



# Seasonal variation in depth-stratified macroalgal assemblage patterns on Marado, Jeju Island, Korea

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Marado is a small rocky island located off the south coast of Jeju Island and acts as the first gateway of the Kuroshio Current to Korean coastal ecosystems. This island is one of the most unpolluted and well preserved sea areas around the Jeju coast. We extensively observed macroalgal assemblages of species and functional forms in the intertidal and subtidal zones through four seasons on Marado, Jeju Island, Korea to demonstrate the seasonality of vertical distribution patterns and biomass. A total of 144 species (14 Chlorophyta, 40 Phaeophyta, and 90 Rhodophyta) were identified in quadrats and were analyzed seasonally and vertically to define the variation patterns. The annual mean biomass of macroalgae was 2,932.3 g wet wt m<sup>-2</sup> and the highest value was recorded in spring and the lowest was in winter. The annual dominant species by biomass was *Ecklonia cava* followed by *Sargassum fusiforme*, *S. macrocarpum*, *Amphiroa galapagensis*, *Chondria crassicaulis*, and *S. thunbergii*. Obvious biomass zonation patterns of macroalgal species were detected in relation to tidal height and depth. Macroalgal biomass, diversity index ( $H'$ ), and community dynamics were the highest in the shallow subtidal zone. Species number was higher in the subtidal than in the intertidal zone and similar throughout the entire subtidal zone. Our results provide revealing insights into the distribution patterns of macroalgal assemblages in an unpolluted sea area around Jeju Island.

**Key Words:** biomass; distribution; Jeju Island; macroalgae; Marado; seasonal variation

## INTRODUCTION

Macroalgal ecologists strive to understand the environmental factors and phenomena that affect macroalgal zonation patterns (Choi and Kim 2004, Balata and Piazzini 2008, Konar et al. 2009, Kang et al. 2011). Macroalgal zonation patterns commonly undergo changes in abundance, diversity, and community dynamics through natural processes along tidal height and depth gradients. The highest level of these patterns is generally found at mean low water (MLW) and decreases with both increasing depth and intertidal height (Garrabou et al. 2002, Choi and Kim 2004, Kang and Kim 2004, Balata et al. 2006, Konar et al. 2009). Although numerous studies have described these

general zonation patterns, recent studies have suggested that these patterns may not be generalizable across geographic regions because peaks in abundance or diversity are not found consistently in particular depth strata (Balata and Piazzini 2008, Konar et al. 2009, Heo et al. 2011, Kang et al. 2011). Therefore, there is great interest in investigating not only these exceptional patterns but also different zonation patterns in species composition, diversity, abundance, and community dynamics among areas at local scales (Konar et al. 2009, Heo et al. 2011, Kang et al. 2011, Shin et al. 2011).

Macroalgal growth is influenced by multi-factorial in-

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Received June 20, 2012, Accepted October 27, 2012

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teractions among abiotic and biotic components, such as tide, light, and water movement (Dawes 1998). Tide and light attenuation are two of the strongest factors that influence vertical macroalgal distribution (Graham et al. 2009). Tide is related to the period of desiccation for macroalgal species living in the intertidal zone, where exposure occurs for significantly longer periods in the upper region than in lower areas (Doty 1946). Macroalgal zonation of the intertidal zone is affected by different photosynthetic recovery capacity after water stress (Davison and Pearson 1996, Ji and Tanaka 2002). The vertical distribution of subtidal macroalgae is mainly controlled by the light gradient which is changed depending on the water depth or turbidity (Irving and Connell 2002, Balata et al. 2006). Light attenuation shows a geometric progression curve and only 15% of sea surface radiation reaches a 40 m depth in the clearest of ocean (Littler et al. 1985, 1986). The compensation irradiance ( $I_c$ ) value for macroalgae is different based on the morphology of each species, and is lower in species that grow in deeper or shaded habitats (Markager and Sand-Jensen 1992, Johansson and Snoeijs 2002).

Littler and Littler (1984) divided various seaweeds into six functional form (F-form) groups based on their morphology, texture, photosynthetic rate, and growth strategy. According to Steneck and Dethier (1994), algal biomass and functional group diversity are highest in habitats with high productivity potential or low disturbance potential dominated by leathery and corticated functional forms. In contrast, habitats with low algal biomass and functional group diversity are dominated by crustose algae having high disturbance potential. Orfanidis et al. (2001, 2003) developed the ecological evaluation index (EEI) to evaluate ecological status based on the characteristic tolerance of each F-form group.

Macroalgal assemblage patterns along the coast of Jeju Island, Korea were initially presented by Lee and Lee (1976). They investigated vertical macroalgal assemblage patterns in the intertidal zone as well as exposure frequency and documented the characteristics of species that were distributed at each vertical level. Although Jeju Island has received considerable attention since the 1970s by phycologists interested in floristic and taxonomic aspects, few ecological studies have examined the abundance, diversity, and community dynamics of macroalgae. Only two spatiotemporally comprehensive studies have been conducted to examine the seasonality of macroalgae in the intertidal / subtidal zone of Jeju Island (Yoo 2003, Kang et al. 2011).

