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Inference Models for Tidal Flat Elevation and Sediment Grain Size: A Preliminary Approach on Tidal Flat Macrobenthic Community

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Abstract – A vertical transect with 4 km length was established for the macrofaunal survey on the Chokchon macrotidal flat in Kyeonggi Bay, Incheon, Korea, 1994. Tidal elevation (m) and sediment mean grain size (ϕ) were inversely predicted by the transfer functions from the faunal assemblages. Three methods: weighted average using optimum value (WA), tolerance weighted version of the weighted average (WAT) and maximum likelihood calibration (MLC) were employed. Estimates of tidal elevation and mean grain size obtained by using the three different methods showed positively corresponding trends with the observations. The estimates of MLC were found to have the minimum value of sum of squares due to errors (SSE). When applied to the previous data (1990~1992), each of three inference models exhibited high predictive power. This result implied there are visible relationships between species composition and faunas' critical environmental factors. Although a potential significance of the two major abiotic factors was re-affirmed, a weak tendency of biological interaction was detected from faunal distribution patterns across the flat. In comparison to the spatial and temporal patterns of the estimates, it was suggested that sediment characteristics were the primary factors regulating the distribution of macrofaunal assemblages, rather than tidal elevation, and the species composition may be sensitively determined by minute changes in substratum properties on a tidal flat.

Key words – inference model, sediment grain size, tidal flat elevation, macrobenthos, macrotidal flat

1. Introduction

A series of spatial observations may be a useful tool for understanding the interrelationships between patterns of species distribution and abiotic factors and even species association, particularly in the intertidal zone. The progressive change in species distribution pattern across a tidal flat is very analogous to temporal successions because it also follows an 'orderly process of community development that is reasonably directional and apparently predictable', as defined by Odum (1969). From this viewpoint, a tidal flat could be a good place either for testing a hypothesis by experimentation or predicting species distribution.

The study area, the Chokchon macrotidal mud flat, is located in a part of Kyeonggi Bay, a large embayment of the east central Yellow Sea, and it experiences maximum tidal ranges of up to 10 m and a maximum horizontal exposure of 7 km long (for detailed information, see 'Environmental Setting' in Frey *et al.* (1987) and references contained therein). Previous works of Frey *et al.* (1987) and Yoo (1998) revealed that macrobenthic assemblages showed tripartite zonation and that substratum types and tidal elevations mainly determine species distributions. In such an environment, quantitative environmental variables may be inversely estimated by function of species distribution data. The function is termed 'transfer function' and its construction is called 'calibration'. However, the implementation may be difficult or almost impossible, because it depends on whether strong governing agents are present or not.

The inference model is currently applied to reconstruction of past environmental conditions (Davis and Anderson 1985; Jones and Juggins 1995; Bennion *et al.* 1996; Wilson *et al.* 1996; Antoniades *et al.* 2005; Hausmann and Kienast 2006). These studies were mainly concerned with diatom

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*Corresponding author. E-mail: jwyoo23@hitel.net assemblages of lakes. Quantitative information from these techniques has revolutionized palaeoecology and helped understanding of environmental variables that control the distribution of organisms (Hausmann and Kienast 2006). There are no examples that deal with macrofaunas or tidal flat environment. Although this study is confined to a local area and is far from a broad-scale approach, observations on the outputs allow us to understand the relationship between macrofaunas and environments and to encompass data of wider spatial ranges. Macrotidal mud flats and the distribution of inhabitants can be precisely studied by drawing out transfer functions and inference models. The next three conditions account for this assumption: (1) the gradual changes in two major environmental variables and faunal assemblages, (2) the higher resolvability owing to longer width, and (3) the abiotic factors prevailing over biological interactions (Levinton, 1982; Reise, 1985; Huston, 1994).

This study aims (1) to construct tidal elevation and sediment grain size inference models, (2) to understand the observed patterns of species distribution in relation to the underlying structures contained by the models and (3) to test possibility and usefulness of inference model based on macrofaunal community in tidal flats.

2. Materials and Methods

Sampling

A total of 41 sites with an interval of 100 m were selected on a transect line running from land toward sea in the Chokchon macrotidal mud flat during spring tides for 2 days in July, 1994 (Fig. 1). Macrofaunas larger than 1 mm were collected by using a can core (15×20×30 cm) and sieve. Total surface area of 0.2 m^2 from 6 cores was sampled at each station. These sampling efforts were determined based on Kang (1993) who suggested that a surface area of 0.16 m^2 is appropriate for sampling macrofaunal assemblages.

Surface sediments were taken and grain size analysis was carried out using both the dry sieving and pipette analysis methods. Mean grain size values of surface sediment were obtained by using the equation of Folk and Ward (1957). Tidal elevation was measured at the same transect in June 1986 (Frey *et al.* 1987) and in July 1997. The vertical range of elevation was 1.5~6.5 m, which is what we used in calibration with the assumption that there was no significant change during the eight years (1986-1994).

