

Article

Crustacean Decapod Assemblage Associated with Seagrass (*Zostera marina*) Beds in Southern Waters of Korea

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Abstract: Decapod assemblages in *Zostera marina* beds from two bays adjacent to unvegetated habitats were investigated to assess their influence on decapod assemblages. Thirty-eight decapod species belonging to four taxa were collected using a small beam trawl at four habitat types from two different locations off the coast of Namhae Island, South Korea. Dominant decapod taxon at all habitats was the caridean shrimps, with *Eualus leptognathus*, *Heptacarpus pandaloides*, *Latreutes anoplonyx*, *La. Laminirostris*, and *Palaemon macrodactylus* being the most abundant caridean species. Crabs were characterized with the highest biomass, but with moderate species richness and abundance. Penaeoid and sergestoid shrimps only accounted for <1% of the total decapod abundance. The number of species and their abundance of decapod assemblages varied greatly by habitat type, season, and diel patterns, but not diversity. Species number and abundance peaked in seagrass beds of southern exposed bays during the autumn and were lowest in unvegetated habitats during the summer months. Diel decapod catch rates were higher at night. Dense seagrass vegetation and nighttime supported higher decapod mean densities, but not species richness and diversity. Multivariate analyses revealed that habitat type and season significantly affected the structure of decapod assemblages, but diel patterns had a minor influence. Among decapod species, *Pa. macrodactylus* and *Pugettia quadridens* characterized the decapod assemblages in seagrass beds at the northern semi-closed bay, while *Telmessus acutidens*, *Crangon affinis*, *Cr. hakodatei*, *Charybdis (Charybdis) japonica*, and *Portunus sanguinolentus* were significantly associated with both vegetated and unvegetated habitats at the southern exposed bay, with the former two species more abundant during the colder season.

Keywords: decapod assemblage; *Zostera marina*; Namhae Island; seagrass vegetation; day/night change

1. Introduction

Seagrass beds have been shown to be highly productive marine habitats, common in estuarine and shallow marine coastal ecosystems throughout the world [1,2]. Among seagrass species, *Zostera marina* is widespread in temperate coastal areas of the Western Pacific, providing shelter for many marine animals, especially their juveniles [3–6]. Seagrass meadows' physical complexity also provides protection from predators [7–9] and allows coexistence of species occupying different ecological niches [10]. As a further benefit, seagrass beds provide nursery grounds and feeding opportunities for vertebrate and invertebrate species, many of which are of commercial and recreational value [4,11–13].

Studies on abundance patterns and community structure according to vegetation cover have shown a higher diversity of vertebrates and invertebrates in vegetated habitats [10,14,15]. Since

seagrasses stabilize sediments from tidal currents and wave action [16,17], they provide a suitable habitat for benthic invertebrates [18,19]. The quality of vegetative cover and the complexity of the physical habitat also have been shown to influence faunal assemblages. Recent studies of faunal assemblages on seagrass-macroalgal beds and its adjacent habitats have shown faunal assemblages structures determined by phenological parameters of seagrass [20,21], substrate structures [22,23], geographical features around seagrass-microalgal beds [24], and other hydrographic factors [25,26]. Further investigations on trophic relationships have also revealed the roles of seagrass habitat complexity structuring fish and macroinvertebrate assemblages [27–29].

Habitat structure complexity has often been associated with biodiversity [30], with a more complex habitat providing a wider range of niches, allowing for a higher number of resident species [31–34]. The diversity of decapod assemblages, similarly, has been shown to be higher in seagrass beds compared with that in non-vegetated habitats. Bloomfield and Gillanders [35] reported similar faunal assemblages between non-vegetated and seagrass habitats in southern Australia, with the caveat of higher loss rates of species richness and abundance in seagrass habitats. More recently, Park and Kwak [36] showed that seagrass beds adjacent to both tidal flats and rocky shores supported greater decapod abundances and diversities than adjacent unvegetated habitats. The importance of large seagrass beds to abundance and diversity [36–38] may be due to the high abundances of eelgrass residents [39]. Comparative studies of decapod assemblages between vegetated and unvegetated seagrass habitats have shown bare habitats with fewer species [36] and associated with considerable diel and seasonal variations in abundance and assemblage structure [36,40–42].

Extensive seagrass beds are common in Namhae Island, South Korea, providing shelter for small fish and invertebrates [43–45]. Although a number of studies comparing fish and decapod assemblages in seagrass meadows have been conducted globally [39,40,46–50], few such studies have been conducted in the eelgrass beds of South Korean waters. Of the few, the focus was limited to estimating the effects on fish communities [36,43,51]. Studies on the effects on decapod diversity, including assessment of bottom sediment structure, presence of seagrasses, and hydrodynamic features, such as water temperature, tidal current, and seasonal storms, might provide key insight into the factors influencing the maintenance of decapod assemblages [52].

