	1,224	807	446	892
Mud content (%)	98.9	99.4	99.2	97.7	90.0	99.0	98.5	99.3	98.9	98.6	99.0

higher than that in the outer part and offshore area of Yeoja Bay (Yb2 and Yb3) (Table 1). According to Lee and Kim (2007), relative proportion of dinoflagellates to diatoms increases from the low salinity and high DIN inner part to the high salinity and lower DIN offshore area of Yeoja Bay. As a result, this may lead to a lower cyst concentration within Yeoja Bay. In addition, Yeoja Bay has a large seasonal variation in salinity due to the intrusion of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◀**Fig. 2** Photomicrographs of some dinoflagellate cysts collected in surface sediments from the southern coastal waters of Korea: **a** *Spiniferites bulloideus,* **b** *Spiniferites bentorii*, **c** *Lingulodinium machaerophorum,* **d** Cyst of *Alexandrium affine* type, **e** *Tuberculodinium vancampoae*, **f** *Cochlodinium* spp., **g** Cyst of *Gymnodinium catenatum*, **h** Cyst of *Oblea acanthocysta,* **i** Cyst of *Protoperidinium americanum,* **j** *Brigantedinium irregulare*, **k** Cyst of *Protoperidinium* cf. *minutum*, **l** *Quinquecuspis concreta*, **m** *Selenopemphix quanta*, **n** *Trinovantedinium applanatum*, **o** Cyst of *Polykrikos kofoidii*, **p** Cyst of *Polykrikos schwartzii,* **q** *Stelladinium reidii*, **r** *Votadinium spinosum*, **s** *Selenopemphix nephroides,* **t** *Votadinium calvum*, **u** *Trinovantedinium pallidifulvum*, **v** *Protoperidinium latissimum*, **w** Cyst of *Alexandrium catenella/tamarense* type under normal light after staining with primuline, and **x** Cyst of *Alexandrium catenella/tamarense* type under UV light after staining with primuline. *Scale bars*: 10 μm

freshwaters, and precipitation that falls mostly in the summer season (from July to September). These specific conditions may also determine the low dinoflagellate cyst concentration of this bay as few species such as *Spiniferites* spp. tolerate low-salinity environments (Pospelova et al. 2004).

The result of cluster analysis shows distributional characteristics of dinoflagellate cyst assemblages in study area: groups I (Yeoja Bay) and II (offshore area of Yeoja Bay and Gamak Bay). Based on the PCA results, we identified that the differences in salinity levels are the main environmental factors affecting distributional characteristics of dinoflagellate cyst assemblages (groups I and II) in studied areas. Group I is affected by the intrusion of freshwaters, and has relatively low salinity levels. The assemblages related to group I are characterized by abundant occurrences of *S. nephroides* and cyst of *P. americanum*. Holzwarth et al. (2007) suggested that *S. nephroides* and cyst of *P. americanum* can be used as a proxy for fluvial influences. However, *S. nephroides* has also been observed in marine environments (Ellegaard 2000; Persson et al. 2000). This species possibly seems to have a tolerance to salinity. Marret and Zonneveld (2003) and Kawamura (2004) reported that the occurrence of *P. americanum* cyst is not restricted to river estuaries or even to coastal environments. In study area the abundant occurrence of *P. americanum* cyst was also observed in the inner part of Gamak Bay, which is affected by urban sewage (Fig. 3). Consequently, the occurrences of this species in study area may be related to low salinity levels.

In general, the distribution of heterotrophic cysts is related to availability of prey such as diatoms and small flagellates (Naustvoll 2000). According to Hwang et al. (2005), the freshwater input into Yeoja Bay brings with it high silicate concentration (mean dissolved inorganic silicate 36 μM in the summer season), and in summer the main primary producers are diatoms (Shim 1980; Lee and Youn 2000). This probably provides a favorable environmental condition for the growth of heterotrophic dinoflagellates. Nevertheless, the relatively low proportions of heterotrophic cysts in Yeoja Bay suggest that heterotrophic dinoflagellates in Yeoja Bay may be controlled by other environmental conditions such as salinity rather than the availability of prey, because heterotrophic dinoflagellates