Analysis

To construct the inference models, we employed three techniques: weighted average using optimum value (WA), tolerance-weighted version of the weighted average (WAT), and maximum likelihood calibration (MLC) (ter Braak, 1987). Species optima (u), tolerance (t) and occurrence probabilities (p_k) were obtained from the Gaussian logit and sigmoid curves fitted in the presence-absence data of each species distribution. This was done by utilizing

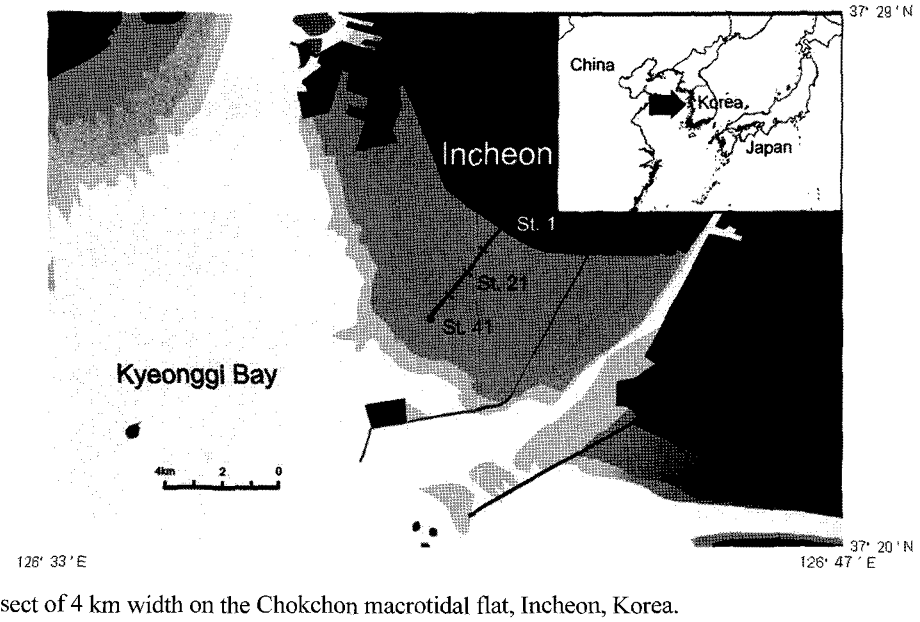

Fig. 1. A survey transect of 4 km width on the Chokchon macrotidal flat, Incheon, Korea.

categorical data modelling procedures (PROC CATMOD) of SAS (Statistical Analysis System). The null hypothesis states that the specific Gaussian logistic model is appropriate for the data.

Species optimum (u), and tolerance (t) of each species were calculated from the following equations: x is an environmental variable and p is a probability of occurrence. The Gaussian logit curve is expressed as $p = [\exp(b_0+b_1x+b_2x^2)]/[1+\exp(b_0+b_1x+b_2x^2)]$. Where $b_2<0$, species optimum (u) is the value of x that gives maximum probability and tolerance (t) is a measure of ecological amplitude. We obtained the estimates by the equations, $u = -b_1/(2b_2)$, and $t = 1/\sqrt{(-2b_2)}$ (ter Braak and Looman, 1987).

Unlike MLC, the WA and WAT methods essentially require species optima (u) and tolerances (t). For MLC that does not require these estimates, the linear predictor (b_0+b_1x) was fitted in the case of species occurring only in either the higher or lower portion of the tidal flat. For WA and WAT methods, u and t of these species had to be obtained by another way. We intentionally made the data symmetrically, and fitted Gaussian response curves. We assumed that u and t estimated in this way did not significantly distort the true u or t of the species present in the area being studied.

Table 1. Parameters and p-values of fitted equations from tidal elevation data (m) for each species.

Species	Taxa[a]	b_0	p-value	b_1	p-value	b_2	p-value	L-ratio	Prob.[b]	Optimum (m)	Tolerance (m)
Eohaustorius longidactylus	CAm	62.4	0.362	-29.6	0.365			6.5	1.000	3.12*	0.24*
Aricidea assimilis	APol	-15.7	0.007	7.8	0.007	-0.9	0.009	36.3	0.453	4.30	0.74
Aedicira pacifica	APol	-12.3	0.008	8.6	0.003	-1.2	0.003	27.9	0.831	3.70	0.66
Borniopsis tsurumaru	MBi	13.6	0.011	-4.5	0.009			12.2	1.000	2.94*	0.28*
Cirrophorus furcatus	APol	-4.0	0.227	4.0	0.049	-0.6	0.028	30.4	0.734	3.41	0.92
Eulima sp.	MGs	-14.1	0.103	13.5	0.056	-2.8	0.038	21.0	0.978	2.38	0.42
Glycera decipiensis	APol	-14.0	0.002	8.7	0.001	-1.1	0.001	30.2	0.740	3.98	0.68
Glycinde gurjanovae	APol	-27.0	0.003	16.2	0.004	-2.0	0.004	16.5	0.998	4.08	0.50
Heteromastus filiformis	APol	-3.9	0.336	4.3	0.087	-0.6	0.062	20.5	0.983	3.58	0.92
Ilyoplax pingi	CDB	-9.9	0.035	4.9	0.054	-0.6	0.059	36.8	0.431	3.89	0.89
Macrophthalmus japonicus	CDB	-20.6	0.020	4.5	0.021			10.5	1.000	6.00*	0.48*
Magelona sp.	APol	25.4	0.063	-7.6	0.063			8.3	1.000	1.39*	0.44*
Magelona japonica	APol	-59.8	0.023	24.3	0.024	-2.4	0.027	19.1	0.991	5.10	0.46
Moerella sp.	MBi	-12.6	0.021	5.6	0.040	-0.5	0.098	31.1	0.701	5.21	0.96
Nephtys californiensis	APol	-21.0	0.021	14.8	0.015	-2.0	0.014	16.7	0.998	3.71	0.50
Phoronis sp.	Ph	-113.8	0.033	49.6	0.033	-5.3	0.034	14.6	0.999	4.67	0.31
Potamocorbula amurensis	MBi	-66.0	0.008	29.5	0.008	-3.1	0.008	17.2	0.997	4.68	0.40
Protankyra bidentata	EHo	44.5	0.136	-13.3	0.136			5.2	1.000		
Reticunassa festiva	MGs	-13.7	0.003	6.9	0.004	-0.8	0.006	35.6	0.486	4.47	0.80
Ruditapes philippinarum	MBi	-22.6	0.022	13.5	0.026	-2.0	0.029	26.7	0.869	3.38	0.50
Solen strictus	MBi	-26.5	0.001	16.3	0.001	-2.2	0.001	20.9	0.979	3.70	0.48
Sthenothyra edogawaensis	MGs	-59.2	0.043	26.6	0.044	-2.9	0.045	20.1	0.985	4.51	0.41
Theora fragilis	MBi	-14.7	0.032	6.4	0.056	-0.6	0.122	28.3	0.816	5.32	0.91
Tugonia sinensis	MBi	-264.4	0.047	111.8	0.047	-11.7	0.048	7.4	1.000	4.79	0.21
Nephtys chemulpoensis	APol	-23.5	0.034	4.6	0.035			8.9	1.000		
Nephtys polybranchia	APol	-1.4	0.783	3.4	0.269	-0.7	0.124	24.9	0.918	2.48	0.86
Monoculodes koreanus	CAm	3.0	0.010	-0.9	0.005			42.3	0.254		
Asthenognathus inequipes	CDB	1.8	0.138	-0.9	0.022			37.2	0.460		
Cyclina sinensis	MBi	-8.6	0.014	1.4	0.034			17.6	0.997		
Macrophthalmus dilatatus	CDB	-16.2	0.113	12.3	0.110	-2.3	0.100	27.1	0.857	2.68	0.47

