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Seasonal and habitat structures of crustacean decapod assemblages associated with *Zostera marina* beds in northern Jinhae Bay, Korea

JOO MYUN PARK[1] AND SEOK NAM KWAK[2]

[1]Department of Biological Sciences, Macquarie University, Sydney, NSW 2109, Australia, [2]Environ-Ecological Engineering Institute Co. Ltd, Busan 48280, Korea

Crustacean decapod assemblages were surveyed in Zostera marina *beds adjacent to tidal flats (ET) and rocky shore (ER), and in unvegetated habitats (UV). Decapod samples were collected monthly throughout 2002 using a small beam trawl from northern Jinhae Bay, Korea. Water temperature, salinity, eelgrass biomass, sediment composition and organic matter were also monitored to assess any correlation between environmental variables and decapod fauna. A total of 31 decapod species belonging to five taxa (three prawns, 13 caridean shrimps, one hermit crab, one mud shrimp and 13 crabs) were collected at three different habitats. To assess variations in decapod assemblages in relation to habitat type and season, various multivariate analyses were used. The dominant caridean shrimps were* Palaemon macrodactylus, Alpheus digitalis *and* Crangon uritai, *and the dominant crabs were* Charybdis japonica, Hemigrapsus penicillatus *and* Charybdis bimaculata. *The number, abundance and diversity of decapod species varied greatly with habitat type and season, peaking in eelgrass beds and during spring, and showing the lowest catch rate in unvegetated habitat and during winter months. The nMDS ordination and multivariate analyses revealed that habitat type and season were determinant factors affecting the structure of decapod assemblages. Seasonal shifts in the abundance of decapods corresponded with changes in eelgrass biomass and loss on ignition (LOI), but not with water temperature or salinity.*

Keywords: caridean shrimps, crabs, spatio-temporal variation, eelgrass beds, south-eastern Korea

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INTRODUCTION

Seagrasses are widely distributed throughout shallow estuaries and coastal areas of temperate and tropical seas, providing vegetative habitat and shelter for various marine animals (Hemminga & Duarte, 2000). Many fish and invertebrate species use seagrass beds as feeding and/or nursery grounds, including many economically important species (Nelson, 1981; Edgar & Shaw, 1995; Haywood *et al*., 1995; Huh & An, 1997; Guidetti & Bussotti, 2000). Seagrass habitats increase the number of microhabitats, sediment deposition and stabilization, food resources, and protection from predators, and reduce hydrodynamic forces (Lewis, 1984; Klumpp *et al*., 1989; Connolly *et al*., 1999; Hemminga & Duarte, 2000). However, despite the importance of these habitats in supporting regional biodiversity, seagrass habitats have been experiencing global declines in coverage, often related to the destruction of physical habitat, increased nutrient and sediment runoff, over-exploitation and decreased water quality due to anthropogenic activities (Dennison *et al*., 1993; Short & Wyllie-Echeverria, 1996; Erftemeijer & Lewis, 2006; Orth *et al*., 2006; Burkholder *et al*., 2007; Cabaço *et al*., 2008).

Zostera marina (eelgrass) is the most common seagrass species in temperate coastal areas around the world. This species forms large eelgrass beds along the coastlines of southern Korea (Huh, 1986; Huh & Kwak, 1997; Lee *et al*., 2000). Although many ecological studies of faunal assemblages in eelgrass beds have been conducted in Korean waters, they have primarily focused on fish species (e.g. Huh, 1986; Go & Cho, 1997; Huh & Kwak, 1997; Kwak *et al*., 2006). Only a few studies in Kwangyang Bay have examined seasonal variation in the species composition and abundance of decapods in eelgrass beds of Korean waters (Huh & An, 1997, 1998). In contrast, many studies in other areas have described decapod assemblages in seagrass habitats (e.g. Holmquist *et al*., 1989; Kwak & Klumpp, 2004; De La Rosa *et al*., 2006) and compared assemblage structure between vegetated and unvegetated habitats (e.g. Lazzari, 2002; Nakamura & Sano, 2005). Because invertebrate epifauna in seagrass meadows may have an essential role in the transfer of primary production to higher trophic level (Bauer, 1985), and in regulating densities of seagrass microbenthic taxa by their predations (Nelson, 1981), decapod crustaceans may potentially affect the structure of the seagrass community.

In many shallow seagrass habitats, vegetation patterns are important factors that control faunal assemblage structure (e.g. Guidetti, 2000; Bloomfield & Gillanders, 2005; Kwak *et al*., 2006; Ribeiro *et al*., 2012), and variation in vegetation coverage may drive differences in habitat preferences among species (Guidetti, 2000). For example, vegetated habitats increase the

Corresponding author:
S.N. Kwak
Email: seoknam@eeei.kr

species richness and abundance of fish and decapod assemblages in South Australia (Bloomfield & Gillanders, 2005). Higher densities of juvenile fishes have been observed in *Posidonia* seagrass and rocky-algal reed habitats compared with unvegetated habitats in the Adriatic Sea (Guidetti, 2000). In addition, vegetated habitat harbours large numbers of fish and crustaceans, and supports a greater diversity of faunal assemblages (Bell & Pollard, 1989; West & King, 1996). Due to the crucial role of seagrass beds and adjacent habitats in sustaining biodiversity, such studies are essential for future conservation efforts, as they elucidate the ecological mechanisms pertinent to the effective management of these areas (Bell & Pollard, 1989; Ferrell & Bell, 1991). Nonetheless, relatively few studies have compared decapod assemblages between vegetated and non-vegetated habitats (e.g. Lazzari, 2002; Bloomfield & Gillanders, 2005; Nakamura & Sano, 2005).

In the present study, we assessed spatial and temporal differences in decapod assemblages inhabiting eelgrass beds and unvegetated habitat in northern Jinhae Bay, Korea. Our objectives were (1) to assess differences in decapod assemblage structure among three types of habitats, and (2) to examine seasonal changes in diversities of decapod assemblages.

