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Distribution of diatoms in the surficial sediments of the Mangyung-Dongjin tidal flat, west coast of Korea (Eastern Yellow Sea)

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Abstract The relationship between the distribution of benthic diatoms and sediment characteristics of the Mangyung-Dongjin tidal flat on the west coast of Korea was investigated during June and July 1988. Diatoms were collected from the upper 5 mm of sediments at 60 sites along eight transect lines running perpendicular to the shore line. Of the 371 taxa encountered in the study area, 88% were pennate diatoms. Genera represented by the greatest number of species were *Navicula*, *Nitzschia*, *Amphora*, *Cocconeis*, *Fragilaria* and *Achnanthes*. The most abundant species were *Paralia sulcata*, *Navicula* sp. #1, *N. arenaria* and *Cymatosira belgica*; all were broadly distributed across the tidal flats. The 60 sites could be assigned to eight clusters with respect to similarity in species composition. Discriminant analysis showed that separation cluster was primarily related to the mean grain size of the sediment. The species could not be separated into groups based on similarities in occurrence; a high degree of spatial overlap was observed. The preferences of the more abundant species for grain size were, therefore, analysed by plotting numerical abundance against mean grain size. There were at least four patterns: species groups could be associated with fine-grained sediments, those of intermediate size and coarser sediments and the last group showed no discernible pattern.

Introduction

Early investigations of littoral diatom communities inhabiting marine sediments were mainly concerned with preparing floral lists and defining associations of species (Brockmann 1950; Round 1979). In several studies, attempts were made to identify distribution patterns with environmental factors, but no rigorous statistical approach was employed. Recently, however, efforts have been made to relate the distribution of benthic diatoms to environmental factors in a quantitative way (McIntire 1973, 1978; Amspoker 1977; McIntire and Moore 1977; Amspoker and McIntire 1978; Sullivan 1978; Sullivan and Moncreiff 1988a). The recognition of distinct diatom assemblages in these studies was typically ascribed to environmental heterogeneities and discontinuities in physical and chemical gradients. Admiraal (1984) listed ecological factors affecting sediment-inhabiting diatoms. However, environmental factors may act differently from one region to another, and an interpretation is therefore valid only within a particular region. Although it is difficult to generalize which factor is most responsible for structuring diatom assemblages, physical and chemical factors (i.e., salinity, elevation, temperature, soil moisture, organic matter content, grazing, etc.) are important structural determinants (Sullivan 1975, 1978, 1982; Amspoker and McIntire 1978; McIntire 1978; Cook and Whipple 1982; Admiraal et al. 1984; Whitting and McIntire 1985; Sullivan and Moncreiff 1988a, b). Some efforts have been made to infer relationships between diatom distribution and sediment characteristics (Amspoker and McIntire 1978; Kosugi 1987). It must be stressed, however, that sediment-related effects may often be masked by substrate instability induced by winds and tidal currents (de Jonge 1985; de Jonge and van den Bergs 1987; de Jonge and van Beusekom 1992). A uniform distribution pattern was observed in a sand beach where the substrate was exposed to extremely strong wave action (Amspoker 1977).

The primary aim of our study was to investigate the relationships between sediment characteristics and distribution of benthic diatoms in a Korean tidal flat. We also examined whether or not distinct diatom assemblages exist which can be segregated based on sedimentary characteristics.

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Study area

Extensive tidal flats occur along the west coast of the Korean Peninsula owing to the macrotidal range (>4 m) and the very gentle bottom slope. They occupy an area of approximately 2850 km^2 and may extend as much as ca. 20 km from the shore line and, therefore, rival those of the North Sea coast in their aerial extent.

The study area was located between 35°42′ and 35°54′N and 126°32′ and 126°42′E along the central west coast of Korea near the cities of Kunsan, Kimje and Buan (Fig. 1). The tidal flat studied is the broadest one in the eastern Yellow Sea. The extreme tidal range and gentle bathymetric gradient (1:2000 to 1:500) produce an intertidal zone which is 20 km broad at its central area and has an area of approximately 170 km^2, as determined by the contour line of mean lowest low water (MLLW) level (Fig. 1). The eastern side of the tidal flat receives the flow of the Mangyung and Dongjin rivers which join with the main two tidal channels; freshwater discharge here is low, however. The study area is dissected by these two channels running in an east-west direction with dendritic patterns of gullies. Depths greater than 5 m, where the subtidal zone may be distinguished from the intertidal, occur largely in the channel areas. The bathymetry was reflected in the flow patterns of tidal currents which dominated over the study area. Major flood and ebb currents were mainly in a NE-SW direction offshore.

Tides are mixed semi-diurnal, with a mean tidal range of 4.3 m, a maximum spring tidal range of 6 m and a minimum neap tidal range of 3 m. Current velocities ranged from 0.8 to 1.8 m s^{-1} at flood tide and 1.2 to 2.4 m s^{-1} at ebb tide (OHAROK 1987). Freshwater discharge was sufficiently small so that year-round salinities in the water column approximated those characteristic of the coastal zone of the eastern Yellow Sea (30 to 32‰).

All field work was carried out along offshore transect. A total of eight transect lines running roughly perpendicular to the shoreline were set up (Fig. 1). The transects ended approximately at the tidal flat margins. They were named after the hamlets located at starting points of each transect. We divided the tidal flat into three regions, which were separated by the main channels (i.e., the Kunsan, Kimje and Buan tidal flats). The Kunsan tidal flat included sites S1–5, E1–4 and C1–3, the Kimje tidal flat included G1–17, W1–7 and U1–5, and the Buan tidal flat consisted of B1–16 and H1–3. These 60 sites were located at 500-m intervals along each transect and were numbered so that the farthest seaward site of each transect received the highest number (Fig. 2).

The elevation profiles of all transects are shown in Fig. 2. The elevation of study sites ranged from −3 to +2 m above mean sea level. The slope of the Sura transect (S1–5) was steeper than that of the Geojon (G1–17) and Gyehwa (B1–16) transects, although all three transects were exposed to the open sea. Most transects changed little in elevation in a seaward direction. A number of small tributary channels crossed the transects; however, the Geojon transect was dissected by a broad tidal channel at about 2 km from the shore line. Field observations indicated that the dominant sediment types on the Sura, Geojon and Gyehwa transects exposed to the open sea were sand and silt, whereas the other transects, except the Hechang transect, were composed mostly of silt. Gravel and sand were dominate on the Hechang transect.