[a] Major taxon for each species indicated as follows: APol, polychaeta; MGs, gastropoda; MBi, bivalvia; CAm, amphipoda; CDB, brachyura; EHo, holothuroidea; Ph, phoronida.

[b] H0 is that fitted model is appropriate for the data. L-ratio denotes likelihood ratio.

* denotes the value obtained by the deliberate data set for WA and WAT (see Materials and Methods).

Table 2. Parameters and p-values of fitted equations from sediment mean grain size data (ϕ) for each species.

Species	Taxa	b_0	p-value	b_1	p-value	b_2	p-value	L-ratio	Prob.	Optimum (ϕ)	Tolerance (ϕ)
Eohaustorius longidactylus	CAm	36.8	0.012	-10.0	0.011			17.9	0.990	1.38*	0.27*
Aricidea assimilis	APol	-51.0	0.037	22.6	0.046	-2.5	0.059	36.0	0.331	4.58	0.45
Aedicira pacifica	APol	-131.0	0.011	63.1	0.012	-7.4	0.013	23.5	0.888	4.25	0.26
Borniopsis tsurumaru	MBi	73.1	0.021	-18.7	0.021			12.2	1.000	1.35*	0.53*
Cirrophorus furcatus	APol	-41.8	0.131	21.2	0.106	-2.5	0.098	22.9	0.907	4.19	0.44
Eulima sp.	MGs	32.1	0.002	-8.3	0.002			19.6	0.977		
Glycera decipiensis	APol	-63.3	0.004	28.2	0.004	-3.0	0.006	32.9	0.471	4.70	0.41
Glycinde gurjanovae	APol	-192.1	0.007	84.5	0.009	-8.9	0.011	9.7	1.000	4.77	0.24
Heteromastus filiformis	APol	-29.0	0.145	13.9	0.099	-1.5	0.084	12.8	0.999	4.78	0.59
Ilyoplax pingi	CDB	-44.4	0.163	19.6	0.192	-2.2	0.215	33.0	0.467	4.50	0.48
Macrophthalmus japonicus	CDB	-46.1	0.011	10.6	0.012			12.0	1.000	7.59*	0.83*
Magelona sp.	APol	59.2	0.014	-14.8	0.014			15.7	0.997	3.33*	0.19*
Magelona japonica	APol	-58.5	0.003	21.9	0.004	-1.9	0.005	21.3	0.942	5.65	0.51
Moerella sp.	MBi	-39.1	0.014	14.6	0.025	-1.2	0.058	32.8	0.478	5.98	0.64
Nephtys californiensis	APol	-111.6	0.028	54.1	0.029	-6.3	0.033	21.5	0.937	4.26	0.28
Phoronis sp.	Ph	-708.9	0.036	323.5	0.037	-36.8	0.038	15.7	0.995	4.40	0.12
Potamocorbula amurensis	MBi	-227.1	0.012	98.1	0.015	-10.4	0.019	11.8	1.000	4.71	0.22
Protankyra bidentata	EHo	270.2	0.278	-67.6	0.278			5.2	1.000		
Reticunassa festiva	MGs	-33.3	0.004	13.1	0.005	-1.2	0.006	38.6	0.230	5.49	0.65
Ruditapes philippinarum	MBi	-1523.6	0.060	750.8	0.060	-92.4	0.060	17.5	0.988	4.06	0.07
Solen strictus	MBi	-159.2	0.008	77.9	0.008	-9.4	0.009	34.4	0.400	4.14	0.23
Sthenothyra edogawaensis	MGs	-524.7	0.046	241.6	0.048	-27.8	0.049	19.6	0.969	4.35	0.13
Theora fragilis	MBi	-37.9	0.016	14.1	0.029	-1.2	0.066	30.1	0.611	6.02	0.65
Tugonia sinensis	MBi	-553.0	0.099	247.8	0.104	-27.7	0.111	14.7	0.998	4.47	0.13
Nephtys chemulpoensis	APol	-38.5	0.048	8.3	0.054			9.2	1.000		
Nephtys polybranchia	APol	13.1	0.005	-3.0	0.008			34.4	0.449		
Monoculodes koreanus	CAm	10.8	0.013	-2.7	0.013			35.7	0.387		
Asthenognathus inequipes	CDB	8.5	0.068	-2.4	0.047			32.2	0.559		
Cyclina sinensis	MBi	-8.3	0.002	1.3	0.015			16.4	0.995		
Macrophthalmus dilatatus	CDB	-497.6	0.092	261.0	0.092	-34.2	0.091	19.5	0.970	3.82	0.12