In this study, we compared decapod assemblages in seagrass beds adjacent to tidal flats and rocky shores with unvegetated habitats in structuring decapod assemblages. More specifically, we a) associated the effects of geographical locations, habitat types, seasons, and diel patterns with assemblage structure; and b) compared diversity and abundance patterns with habitat. We anticipate this study to aid in understanding the implications of habitat complexity in resource management and conservation of decapods in Korea.

2. Materials and Methods

2.1. Study Area

Data for this study were gathered from a bay of Namhae Island and one of the adjacent Changseon-Do Island, South Korea, with two study sites within each bay (Figure 1). Bays were comprised of a northern semi-enclosed (Dongdae Bay) and southern exposed (Aenggang Bay) body of water. Dongdae Bay is geographically rich and inland-facing, rich in tidal flats, rocky shores, small islands and reefs. Aenggang Bay is exposed to open ocean from a southern inlet, allowing seawater circulation to the bay. The two study sites in each bay were seagrass beds adjacent to tidal flats (DS(t)) and to rocky shore (DS(r)) at Dongdae Bay, and seagrass beds (AS) and unvegetated habitat (AU) at Aenggang Bay (Figure 1). Dongdae Bay sediment composition consists of compact particles (e.g., clay-silt). Sediment at Aenggang Bay, conversely, mostly comprises coarse particles (Kim et al., unpublished data). Seagrass beds from both bays are characterized by *Zostera marina*, forming subtidal habitats (2.7–3.3 km in width) in shallow water (<5 m). Seagrass biomass fluctuate with season, peaking during the spring, and seagrass density. Biomass is typically five times higher at Dongdae Bay

than at Aenggang Bay [45]. Typical water temperature fluctuations are between 7.4 °C and 27.7 °C at Dongdae Bay and between 7.7 °C and 30.7 °C at Aenggang Bay. Salinity is between 19.5 and 34.2 psu (practical salinity unit) at Dongdae Bay and between 16.5 and 34.8 psu at Aenggang Bay. At both bays, values in the summer are lowest for salinity [45].

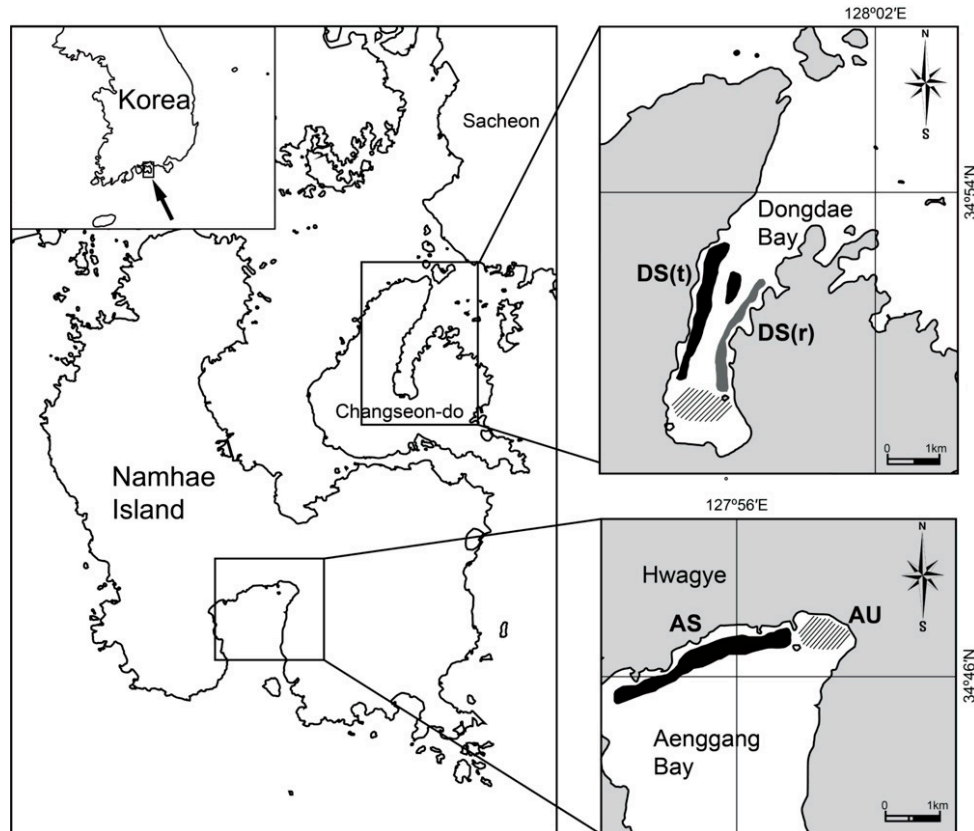


Figure 1. Namhae Island, South Korea, area of investigation. Black area = seagrass bed adjacent tidal flat (DS(t), AS), gray area = seagrass bed adjacent rocky shore (DS(r)), oblique area = unvegetated site (AU).