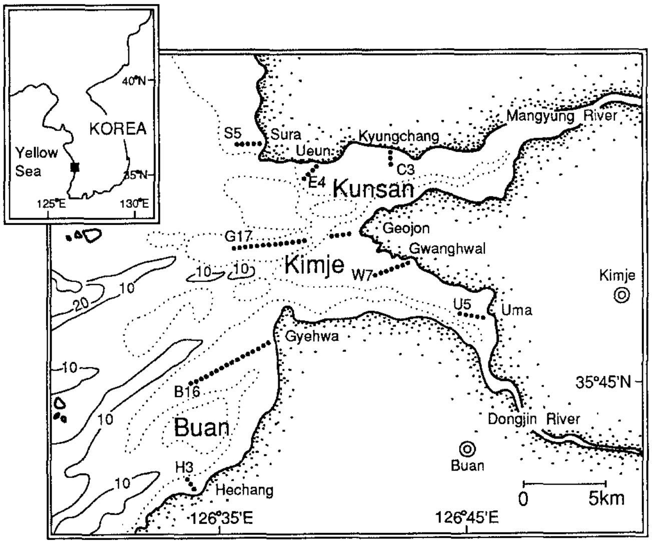


Fig. 1 Mangyung-Dongjin tidal flat, showing locations of the 60 sampling sites. Study sites (●) numbered so that the farthest seaward site of each transect received the highest number. Dotted contour lines (...) present extent of the tidal flat corresponding to the mean lowest low water (MLLW) level

Materials and methods

Samples were collected on three occasions at 2-wk intervals in June and July 1988. The sampling times of the spring tide were selected so that we encountered the lowest low water during the daytime. The transects on the Kunsan tidal flat were investigated on 14–15 June, those on the Kimje tidal flat on 28–30 June and those on Buan on 15–16 July 1988. Transects were established along the paths leading the fishermen to fishing grounds on the tidal flat, but samples were collected from undisturbed sites that had not been trampled by fishermen. The farthest sites on the Geojon transect could be reached only by a fish cutter and on the Gyehwa transect by a motorized cart used frequently by fishermen.

For the analysis of grain size and organic content of the sediment, approximately 100 g of surface sediment were collected at each site by means of a plastic pan which enabled us to isolate the uppermost layer of sediment. The grain size analysis was done using the standard dry sieve and pipette method (Carver 1971). Grain diameter (mm) was expressed as its negative logarithm to base 2, the phi (ϕ) scale. Based on particle diameter in ϕ units, coefficients of sorting and skewness were calculated by the formulas suggested by Folk and Ward (1957). The organic matter content (%) was estimated by ignition at 550°C for 1.5 h (Carver 1971). Mean tidal levels at the study sites were calculated from tidal elevations recorded at Kunsan Outer Harbour from 1 January to 31 December 1986 (OHAROK 1987). The elevations of study sites were then drawn as depth contour maps on a 1:5000 scale.

To estimate the absolute densities (cells cm^{-2}) of epipelic and epipsammic diatoms, the upper 5 mm of the sediment layer were sampled with a plastic core 30 mm in diameter. Three replicate cores were taken at each site to avoid sampling bias due to any differences in sediment type; these were then combined to yield a composite sample. In order to observe the frustle structure of diatoms for identification purposes, each composite sample was treated with hydrochloric acid (Simonsen 1974). Microscopic observation indicated

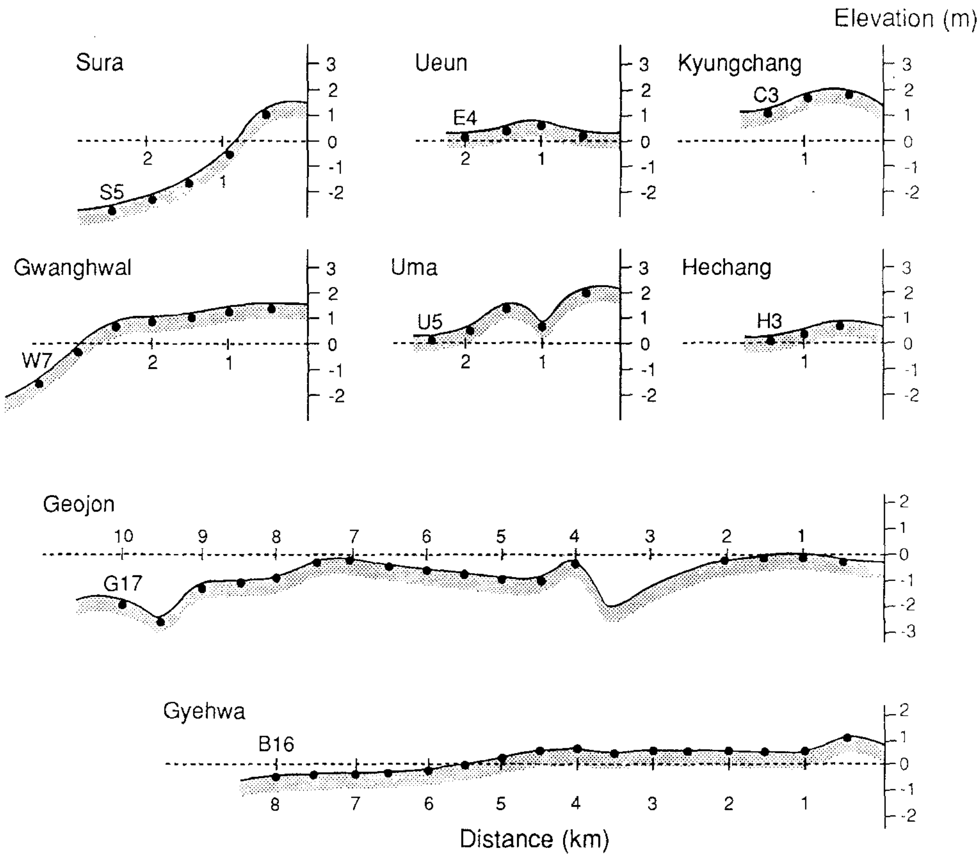


Fig. 2 Cross-sectional view showing elevation of transects above mean sea level (dashed line). Horizontal axis indicates distance of sampling sites (●) from shoreline

that most sand grains were free of epipsammic diatoms after the acid treatment. Diatom cells were eluted from sediment samples by passive settling and repeated washing (Lohman 1972). A maximum of 20 washes was enough to exclude the sediment from the mixture. The elutant was diluted to a volume of 100 to 500 ml from which 0.01 to 0.02 ml were subsampled. The subsamples were dropped onto a cover glass, dried and mounted in Hyrax. The permanent slides were then used for both identification and counting of diatom taxa. Only cleaned materials were employed for counting due to difficulties in identifying the smaller species.