The top 30 dominant species, screened by using Le Bris Index (1988), were included in the training data set for MLC. In WA and WAT, 25 and 23 species were allocated in tidal elevation and sediment grain size calibration. Species with a frequency below 15 % were discarded. Species included in the training data set, their parameters (b_0, b_1 and b_2), significances (p-values), optima (u) and tolerances (t) are listed in Table 1 (tidal elevation) and 2 (sediment grain size), respectively.

In the course of maximum likelihood estimation, likelihoods were obtained at the intervals of 0.1 m for tidal elevation and 0.08 ϕ for sediment grain size. The maximum likelihood estimate is the value representing the maximum probability of the observed combination of species (Fig. 2) (ter Braak, 1987).

Linear regression analysis between observed and estimated values was performed in order to compare the approximation and to verify the inference models. No constant option ($\beta_0 = 0$) was used in the analysis to assess the accuracy on the basis of bias ($\beta_1 \rightarrow 1$) and precision ($\gamma^2 \rightarrow 1$).

Finally, past seasonal biological data (1990~1992) from Seo (1994) were applied to test the validity of the established inference models. The frequency of data gathered during the period was twice in the fall, twice in the winter, twice in the spring and once in the summer. Data from high, middle and low flat stations marked with stakes were included and were made to correspond to St. 5, 15 and 30 of this study. In the case of tidal elevation, the observed

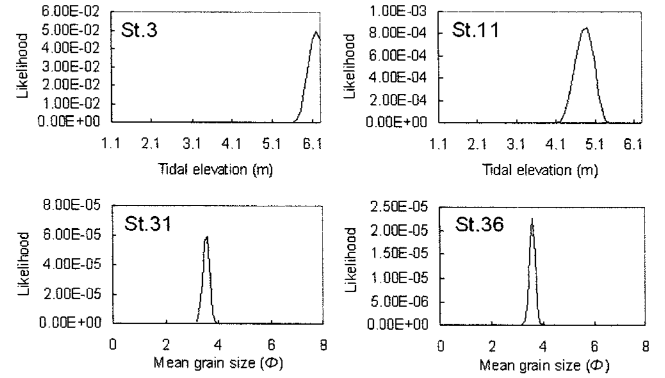

Fig. 2. Procedures for estimating tidal elevation (St. 3 and 11) and sediment mean grain size (St. 31 and 36). Likelihoods were calculated at the interval of 10 cm and 0.08 ϕ.

values taken in June 1986 and July 1997 were compared with estimates obtained from this study in July 1994. For sediment grain size, owing to the availability of data for each sample from 1990 to 1992, one-way ANOVA was carried out to test the differences between means of the observed and estimated values (H0: $u_{observed}=u_{estimated}$). These values were also compared with observed and estimated values from this study in July 1994.

3. Results

Response curves of species to environmental variables

Representative species were displayed together with their occurrence probabilities along two different environmental variables: tidal elevation and sediment mean grain size (Fig. 3). In Fig. 3A, the species differed in their optimum ranges and could be classified into widely distributing (*e.g.* a capitellid polychaete, *Heteromastus filiformis* (Claparède)) and relatively narrowly distributing species (*e.g.* a magelonid polychaete, *Magelona japonica* Okuda). They also differed in their optimum conditions or preferences (*e.g.* a nephtyid polychaete, *Nephtys chemulpoensis* Jung and Hong in higher elevation and a solenid bivalve, *Solen strictus* Gould in mid elevation). In Fig. 3B, the species that occurred in finer sediments manifested their wider ecological amplitudes, and this was ascribed to a sharp decline in mean grain size values at a higher elevation (*e.g. Magelona japonica*). Many of the presented species showed occurrence probabilities close to 100 %, while that of the ocypodid crab, *Ilyoplax pingi* Shen, was predicted to be less than 50 % (Fig. 3A and B).