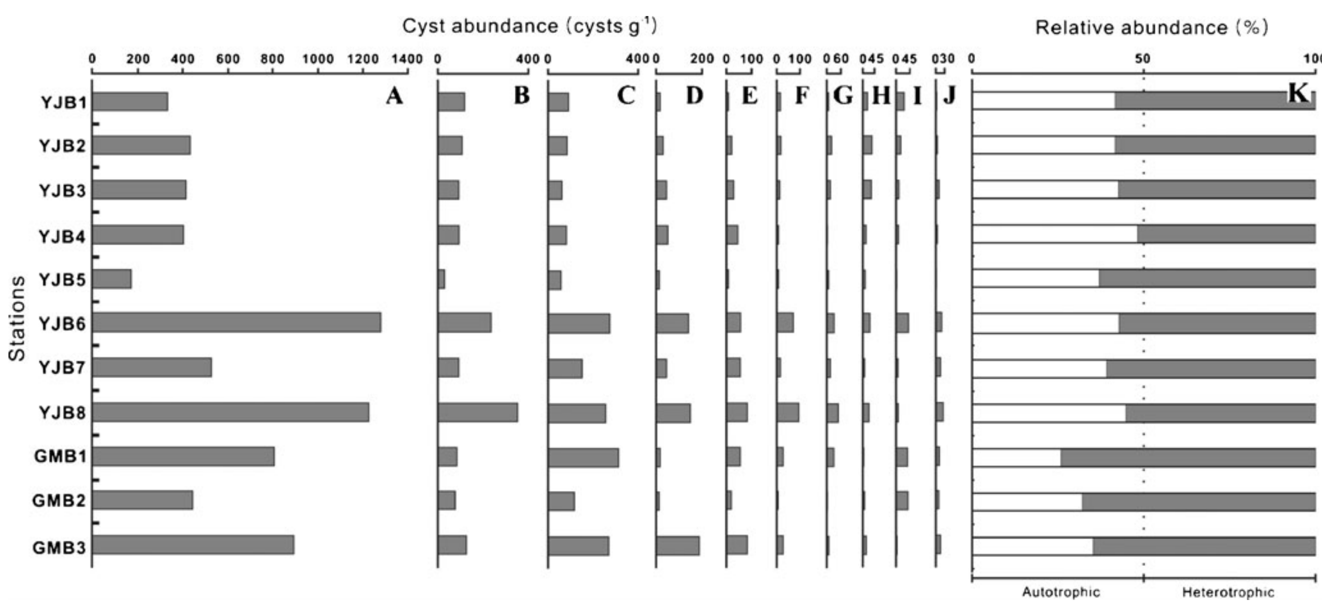

Fig. 3 Concentrations of total number of cysts (*A*), and the most dominant cyst taxa: *Spiniferites* spp. (*B*), *Brigantedinium* spp. (*C*), cysts of *Polykrikos kofoidii/schwartzii* (*D*), cysts of *Alexandrium tamarense/catenalla* type (*E*), *Spiniferites bulloideus* (*F*), *Selenopemphix quanta* (*G*), *Selenopemphix nephroides* (*H*), cysts of *Protoperidinium americanum* (*I*), *Lingulodinium machaerophorum* (*J*), and relative abundances (%) of autotrophic and heterotrophic dinoflagellate cysts (*K*) in surface sediments from the southern coast of Korea