Abundance data for diatom taxa at each study site on a given date were based on two permanent slides where all cells on each slide were counted in contiguous, non-overlapping fields with an oil immersion (×1000). Actual counts fell mostly into the range between 900 and 1200 cells. Only complete cells were counted since valves or fragments of valves were not frequently observed, although the sediments were treated with hydrocloric acid. Diatom cell density cm^{-2} surface sediment was calculated by multiplying the number of cells of a taxon by the dilution factor and adjusting this value to the actual area of the sample core. The abundance data subjected to numerical analysis in the present study was the actual cell counts cm^{-2}. The raw data differed, therefore, from that employed in previous studies which applied the relative abundance data obtained from the ratio of abundance of certain taxon to a fixed total count, e.g. 500 cells (Amspoker and McIntire 1978; Sullivan and Moncreiff 1988a).

Species-abundance data at the sampling sites were subjected to numerical analysis. The Shannon-Wiener diversity index (*H'*) was calculated for each sample using $\log_2$. Both the study sites and diatom taxa were clustered on the basis of similarities in the diatom taxa and of study sites where the diatom taxa occurred, respectively. These cluster analyses employed the similarity index of Bray-Curtis and the unweighted pair group method average (UPGMA). However, diatom taxa were not assigned to clusters (see "Discussion") and, therefore, only the eight study site clusters were subjected to discriminant analysis to identify those environmental factors with the most discriminating power. Discriminant functions were derived using the direct method which considered all variables simultaneously in extracting the functions (Cooley and Lohnes 1971). Discriminating variables included elevation and mean grain size, sorting value, skewness, and organic matter content of surface sediments at the 60 study sites. The discriminant analysis program of SPSS was used (Norusis 1986).

Results

The inner transects (C1–3, E1–4, U1–5, W1–7) located within the mouths of the two rivers were composed of fine-grained materials, whereas coarser sediments predominated on the outer transects more exposed to the open sea (Table 1). There was some consistency between the size distribution of sediments and the degree of sorting. Well-sorted sediments were generally restricted to the outer flats. The most poorly sorted sediments were found in the Hechang (H1–3) transect, where gravel and pebble-sized grains dominated. This transect was located in the backwash area of a tidal channel where strong tidal currents could alter the sediment facies. The organic matter content of the sediments was generally low over the entire area, with the lowest values being found in the outer transects. The raw data on sediment charactistics, tidal level and the duration of exposure at each site were provided by Oh and Koh (1991).

Table 1 Mean values ($\bar{x}$ ± SD) for environmental factors along eight transect lines on tidal flats in the Mangyung-Dongjin area, west coast of Korea. The ϕ value in grain size was based on $-\log_2$ mm

Tidal flat	Transect line	No. of sites	Sampling dates (1988)	Tidal level (cm)	Grain size (ϕ)	Sorting coefficient	Skewness	Content of organic matter (%)
Kunsan	Kyungchang	C1–3	14–15 June	156.7 × 26.2	6.7 × 1.0	2.2 × 0.1	1.4 × 0.6	3.6 × 0.6
	Ueun	E1–4		50.0 × 15.8	4.5 × 0.6	1.6 × 0.5	1.9 × 0.8	1.4 × 0.2
	Sura	S1–5		–92.0 × 143.0	2.9 × 0.7	1.1 × 0.4	1.2 × 0.1	1.1 × 0.2
Kimje	Uma	U1–5	28–30 June	108.0 × 76.8	5.1 × 0.7	1.7 × 0.2	1.8 × 0.3	2.7 × 0.3
	Gwanghwal	W1–7		98.6 × 99.3	4.5 × 0.6	1.5 × 0.4	1.6 × 0.2	2.0 × 0.3
	Geojon	G1–17		–69.4 × 65.2	3.8 × 0.6	1.2 × 0.5	1.6 × 0.2	1.5 × 0.6
Buan	Gyehwa	B1–16	15–16 July	26.9 × 47.3	3.9 × 0.8	1.1 × 0.6	1.9 × 0.5	1.6 × 0.6
	Hechang	H1–3		50.0 × 24.5	3.3 × 1.4	2.6 × 0.8	0.9 × 0.4	1.9 × 1.1

The percentages of sand, silt, and clay, plotted on Folk's triangular diagram (Folk and Ward 1957), are shown in Fig. 3. Sand, silty-sand, and sandy-silt facies predominated at most of the investigated sites. Sand and silty-sand facies were dominant in the outer tidal flats, whereas sandy-silt and silt facies were typical of the inner flats. Mud and clay facies were rare.

It was not possible to identify 137 (37%) of the 371 diatom taxa to the species level. Unidentified species belonged mainly to the genera *Amphora*, *Navicula*, *Nitzschia* and *Cocconeis*. When a particular diatom could not be identified to species after an exhaustive search of the literature, it was photographed and assigned a temporary number.

The diatom flora was represented by 58 genera belonging to 14 families. The families Diatomaceae, Achnanthaceae, Naviculaceae, and Nitzschiaceae accounted for 303 (82%) of the 371 taxa. Of the 58 genera encountered, *Navicula*, *Paralia*, *Amphora*, *Nitzschia*, *Cocconeis*, *Fragilaria*, and *Achnanthes* were most dominant in terms of cell numbers. *Navicula* was the single most abundant genus with 31% of all cells counted, followed by the genera *Paralia* with 16%, *Amphora* with 14% and *Nitzschia* with 5%. All taxa representing >0.2% of the total cell number are listed in Table 2. The single most abundant species was *Paralia sulcata*, which accounted for 16% of all cells counted and was collected from 59 of the 60 sampling sites (Table 2). The fresh sediment was examined microscopically before cleaning; however, it was difficult to observe how firmly the chains of *P. sulcata* were attached to sediment particles. Most cells were alive with healthy, golden-brown chloroplasts. *Navicula* sp. #1 and *N. arenaria* represented 11 and 10% of the flora, respectively, and were collected from 44 and 52 sites, respectively. A large number of taxa (94% of the total) represented less than 0.2% of the total cell count and were, therefore, considered as rare species.

Total cell number at the sampling sites ranged from 9.6 to 631.6×10^4 cells cm^{-2} with an average value of $96.3 \pm 92.0 \times 10^4$ cells cm^{-2}. The highest diatom densities were found at sites U1, C1, and W1, located on the upper intertidal of the inner tidal flats; the lowest densities were found at sites G17 and G3, located near the channel of the outer tidal flat.