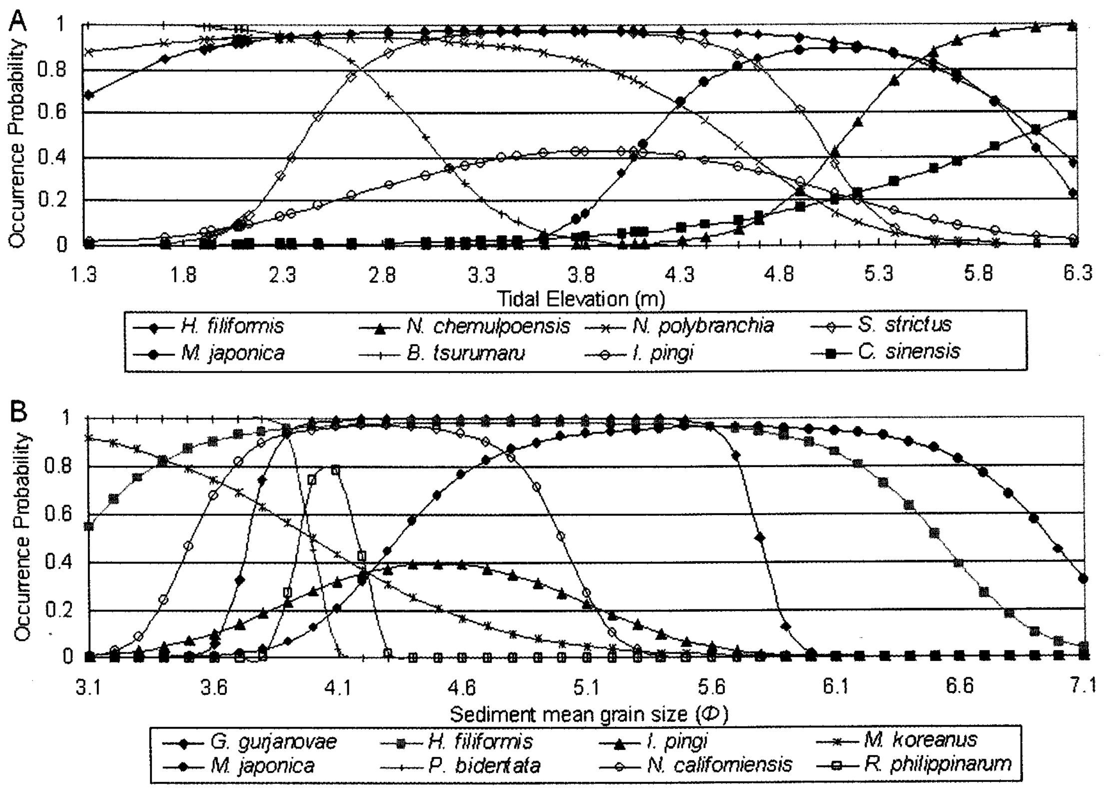

Fig. 3. Response curves and occurrence probability of the species (A) vs. tidal elevation and (B) vs. sediment mean grain size.

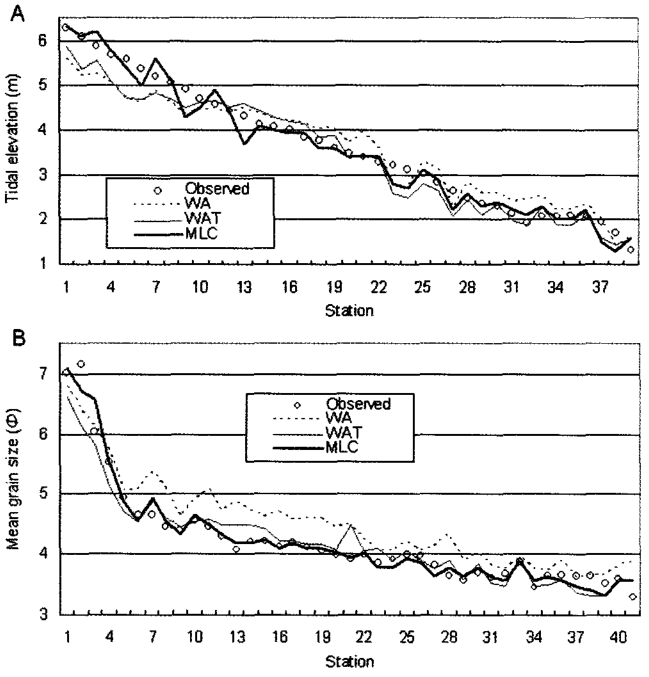

Fig. 4. Comparisons of estimates from WA, WAT, and MLC- (A) Tidal elevation and (B) sediment mean grain size.

Estimates of WA, WAT and MLC

Observed and estimated values of WA, WAT, and MLC were compared with one another (Fig. 4). The gradients in the estimates coincided well with those in the observed values. For tidal elevation, estimates from WA and WAT showed a deviation at a higher elevation, while MLC estimates were generally good approximations of the observed values. However, relatively larger residuals occurred in mid elevation from about St. 6 to 13 (Fig. 4A). For sediment grain size, estimates of WA showed a larger deviation from St. 6 to 21. Estimates of the other two models (WAT and MLC) fitted well with the observed values along the tidal transect (Fig. 4B).

Verification procedures were then carried out in order to examine the approximation between the observed and estimated values (Fig. 5). In tidal elevation and sediment grain size calibration, all estimates were found to have significant correlation. However, MLC was the best model in terms of the intensity of linear relationship (r^2) and slopes (b_1). Residuals of WA and WAT showed weak trends in that residuals in the middle of the x-axis were positive and those in the higher end were negative (see Fig. 5A, B, D and E).

Application to the previous data

In Fig. 6, elevation estimates (MLC) based on 1990-1992 biological data were compared with estimates from