2.2. Sampling

Crustacean decapod samples were collected monthly in 2005 using a 3-m beam trawl with 1.9-cm mesh surrounded by a 0.6-cm mesh liner. Tows (four; 6 min duration) both during the day (between 10:00 and 12:00) and night (between 20:00 and 22:00) at spring tide in all habitats were conducted, with estimated 280 m² coverage per sampling event. A total of 384 beam trawl hauls were conducted during the study period. The number of individuals per 100 m² was the variable recorded. A solution of 5% formalin with seawater at sampling, followed by 70% ethanol for long-term storage was used to preserve specimens. All individual decapods were identified to the lowest taxa possible and weighed to the nearest milligram. All scientific names were checked against the WoRMS database [53].

2.3. Data Analyses

The Shannon–Wiener index (H' ; [54]) was used to estimate community-level diversity. Prior to ANOVA analysis, the assumption of homogeneity of variance was tested using Levene's test [55]. Since there was no evidence for heteroschedasticity, three-way analysis of variance (ANOVA) was used to assess spatial and temporal differences in species richness (number of species), abundance (number of individuals), and diversity. Station (combined factor of location and habitat; i.e., study location across seagrass vegetation), season, and diel patterns were fixed factors, with Tukey's honest significant different (HSD) test for post-hoc ANOVA tests. Abundances for all species were $\log(x +$

1)-transformed. Three stations were seagrass bed in Dongdae Bay, and both were seagrass bed and bare habitat in Aenggang Bay. The four seasons were winter (December–February), spring (March–May), summer (June–August), and autumn (September–November).

Inferential and descriptive analyses were performed to further assess abundance trends with diel patterns, seasons, and habitat. Permutation multivariate analyses of variance (PERMANOVA) on $\log(\text{abundance} + 1)$ based on Bray–Curtis similarity matrices were conducted [56]. Analysis factors for the PERMANOVA were location (two fixed levels: Aenggang and Dongdae), habitat (nested within location, three random levels), season (four fixed levels: winter, spring, summer, and autumn), and diel patterns (two fixed levels: day and night). Similarity matrices were used in a PERMANOVA to test for factor effects. In cases in which PERMANOVA detected a significant difference at the 0.05 level, posteriori pairwise PERMANOVA comparisons were used to determine which interaction terms differed significantly among variables within each level of factors. PERMANOVA assigns components of variation (COV) of differing magnitudes to the main factors and interaction between combinations of main factors. The larger COV indicates the greater the influence of a particular factor or interaction term on the structure of the data [57]. The metric multidimensional scaling (mMDS) ordination technique was used to visualize factor effects. To assess statistical significance among factor levels, a canonical analysis of principal coordinates (CAPs) was used [57]. Correlation coefficients between each factor and the canonical axis were used as evidence for species contributions to observe differences. Individual species with both correlations higher than 0.4 and total abundance larger than 1% were plotted on CAP axes 1 and 2 for additional visualization of results.

Statistical software used was Systat (Systat version 18, SPSS Inc., Chicago, IL, USA) and PRIMER v7 with the PERMANOVA+ module [57,58]. A 0.05 level for statistical significance was used in analyses.

3. Results

3.1. Decapod Species Composition

Thirty-eight decapod species from four taxa were sampled in this study (Table 1). Ranks by number were Caridea (19 species), followed by Brachyura (13 species), Penaeoidea (4 species), and Sergestoidea (2 species). Aenggang Bay seagrass bed (AS) yielded the largest number of species, and the lowest at the seagrass bed adjacent to the rocky shore at Dongdae Bay (DS(t)). The seagrass bed of Aenggang Bay produced the largest abundance of decapods and the lowest at the bare habitat of Aenggang Bay (AU). Overall, the study areas were dominated by the Caridea genera of *Eualus*, *Heptacarpus*, and *Latreutes*. The species with highest abundance at all study sites were *Heptacarpus pandaloides*, followed by *Eualus leptognathus*, *Latreutes anoplonyx*, and *La. laminirostris*. Among decapods, *Palaemon* species was dominant at Dongdae Bay, and *Crangon affinis* and *Portunus sanguinolentus* were dominant at Aenggang Bay (Table 1).

3.2. Spatio-temporal Changes in Species Richness, Abundance, and Diversity

Abundance and mean richness varied by factors of station, season, and diel patterns, but not diversity. Three-way ANOVA showed species richness and abundance of decapod assemblage differed significantly among stations, seasons, and diel patterns, except species richness between day and night. Diversity patterns were not significant for any factors (Table 2). No two- or three-way interactions were significant between most factors. Only the station \times day/night interaction for abundance had a significant influence on decapod assemblage (Table 2).

Table 1. Decapod species and total abundance (per 100 m⁻²) in seagrass beds adjacent to tidal flat (DS(t)) and rocky shore (DS(r)) of Dongdae Bay, seagrass beds (AS) and adjacent habitats to the unvegetated areas (AU) of Aenggang Bay, Namhae Island, South Korea.