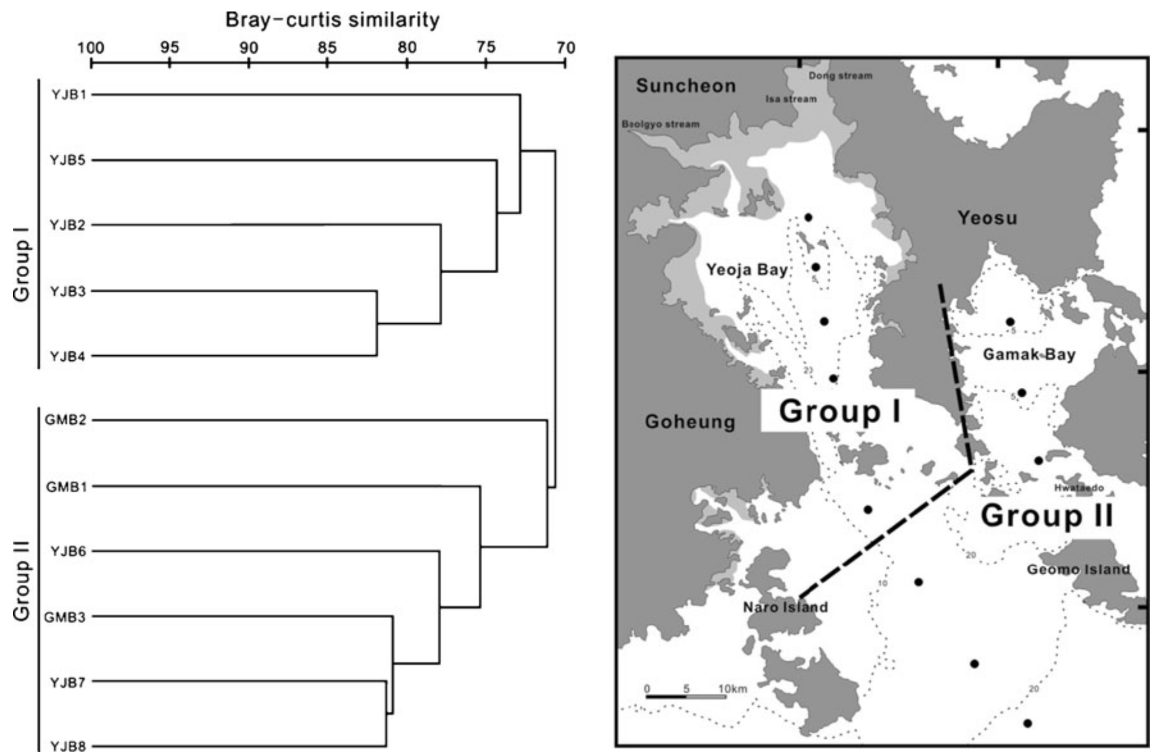

Fig. 4 Dendrogram and separated areas based on results from cluster analysis

that can endure low-salinity stress can graze on the preys such as diatoms (Shin et al. 2010b).

Group II is frequently affected by the intrusion of open seawaters, and is characterized by relatively low DIN in August. In particular, DIN in Gamak Bay (Gb1 and Gb2) exhibit a large differential gradient in between August and February, possibly due to nitrogen uptake by dinoflagellates in summer (Shim 1980) (Table 1). According to Kim (2002), the limiting nutrient responsible for the growth of dinoflagellates in Gamak Bay and the offshore area of Yeoja Bay is nitrogen, which suggests that the distribution of dinoflagellate cysts in group II may be closely related to DIN and that environmental conditions in group II are favorable for the growth of dinoflagellates compared with that of group I. The cyst assemblages related to group II were generally characterized by high abundance of heterotrophic dinoflagellate cysts such as *Protoperidinium* cysts (*S. quanta* and *Brigantedinium* spp.) and *Polykrikos* cysts. In particular, *Brigantedinium* spp. were highly abundant in this group. According to Holzwarth et al. (2007), high relative abundances of heterotrophic cysts are related to high chlorophyll *a* concentrations, which can be used as a productivity indicator (Zonneveld et al. 2001; Marret and Scourse 2002). PCA result showed that the inner part of Yeoja Bay (Yb1) and Gamak Bay (Gb1 and Gb2) has a positive relationship to chlorophyll *a* concentrations in August. As such, the abundance of heterotrophic cysts is likely to be used as productivity indicators within our study area. *Brigantedinium* spp. are also abundant in areas with nutrient-rich waters, such as upwelling areas (Marret 1994; Wall et al. 1977; Pospelova et al. 2008). According to Marret and Zonneveld (2003), their distribution is not restricted to any salinity or nitrate concentration ranges, whereas recently Shin et al. (2010b) reported that although the environmental conditions such as nutrients are favorable for the growth of dinoflagellates, low salinity levels in

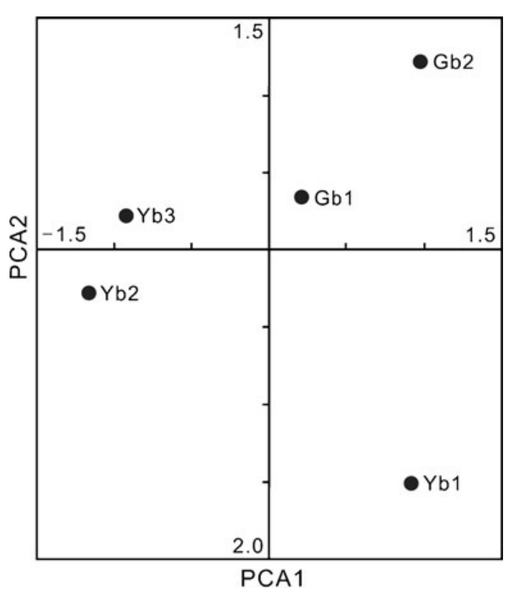

Fig. 5 PCA ordination of stations based on environmental parameters

Yeoja Bay may hamper the growth. Consequently, their relatively higher concentration may be attributed to the intrusion of open seawaters characterized by high salinity.