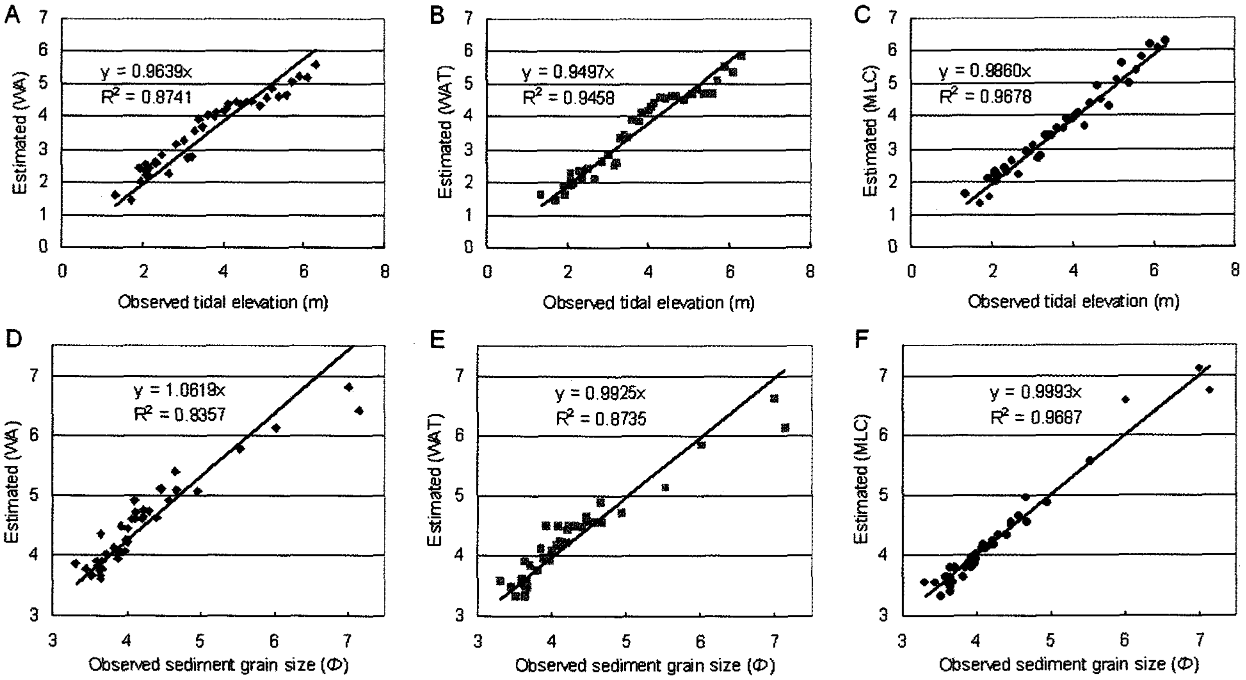

Fig. 5. The result of regression analysis between observed and estimated values with no constant option. (A-C) Tidal elevation; (D-F) Sediment mean grain size.

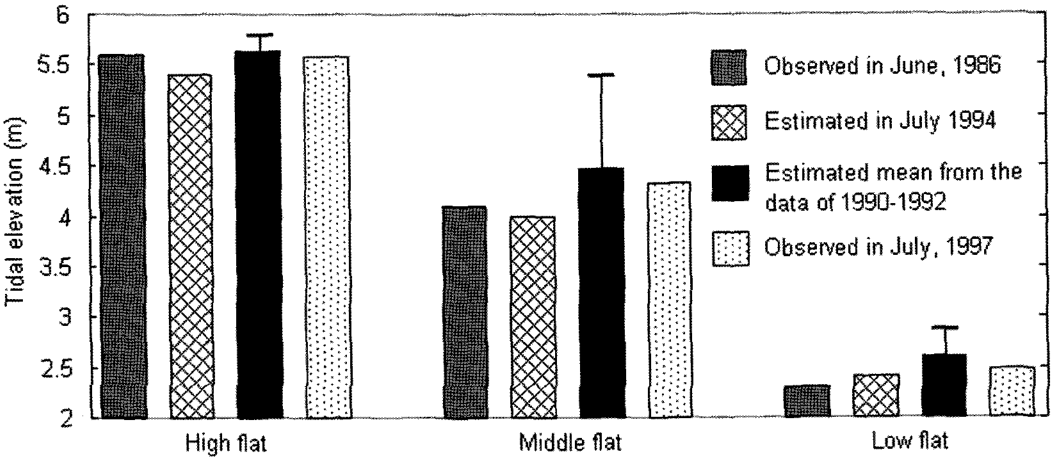

Fig. 6. Comparisons between estimates and observed values of tidal elevation. Error bar indicates the 68 % confidence level (Standard deviation) of data.

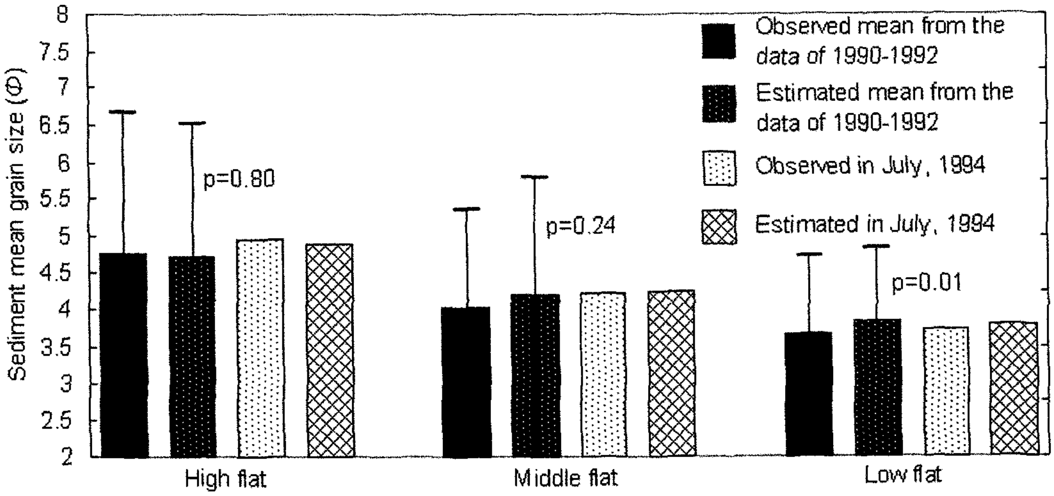

Fig. 7. Comparisons between estimates and observed values of sediment grain size. Error bar indicates the 68 % confidence level (Standard error) of data. Oneway ANOVA was carried out between observed and estimated means of 1990-1992.

this study and with observations made in 1986 and 1997. The averages of estimates from the three locations (high, middle and low flats) approached the other estimated and observed values. Variation in estimates from the high and low flats ranged narrowly (Standard deviation, SD=±0.15 and ±0.27 m). However, the estimates from the middle flat showed a larger variation (SD=±0.93 m).