Taxa	Species Name	Dongdae Bay		Aenggang Bay	
		DS(t)	DS(r)	AS	AU
Penaeoidea	<i>Metapenaeopsis tenella</i>	3.3	3.3	3.9	1.1
	<i>Mierspenaeopsis hardwickii</i>		0.6		
	<i>Penaeus japonicus</i>			0.6	
	<i>Trachysalambria curvirostris</i>	3.9		0.6	
Sergestoidea	<i>Acetes chinensis</i>	5.6		1.7	3.9
	<i>Acetes japonicus</i>	0.6		0.6	
Caridea	<i>Alpheus brevicristatus</i>	2.2		0.6	1.1
	<i>Alpheus digitalis</i>		0.6	1.1	
	<i>Crangon affinis</i>	1.7	2.2	76.7	92.8
	<i>Crangon hakodatei</i>	0.6		24.4	14.4
	<i>Eualus leptognathus</i>	1380.6	544.4	347.2	9.4
	<i>Eualus middendorffi</i>	3.9	1.7		
	<i>Hayashidonus japonicus</i>			7.8	3.3
	<i>Heptacarpus futilirostris</i>	61.7	0.6	16.7	1.1
	<i>Heptacarpus pandaloides</i>	2462.2	925.0	5067.2	882.2
	<i>Heptacarpus rectirostris</i>	17.8	7.2	108.9	0.6
	<i>Latreutes anoplonyx</i>	334.4	578.3	2220.6	106.1
	<i>Latreutes laminirostris</i>	415.6	185.6	123.9	52.8
	<i>Latreutes planirostris</i>	0.6		3.3	
	<i>Leptochela gracilis</i>			0.6	
	<i>Lysmata vittata</i>		0.6	0.6	
	<i>Palaemon carinicauda</i>	1.1	1.7		
	<i>Palaemon macrodactylus</i>	224.4	46.7	4.4	5.6
	<i>Palaemon orientis</i>	18.9	3.9		
	<i>Palaemon ortmanni</i>	92.8	30.6	40.0	8.3
	Brachyura	<i>Arcania undecimspinosa</i>			
<i>Charybdis (Charybdis) japonica</i>		5.0	8.3	94.4	20.0
<i>Charybdis (Charybdis) sagamiensis</i>				3.3	
<i>Hemigrapsus penicillatus</i>		20.0	11.1	6.1	0.6
<i>Hemigrapsus sanguineus</i>					0.6
<i>Paradorippe granulata</i>				0.6	
<i>Pilumnus minutus</i>			0.6		
<i>Portunus sanguinolentus</i>		5.0		28.9	2.8
<i>Portunus trituberculatus</i>				1.7	1.1
<i>Pugettia quadridens</i>		33.3	26.1	23.3	1.7
<i>Telmessus acutidens</i>		11.1	1.1	35.0	2.8
<i>Thalamita sima</i>				8.3	1.1
Xanthidae sp.		0.6			
Total		5106.7	2380.0	8252.8	1213.9
Number of species		25	21	30	23

Tukey's post-hoc tests indicated that mean species richness was lower at unvegetated habitat than seagrass beds in Aenggang Bay, and during summer than autumn (Figure 2). Mean abundance was the highest at seagrass beds than unvegetated habitats in Aenggang Bay, and during autumn than summer (Figure 2). Diel patterns in decapod assemblage showed that only decapod abundance was significantly higher during the night than day (Figure 2). No patterns in diversity were found with all three factors combined (Figure 2).

Table 2. Abundance (100 m⁻²), number of species, and diversity three-way ANOVA for decapod assemblages in South Korea. Boldface values are significance at *p* < 0.05.

Source	df	Species Richness		Abundance		Diversity	
		F	<i>p</i>	F	<i>p</i>	F	<i>p</i>
Main test							
Station (St)	2	3.373	0.030	5.930	0.005	1.269	0.289
Season (Se)	3	3.035	0.037	7.318	0.001	0.385	0.764
Day/Night (D/N)	1	0.004	0.953	4.513	0.039	0.266	0.608
Interactions							
St × Se	6	1.085	0.383	2.245	0.052	1.178	0.117
St × D/N	2	2.319	0.108	5.186	0.009	1.132	0.330
Se × D/N	3	0.885	0.455	1.228	0.309	0.221	0.882
St × Se × D/N	5	0.298	0.912	1.212	0.316	0.470	0.797