MATERIALS AND METHODS

Study area

Investigations were conducted in the northern part of Jinhae Bay located along the south-eastern coast of Korea (Figure 1). Jinhae Bay is semi-closed and connected by two inlets, the north-eastern and south-western inlets, to the open sea. Eelgrass beds are well-developed in the northern Jinhae Bay and provide habitat for a variety of invertebrates and small fish, which in turn serve as potential prey items for large fishes (Kwak *et al*., 2014). The eelgrass bed within the study area forms subtidal bands in shallow waters (<7 m) and is distributed as patches along the shorelines. In the study area, seagrass beds are dominated by *Zostera marina*. The mean tidal ranges of the study area are 1.8 and 0.7 m at spring and neap tide, respectively. Three study sites were chosen in northern Jinhae Bay to examine differences in decapod assemblages among three types of habitat: eelgrass beds adjacent to tidal flats (ET) or rocky shore (ER), and unvegetated habitat (UV).

Sampling

Decapod samples were collected using a 3 m beam trawl (1.9 cm mesh wing and body, 0.6 cm mesh liner). For each monthly sampling, four 6-min tows were conducted during the daytime at spring tide throughout 2002. The study area was $\sim$180 m^2 for each sampling event. The total area swept by 144 trawl hauls was 25,920 m^2 (4 samplings $\times$ 12 months $\times$ 3 habitats $\times$ 180 m^2). Although this method may be destructive to seagrass beds, beam trawl survey is also beneficial to estimate actual densities of benthic marine organisms in seagrass habitats (Coles, 1986). Specimens were preserved immediately after capture in 5% formalin and later transferred to 70% isopropanol for storage. Samples were identified to the species level.

Surface water temperature and salinity were monitored monthly at each sampling using a thermometer and a salinometer, respectively. Eelgrass biomass was estimated by collecting all plants at the sea bottom from an area of 0.1 m^2. The plants were dried at 80 °C for 24 h and then weighed to the nearest 0.1 g. Eelgrass biomass was expressed as dry weight per square metre (DW/m^2). The sediments of each site were examined monthly throughout the year for both particle size and loss on ignition (LOI) analyses. The top 5 cm of sediments from the bottom were collected using three replicate 10 cm diameter cores. Sediment samples were first analysed to determine grain size and texture after drying at 80 °C for 24 h (Gee & Bauder, 1979). Sediment composition was based on four grain-size classes: gravel ($>$2.0 mm), sand (2.0–0.05 mm), silt (0.002–0.05 mm) and clay ($<$ 0.002 mm). The proportion of each component size class was calculated for each sample. Next, because organic matter derived from microalgae (e.g. seagrass) may constitute the food source for deposit feeders such as decapods in coastal environments (MacIntyre *et al*., 1996), LOI was determined at 500–550 °C (4 h) to estimate organic content, following Heiri *et al*. (2001).

Data analysis

Differences in environmental variables in relation to habitat type were examined using univariate analyses. Student's *t*-test was used to determine eelgrass biomass between two eelgrass beds (ET and ER), and one-way analysis of variance (ANOVA) was applied to test spatial differences in LOI. One-way analysis of similarity (ANOSIM) was performed to test significant differences in sediment composition among three different habitats.

Diversity (H') (Shannon & Weaver, 1949) was calculated as: $H' = -\sum (n_i/N) \times \log (n_i/N)$, where n is the number of individuals (abundance) of each species i in a sample, and N is the total number of individuals. Two-way ANOVAs were used to assess habitat and seasonal differences in abundance (number of individuals) and diversity of decapod assemblage. Habitat and season were considered fixed factors, and Tukey's test was used for post-hoc comparisons after ANOVA. The relationships between decapod abundance and environmental variables were analysed using linear regression. All species were considered in the analyses, and abundances were log $(x + 1)$-transformed. For each of six numerically abundant species which constituted $>$4% in total abundance, spatial and seasonal variations in mean abundance were analysed.

To examine differences in decapod assemblages among habitats and among seasons, assemblage data were log $(x + 1)$-transformed, and Bray–Curtis similarity matrix was constructed (Clarke *et al*., 2006) and then visualised using nMDS ordination. The matrix was then subjected to a series of two-way permutational multivariate analyses of variances (PERMANOVAs) to test for significant effects of habitat (three levels) and season (four levels) as well as their two-way interactions. PERMANOVA is a non-parametric distance-based analysis of variance that uses permutation procedures to test hypotheses. Two-way crossed ANOSIMs were used to test for significant differences in assemblage structure with respect to habitat or season based on the same factors used in the PERMANOVA (see above) and with the magnitude of the *R*-statistic indicating the relative importance of any such differences (Clarke *et al*., 2014). Global *R*-statistic values from the ANOSIM represent differences in the similarities (distance) within and among defined groups; *R*-values vary