For an accurate interpretation of the obtained data, it is essential to know the species-selective degradation of dinoflagellate cysts as a result of oxidation. According to Zonneveld (1997), cysts produced by *Protoperidinium* species, especially *Brigantedinium* spp., appear to be sensitive to decay in relation to oxygen availability, except for some species (e.g., *Impagidinium* species). This suggests that bottom oxygen concentration is an important factor that can affect dinoflagellate cyst assemblages (Zonneveld et al. 2007). In this study, Gamak Bay has been characterized by relatively low bottom oxygen concentrations (Kim et al. 2006), whereas bottom oxygen concentrations of Yeoja Bay and the offshore area of Yeoja Bay range from 2.73 to 6.09 ml/L (Shim 1980). According to Reichart and Brinkhuis (2003), the relative abundances of *Protoperidinium* species at oxygen concentrations of above 2.5 ml/L rapidly decreased. However, since sedimentation rates in our study area are very high, which indicates shorter exposure to bottom water conditions, good preservation of dinoflagellate cysts in sediment samples is expected. Consequently, we assume that there are no systematic errors in the interpretations of data based on dinoflagellate cyst assemblages from our study area.

Dinoflagellate Cysts as Indicator of Eutrophication in Gamak Bay

The utilization of dinoflagellate cysts as an indicator of eutrophication has been well documented (e.g., Dale et al. 1999; Matsuoka 1999; Matsuoka et al. 2003; Pospelova et al. 2002, 2005). For instance, total cyst concentration and the number of *L. machaerophorum* in Oslofjord increased with eutrophication (Dale et al. 1999), while high relative abundance of *S. quanta* with *L. machaerophorum* has been associated with eutrophication in estuaries of Massachusetts (Pospelova et al. 2002). Eutrophication in Tokyo Bay has also led to increased ratios of heterotrophic dinoflagellate cysts (Matsuoka 1999). Gamak Bay is an anthropogenically eutrophied area characterized by high nutrient levels. The abundance of *L. machaerophorum* in Gamak Bay ranged from 2 to 16 cysts g^{-1} and its relative abundance was only 1.9% of the total cyst assemblages. Pospelova et al. (2002) reported that *L. machaerophorum* occasionally tend to response negatively to eutrophication. However, vertical change in concentration of *L. machaerophorum* did not show a particular trend (Shin et al. 2010a). These occurrences are different from Oslofjord where relative abundances of *L. machaerophorum* varied from more than 5 to ca. 50% of the assemblages (Dale et al. 1999). In addition, the concentration of *S. quanta* cysts is not remarkable in Gamak Bay. In Korean coastal areas, *L. polyedrum* (the biological name of *L. machaerophorum*) is not abundant, and large bloom of this species has never been reported (Shim 1980; Kim et al. 1990; Lee et al. 1999). This suggests that *L. machaerophorum* do not respond to eutrophication in Gamak Bay, and as such cannot be used as an indicator species for eutrophication. More recently, Smayda and Reynolds (2003) formulated the ecological strategies of marine dinoflagellates, with emphasis on various bloom-forming species. According to their results, *L. polyedrum* is an upwelling relaxation taxa, and as such their cysts are reported as abundant in upwelling area (Sprangers et al. 2004). Upwelling and anthropogenic eutrophied areas generally have different mechanisms of nutrient enrichment. The major nutrients for the growth of dinoflagellates in Gamak Bay, especially nitrogen, are supplied by the inflow of sewage and bacterial decomposition of organic matters derived from aquaculture activities (Kim 2002; Noh et al. 2006). Consequently, although nutrients are satisfied, discharged organic matters do not allow the growth of *L. polyedrum* in Gamak Bay, possibly due to limited light penetration in the turbid waters.

Matsuoka (1999) suggested that an increase of heterotrophic dinoflagellate cysts is probably a good indicator for eutrophication based on the observation of dinoflagellate cyst assemblages in Tokyo Bay. Our results indicate that Gamak Bay is characterized by high abundance of heterotrophic dinoflagellate cysts, dominated by *Polykrikos* cysts and *Brigantedinium* spp. In general, increases of heterotrophic dinoflagellate cysts have been observed in both upwelling and eutrophied areas, characterized by high primary production and nutrient level (Marret 1994; Dale et al. 2002; Radi and de Vernal 2004). For this reason, a eutrotrophic indicator is difficult to distinguish from an upwelling indicator (Dale 2009). However, increase of *Polykrikos* cysts has been frequently observed in eutrophied areas such as Tokyo Bay, Japan (Matsuoka 1999; Matsuoka et al. 2003), and in Apponagansett Bay, Massachusetts, where nutrient enrichment has continued to increase since the beginning of the 20th century (Pospelova et al. 2002). Matsuoka et al. (2003) suggested that the high abundance of *Polykrikos* cysts observed from surface sediments in Tokyo Bay may reflect a hypertrophic nutrient condition developed from a nutrient rich condition. In addition, Shin et al. (2010a) reported that the changes in nutrient levels in Gamak Bay are coincided with the increase in the proportion of heterotrophic cysts. It is therefore possible that high abundance of heterotrophic dinoflagellate cysts dominated by cysts of *Polykrikos* cysts in Gamak Bay may have resulted from a response to anthropogenic eutrophication like Tokyo and Apponagansett Bays, although the relationship between *Polykrikos* cysts and eutrophication still requires verification.