The averages of estimated and observed sediment grain sizes from the 1990 ~ 1992 data were compared as shown in Fig. 7, which yielded no significant difference in higher ($p = 0.80$) and middle elevation ($p = 0.24$). A significant difference between means (0.166 ϕ, $p = 0.01$) was found in the lower elevation, but the result was negligible when compared with those of the other two elevations (high flat, 0.050 ϕ and middle flat, 0.179 ϕ). The small variation of the estimates (±0.044 ϕ), which appears to be caused by a low sensitivity of the inference model or a high stability of species occurrence patterns in the low flat, may be a probable cause of the significant difference obtained. The high stability in species number in the low flat of the study area was already noted by Seo (1994) as corresponding to 25±5 species/m^2 in the high flat and 38±3 in the low flat from bimonthly samples for 2 years.

4. Discussion

Abiotic vs. biotic factors

Benthic faunas on a tidal flat are strongly governed by a set of abiotic factors. Various authors have extensively described a pool of physiological stress such as desiccation and osmotic shock as a probable major factor (Vernberg, 1981; Peterson, 1991; McLachlan and Jaramillo, 1995). Another important determinant on faunal communities is sediment texture. Sediment-animal relationships have explained most variation patterns of macrofaunal distribution since the investigation by Sanders (1958). The relationship's role involves trophic amensalism and enhancement of proper feeding groups (Rhoads and Young, 1970). Although Snelgrove and Butman (1994) expressed skepticism over the traditional belief, many correlative studies on macrobenthic faunas reported significant relationships between grain size and faunal distribution pattern.

Peterson (1991) classified faunal groups of tidal flats into substratum- and elevation-specific species. The general features of benthic distribution on a tidal flat are largely dependent on two factors, sediment types and tidal elevation. However, other types of regulating factors may affect species distribution on a different scale and from a different viewpoint. If we examine other biological parameters such as growth rate, reproductive rate, life cycle and densities of some populations, the imprint of biological interaction can be detected easily (Holland and Polgar, 1976; Croker and Hatfield, 1980; Reise, 1985; Peterson and Black, 1988).

In this study, it was found that some species' distribution patterns along the explored transect were approximately bimodal (Fig. 8). This means that those species are not governed by abiotic factors, and that the trough in the middle flat may be regarded as a reflection of biological interaction (Huston, 1994). However, the case was limited to few species only, because most of them showed unimodal distribution. Although reliability problems may have occurred, this result was accepted as quite a different response from those of the other species. The persuasive and reliable interpretation recognized from the overall distribution pattern is that the abiotic factors are predominant in this environmental regime. The extraction of a practical transfer function from a community is an important procedure in estimating quantitative environmental variables, and this is determined by whether biological assemblages are regulated by strong governing agents or not. Many studies regarding the quantitative inference models are based on this property, and selection of highly related variables was carried out prior to construction (Davis and Anderson, 1985; Reavie *et al.*, 1995; Wilson *et al.*, 1996). The satisfactory estimation obtained in this study proved that sediment textures and tidal elevation are governing factors, while biological interactions are the 2nd order factors in the present soft-bottom intertidal area.

Tidal elevation vs. substratum effect

The application of this model to previous data seems to be successful in that estimates and observed data almost overlapped, indicating a convincing trend, and most of the values were included within 1×SD ranges (68% confidence interval). However, a relatively marked variation in elevation estimates was detected in the middle flat. At this step, it is possible to interpret the phenomenon as

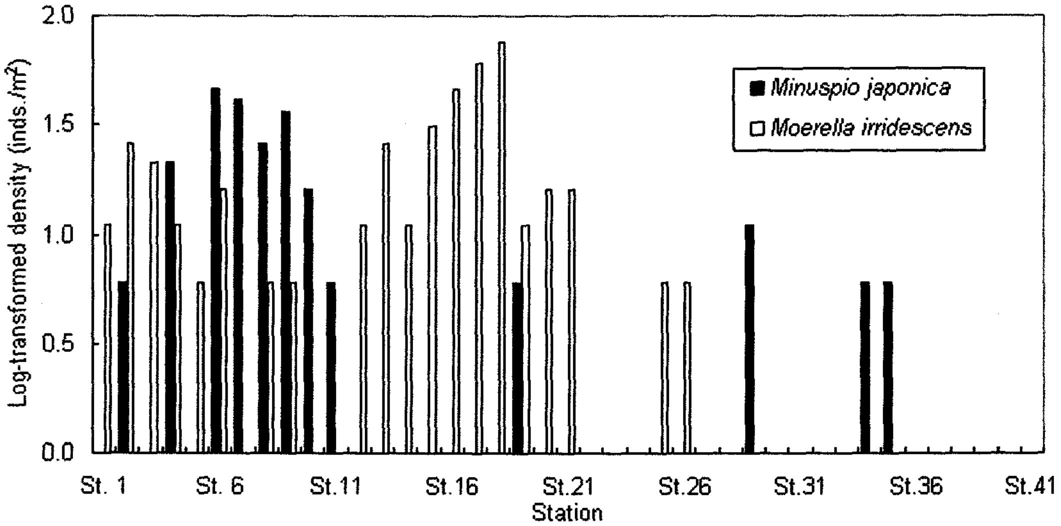

Fig. 8. Bimodal distribution patterns of polychaete, *Minuspio japonica* and bivalve, *Moerella iridescens* along the transect.

reflecting a few probable situations: (1) natural variation in elevation occurred, (2) temporal variations in species composition are larger, especially in the middle flat or (3) tidal elevation is less important in determining faunal composition.