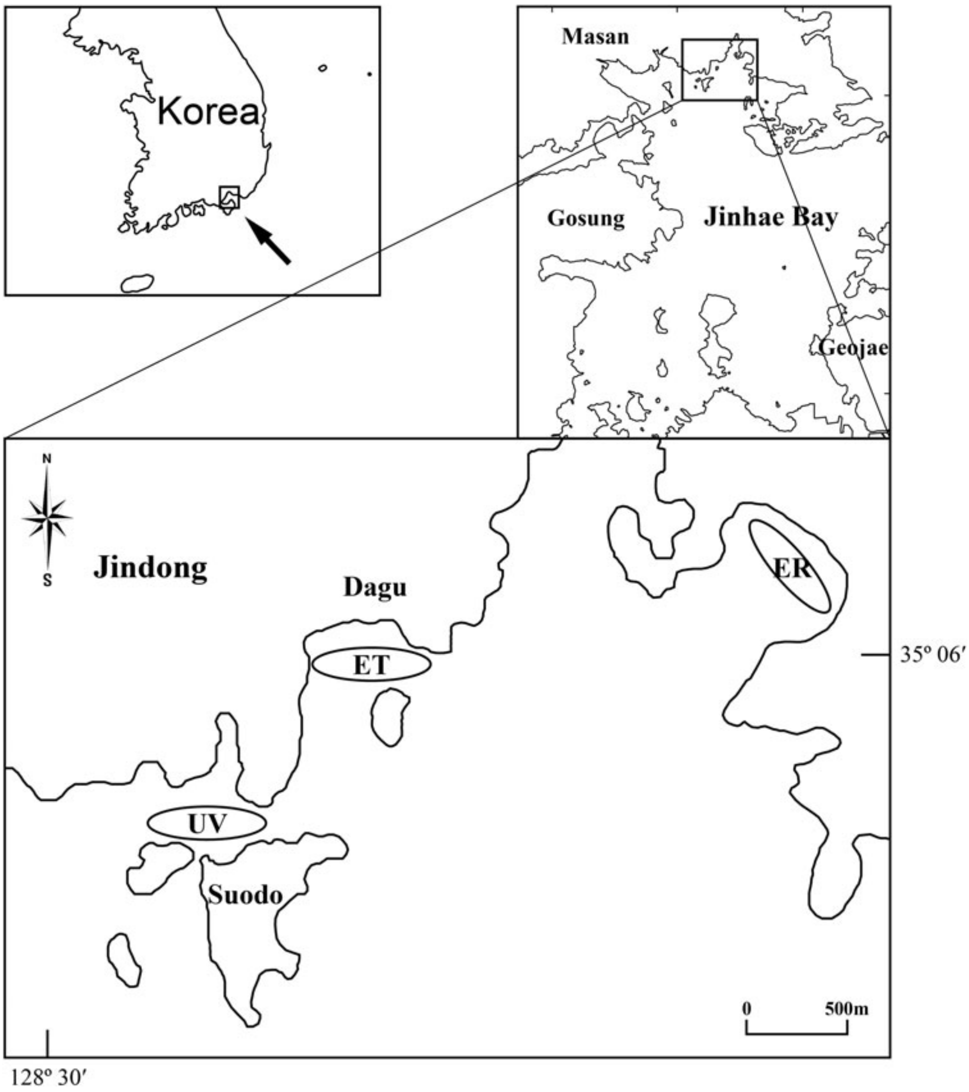

Fig. 1. Locations of the study sites of eelgrass beds adjacent to tidal flats (ET) and rocky shore (ER) as well as unvegetated habitat (UV) in northern Jinhae Bay, Korea.

between 0 and 1. An *R*-value of zero indicates no differences in the average similarity among and within groups, and an *R* value of 1 indicates that the compositions of all samples within each group are more similar to each other than to any of the samples from any other group (Clarke *et al*., 2014). In cases in which ANOSIM detected a significant difference, pairwise ANOSIM comparisons were then used to determine which comparisons between habitats and between seasons were significantly different. To discriminate significant effects obtained by PERMANOVA and ANOSIM, canonical analyses of principal coordinates (CAPs) were used (Anderson *et al*., 2008). The relative contributions of species to the observed differences were assessed using correlation coefficients among each habitat or season and the canonical axis, and the correlations of individual species $>$0.50 with CAP axes 1 and 2 were plotted.

ANOVA and regression analyses were conducted using SYSTAT software (Systat version 18, SPSS Inc., Chicago), and multivariate analyses were performed using routines in the PRIMER v7 multivariate statistics package (www.primer-e.com) and the PERMANOVA + add-on module (Anderson *et al*., 2008; Clarke & Gorley, 2015). Statistical differences were determined at the 0.05 significance level.

RESULTS

Environmental variables

Water temperature in the study area ranged from 7.4 to 27.7 °C, with a peak in July followed by a decline in October and reaching a minimum during winter. Salinity ranged from 25.4 to 34.2‰, with lower values in August and September when salinity dropped to about 25‰ (see also Kwak *et al*., 2006). Average eelgrass biomass ranged from 29.2 to 269.7 g DW m^{-2} at ET and from 38.7 to 278.5 g DW m^{-2} at ER (Figure 2), and the values varied greatly across the seasons in both eelgrass beds, although the average biomass did not significantly differ between the two eelgrass habitats (*t*-test, $P >$ 0.05). Peak eelgrass biomass occurred during spring at both sites, followed by a sharp decline in winter (Figure 2). LOI also fluctuated seasonally, with a peak between spring and summer at all three study sites (Figure 2). Mean LOIs significantly differed among the three habitats (one-way ANOVA, $P <$ 0.05). Tukey's post-hoc test revealed that mean LOIs were significantly higher in the two eelgrass habitats than in the unvegetated area, but values did not significantly differ

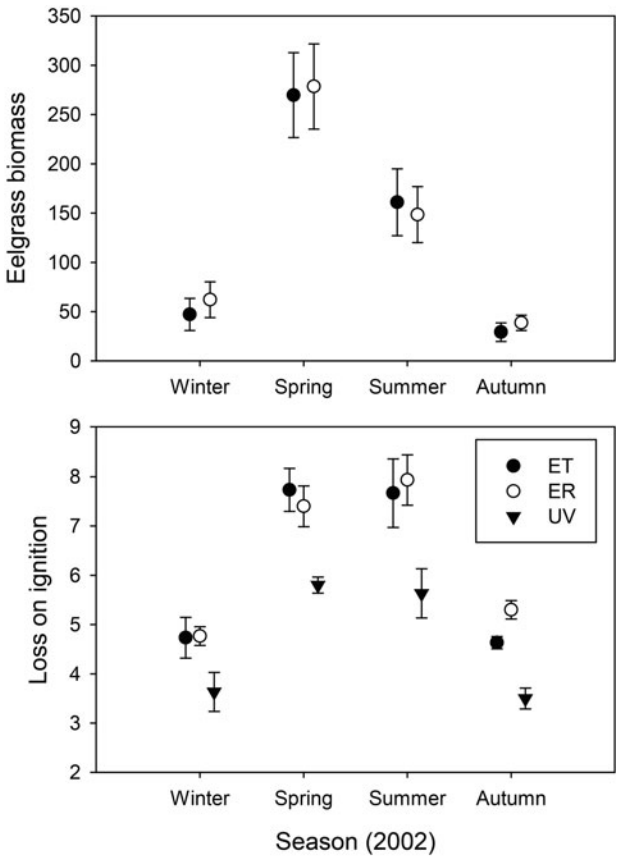

Fig. 2. Seasonal variation in eelgrass biomass (DW m^{-2}) and loss on ignition (LOI) in eelgrass beds adjacent to tidal flats (ET) and rocky shore (ER), and unvegetated habitat (UV) in northern Jinhae Bay, Korea. Error bars represent standard deviations.

between the eelgrass habitats. The proportion of sediment particle sizes significantly differed among habitats (one-way ANOSIM, $P < 0.05$; Table 1). The two eelgrass habitats contained relatively higher proportions of coarse particles (e.g. sand and silt), whereas the proportion of compact particles (e.g. clay) was higher in unvegetated habitat (Table 1).