According to Sætre et al. (1997), low concentration of dinoflagellate cysts dominated by heterotrophic dinoflagellate cysts is related to industrial pollution in Frierfjord, Norway. Cyst concentrations in Gamak Bay are low in comparison with those of the offshore area of Yeoja Bay, which is affected to a lesser extent by direct anthropogenic activities. This result is similar to observations from New Bedford Harbor, Massachusetts, USA (Pospelova et al. 2002, 2005) and Frierfjord, Norway, which is affected by both industrial pollution and eutrophication (Sætre et al. 1997). However, low cyst concentration dominated by high abundance of heterotrophic dinoflagellate cysts in Gamak Bay needs to be further investigated in relation to the effect of industrial pollution, as the concentrations of heavy metals in surface sediments are low (Kim 2002), although human activities such as aquaculture farms are permitted within the bay.

Conclusions

Although the relationship between dinoflagellate cysts and environmental conditions has been widely investigated in many coastal areas of the world, the knowledge-base in Korean coastal areas remains limited. Here, we present dinoflagellate cyst assemblages in relation to environmental conditions from southern coastal waters of Korea. Since the study area is affected by both open seawaters with relatively high salinity levels and fresh waters, the differences in salinity levels are related to the distribution of dinoflagellate cysts.

Dinoflagellate cysts as an indicator for eutrophication in Gamak Bay was not *L. machaerophorum* suggested in Oslo Fjord, however the proportions of heterotrophic cysts dominated by *Polykrikos* cysts reflected the eutrophicated condition in Gamak Bay. This indicates that dinoflagellate cysts as indicators of eutrophication may vary with environmental characteristics a given study area.

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References

Beardsely, R.C., R. Limeburner, H. Yu, and G.A. Cannon. 1985. Discharge of the Changjiang (Yangtze River) into the East China Sea. *Continental Shelf Research* 4: 57–76.

Cho, H.J., and K. Matsuoka. 2001. Distribution of dinoflagellate cysts in surface sediments from the Yellow Sea and East China Sea. *Marine Micropaleontology* 42: 103–123.

Choi, H.Y. 2001. Oceanographic condition of the coastal area between Naro Is. and Sorido Is. in the southern sea of Korea and its relation to the disappearance of red tide observed in summer 1998. *Journal of the Korean Society of Oceanography* 6: 49–62.

Dale, B. 1996. Dinoflagellate cyst ecology: modeling and geological applications. In *Palynology: principles and application, volume 3*, ed. J. Jansonius and D.C. McGregor, 1249–1275. College Station: American Association of Stratigraphic Palynologists Foundation.

Dale, B. 2001. Marine dinoflagellate cysts as indicators of eutrophication and industrial pollution: a discussion. *The Science of the Total Environment* 264: 235–240.

Dale, B. 2009. Eutrophication signals in the sedimentary record of dinoflagellate cysts in coastal waters. *Journal of Sea Research* 61: 103–113.

Dale, B., T.A. Thorsen, and A. Fjellsa. 1999. Dinoflagellate cysts as indicators of cultural eutrophication in the Oslofjord, Norway. *Estuarine, Coastal and Shelf Science* 48: 371–382.

Dale, B., A.L. Dale, and J.H.F. Jansen. 2002. Dinoflagellate cysts as environmental indicators in surface sediments from the Congo deep-sea fan and adjacent regions. *Palaeogeography, Palaeoclimatology, Palaeoecology* 185: 309–338.

de Vernal, A., J.L. Turon, and J. Guiot. 1994. Dinoflagellate cyst distribution in high-latitude marine environments and quantitative reconstruction of sea-surface salinity, temperature, and seasonality. *Canadian Journal of Earth Sciences* 31: 48–62.

Ellegaard, M. 2000. Variations in dinoflagellate cyst morphology under conditions of changing salinity during the last 2000 years in the Limfjord, Denmark. *Review of Palaeobotany and Palynology* 109: 65–81.

Head, M.J. 1996. Modern dinoflagellate cysts and their biological affinities. In *Palynology: Principles and applications, volume 3*, ed. J. Jansonius and D.C. McGregor, 1197–1248. College Station: American Association of Stratigraphic Palynologists Foundation.