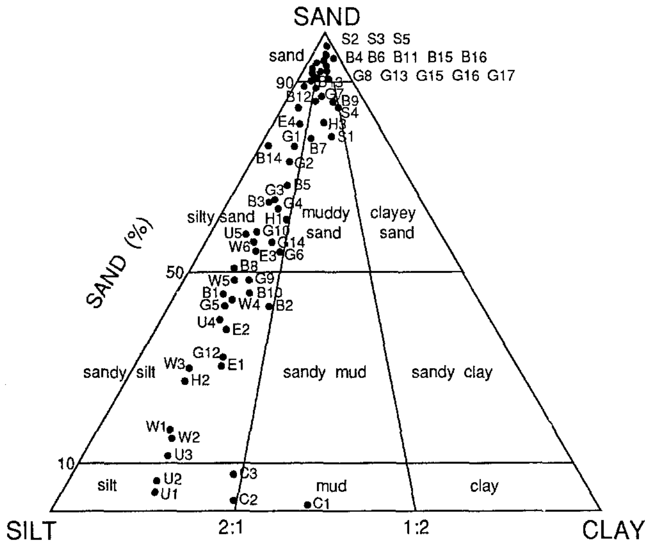


Fig. 3 Ternary diagram showing grain-size composition of surface sediments collected from the 60 sampling sites on the Mangyung-Dongjin tidal flat. Location of study sites shown in Fig. 1

Cluster analysis based on species-abundance data for the 60 sampling sites produced eight distinct clusters including four subclusters (Fig. 4). Cluster A contained all sites of the Sura (S) transect and site E4. Cluster B was composed of the higher intertidal zone sites of the Gyehwa (B) transect and all three sites of the Hechang (H) transect. The lower intertidal sites of the former transect, with the exception of B10, fell in Cluster E. Cluster C was composed of four subclusters and for the most part included the sites of those transects located along the inner inlets. Subcluster C3 was an exception as it included the lower intertidal sites of the Geojon (G) transect. The sites belonging to Cluster D were largely found on the Geojon (G) transect, but they could not be assigned to a particular habitat, as both higher and lower intertidal sites were included.

Discriminant analysis is a multivariate technique that allows one to determine how well a set of variables can differentiate cases belonging to preassigned groups. The eight clusters identified in Fig. 4 were the groups, and the

Table 2 Total number of cells counted at 60 sampling sites and frequency (occurrence at 60 sampling sites) of the 23 most abundant diatom taxa on the Mangyung-Dongjin tidal flats. For both total number of cells and frequency, numbers in parentheses are % values. Community structure indices and sediment characteristics for clusters also given as mean values for all sites of a given cluster. Numbers associated with clusters are the percent contribution of each taxon to total cell numbers for all sites of a given cluster. 0.0 indicates an abundance less than 0.05% but >0.00%. Blank indicates that no cells were present at any cluster site

Taxon	Total cell no. (10^4cells)	Frequency	Clusters							
			A	B	C1	C2	C3	C4	D	E
Paralia sulcata (Ehr.) Cleve	909.7 (15.8)	59 (98.3)	5.7	12.8	13.9	14.4	28.7	28.3	13.1	1.4
Navicula sp.#1	640.0 (11.1)	54 (73.3)	7.5	3.6	24.0	9.3	8.2	5.3	11.1	0.9
Navicula arenaria Donkin	608.1 (10.5)	52 (86.7)	3.7	1.3	18.0	31.6	3.3	1.4	4.9	0
Cymatosira belgica Grun.	267.2 (4.6)	58 (96.7)	3.2	5.5	3.1	3.2	8.9	6.8	7.2	1.7
Amphora holsatica Hust.	211.2 (3.7)	45 (75.0)	4.4	1.4	0.1	8.4	10.4	0.1	17.2	1.7
Amphora coffeaeformis Kuetz.	198.1 (3.4)	45 (75.0)	11.2	13.7	2.8		0.3	0.9	1.9	1.6
Achnanthes hauckiana Grun.	166.6 (2.9)	38 (63.3)	3.7	5.2	0.7	0.3	0.1	0.1	1.7	16.4
Rhaphoneis amphiceros Ehr.	48.0 (2.6)	55 (91.7)	1.0	1.3	1.6	3.1	5.8	4.4	2.5	1.0
Thalassionema nitzschioides (Grun.) Grun. ex Hust.	36.3 (2.4)	47 (78.3)	0.4	0.4	1.7	3.6	2.1	7.3	1.7	0.1
Navicula sp.#2	100.8 (1.8)	35 (58.3)	3.3	2.9	2.5	2.6	0.1	0.9	0.0	0.1
Dimeregramma minor Ralfs	71.6 (1.2)	14 (23.3)	0.5	0.4						11.0
Amphora sp.#1	69.3 (1.1)	13 (21.7)	1.7	0.0	3.3	0.0	0.6	0.0	1.1	0.0
Cyclotella atomus Hust.	60.8 (1.1)	38 (63.3)	0.4	0.4	1.0	0.1	1.1	3.8	0.6	
Cyclotella striata (Kuetz.) Grun.	60.8 (1.1)	38 (63.3)	0.2	0.4	1.0	0.8	1.6	2.3	0.3	0.4
Nitzschia sp.#26	58.2 (1.0)	35 (58.3)	1.2	2.3	1.2	1.3	0.5	0.7	0.1	0.0
Stephanodiscus sp.#1	57.9 (1.0)	43 (71.7)	0.2	0.8	0.3	0.5	0.1	5.7	0.1	0.1
Cocconeis sp.#1	47.3 (0.8)	16 (26.7)	0.0	1.5				0.1	0.8	5.8
Opephora martyi Herib	47.2 (0.8)	14 (23.3)	0.0	0.5				0.2		6.9
Catenula adhaerens Mereschkowsky	26.3 (0.5)	18 (30.0)	0.0	1.1	0.2	0.1				2.4
Dimeregramma minor var. *nana* (Greg.) Ralfs	24.9 (0.4)	15 (25.0)	0.4	0.4						3.4
Fragilaria virescens var. *oblongella* Grun.	19.2 (0.3)	15 (25.0)	0.1	0.7		0.1			0.1	2.1
Fragilaria virescens Ralfs	16.0 (0.3)	18 (30.0)		0.2	0.1		0.2	0.1		1.8
Cocconeis grata A. Smith	13.5 (0.2)	15 (25.0)	0.3	0.1						1.9
Community structure indices										
Density (10^4 cells cm^{-2})			45.6	68.1	219	102	73.9	198	34.2	76.7
Diversity (H')			3.0	3.1	2.8	2.5	2.8	3.0	2.9	3.2
No. taxa $site^{-1}$			50.5	55.8	58.9	43.0	58.9	60.5	44.5	55.6
Sediment characteristics										
Grain size (ϕ)			3.1	4.0	5.0	4.7	4.1	6.5	3.5	3.4
Sorting coefficient			1.1	1.9	1.8	1.6	1.4	2.1	0.7	0.7
Organic matter content (%)			1.1	1.9	2.3	1.9	2.0	3.3	1.2	1.2