General descriptions of decapod assemblages

A total of 4195 decapods belonging to 31 species and five taxa (Penaeidae, Caridea, Anomura, Gebiidea and Brachyura) were collected during the study period, with caridean shrimps (13 species) and crabs (13 species) as the most widely represented taxa (Table 2). In terms of abundance, the dominant caridean shrimps were *Palaemon macrodactylus* (18.7%), *Alpheus digitalis* (4.2%) and *Crangon uritai* (3.5%), whereas *Charybdis japonica* (24.3%), *Charybdis bimaculata* (10.1%), and *Hemigrapsus penicillatus* (7.8%) were the most abundant crab species, and *Trachysalambria curvirostris* (2.7%) was the dominant prawn species. Only a species of hermit crab (*Pagurus dubius*) was caught during the study period.

Table 1. Mean proportions (± SE) of sediment grain size in eelgrass beds adjacent to tidal flats (ET) and rocky shore (ER), and unvegetated habitat (UV) in northern Jinhae Bay, Korea.

	Habitats		
Sediment grain size	**ET**	**ER**	**UV**
Gravel	2.0 ± 0.0	2.6 ± 0.2	1.9 ± 0.3
Sand	19.4 ± 0.6	18.8 ± 0.5	17.3 ± 0.6
Silt	56.9 ± 0.5	57.0 ± 0.5	51.4 ± 0.9
Clay	23.0 ± 0.5	22.8 ± 0.6	30.0 ± 0.8

The total number of decapod species was highest at the ET site (29 species), followed by ER (16 species) and UV (13 species). Only nine species were found at all three habitats, 15 occurred at both seagrass beds, but no species were exclusive of the UV. The highest abundance (2039 individuals) was also recorded at ET, whereas the lowest occurred at UV. In terms of taxa, the abundances of prawns, caridean shrimps and hermit crabs were highest at ET, but crabs exclusively occurred at ER. Among commercially important species, eight and four species were caught at ET and ER, respectively, but no commercial species were found in the unvegetated habitat. Overall, the number and abundance of decapod species (including commercial species) tended to be higher within seagrass beds than in unvegetated habitat in the study area. Only *P. macrodactylus* (caridean shrimps) and *C. bimaculata* (crabs) were numerically dominant in UV.

Spatial and seasonal variations in decapod abundance and diversity

Mean abundance and diversity were highest at ET, followed by ER and UV, during all seasons with the exception of autumn, when abundance was highest at ER (Figure 3). In terms of season, the two variables tended to be higher in spring, followed by winter and summer, and they were lowest during autumn (Figure 3). Two-way ANOVAs revealed that abundance and diversity of decapod assemblages differed significantly among habitats and among seasons (Table 3). The habitat × season interaction was not significant for abundance or diversity (Table 3). Tukey's post-hoc test indicated that eelgrass beds harboured significantly higher mean abundance and diversity compared with unvegetated areas, and values of all variables were highest during the spring (Table 3).

Spatial and seasonal variations in abundances of dominant species

The mean abundances for each of the six dominant species varied with habitat and season (Figure 4). The mean abundance of *C. japonica* in ER was higher than in ET (Figure 4A), but did not differ seasonally. The mean abundance of *P. macrodactylus* and *H. penicillatus* differed between vegetated and unvegetated habitats, and between colder (winter and spring) and warmer (summer and autumn) seasons, with higher abundance during winter and spring at seagrass beds (Figure 4B and D). *Charybdis bimaculata* exhibited higher abundances in summer in both ER and UV compared with ET (Figure 4C), and those of *P. dubius* and *A. digitalis* differed among both habitats and seasons, with the highest values for both species occurring at ET, followed by ER and UV (Figure 4E and F).

Decapod assemblage structure

Two-way PERMANOVAs revealed that the decapod assemblages differed significantly across habitats and seasons, with

Table 2. Species composition of decapod assemblages and total abundance of species (N) in eelgrass beds adjacent to tidal flats (ET) and rocky shore (ER), and unvegetated habitat (UV) in northern Jinhae Bay, Korea.

Taxa/Species	**Total**		**ET**		**ER**		**UV**	
	N	**%**	**N**	**%**	**N**	**%**	**N**	**%**
Penaeidae total	133	3.2	105	5.1	28	1.9		
Marsupenaeus japonicus[a]	12	0.3	12	0.6				
Metapenaeus joyneri[a]	7	0.2	7	0.3				
Trachysalambria curvirostris[a]	114	2.7	86	4.2	28	1.9		
Caridea total	1638	39.0	983	48.2	289	19.8	366	52.8
Alpheus digitalis	176	4.2	142	7.0	27	1.8	7	1.0
Crangon affinis	138	3.3	127	6.2			11	1.6
Crangon hakodatei	25	0.6	18	0.9			7	1.0
Crangon uritai	146	3.5	119	5.8	14	1.0	13	1.9
Eualus leptognathus	57	1.4	38	1.9	19	1.3		
Heptacarpus pandaloides	87	2.1	13	0.6	8	0.5	66	9.5
Latreutes anoplonyx	61	1.5	61	3.0				
Latreutes planistris	5	0.1			3	0.2	2	0.3
Lysmata vittata	4	<0.1	4	0.2				
Palaemon gravieri	15	0.4	15	0.7				
Palaemon macrodactylus	784	18.7	395	19.4	141	9.6	248	35.8
Palaemon ortmanni	124	3.0	41	2.0	71	4.9	12	1.7
Tozeuma tomentosum	16	0.4	10	0.5	6	0.4		
Anomura total	319	7.6	181	8.9	88	6.0	50	7.2
Pagurus dubius	319	7.6	181	8.9	88	6.0	50	7.2
Gebiidea total	58	1.4	58	2.8				
Upogebia major[a]	58	1.4	58	2.8				
Brachyura total	2047	48.8	712	34.9	1058	72.3	277	40.0
Carcinoplax vestita	1	<0.1	1	<0.1				
Charybdis bimaculata	422	10.1	171	8.4	45	3.1	206	29.7
Charybdis japonica[a]	1020	24.3	310	15.2	710	48.5		
Gaetice depressus	7	0.2	7	0.3				
Hemigrapsus penicillatus	328	7.8	132	6.5	132	9.0	64	9.2
Hemigrapsus sinensis	1	<0.1	1	0.0				
Portunus sanguinolentus[a]	6	0.1	3	0.1	3	0.2		
Portunus trituberculatus[a]	17	0.4	17	0.8				
Pugettia quadridens	139	3.3	47	2.3	87	5.9	5	0.7
Sesarma pictum	83	2.0			81	5.5	2	0.3
Sphaerozius nitidus	7	0.2	7	0.3				
Telmessus acutidens	10	0.2	10	0.5				
Tritodynamia rathbuni	6	0.1	6	0.3				
Total abundance	4195		2039		1463		693	
Number of decapod species	31		29		16		13	
Number of commercial species[a]	7		7		3		1	