Slight seasonal variations in elevation commonly occur in the tidal flats of the West Coast of Korea. KORDI (1995) reported that the sedimentation rate was ca. 3 cm/ 5 months in the lower part of a transect. In the middle flat, the sedimentation rate was not homogeneous but rather fluctuated in a minute scale (< 2 cm/5 months). An annual comparison of topographic profiles between May 1986 and June 1988 in this study area reported net changes of +10~+30 cm in elevation in the middle and low flats (KORDI, 1989). Based on these results, a larger variation in tidal elevation seems probable. However, the variation of estimated elevation from 1990 to 1992 was pegged at ±1 m.

The middle flat is described as a transitional zone where the suspension-dominant sedimentation process in the high flat and the bedload-dominant transport in the low flat are mixed, and are involved in an interactive relationship (Park, 1995). The hydrodynamic process is intermediate and the resultant sediment type is mud and sand-mixed sediment that contains either sand or mud bottom-specific species. An edge effect may act upon the middle flat community and a higher variation in species occurrence pattern may be produced. High flat inhabitants, including an ocypodid crab, *Macrophthalmus japonicus* De Haan, were found in the middle flat with a frequency of 29 % (100 % at the high flat in all seasons) from 1990 to 1992. A venerid bivalve, *Cyclina sinensis* (Gmelin), was yielded with a frequency of 43 % (86 % at the high flat). A synaptid holothurian, *Protankyra bidentata* (Woodward et Barrett), occurred with a frequency of 43 % (100 % at the low flat during all seasons). However, the presence of these inhabitants could not be a main reason for a larger variance being observed in estimating tidal elevation, in spite of the fact that a species data set was applied to both models. Finally, an attempt to determine whether tidal elevation effect is a causative or just a correlative factor was undertaken. Yoo (1998) hypothesized that the tidal elevation effect is not important in determining species composition but in regulating density and biomass in high flat communities. Proof of this relative importance was suggested in the postulations outlined below. Modulation of mean grain size along an estimated trend was observed in this study area (-0.4~ +0.3 ϕ in Yoo (1998) and -0.8 ~ +0.6 ϕ in Frey *et al.* (1989)). Those small reversals along the exponentially decreasing trend could be seen in Fig. 5b. Although we do not know the exact process at the moment, the reversals could imply a significant event because the inference model approximately reflected these minute variations. The realization of small reversals gave an idea that the responses of biological assemblages are congruent with the variation of sediment types and partly independent of linearly decreasing tidal elevation.

In estuaries where the environmental characteristics are similar with the intertidal area in terms of the predominance of abiotic factors, sediment composition is an important factor in explaining the variation in macrofaunal community structures (Mannino and Montagna, 1997). Moore (1978) studied the intertidal flat in the lower Mersey Estuary, U.K., and reported that seasonal changes in sediment composition were responsible for the variation of macrofaunal assemblages.

The results of this study tells us some implications that (1) substratum properties (*e.g.*, sediment texture) may be a primary factor in governing the distribution of macrobenthos community and (2) the species composition may be sensitively determined by small differences in substratum properties on a tidal flat. Potential re-adjustments on a small, temporal and spatial scale are expected in soft bottom intertidal communities.

Application to tidal flat environment

Nowadays, transfer function techniques are widely used in ecology and environmental sciences, mainly for reconstructing past environments based on contemporary controlling factors (Hausmann and Kienast, 2006). As previously described, major taxa of training data in inference modeling were confined to the planktonic community and the purposes were, in general, to estimate changes of eutrophication status; however, it can be applied to diverse fields of ecology from detecting positional or locomotory behavior of plankton and fishes to monitoring responses of macrofaunal composition to disturbance sources.

This study has shown the possibility of an inference model that predicts critical environmental factors based on tidal flat macrofaunal community. Although significant effects of abiotic and biotic factors were found, this study has rather a preliminary characteristic that determines our further planned direction for combining other critical environmental variables of macrofaunal distribution. At present, the established model is not applicable to other sites because of limitation of data and small number of environmental variables. However, an inference model based on local faunal data can still be useful as a solution to local problems. For example, one of our longstanding questions in coastal management is monitoring environmental changes due to local area developments (*e.g.* land reclamation, port construction, *etc.*). These may result in changes of substratum properties and elevation in tidal flats. Working conditions in tidal flats are so severe that only a transect line survey design is adopted for measuring tidal flat elevation and sampling sediment. After an appropriate validation and testing procedure, in a local area, this kind of approach (*i.e.* application of inference model on ordinary monitoring data of macrofaunal community) can provide more rapid and easier chances to get information on environmental changes due to anthropogenic impact.

High performance models from this study can invoke a development of more robust model that is not restricted to a local faunal data and may be applied to tidal flats nationwide. Based on the effective response of macrofaunas to eutrophication, the inference model for biological evaluation of water quality can be said to be a promising tool. A by-product of the model is a gain in knowledge of habitat requirement (*i.e.* optimum and tolerance range of habitat) of principal species in the study area. This kind of information could play a vital role in the intertidal habitat restoration if we obtain faunal occurrence data from a diverse type of tidal flats in and around a target area.

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