discriminating variables were tidal level, mean grain size, coefficient of sorting, skewness, and organic matter content (%) of the sediments. A total of 73% of the discriminating power residues in the first discriminant function (DF1) and 15 and 10% in DF2 and DF3, respectively (Table 3). There was virtually no discriminating power in either DF4 or DF5; hence, they need not be considered further. Although DF3 possessed 10% of discriminating power, it was not considered to be a factor responsible for the separation because of its low significance level (p=0.15). Both DF1 and DF2 were significant (p< 0.01). DF1 showed the highest correlation with mean grain size (r=0.96, see Table 3), leading to the interpretation that the primary factor separating clusters was sediment grain size. DF2 had a high correlation with tidal level (r=0.96), which was considered as the second most important discriminating factor. Figure 5 depicts the relative positions of clusters in two dimensional (DF1 and DF2) discriminant space. The correlations between discriminant functions and environmental variables given in Table 3 resulted in the angles of axis between discriminant functions and variables (i.e., between DF1 and mean grain size and between DF2 and tidal level). The clusters were positioned in discriminant space according to the values of cluster centroids in Table 3. It was clear from Fig. 5 that DF1 possesses a much higher separating power than DF2; the clusters are positioned broadly along a gradient of mean grain size. A total of 60% (36) of the 60 study sites (cases) were correctly classified into clusters (Table 3).

The 60 study sites were divided into eight clusters as shown in Fig. 4, and the discriminant analysis based on environmental factors correctly assigned a majority of sites to the correct cluster. However, the cluster analysis employing the 23 most abundant diatom taxa exhibited only a diffuse dendrogram. To define the characteristics of clusters with respect to diatom taxa, we examined the distribution of the 23 most abundant taxa (Table 2), all of which represented >0.2% of the total cell count. The following description is based largely on the percent contribution of each taxon to the total cell count.

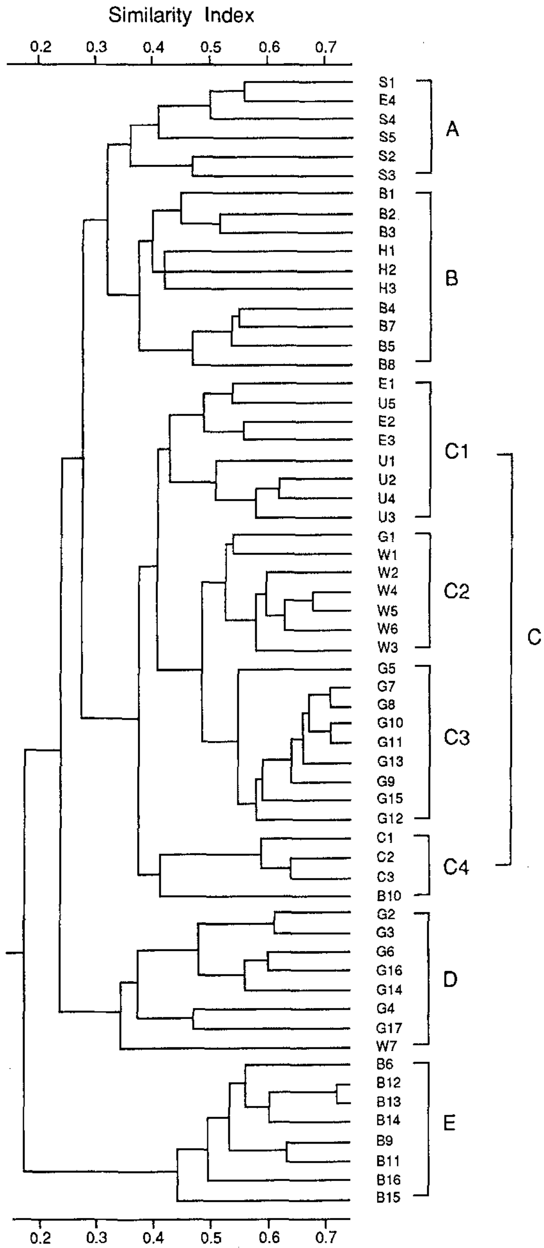


Fig. 4 Dendrogram for clustering the 60 sampling sites using the Bray-Curtis index and the unweighted pair group method average linkage strategy. Location of study sites shown in Fig. 1

Mean cell density was highest in Clusters C1 and C4, where the sediments were relatively fine (Table 2). *H′* showed little variation among cluster (range: 2.8 to 3.2 for all except Cluster C2). The distribution of diatom taxa among clusters showed some considerable differences. Cluster A, where the sediment was composed of coarser particles, had as its most abundant species *Amphora coffeaeformis*, *Navicula* sp. #1, *Paralia sulcata* and *A. holsatica*. *A. coffeaeformis* and *P. sulcata* were the most abundant diatoms in Cluster B, where the sediment was finer than that of Cluster A. Clusters C1 and C2 were composed largely of *Navicula arenaria*, *Navicula* sp. #1. and *P. sulcata*. The sediment grains at these sites were finer than those of Cluster B. The highest densities of *P. sulcata* were observed in Clusters C3 and C4. The four centric diatoms, *Thalassionema nitzschioides*, *Cyclotella striata*, *C. atomus*, and *Stephanodiscus* sp. #1, which were abundant in the plankton samples from the same area (Oh 1994), were noticeably most abundant at C4. Cluster C4 contained sites with the finest sediments in the entire study area. Cluster D was similar to C3 in terms of dominant species. The most abundant species occurring in sites of Cluster E were *Achnanthes hauckiana* and *Dimeregramma minor*; it should be noted that the latter taxon was absent from all sites in the four C subclusters.

Species assemblages which might correspond to clusters could not be ascertained by the cluster analysis as mentioned above. We, therefore, synthesized abundance data for the 60 most abundant diatom taxa and plotted these against sediment grain size (Fig. 6). Only 39 taxa are shown in Fig. 6, since the remaining 21 species showed no discernible patterns along the gradient of grain size. The allocation of taxa into separate figures (Fig. 6) was arbitrary, but the similarities in the distribution of cell numbers against mean grain size were apparent. There were at least four categories of diatom taxa (Fig. 6a–d, e–f, g, h) showing a specific affinity for various grain diameters: the first predominated largely in fine deposits (Fig. 6a–d), the second was largely restricted to a grain size of 3.0 to 3.5 phi units (Fig. 6e–f), the third exhibited much denser populations on coarser sediments (Fig. 6g), and the last was characterized by a broad distribution pattern over the spectrum of sediment diameter (Fig. 6h). An interesting feature was that species listed in Fig. 6b and some in Fig. 6a and c showing a preference for fine-grained sediments also occurred in coarser sediments. The taxa in Fig. 6b were the three most abundant species encountered in the study area.