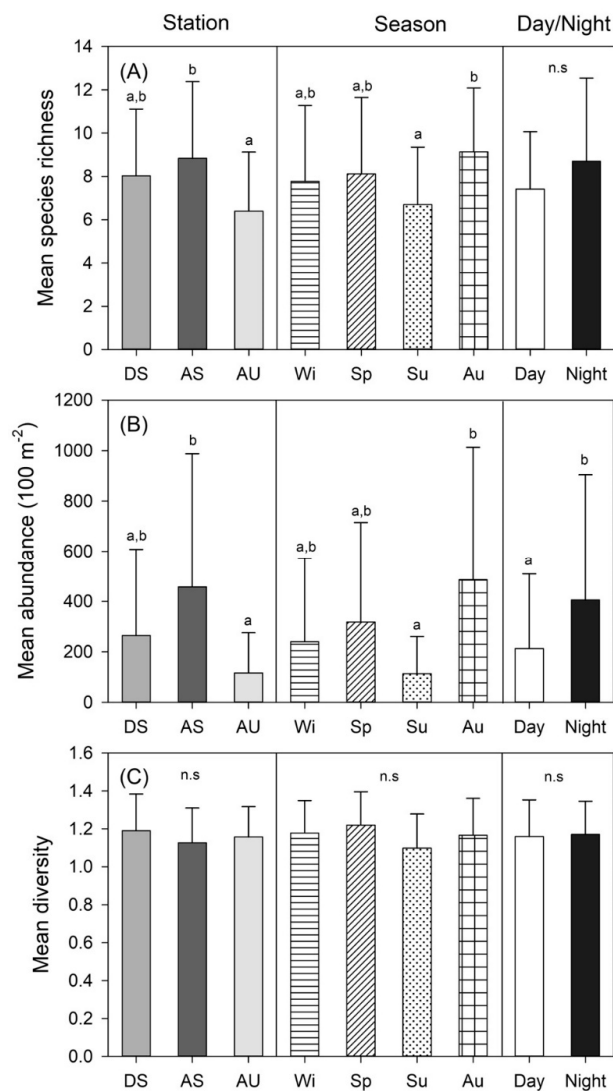


Figure 2. Mean species richness (A), abundance (B), and diversity (C) of decapod assemblages with station, season, and diel patterns. DS = seagrass beds in Dongdae Bay, AS = seagrass bed in Aenggang Bay, AU = unvegetated habitat in Aenggang Bay; Wi = winter, Sp = spring, Su = summer, Au = autumn.

3.3. Decapod Assemblage Structure

PERMANOVA tests revealed decapod assemblages were significantly associated with study location, habitat type, and season, with COV of location being the highest, indicating the strongest factors determining variation within samples (Table 3). Only one statistically significant two-way interaction between location and season was observed (Table 3). Pairwise comparisons of location and season showed evidence of differences in decapod assemblage structures between Dongdae and Aenggang bays during spring, summer, and autumn (Table 4). Significant differences between seasons within each location were also observed, except between winter and spring at both locations, and autumn versus other seasons at Dongdae Bay (Table 4). At Dongdae Bay, only differences between spring and summer and between winter and summer were significant. Seasonal comparisons between colder (winter and spring) and warmer (summer and autumn) seasons, and within warmer seasons (summer and autumn) were significant at Aenggang Bay (Table 4).

Table 3. Mean squares (MS), pseudo-F ratios, significance levels (*p*), and components of variation (COV) for PERMANOVA tests using Bray–Curtis similarity matrices from abundance of decapod assemblages showing differences in location (Lo), habitat (Ha nested within Lo), season (Se), day/night (D/N), and interactions terms; bold letters indicate significance at *p* < 0.05.

Source	df	MS	Pseudo-F	<i>p</i>	COV
Main test					
Lo	1	15294.0	9.538	0.001	21.269
Ha (Lo)	1	3747.8	2.337	0.031	12.847
Se	3	6363.6	3.969	0.001	16.936
D/N	1	2968.8	1.851	0.086	6.761
Interactions					
Lo × Se	3	4450.4	2.775	0.001	18.522
Lo × D/N	1	3102.2	1.935	0.074	11.045
Ha (Lo) × Se	3	2404.0	1.499	0.073	14.443
Ha (Lo) × D/N	1	2666.6	1.663	0.114	12.936
Se × D/N	3	2618.4	1.633	0.065	10.017
Lo × Se × D/N	3	1568.2	0.978	0.497	-2.915
Ha (Lo) × Se × D/N	2	2297.5	1.433	0.151	18.001
Residual	54	1603.5			40.044

Table 4. Pairwise PERMANOVA tests for the location–season interaction within each study location, or season; bold letters indicate significance at *p* < 0.05.

Location	Winter		Spring		Summer		Autumn	
	t	<i>p</i>	t	<i>p</i>	t	<i>p</i>	t	<i>p</i>
Dongdae-Aenggang	1.509	0.063	2.296	0.008	2.5082	0.001	2.213	0.001
Season	Dongdae		Aenggang					
	t	P	t	P				
Winter-Spring	1.177	0.221	1.012	0.374				
Winter-Summer	1.648	0.011	1.764	0.008				
Winter-Autumn	1.245	0.151	2.878	0.002				
Spring-Summer	1.717	0.012	1.603	0.026				
Spring-Autumn	1.214	0.175	2.793	0.001				
Summer-Autumn	1.045	0.373	2.492	0.001				

Metric MDS ordination of similarity of mean decapod assemblages showed clear differences in decapod assemblages by study location, habitat type, season, and the location × season interaction (Figure 3). Samplings from different locations and habitats showed distinct clustering patterns, indicating no overlaps of the multivariate dispersions between locations or habitats (Figure 3A,B). Taking seasonal data pooled by study location and habitat type also showed clear clustering. Bootstrap

averages of samples between warmer seasons (i.e., summer and autumn) showed clear separation, compared with the average assemblages between colder seasons (Figure 3C). In addition, samples of seasonal decapod assemblage were clearly divided between warmer and colder seasons along with the Y axis in mMDS ordination. In terms of the location–season interaction, decapod assemblages displayed discrete groups according to both study location and season in the ordination plot (Figure 3D). Within each study location, Aenggagn samples showed clear separation in the summer and autumn, while those in Dongdae showed no apparent groupings.