[a] Decapod species of commercial value.

a higher F value for habitat compared with season (habitat: pseudo-$F = 22.655$, $P = 0.001$; season: pseudo-$F = 13.331$, $P = 0.001$). The habitat × season interaction was also significant (pseudo-$F = 1.738$, $P = 0.020$). Results of two-way crossed ANOSIM tests also indicated that the decapod assemblages differed significantly among habitats (global-$R = 0.877$, $P = 0.001$) and among seasons (global-$R = 0.665$, $P = 0.001$). Pairwise ANOSIM tests revealed that decapod assemblages differed significantly between all habitat and season comparisons (pairwise comparisons; $P < 0.05$), with the exception of the pairwise comparison between summer and autumn. The habitat differences were strongest between ER and UV (global-$R = 0.963$, $P = 0.001$).

The decapod assemblages plotted on the nMDS ordination axes exhibit discrete groups of samples according to both habitat and season (Figure 5). In terms of habitat, clear separation occurred between eelgrass beds and unvegetated habitat, whereas the sampling sites for the two eelgrass beds exhibited considerable overlap. In terms of season, two distinct seasonal groups, warmer (summer and autumn) or colder (spring and winter), were clearly separated on the ordination plot.

Because the PERMANOVA results indicated that both habitat and season significantly influenced decapod assemblage structure, CAP analyses were performed to discriminate among habitats and seasons (Figure 6). In the CAP plot for habitat, *C. japonica* and *Sesarma pictum* distinguished the ER from the other habitats, whereas multiple species characterized the decapod assemblages of the ET (Figure 6A). No species were significantly correlated with UV. *Palaemon macrodactylus* and *C. bimaculata* tended to be positively correlated with both ET and UV. In the CAP plot for season, each season exhibited clear separation, but some overlap occurred between summer and autumn samples (Figure 6B). Most species were highly correlated with spring samples, while *C. bimaculata* and *H. penicillatus* were correlated with summer and winter samples, respectively. However, no species were correlated with autumn samples (Figure 6B).

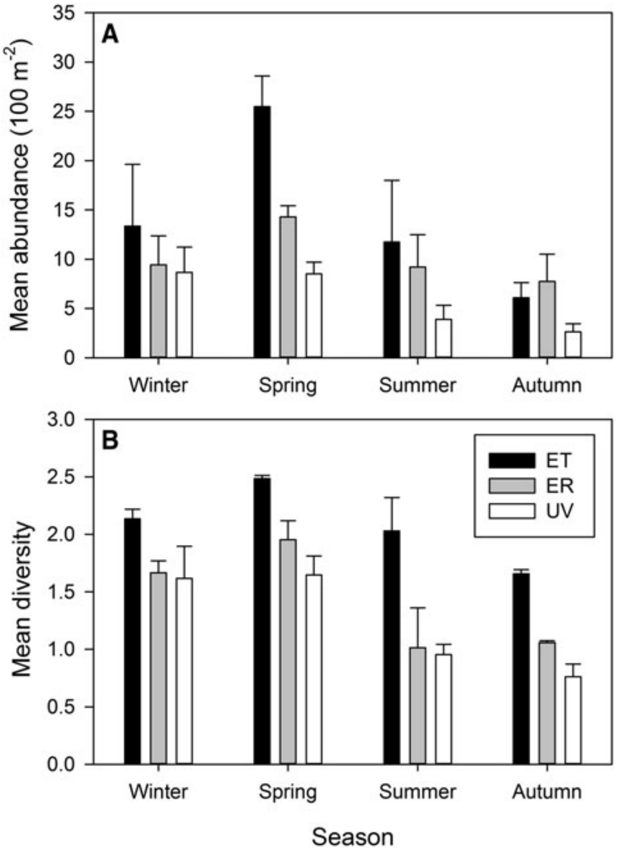

Fig. 3. Mean abundance and diversity of decapod species during different seasons in eelgrass beds adjacent to tidal flats (ET) or rocky shore (ER) or in unvegetated areas (UV) in northern Jinhae Bay, Korea. Error bars represent standard deviations.

Relationships between decapod abundance and environmental variables

Linear regression revealed that decapod abundances were significantly correlated with eelgrass biomass and the LOI of sediment throughout the study period (Figure 7; $P < 0.05$); however, neither water temperature nor salinity was significantly related to the abundance of decapods ($P > 0.05$).

DISCUSSION

A total of 31 decapod species, primarily caridean shrimps and crabs, was collected from the study area. *Palaemon macrodactylus*, *C. affinis* and *A. digitalis* were the most abundant caridean shrimps, and *C. japonica* and *C. bimaculata* (Portunidae), *H. penicillatus* (Grapsoidea) and *P. quadridens* (Majoidea) were the dominant crab species. Similar to Jinhae Bay, those shrimps and crabs were also the dominant decapod species in eelgrass beds of Kwangyang Bay, Korea (Huh & An, 1997, 1998). In other unvegetated coastal habitats of southern Korea, however, those species were not common decapod species. For example, *Trachysalambria curvirostris* (prawn) and *Crangon hakodatei* (caridean shrimp) were dominant decapod species in southern Geojo Island (Cho *et al*., 2013), while *C. hakodatei*, *Plesionika izumiae* and *C. bimaculata* were common decapod species in Nakdong River estuary (Lee *et al*., 2009). Thus, although abundant decapod species are often similar in seagrass beds, different dominances of these taxonomic groups were evident between vegetated and non-vegetated habitats indicating differences of habitat preferences of each decapod species.