Discussion

It was our purpose here to document the abundances of diatom taxa on a Korean tidal flat and relate distributional patterns to selected environmental factors using a multivariate statistical analysis. The most abundant species in this region were *Paralia sulcata*, *Navicula* sp. #1 and *N. arenaria*. The centric diatom *P. sulcata* is considered a cosmopolitan species (Roelofs 1984), but only a few studies have reported it as being abundant in the benthic zone of any other coastal area. Roelofs (1984) found that this taxon represented >2% of the total diatom cell count in surface sediments of southern British Columbia inlets. He also noted that *P. sulcata* constituted a major component of the phytoplankton community in this area. *P. sulcata* was present in the plankton samples taken from coastal waters off our study area (Shim and Yang 1982; Choi and Shim 1986). In water samples from stations including our study area, more than 10% of the total cell counts in December could be attributed to this taxon (Shim et al. 1991). Al-

Table 3 Descriptive data for discriminant analysis employing eight clusters as groups and five environmental variables as discriminating variables. (*DF* discriminant function)

	DF1	DF2	DF3	DF4	DF5
Separation power of each discriminant function (DF)					
Relative percent of discriminating power	73.01	14.59	10.05	2.32	0.02
Eigenvalue	2.72	0.54	0.37	0.09	0.0007
Test of significance					
Chi-squared value	110.63	43.01	20.67	4.30	0.04
Significance level	p<0.0001	p<0.01	p=0.15	p=0.83	p=0.998
Degree of freedom	35	24	15	8	3
Standardized discriminant coefficients for each variable					
Variables					
Tidal level	0.33	–0.99	–0.09	0.13	–0.17
Mean grain size	0.60	0.22	–0.59	–0.59	0.54
Sorting coeffient	0.20	0.18	0.99	0.16	0.67
Skewness	–0.17	0.16	0.13	1.03	0.57
Organic matter content	0.25	0.48	0.003	0.73	–0.80
Correlations between DFs and variables					
Variables					
Tidal level	0.13	0.96	0.16	0.20	0.06
Mean grain size	0.96	0.05	0.25	0.09	0.10
Sorting coeffient	0.06	0.05	0.17	0.96	–0.23
Skewness	0.07	0.02	–0.12	–0.26	0.95
Organic matter content	0.17	0.04	0.96	0.20	–0.13
Canonical DFs evaluated at group centroids					
Clusters					
A	–1.86	–1.22	–1.90	-1.21	0.10
B	–0.03	0.65	0.53	1.25	–0.73
C1	1.58	1.13	1.74	1.41	–0.43
C2	0.91	1.28	0.66	0.62	–0.11
C3	–0.10	–0.92	0.16	0.001	–0.06
C4	3.91	1.73	4.07	2.83	–1.04
D	–1.28	–1.43	–1.80	–1.92	0.66
E	–1.31	–0.40	–1.76	–1.93	1.23

Classification matrix for 60 cases (sites)

Original cluster	No. sites	Predicted cluster							
		A	B	C1	C2	C3	C4	D	E
A	6	3 (50%)	1	0	0	0	0	1	1
B	10	1	7 (70%)	0	0	1	0	0	1
C1	8	0	0	4 (50%)	3	0	1	0	0
C2	7	0	0	3	3 (43%)	0	0	0	1
C3	9	0	1	0	0	5 (56%)	0	3	1
C4	4	0	1	0	0	0	3 (75%)	0	0
D	8	0	0	0	0	1	0	4 (50%)	3
E	8	1	0	0	0	0	0	0	7 (88%)

though a tychoplanktonic species, *P. sulcata* is predominantly benthic; it was a major constituent of the diatom assemblage throughout the year with relative abundances ranging between 21 and 37% on a mud flat located 20 km to the north of the Kunsan tidal flat (Kim and Cho 1985). In the present study, *P. sulcata* was abundant in coarse as well as in fine sediments. The importance of this taxon in both sediments and the water column reflected the significant tidal mixing that occurs in the study area. Entrainment of benthic diatoms into the water column of shallow estuarine systems is well documented (Shaffer and Sullivan 1988).

Difficulties in defining diatom assemblages arose when 60 species were subjected to cluster analysis. This may be because the taxa exhibited a broadly overlapping distribution. Some species showed high abundances in the narrow range of grain sizes (Fig. 6). The three most abundant species achieved their highest densities in fine-grained sediments but were also found in coarser sediments. Rare species were mostly encountered sporadically over the whole area.

It is generally known that benthic diatoms are not randomly distributed but exhibit distributional patterns which are related to habitat type and environmental gradients (re-

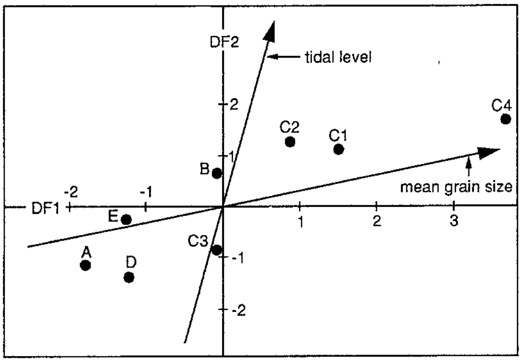
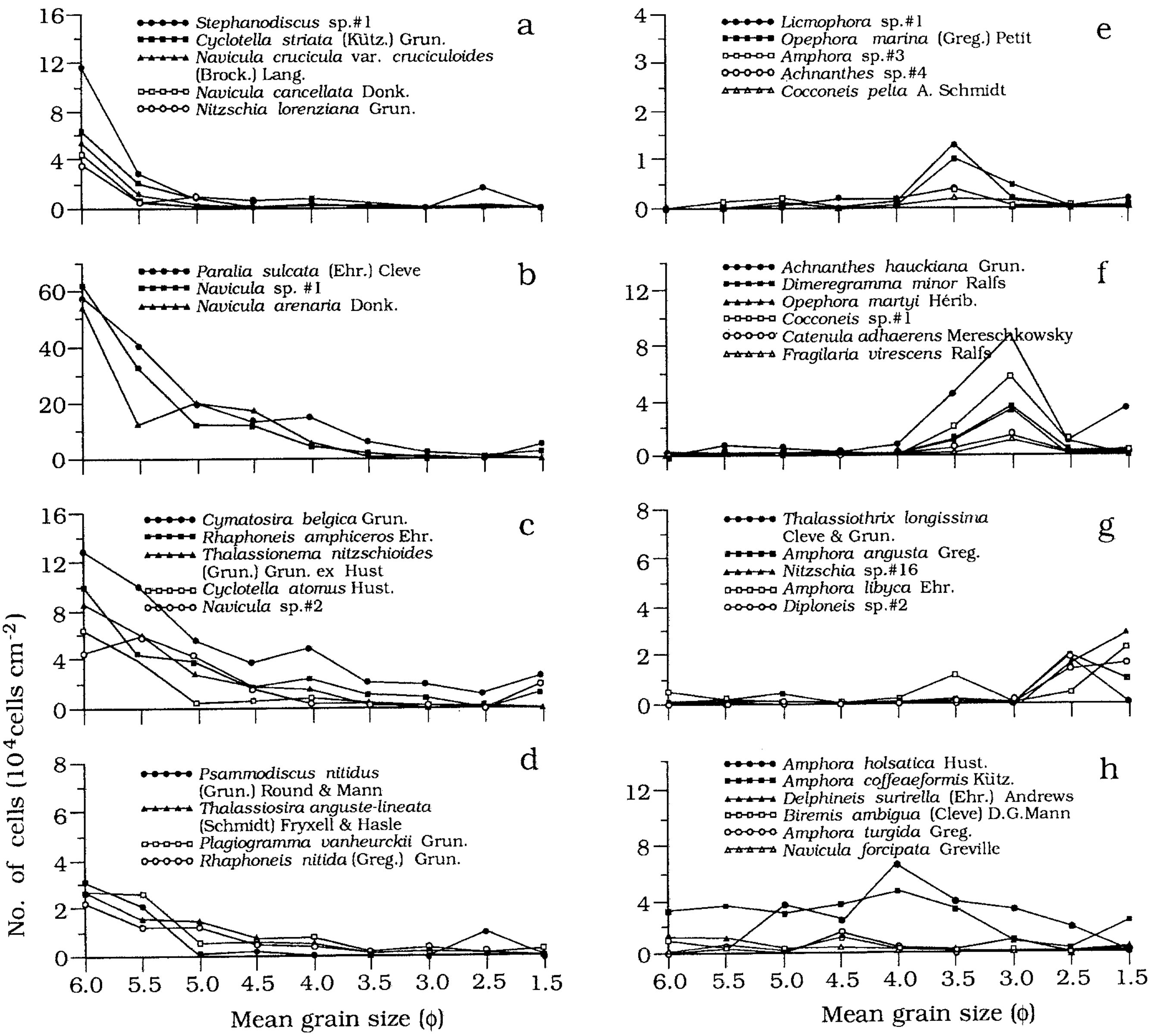