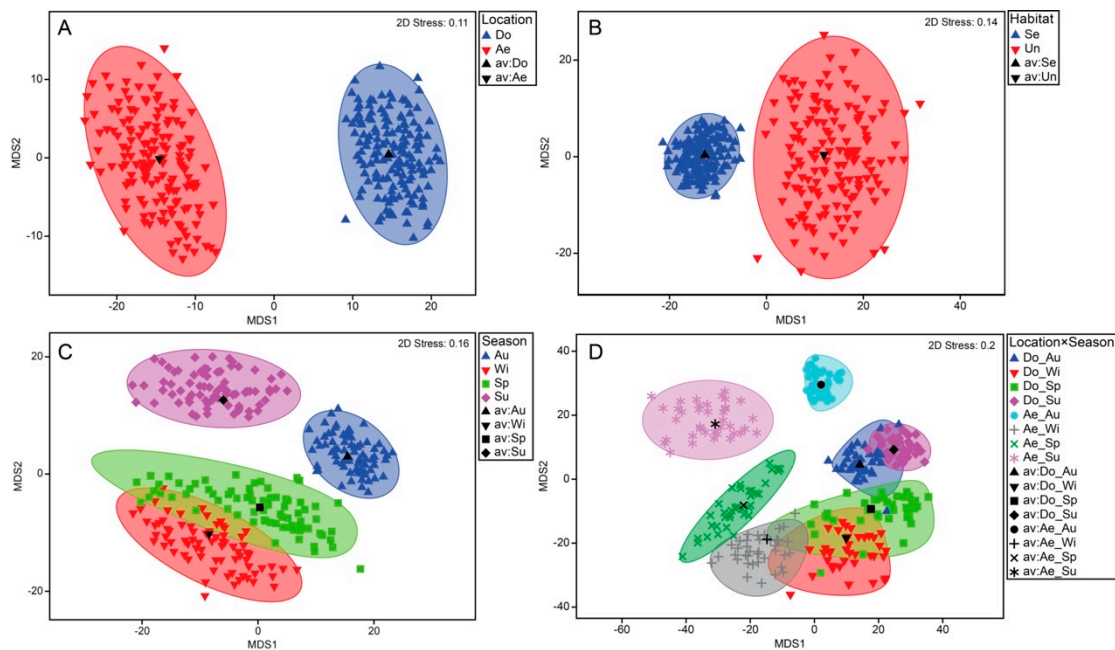


Figure 3. Metric multidimensional scaling (mMDS) for decapod assemblages from the two study locations (A), two habitat types (B), four seasons (C), and eight locations at each season (D); Do = Dongday Bay, Ae = Aenggagn Bay, Se = seagrass bed, Un = unvegetated habitat; Wi = winter, Sp = spring, Su = summer, Au = autumn.

Canonical analyses on principal coordinates were performed on significant interactions as a further test on PERMANOVA analyses. The CAP plot for the location–season interaction showed strong evidence for factor group separation (Figure 4). *Palaemon macrodactylus* and *Pugettia quadridens* contributed to separate the sites of Dongdae Bay from those in Aenggagn Bay. *Telmessus acutidens*, two crangonid shrimps (*Cr. affinis* and *Cr. hakodatei*), and two portunid crabs (*Ch. japonica* and *Portunus trituberculatus*) characterized the decapod assemblages in Aenggagn Bay (Figure 4). Weak seasonal differences in decapod assemblages were found at Dongdae Bay, although there were some trends on species contribution of *Pa. macrodactylus* and *Pu. quadridens* on colder and warmer season assemblages, respectively. Conversely, clear seasonal classifications in decapod assemblages were evident at Aenggagn Bay sites. *Te. acutidens* and *Cr. affinis* contributed to the colder season samples, and *Cr. hakodatei*, *Ch. japonica*, and *Po. trituberculatus* to the warmer season samples, regardless of seagrass vegetation (Figure 4).