Holzwarth, U., O. Esper, and K. Zonneveld. 2007. Distribution of organic-walled dinoflagellate cysts in shelf surface sediments of the Benguela upwelling system in relationship to environmental conditions. *Marine Micropaleontology* 64: 91–119.

Hue, H.K., D.H. Kim, S.H. Ahn, and K.W. Park. 2000. Characteristics of the sedimentary environment in Yoja Bay in the summer of 1998. *Korean Journal of Environmental Biology* 18: 227–235.

Hwang, D.W., G.B. Kim, Y.W. Lee, and H.S. Yang. 2005. Estimating submarine inputs of groundwater and nutrients to a coastal bay using radium isotopes. *Marine Chemistry* 96: 61–71.

Kawamura, H. 2004. Dinoflagellate cyst distribution along a shelf to slope transect of an oligotrophic tropical sea (Sunda Shelf, South China Sea). *Phycological Research* 52: 355–375.

Kim, K.Y. 2002. A study on physico-chemical environmental characteristics and the behavior of metals in sediments in Kamak Bay. Ph.D. dissertation, Yeungnam University, Korea.

Kim, H.G., J.S. Park, and S.G. Lee. 1990. Coastal algal blooms caused by the cyst-forming dinoflagellates. *Journal of the Korean Fisheries Society* 23: 468–474.

Kim, D.S., J.G. Je, and S.H. Shin. 2000. Utilization of meiobenthos for pollution monitoring in the Gamak Bay, Korea. *Journal of the Korean Fisheries Society* 33: 307–319.

Kim, H.C., C.K. Lee, S.G. Lee, H.G. Kim, and C.K. Park. 2001. Physico-chemical factors on the growth of Cochlodinium polykrikoides and nutrient utilization. *Journal of the Korean Fisheries Society* 34: 445–456.

Kim, J.B., S.Y. Lee, J. Yu, Y.H. Choi, C.S. Jung, and P.Y. Lee. 2006. The characteristics of oxygen deficient water mass in Gamak Bay. *Journal of Korean Society for Marine Environmental Engineering* 9: 216–224.

Kim, C.J., H.G. Kim, C.H. Kim, and H.M. Oh. 2007. Life cycle of the ichthyotoxic dinoflagellate Cochlodinium polykrikoides in Korean coastal waters. *Harmful Algae* 6: 104–111.

Koo, B.J., J.G. Je, and S.H. Shin. 2004. Benthic pollution assessment based on macrobenthic community structure in Gamak Bay, southern coast of Korea. *Ocean and Polar Research* 26: 11–22.

Lee, G.H. 1992. The pattern of sea water circulation in Kamak Bay. *Bulletin of the Korean Society of Fisheries Technology* 28: 117–131.

Lee, Y.S. 2006. Factors affecting outbreaks of high-density *Cochlodinium polykrikoides* red tides in the coastal seawaters around Yeosu and Tongyeong, Korea. *Marine Pollution Bulletin* 52: 1249–1259.

Lee, K.H., and K.D. Cho. 1990. Distributions of the temperature and salinity in Kamak Bay. *Journal of the Korean Fisheries Society* 23: 25–39.

Lee, Y.W., and G.B. Kim. 2007. Linking groundwater-borne nutrients and dinoflagellate red-tide outbreaks in the southern sea of Korea using a Ra tracer. *Estuarine, Coastal and Shelf Science* 71: 309–317.

Lee, J.B., and K. Matsuoka. 1994. Distribution of dinoflagellate cyst from surface sediments in southern Korean waters. In: Proceeding of Second International Symposium on Marine Science Exploitation of Marine Resources, Korea, 1–20.

Lee, J.B., and K.I. Yoo. 1991. Distribution of dinoflagellate cysts in Masan Bay, Korea. *The Journal of the Oceanological Society of Korea* 26: 304–312.

Lee, J.H., and S.M. Youn. 2000. Water quality and phytoplankton communities in Yeoja Bay of Korea. *Algae* 15: 89–98.

Lee, M.H., J.B. Lee, J.A. Lee, and J.G. Park. 1999. Community structure of flagellates and dynamic of resting cysts in Kamak Bay, Korea. *Algae* 14: 255–266.

Lee, Y.G., Y.S. Chu, K.K. Jung, H.J. Woo, and H.J. Lee. 2000. Depositional processes of fine-grained sediments and foraminiferal imprint of estuarine circulation by summer floods in Yoja Bay, southern coast of Korea. *Journal of the Korean Society of Oceanography* 35: 109–123.

Lopes, C.B., A.I. Lillebø, J.M. Dias, E. Pereira, C. Vale, and A.C. Duarte. 2007. Nutrient dynamics and seasonal succession of phytoplankton assemblages in a Southern European Estuary: Ria de Aveiro, Portugal. *Estuarine, Coastal and Shelf Science* 71: 480–490.