Fig. 5 Ordination of clusters on discriminant function 1 (*DF1*) and discriminant function 2 (*DF2*)

Fig. 6 Plot of cell numbers (10^4 cells cm^{-2}) of the most abundant diatom taxa against mean grain size. Species were assigned to eight clusters (**a–h**) based on their density at specific grain sizes



viewed in Round 1971). However, a high degree of spatial overlap of species shown in the present study is not an uncommon finding in other studies. A broadly overlapping distribution of diatom taxa along environmental gradients were frequently found in an estuary (Amspoker and McIntire 1978), a salt marsh (Cook and Whipple 1982; Sullivan and Moncreiff 1988a), and an intertidal shore crossing a salt marsh, sand flat and mud flat (Oppenheim 1988). Even a uniform distribution of diatom taxa along the environmental gradients was reported in a sand beach (Amspoker 1977). Our study area was characterized by differences in its areal extent compared to these other study areas; it covered an area of approximately 170 km^2, was exposed to the open sea, and included silty to sandy facies. Neverthless, the species which were typical of the inner tidal flat were also present in significant numbers on the outer tidal flat.

Multivariate analyses were employed to collapse the multi-dimensional data set into several orthogonal uncorrelated dimensions and to identify those environmental factors potentially controlling the distribution of benthic diatoms on the tidal flats. Primary factors identified in previous studies using a multivariate approach included salinity on estuarine tidal flats (Amspoker and McIntire 1978; McIntire 1978), elevation in salt marshes (Sullivan 1975, 1978, 1982), wave action on an exposed sand beach (Amspoker 1977). Other factors (i.e., temperature, desiccation, insolation, soil moisture, and sediment characteristics) were also found to be important determinants (Amspoker and McIntire 1978; McIntire 1978; Sullivan and Moncreiff 1988a). In the present study, however, mean grain size appeared to be the most important factor (Figs. 5, 6). The distribution of diatom taxa along gradients of sediment grain size and sorting have been well documented (McIntire and Moore 1977; Amspoker and McIntire 1978). Kosugi (1987) collected sedimentary benthic diatoms from 110 localities throughout Japan and found that the distributional patterns were determined by the properties of the substratum. Amspoker and McIntire (1978) showed that the distribution of diatoms on the tidal flats of Yaquina estuary, Oregon was primarily regulated by the physical properties of the sediment as well as a discontinuity in salinity.

The relatively high abundance of epipelic diatoms in the coarser sediments of our study area can be explained by the size distribution of sediment particles. The proportion of larger grains was great; however, there was still about 10% clay in most of these study sites (Fig. 3), and this would be advantageous for epipelic forms. The continual disturbance and resuspension of sediments could also be a factor responsible for the wide distribution of epipelic diatoms on a tidally dominated flat such as our study area (see Ballie and Welsh 1980). Relatively weak currents (10 cm s^{-1}) cause an obvious resuspension and displace sediment particles and benthic diatoms in estuarine systems (de Jonge and van den Bergs 1987). Tidal currents are mainly responsible for this redistribution of the resuspended materials (de Jonge and van Beusekom 1992).

We observed the greatest diatom abundance in the higher intertidal where finer sediments predominated. The density of cells was highest in Clusters C1 and C4, which except for site B10 included only sites of the innermost tidal flats. Tidal elevations were highest at these sites, and the sediments were characterized by the highest ϕ values and organic matter content. Fine particles can stimulate diatom growth by supplying more nutrients or protecting the cells against mechanical stress caused by wave action (Admiraal and Peletier 1979; Aston 1980; de Jonge 1985). Cook and Whipple (1982) found the greatest abundance of edaphic diatoms in the less tidally influenced upper reaches of a Louisiana salt marsh. Colijn and de Jonge (1984) reported a positive correlation between benthic microalgal primary production in sediments and tidal level. It has been claimed that a longer photoperiod for the more elevated portions of the tidal flat was responsible for the high primary production rates of benthic diatoms (Colijn and de Jonge 1984). However, the influence of elevation alone could not account for the high abundance of diatoms in the upper intertidal. Indeed, Riznyk and Phinney (1972) reported dense diatom populations in the lower intertidal where exposure to desiccation would be limited. McIntire and Wulff (1969) showed experimentally a relationship between desiccation and low diatom density in the upper intertidal. The distribution of benthic diatoms along environmental gradients may differ from one region to another; therefore, additional field work encompassing a yearly cycle and laboratory experiments are required to better define those environmental factors determining the spatial and temporal distributional patterns of diatom abundance on the Mangyung-Dongjin tidal flats. This will allow geographical comparisons to be made and enlarge our fragmentary knowledge of the biogeography of benthic marine diatoms.