In the present study, decapod assemblages exhibited clear differences in terms of species richness (i.e. number of species), abundance and diversity among habitats. A total of 29 and 16 species were found in the two seagrass habitats (ET and ER), respectively, whereas 13 species were caught in the unvegetated area. Decapod abundance and diversity were also significantly higher in seagrass *vs* unvegetated habitats, with the highest values occurring in eelgrass beds adjacent to tidal flats (two-way ANOVA post-hoc comparison, $P < 0.05$). Similarly, Bloomfield & Gillanders (2005) documented significantly higher abundances of fishes and invertebrates in seagrass beds compared with non-vegetated habitats in southern Australia. Several studies comparing fish abundances between vegetated and non-vegetated habitats have reported similar results (e.g. Guidetti, 2000; Kwak *et al*., 2006), as seagrass vegetation often supports higher densities and species richness of fish and decapod assemblages (Lazzari, 2002).

The nMDS ordination and multivariate analyses confirmed that decapod assemblage structure differed significantly among habitats. These differences in assemblages were caused by variation in habitat use by individual decapod species. For example, *C. japonica* was limited to eelgrass beds, with its highest abundance in eelgrass beds adjacent to rocky shore. Penaeid and Crangonid shrimps (*C. affinis* and *C. uritai*) were also highly dependent on *Zostera marina* beds. All of the above decapod species are closely associated with seagrass habitats in Korean waters (e.g. Huh & An, 1997, 1998). Although the two eelgrass habitats exhibited

Table 3. Results of two-way ANOVAs for abundance and diversity of decapods among eelgrass beds adjacent to tidal flats (ET) or rocky shore (ER) or in unvegetated areas (UV) over the four seasons in northern Jinhae Bay, Korea.

Source	df	MS	*F*	*P*	Tukey's HSD
Abundance					
Habitat	2	0.630	23.004	<0.001	UV < ET = ER
Season	3	0.317	11.571	<0.001	Au = Su < Wi = Su < Sp
Habitat × Season	6	0.017	0.623	0.710	
Error	24	0.021			
Diversity					
Habitat	2	2.300	73.205	<0.001	UV = ER < ET
Season	3	1.470	46.782	<0.001	Wi = Au < Su = Sp
Habitat × Season	6	0.068	2.157	0.084	
Error	24				

Tukey's test: $P < 0.05$. df = degrees of freedom; MS = mean square; Wi = winter; Sp = spring; Su = summer; Au = autumn.

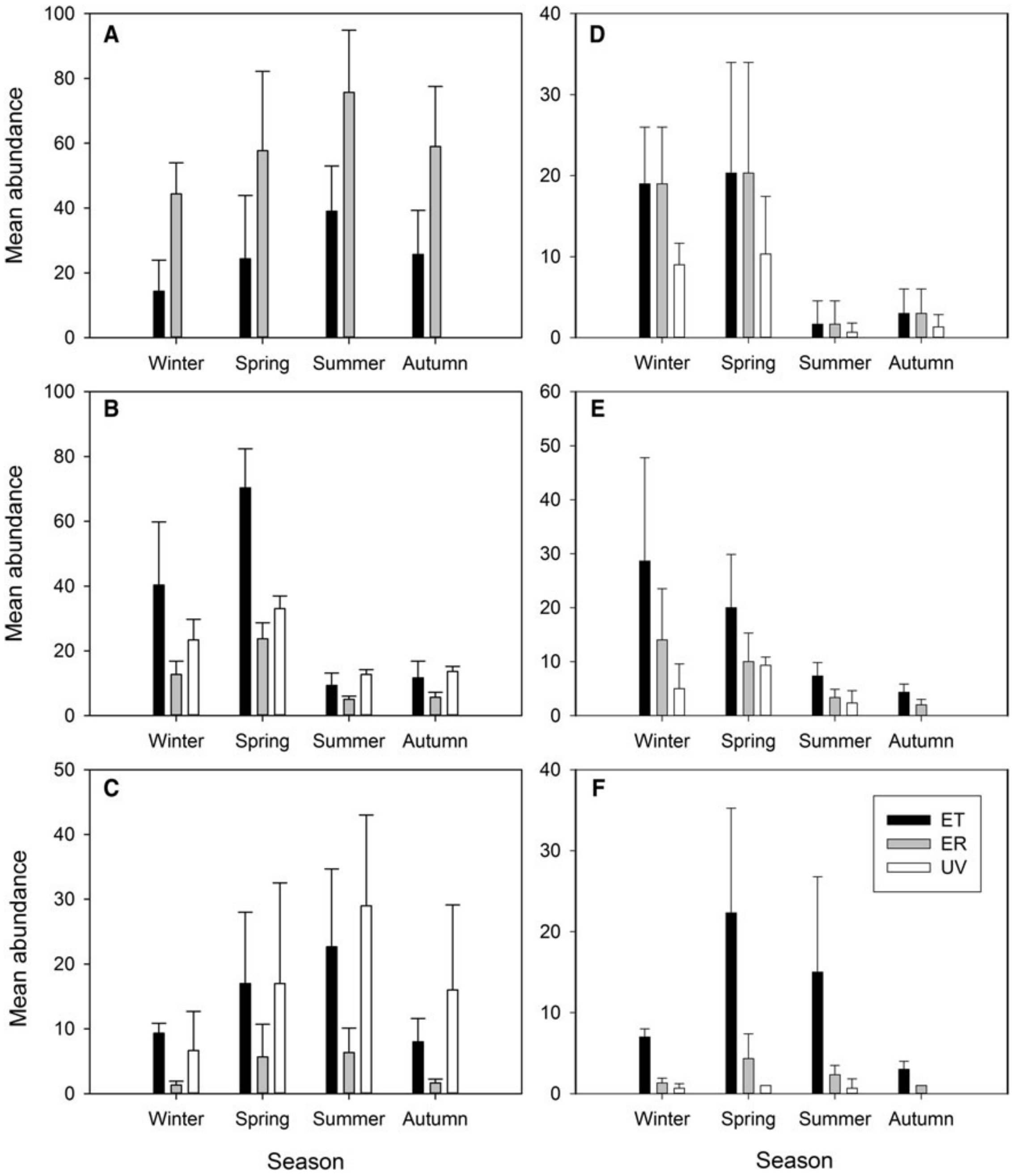

Fig. 4. Mean abundance of six common decapod species during different seasons in eelgrass beds adjacent to tidal flats (ET) or rocky shore (ER) or in unvegetated areas (UV) in northern Jinhae Bay, Korea. Error bars represent standard deviations. (A) *Charybdis japonica*; (B) *Palaemon macrodactylus*; (C) *Charybdis bimaculata*; (D) *Hemigrapsus penicillatus*; (E) *Pagurus dubius*; and (F) *Alpheus digitalis*.