4. Discussion

Dominant caridean shrimps were *Ha. pandaloides*, *La. anoplonyx*, *Eu. leptognathus*, *La. laminirostris*, and *Pa. macrodactylus*, and abundant crab species were *Ch. japonica*, *Pu. quadridens*, and *Te. acutidens*. Similar community structures from other South Korean regions were reported. *Heptacarpus*, *Latreutes*, *Eualus*, and *Palaemon* were the dominant shrimp genera at the seagrass habitats in Kwang Bay and Jinhae Bay [4,36,59]. *Charybdis* (*Charybdis*) *japonica*, *Pu. quadridens*, and *Te. acutidens* were the common

crab species at the seagrass beds of Jinhae Bay, but they were not in adjacent unvegetated areas of the bay [36]. Compared with seagrass beds of temperate regions worldwide, the genera *Eualus*, *Heptacarpus*, and *Latreutes* were the principally North Pacific caridean genera often abundant in *Zostera* meadows [42]. *Crangon* and *Palaemon* also dominated the decapod communities of seagrass beds in Western Port Bay, Australia [5,60]. *Charybdis* (*Charybdis*) *japonica* and *Pu. quadridens*, in particular, were the seagrass-dependent crab species in northwestern Pacific regions [61,62]. The above taxonomical groups, therefore, show common decapods inhabiting seagrass beds of temperate Pacific regions, regardless of locations.

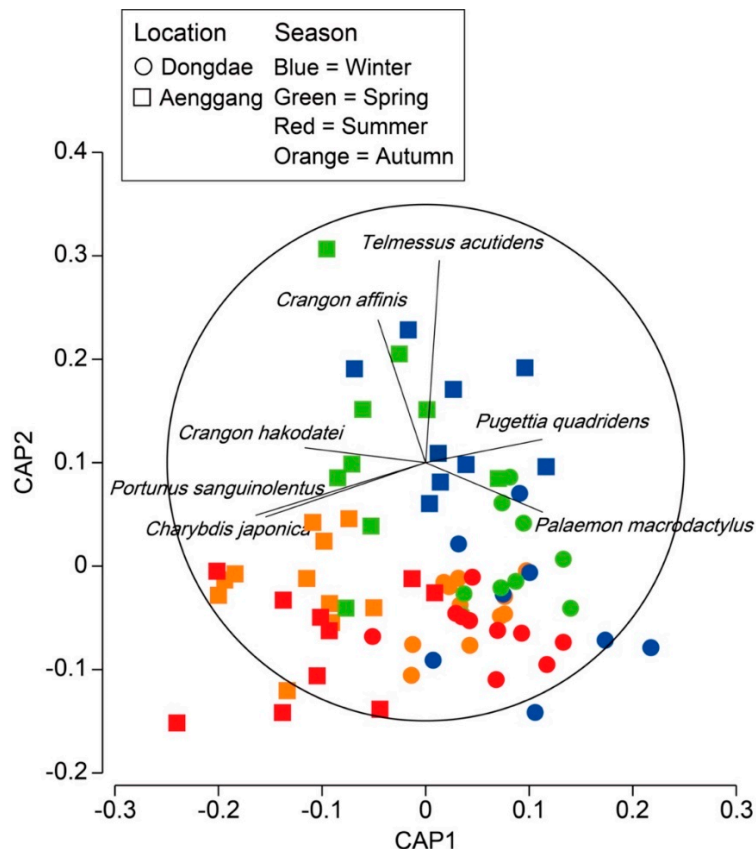


Figure 4. Ordination plots for canonical analysis of principal coordinates of decapod assemblage location–season interaction term.

Seagrass beds are highly productive, showing higher abundances and diversity of marine organisms compared with bare habitats [6,36,63]. This is due to the higher capacity of seagrass vegetation in supporting higher abundance and richness of faunal assemblages [39]. This study corroborated the expected by showing higher species richness and abundance in seagrass beds. There were also tendencies of differences in species richness and abundance between seagrass beds within Dongdae Bay. No evidence of differences in diversity, however, were evident among habitat types. Several studies have shown significantly higher decapod abundances at vegetated habitats [35,36]. Park and Kwak [36] documented that decapod abundances within seagrass habitats were also significantly influenced by habitat structures associated with adjacent environments, where seagrass bed associated with vegetated tidal flats had a higher decapod abundance than seagrass beds adjacent to rocky shores or unvegetated habitats. Physical habitat structure (i.e., both seagrass vegetation and adjacent environment), therefore, is one of the main forces driving abundance of coastal marine animals in seagrass habitat [64].

High seagrass biomass is indicative of high species richness and abundance of faunal assemblages in seagrass habitats [36,65], because increased seagrass biomass provides refuge from predation and favors food availability [6,66]. Although noticeable differences in seagrass biomass between the two study bays were evident, with Dongdae Bay having higher seagrass biomass than Aenggang Bay [45], species richness and abundance of decapod assemblages were not associated with seagrass density in the study area. Hori et al. [67] reported intermediate, instead of high, seagrass biomass more conducive to increased abundance of faunal communities. Moranta et al. [68], similarly, reported denser meadows hosting higher densities of small-sized fishes, but not necessarily larger adults. Thus, decapod assemblage among seagrass beds in this study may not be influenced solely by seagrass biomass, but other physical factors, such as shoreline characteristics, may influence decapod abundance. In Cádiz Bay of southwestern Spain, inner bay habitats with higher vegetative cover and relatively limited water renewal support lower species richness compared with the outer bay [69]. Similarly, in this study, higher accessibility due to exposure to open ocean promoted the occurrence of marine organisms, whereas enclosed bays hindered habitat accessibility to marine fauna. Habitat accessibility to macroinvertebrates has also been shown to be a factor of exposure levels in seagrass beds [24]. Thus, the effects of coastline patterns and meadow structure may interact, producing the patterns in decapod communities observed in this study.