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References

Admiraal W (1984) The ecology of estuarine sediment-inhabiting diatoms. Prog phycol Res 3:269–322

Admiraal W, Peletier H (1979) Influence of organic compounds and light limitation on the growth rate of estuarine benthic diatoms. Br Phycol J 14:197–206

Admiraal W, Peletier H, Brouwer T (1984) The seasonal succession patterns of diatom species on an intertidal mudflat: an experimental analysis. Oikos 42:30–40

Amspoker MC (1977) The distribution of intertidal epipsammic diatoms on Scripps Beach, La Jolla, California, USA. Bot mar 20: 227–232

Amspoker MC, McIntire CD (1978) Distribution of intertidal diatoms associated with sediments in Yaquina estuary, Oregon. J Phycol 14:387–395

Aston SR (1980) Nutrients, dissolved gases and general biogeochemistry in estuaries. In: Olausson E, Cato I (eds) Chemistry and biogeochemistry of estuaries. John Wiley and Sons, Ltd., London, pp 223–262

Ballie PW, Welsh BL (1980) The effect of tidal resuspension on the distribution of intertidal epipelic algae in an estuary. Estuar cstl mar Sci 10:165–180

Brockmann C (1950) Die Watt-Diatomeen der Schleswig-Holsteinischen Westküste. Abh senkenb naturforsch Ges 478:1–26

Carver RE (ed) (1971) Procedures in sedimentary petrology. Wiley-Interscience, New York

Choi JK, Shim JH (1986) The ecological study of phytoplankton in Kyeonggi Bay, Yellow Sea. III. Phytoplankton. J oceanogr Soc Korea 21:156–170

Colijn F, Jonge VN de (1984) Primary production of microphytobenthos in the Ems-Dollard estuary. Mar Ecol Prog Ser 14:185–196

Cook LL, Whipple SA (1982) The distribution of edaphic diatoms along environmental gradients of a Louisiana salt marsh. J Phycol 18:64–71

Cooley WW, Lohnes PR (1971) Multivariate data analysis. Wiley, New York

Folk RL (1954) The distinction between grain size and mineral composition in sedimentary rock nomenclature. J Geol 62:334–359

Folk RL, Ward WC (1957) Brazos River bar, a study in the significance of grain size parameters. J sedim Petrol 27:3–26

Jonge VN de (1985) The occurrence of 'epipsammic' diatom populations: a result of interaction between physical sorting of sediment and certain properties of diatom species. Estuar cstl Shelf Sci 21:607–622

Jonge VN de, Bergs J van den (1987) Experiments on the resuspension of estuarine sediments containing benthic diatoms. Estuar cstl Shelf Sci 24:725–740

Jonge VN de, Beusekom JEE van (1992) Contribution of resuspended microphytobenthos to total phytoplankton in the Ems estuary and its possible role for grazers. Neth J Sea Res 30:91–105

Kim JH, Cho KJ (1985) The physico-chemical properties of sediment, the species composition and biomass of benthic diatoms in the intertidal zone of Keum River estuary. Korean J Ecol 8: 199–207

Kosugi M (1987) Limiting factors on the distribution of benthic diatoms in coastal regions – salinity and substratum. Diatom 3: 21–31

Lohman K E (1972) A procedure for the microscopical study of diatomaceous sediments. Nova Hedwigia (Beih) 39:267–283

McIntire CD (1973) Diatom associations in Yaquina estuary, Oregon: a multivariate analysis. J Phycol 9:254–259

McIntire CD (1978) The distribution of estuarine diatoms along environmental gradients: a canonical correlation. Estuar cstl mar Sci 6:447–457

McIntire CD, Moore WM (1977) Marine littoral diatoms – ecological considerations. In: Werner D (ed) The biology of diatoms. Blackwell Scientific Publications, Oxford, pp 333–371

McIntire CD, Wulff BL (1969) A laboratory method for the study of marine benthic diatoms. Limnol Oceanogr 14:667–668

Norusis MJ (1986) SPSS/PC+ for the IBM PC/XT/AT. SPSS Inc, Chicago

Oh JS (1994) Ecological and taxonomical study of phytoplankton in the estuarine system of the Mangyung and Dongjin Rivers. M.Sc. thesis, Seoul National University, Seoul

Oh SH, Koh CH (1991) Distribution pattern of dominant benthic diatoms on the Mangyung-Dongjin tidal flat, west coast of Korea. J oceanol Soc Korea 26:24–37

OHAROK: Office of Hydrographic Affairs, Republic Of Korea (1987) Tide tables, Vol. 1. OHAROK, Pusan

Oppenheim DR (1988) The distribution of epipelic diatoms along an intertidal shore in relation to principal physical gradients. Bot mar 31:65–72

Rizynk RZ, Phinney HK (1972) The distribution of intertidal phytopsammon in an Oregon estuary. Mar Biol 13:318–324

Roelofs AK (1984) Distributional patterns and variation of valve diameter of *Paralia sulcata* in surface sediments of southern British Columbia inlets. Estuar cstl Shelf Sci 18:165–176

Round FE (1971) Benthic marine diatoms. Oceanogr mar biol A Rev 9:83–139

Round FE (1979) A diatom assemblage living below the surface of intertidal sand flats. Mar Biol 54:219–223

Shaffer GP, Sullivan MJ (1988) Water column productivity attributable to displaced benthic diatoms in well-mixed shallow estuaries. J Phycol 24:132–140

Shim JH, Shin YK, Yeo HG (1991) Abiotic environment and primary producers of estuarine pelagic ecosystem in the lower water of the Mangyung River and the Dongjin River. J oecanogr Soc Korea 26:155–168

Shim JH, Yang JS (1982) The community structure and distribution of phytoplankton of the Keum River estuary. J oceanogr Soc Korea 17:1–11

Simonsen R (1974) The diatom plankton of the Indian Ocean expedition of R.V. "Meteor" 1964–65. "Meteor" ForschErgebn 19: 1–66

Sullivan MJ (1975) Diatom communities from a Delaware salt marsh. J Phycol 11:384–390

Sullivan MJ (1978) Diatom community structure: taxonomic and statistical analysis of a Mississippi salt marsh. J Phycol 14:468–475

Sullivan MJ (1982) Distribution of edaphic diatoms in a Mississippi salt marsh: a canonical correlation analysis. J Phycol 18: 130–133

Sullivan MJ, Moncreiff CA (1988a) A multivariate analysis of diatom community structure and distribution in a Mississippi salt marsh. Bot mar 31:93–99

Sullivan MJ, Moncreiff CA (1988b) Primary production of edaphic algal communities in a Mississippi salt marsh. J Phycol 24:49–58

Whitting MC, McIntire CD (1985) An investigation of distributional patterns in the diatom flora of Netarts Bay, Oregon by correspondence analysis. J Phycol 21:655–661