similar patterns of species distributions, taxonomic composition did differ to some degree; for example, caridean shrimps were more strongly associated with tidal flats, whereas crabs were predominantly found in eelgrass near rocky shores. Portunid and grapsoid crabs tend to be associated with rocky habitats and are frequently found along rocky shores in shallow marine habitats (Hong, 2006). Thus, the rocky shore habitat likely supports high abundances of crabs when adjacent to seagrass habitats. In unvegetated areas, *P. macrodactylus* (caridean shrimps) and *C. bimaculata* (crabs) were the most dominant species, although they also occurred in eelgrass beds. *Charybdis bimaculata* prefer to inhabit silt-clay bottoms in coastal areas (Narita *et al.*, 2008) and were similarly abundant in other non-vegetated coastal habitats of Korea (e.g. Huh *et al.*, 2010).

Although the overall sediment composition was similar among habitats, sediments of the unvegetated areas contained more clay compared with the eelgrass beds. Generally, seagrasses stabilize their underlying sediments by baffling tidal currents and dampening wave action (Orth, 1977). In unvegetated environments, sediments are frequently resuspended and transported by wave and tidal currents, resulting in an unstable environment for many benthic invertebrates. However, due to a geographic feature protecting UV from wave action, our unvegetated study site could have more clay sediment than seagrass beds. In addition, fine sediments

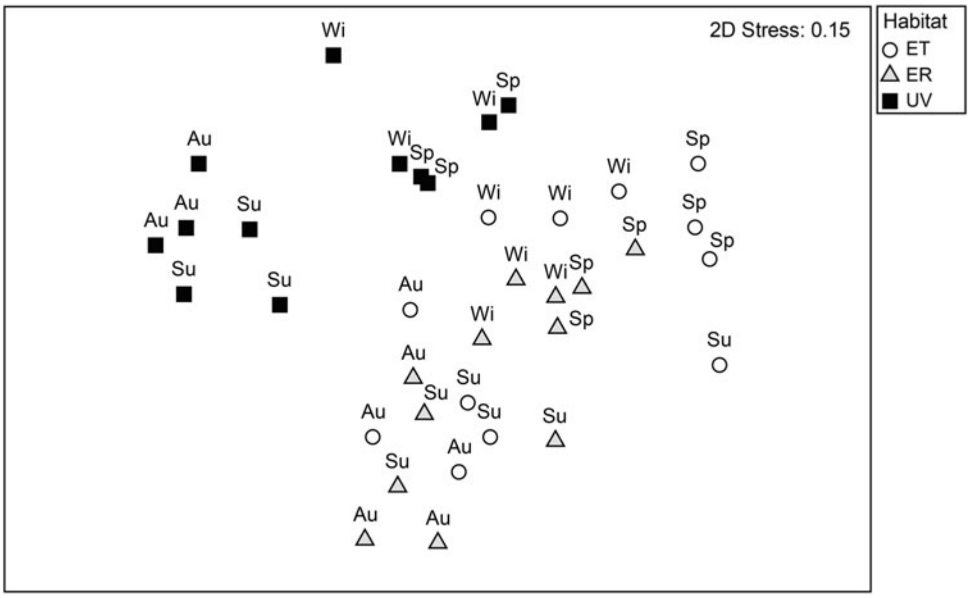

Fig. 5. nMDS ordination of decapod assemblages constructed from Bray–Curtis similarity matrix of the three habitats and four seasons. Wi = winter, Sp = spring, Su = summer, Au = autumn.

(e.g. clay-rich sediments) provide suitable environments for burrowing benthic invertebrates, whereas larger grain sizes provide more suitable habitat and/or shelter for larger crustaceans, i.e. decapods (Riddle, 1988). Consequently, in the present study area, the silt-clay dominant sediment may be suitable for the development of *Zostera marina* and its many resident decapod species.

Seasonal variation in both species composition and abundance tends to be considerable for decapod communities utilizing eelgrass beds. In the present study, the peak in decapod abundance corresponded closely to peak eelgrass biomass and LOI. When eelgrass biomass increased in spring, the number of decapod individuals also increased, followed by population declines with decreases in eelgrass biomass beginning in autumn. Because high seagrass density provides shelters and/or food resources for decapods (Hemminga & Duarte, 2000; March & Pringle, 2003), variations of decapod abundance corresponded to eelgrass biomass. A number of other studies have also demonstrated positive correlations between faunal richness or abundance and the above-ground biomass of seagrass beds (e.g. Leber, 1985; Bell & Pollard, 1989; Heck & Weinstein, 1989; Huh & Kwak, 1997; Connolly *et al*., 1999). Other studies of fish communities in eelgrass beds have reported similar patterns of variable faunal abundance in Korea. For example, fish abundance increased with increasing eelgrass biomass and water temperature in Angol