Multivariate analyses agreed with analyses from ANOVA in that decapod assemblage structure was influenced by study location, habitat type, and season, especially between colder (winter and spring) and warmer (summer and autumn) seasons. Such a difference, however, was likely not only due to vegetative cover. The differences in assemblage may have also been due to habitat use variation by individual decapod species in different habitats and seasons. Canonical analysis of principal coordinates showed strong associations between decapod assemblages and habitat, as well as season. As an example, crangonid shrimps were limited to Aenggang Bay, whereas *Pu. quadridens* and *Pa. macrodactylus* were highly associated with seagrass beds of Dongdae Bay. In this study, the differences of decapod assemblages are likely associated with sediment compositions (i.e., compact versus coarse particles) and degree of exposure to open sea between study locations [45]. Among decapod species, crangonid shrimps showed sediment preferences in coarse sand bottoms related to its borrowing ability [70,71], whereas *Palaemon* species inhabited mainly seagrass-covered beds [72,73] with mud bottoms [74]. De La Rosa et al. [69] also showed structures of decapod assemblages influenced by variability of granulometric composition in Cádiz Bay, southwestern Spain, with low granulometric variability and fine sediment associated with structural heterogeneity. In addition, high circulation at exposed habitats (i.e., Aenggang Bay) may allow accessibility for various marine species, including swimming crabs (Portunidae). Since our sampling locations all provided adequate habitats, the observed differences in assemblage may have been due to different sediment structure and habitat exposures at each location. Nonetheless, several minor decapod groups, including *Eualus* and *Palaemon* shrimps, and *Pu. quadridens* and *Te. acutidens* crabs, consistently preferred vegetated habitats, regardless of geographical difference and sediment compositions.

Seasonal variation in both species richness and abundance was significant for seagrass decapod communities, with similar patterns among winter, spring, and autumn, but considerably lower in the summer. The pattern observed was probably more due to stable and dense vegetative cover and less to hydrographic factors [52]. Lower abundance of seagrass organisms during summer suggests that some marine animals select against high temperatures [75] or low salinities [76]. Decapod assemblages, however, were highly variable between colder and warmer seasons, especially at Aenggang Bay. This seasonal structural difference was mainly due to contributions of several crab species in each season; i.e., swimming crabs (Portunidae) were more associated with decapod assemblage during the warmer season, while *Telmessus acutidens* contributed to colder season assemblages. Spawning, coinciding with development of the seagrass, may have been the driver for the observed pattern [45,77,78], probably due to migration from deeper waters to shallow habitats for reproduction. In addition, although two crangonid shrimps were highly associated with Aenggang Bay, their occurrence pattern between colder

and warmer seasons was apparent for this bay. Such temporal segregations among sympatric species have also been reported for palaemonid shrimps, with varying freshwater inputs and salinity between dry and wet season in estuarine habitats [79], allowing coexistence of closely related species in a given habitat through resource partitioning [80].

Overall abundance of decapods was higher at night than during the day. No significant diel patterns in assemblage structure, however, were evident. Decapod assemblage patterns in seagrass beds and shallow marsh creeks from sub-tropical and temperate estuaries supported our observation [40,42,81–83]. Diel difference in abundance might relate to diurnal changes in decapod behavior associated with variation in light intensity, turbidity, and tide forcing [84,85]. Rountree and Able [81] reported that young-of-the-year decapod were significantly more abundant at night due to their nocturnal movement into shallow marsh creeks. From both field and laboratory observations, Bauer [42] found that mean abundance of caridean shrimps from seagrass meadows was consistently higher at night, because of nocturnal emergence from daytime burrows. Several studies also reported nocturnal movement from substrate into the water column [86,87], increasing abundance of epiphytic crustaceans at night in shallow seagrass habitats [82,88]. More recently, Hampel et al. [83] showed densities of faunal assemblages influenced by the interplay of light intensity and tidal cycles in an intertidal salt marsh creek, with the highest densities during low tide and at night.

5. Conclusions

This study provides important insights into the spatio-temporal variabilities of decapod assemblages in seagrass beds and unvegetated areas from two locations at Namhae Island in South Korean waters. Findings herein showed that habitat type, location, and season, driven principally by variations in the abundance of common decapod species, influence decapod assemblage structure. Moreover, density of seagrass beds and abundance of decapods were positively related, with higher abundances during the night. Since seagrass habitats are associated with high abundance of ecologically and economically important marine organisms, preservation and management of such habitats must be a priority. Investigations of relationships between faunal assemblages and habitat types, such as this, establish much-needed baselines for future research and management interventions toward marine biodiversity, especially in areas where research is limited or lacking, as in South Korean waters.

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