Marret, F. 1994. Distribution of dinoflagellate cysts in recent marine sediments from the east Equatorial Atlantic (Gulf of Guinea). *Review of Palaeobotany and Palynology* 84: 1–22.

Marret, F., and J. Scourse. 2002. Control of modern dinoflagellate cyst distribution in the Irish and Celtic seas by seasonal stratification dynamics. *Marine Micropaleontology* 47: 101–116.

Marret, F., and K.A.F. Zonneveld. 2003. Atlas of modern organic-walled dinoflagellate cyst distribution. *Review of Palaeobotany and Palynology* 125: 1–200.

Matsuoka, K. 1985. Organic-walled dinoflagellate cysts from surface sediments of Nagasaki Bay and Senzaki Bay, West Japan. *Bulletin of the Faculty Liberal Arts, Nagasaki University (Natural Science)* 25: 21–115.

Matsuoka, K. 1999. Eutrophication process recorded in dinoflagellate cyst assemblages—a case of Yokohama Port, Tokyo Bay, Japan. *The Science of the Total Environment* 231: 17–35.

Matsuoka, K. 2001. Further evidence for a marine dinoflagellate cyst as an indicator of eutrophication in Yokohama Port, Tokyo Bay, Japan. *The Science of the Total Environment* 264: 221–233.

Matsuoka, K., and Y. Fukuyo. 2000. Technical guide for modern dinoflagellate cyst study. 29. Japan: Japan Society for the Promotion of Science.

Matsuoka, K., L.B. Joyce, Y. Kotani, and Y. Matsuyama. 2003. Modern dinoflagellate cysts in hypertrophic coastal waters of Tokyo Bay, Japan. *Journal of Plankton Research* 25: 1461–1470.

Naustvoll, L.J. 2000. Prey size spectra and food preferences in thecate heterotrophic dinoflagellates. *Phycologia* 39: 187–198.

Noh, I.H., Y.H. Yoon, D.I. Kim, and J.S. Park. 2006. The spatio-temporal distribution of organic matter on the surface sediment and its origin in Gamak Bay, Korea. *Journal of Korean Society for Marine Environmental Engineering* 9: 1–13.

Park, J.S., and Y.H. Yoon. 2003. Marine environmental characteristics by distribution of dinoflagellate cysts in the southwestern coastal waters of Korea. 1. Spatio-temporal distribution of dinoflagellate cysts in Gamak Bay. *Journal of the Korean Fisheries Society* 36: 151–156.

Persson, A., A. Godhe, and B. Karlson. 2000. Dinoflagellate cysts in recent sediments from the West Coast of Sweden. *Botanica Marina* 43: 66–79.

Pospelova, V., G.L. Chmura, W.S. Boothman, and J.S. Latimer. 2002. Dinoflagellate cyst records and human disturbance in two neighboring estuaries, New Bedford Harbor and Apponagansett Bay, Massachusetts (USA). *The Science of the Total Environment* 298: 81–102.

Pospelova, V., G.L. Chmura, and H.A. Walker. 2004. Environmental factors influencing the spatial distribution of dinoflagellate cyst assemblages in shallow lagoons of southern New England (USA). *Review of Palaeobotany and Palynology* 128: 7–34.

Pospelova, V., G.L. Chmura, W.S. Boothman, and J.S. Latimer. 2005. Spatial distribution of modern dinoflagellate cysts in polluted estuarine sediments from Buzzards Bay (Massachusetts, USA) embayments. *Marine Ecology Progress Series* 292: 23–40.

Pospelova, V., A. de Vernal, and T.F. Pedersen. 2008. Distribution of dinoflagellate cysts in surface sediments from the northeastern Pacific Ocean (43–25°N) in relation to sea-surface temperature, salinity, productivity and coastal upwelling. *Marine Micropaleontology* 68: 21–48.

Radi, T., and A. de Vernal. 2004. Dinocyst distribution in surface sediments from the northeastern Pacific margin (40–60°N) in relation to hydrographic conditions, productivity and upwelling. *Review of Palaeobotany and Palynology* 128: 169–193.

Radi, T., A. de Vernal, and O. Peyron. 2001. Relationship between dinoflagellate cyst assemblages in surface sediment and hydrographic conditions in the Bering and Chukchi seas. *Journal of Quaternary Science* 16: 667–680.

Radi, T., V. Pospelova, A. de Vernal, and V.J. Barrie. 2007. Dinoflagellate cysts as indicators of water quality and productivity in British Columbia estuarine environments. *Marine Micropaleontology* 62: 269–297.