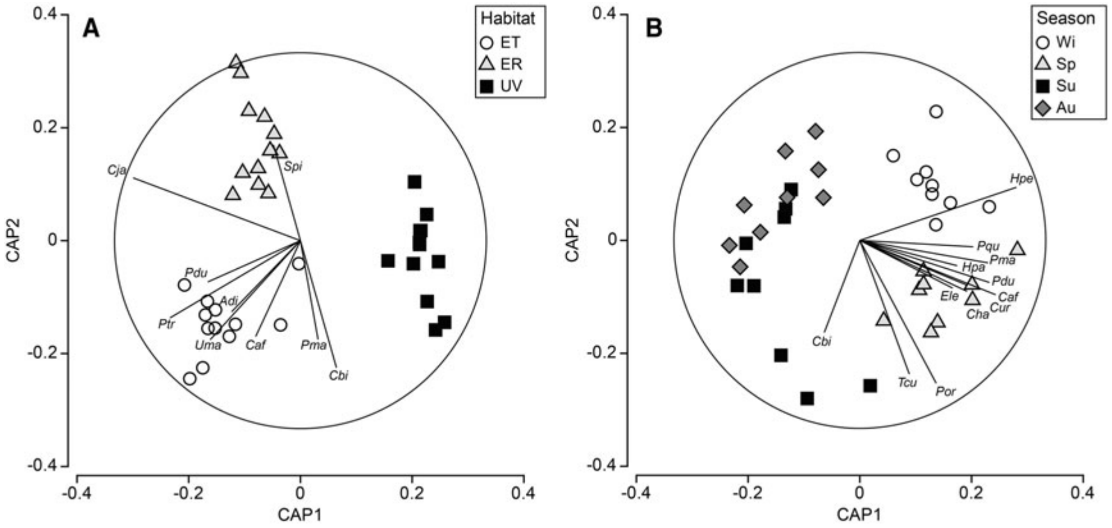

Fig. 6. Canonical analysis of principal coordinates (CAP) ordination plots of decapod assemblages to assess differences among habitats (A) and among seasons (B). Species correlations with each canonical axis are represented as vectors for species with correlations greater than 0.5. Vectors represent Pearson correlations, and the circle indicates a correlation of 1. *Adi, Alpheus digitalis*; *Caf, Crangon affinis*; *Cbi, Charybdis bimaculata*; *Cha, Crangon hakodatei*; *Cja, Charybdis japonica*; *Cur, Crangon uritai*; *Ele, Eualus leptognathus*; *Hpa, Heptacarpus pandaloides*; *Hpe, Hemigrapsus penicillatus*; *Pdu, Pagurus dubius*; *Pma, Palaemon macrodactylus*; *Por, Palaemon ortmanni*; *Pqu, Pugettia quadridens*; *Ptr, Portunus trituberculatus*; *Spi, Sesarma pictum*; *Tcu, Trachysalambria curvirostris*; *Uma, Upogebia major*.

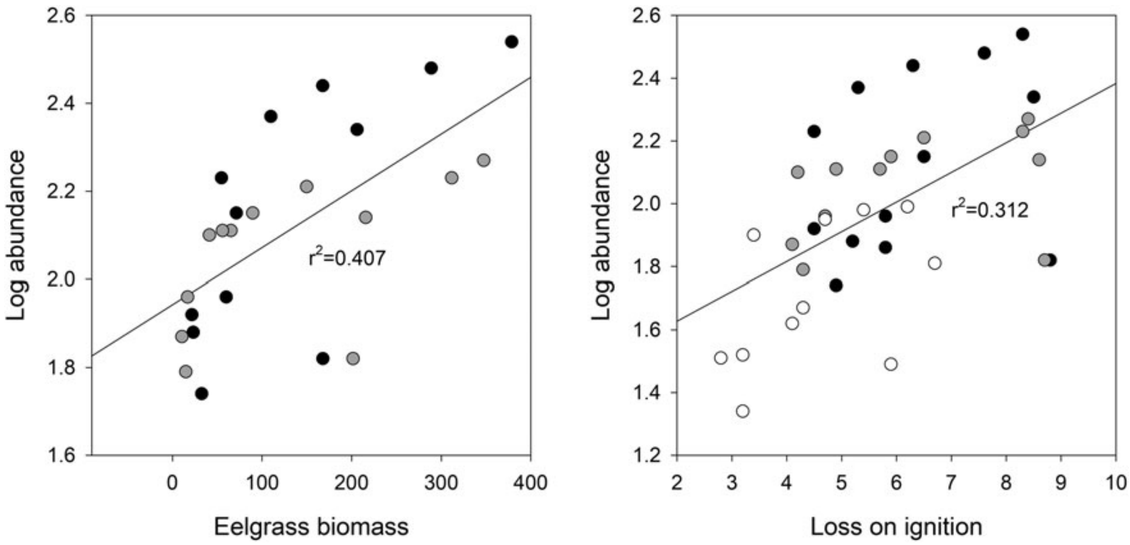

Fig. 7. Relationships between decapod abundance and eelgrass biomass (DW m^{-2}) and loss on ignition at three stations in northern Jinhae Bay, Korea. Black, grey and open symbols indicate eelgrass beds adjacent to tidal flats (ET), rocky shore (ER) and unvegetated areas (UV), respectively.

Bay (Lee *et al.*, 2000) and in Hamduck off of Cheju Island (Go & Cho, 1997). Kwak & Klumpp (2004) demonstrated that seasonal variation of decapod abundance in Cockle Bay, Australia, was positively correlated with seagrass biomass. In addition, Ávila *et al.* (2015) reported that seagrass shoot density and leaf length influenced the distribution of associated macrofaunal assemblages. The abundance of caridean shrimps was significantly associated with eelgrass biomass in Kwangyang Bay, Korea (Huh & An, 1997). High seagrass densities provide a favourable habitat for many seagrass-associated decapods, whereas decapods common to unvegetated areas, such as *C. bimaculata* and *P. macrodactylus*, exhibited peak abundance in summer when water temperatures were highest. Although those species were also caught in all habitats, even abundant at seagrass beds, seasonal variations in their abundances seem to be related to water temperature, regardless of seagrass biomass.

This study provides important insights into the spatio-temporal variation in decapod assemblages in eelgrass beds and unvegetated areas of northern Jinhae Bay, Korea. Our findings document that decapod assemblage structure is significantly affected by both habitat type and season. These compositional differences were caused by variation in the abundances of the most common species. Moreover, decapod abundance was significantly higher in eelgrass beds compared with unvegetated habitat. Because the seagrass habitats supported high abundances of marine organisms, including commercially important species, these habitats play crucial roles, both ecologically and economically. In addition, studies of crustacean assemblages in seagrass habitats are meaningful in light of conservation and habitat monitoring efforts, because seagrass-associated crustaceans are less mobile and closely dependent on seagrass habitat, and thus, more easily influenced by environmental variations than most of the fishes.

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Correspondence should be addressed to:
Seok Nam Kwak
Environ-Ecological Engineering Institute Co. Ltd, Busan 48280, Korea
email: seoknam@eeei.kr