Reichart, G.J., and H. Brinkhuis. 2003. Late quaternary Protoperidinium cysts as indicators of paleoproductivity in the northern Arabian Sea. *Marine Micropaleontology* 49: 303–315.

Sætre, M.M.L., B. Dale, M.I. Abdullah, and G.P. Sætre. 1997. Dinoflagellate cysts as potential indicators of industrial pollution in a Norwegian Fjord. *Marine Environmental Research* 44: 167–189.

Shim, J.H. 1980. Biological oceanography of the Gamagyang Bay—the Yeoja Bay water system. *Journal of the Oceanological Society of Korea* 15: 89–99.

Shin, H.H., Y.H. Yoon, and K. Matsuoka. 2007. Modern dinoflagellate cysts distribution off the eastern part of Geoje Island, Korea. *Ocean Science Journal* 42: 31–39.

Shin, H.H., K. Mizushima, S.J. Oh, J.S. Park, I.H. Noh, M. Iwataki, K. Matsuoka, and Y.H. Yoon. 2010a. Reconstruction of historical nutrient levels in Korean and Japanese coastal areas based on dinoflagellate cyst assemblages. *Marine Pollution Bulletin* 60: 1243–1258.

Shin, H.H., K. Matsuoka, Y.H. Yoon, and Y.-O. Kim. 2010b. Response of dinoflagellate cyst assemblages to salinity changes in Yeoja Bay, Korea. *Marine Micropaleontology* 77: 15–24.

Smayda, T.J., and C.S. Reynolds. 2003. Strategies of marine dinoflagellate survival and some rules of assembly. *Journal of Sea Research* 49: 95–106.

Sprangers, M., N. Dammers, H. Brinkhuis, T.C.E. van Weering, and A.F. Lotter. 2004. Modern organic-walled dinoflagellate cyst distribution offshore NW Iberia; tracing the upwelling system. *Review of Palaeobotany and Palynology* 128: 97–106.

Taylor, F.J.R. 1987. *Botanical Monograph 21: The biology of the dinoflagellates, 784*. Oxford: Blackwell.

Teague, W.J., G.A. Jacobs, D.S. Ko, T.Y. Tang, K.-I. Chang, and M.-S. Suk. 2003. Connectivity of the Taiwan, Cheju, and Korea straits. *Continental Shelf Research* 23: 63–77.

Vaquer, A., M. Troussellier, C. Coutries, and B. Bibent. 1996. Standing stock and dynamics of phytoplankton in the Thau Lagoon (northwest Mediterranean coast). *Limnology and Oceanography* 41: 1821–1828.

Wall, D., B. Dale, G.P. Lohmann, and W.K. Smith. 1977. The environmental and climatic distribution of dinoflagellate cysts in modern marine sediments from regions in the North and South Atlantic oceans and adjacent seas. *Marine Micropaleontology* 2: 121–200.

Wang, Z., K. Matsuoka, Y. Qi, and J. Chen. 2004. Dinoflagellate cysts in recent sediments from Chinese coastal waters. *Marine Ecology* 25: 289–311.

Yamaguchi, M., S. Itakura, I. Imai, and Y. Ishida. 1995. A rapid and precise technique for enumeration of resting cysts of *Alexandrium* spp. (Dinophyceae) in natural sediments. *Phycologia* 34: 207–214.

Yoon, Y.H. 2000. Variational characteristics of water quality and chlorophyll *a* concentration in the northern Kamak Bay, Southern Korea. *Journal of the Korean Environmental Sciences Society* 9: 429–436.

Zonneveld, K.A.F. 1997. Dinoflagellate cyst distribution in surface sediments from the Arabian Sea (northwestern Indian Ocean) in relation to temperature and salinity gradients in the upper water column. *Deep-Sea Research* 44: 1411–1443.

Zonneveld, K.A.F., A. Brune, and H. Willems. 2000. Spatial distribution of calcareous dinoflagellate cysts in surface sediments of the Atlantic Ocean between 13°N and 36°S. *Review of Palaeobotany and Palynology* 111: 197–223.

Zonneveld, K.A.F., G.J.M. Versteegh, and G.J. de Lange. 2001. Palaeoproductivity and post-depositional aerobic organic matter decay reflected by dinoflagellate cyst assemblages of the Eastern Mediterranean S1 sapropel. *Marine Geology* 172: 181–195.

Zonneveld, K.A.F., F. Bockelmann, and U. Holzwarth. 2007. Selective preservation of organic walled dinoflagellate cysts as a tool to quantify past net primary production and bottom water oxygen concentrations. *Marine Geology* 237: 109–126.