Marado is a small rocky island located off the south

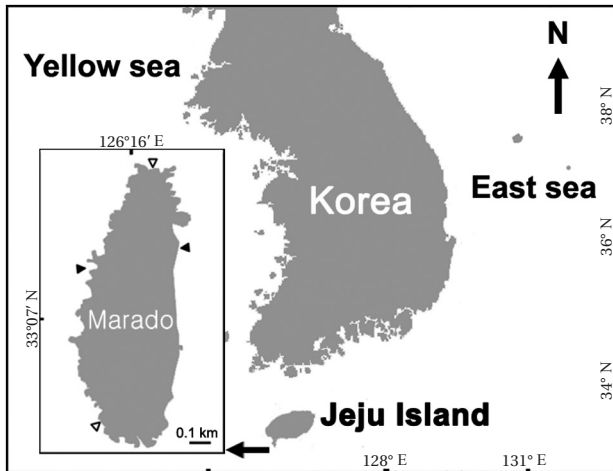
coast of Jeju Island, the southernmost part of the Korean coast. It acts as the first gateway of the Kuroshio Current to Korean coastal ecosystems. This area is important both geopolitically and in terms of marine ecology, but the study of macroalgal assemblage patterns around Marado has been lacking.

The present study describes the characteristics of the vertical macroalgal assemblages on the Marado coast and provides baseline data necessary for long-term monitoring. The specific objectives were to examine seasonal variations in vertical assemblage patterns and biomass of macroalgal functional forms in an unpolluted sea area. This is the first study that has intensively examined macroalgal assemblages in the intertidal and subtidal zones of Marado.

## MATERIALS AND METHODS

Marado is located 8 km south of Jeju Island (Fig. 1). It is elliptical, measuring 0.5 km along its smaller east-west axis and 1.3 km across its north-south axis. The eastern and western coasts are composed of vertical cliffs, but the northern and southern areas are gently sloped. The intertidal substrate consists mainly of basaltic bedrock, but the eastern and western parts of the subtidal zone have accumulated rocks and boulders.

Macroalgal assemblages were examined seasonally from June 2010 to May 2011. Three quadrats (0.25 m<sup>2</sup>) were randomly placed at each of the high-, mid-, and low-intertidal levels in the southern and northern parts of the island. Nine quadrats were placed at intervals of 2 m depth in the subtidal zone, at each site in the eastern and western parts (Fig. 1). These sites were selected because the eastern and southern coasts cannot be approached by land due to the presence of vertical cliffs, and the northern and southern coasts have strong tidal currents that hamper underwater investigations. We divided the areas into three subtidal levels (0-6, 7-12, and 13-18 m deep from the MLW) to examine variations in macroalgal assemblage with seawater depth. Therefore, three quadrats were placed at each vertical level for each season. All macroalgae, except melobesioidean algae, were collected in the quadrats, and the biomass of each macroalgal species was measured (g wet wt m<sup>-2</sup>) in the laboratory. Samples were identified using a microscope based on the descriptions of Lee (2008) and Yoshida (1998). We divided all macroalgae into six functional forms using the criteria of Orfanidis et al. (2001) and compared each percentage among the vertical levels. We calculated diversity ( $H'$ )



**Fig. 1.** Map showing the collection sites for the macroalgal samples applied to a quantitative analysis on the intertidal (white triangle marks) and subtidal zones (dark triangle marks) of Marado.

and dominant ( $D$ ) indices for each seasonal vertical level using the Shannon-Wiener index (Shannon and Wiener 1949) and performed cluster analysis using the  $\chi^2$  method by frequency (SPSS version 17.0; SPSS Inc., Chicago, IL, USA) based on the biomass of each macroalgal species.

## RESULTS

A total of 144 macroalgal species, including 14 Chlorophyta, 40 Phaeophyta, and 90 Rhodophyta, were identified during the study period. Species richness was maximum in the spring and minimum in the summer (Table 1). The annual dominant species by biomass (g wet wt  $m^{-2}$ ) was *Ecklonia cava* (965.3), followed by *Sargassum fusiforme* (254.1), *Sargassum macrocarpum* (198.3), and *Amphiroa galapagensis* (156.8) (Table 1).

The biomass of dominant seaweeds showed seasonal and vertical variations (Fig. 2). Obvious zonation patterns were observed in the biomass of macroalgal species in relation to tidal level and depth. The annual dominant species at each of the six vertical levels were *Ishige okamurae*–*S. fusiforme*–*A. galapagensis*–*E. cava*–*E. cava*–*E. cava*. *I. okamurae* was nearly restricted to the high-intertidal zone, and its biomass was the highest between summer and autumn. *S. fusiforme* and *Sargassum thunbergii* were distributed throughout the intertidal level particularly concentrated in the mid-intertidal zone and they were abundant during winter to spring. *Chondria crassicaulis* emerged in summer and spring at mid- to low-intertidal levels. *A. galapagensis* and *Corallina pilulifera* were dis-

tributed in the mid- to low intertidal zones. *Sargassum nipponicum* and *Sargassum yezoense* were only found in the low intertidal zone. *Dictyopteris prolifera*, *Undaria pinnatifida*, *Sargassum horneri*, and *Sargassum coreanum* were concentrated near the MLW and their abundance changed seasonally. *Marginisporum aberrans*, *M. crassimum*, *Cladophora wrightiana* and *S. macrocarpum* were found throughout the subtidal levels, and their abundance was unevenly distributed throughout the vertical range and seasons. The macroalgae with the widest vertical distribution was *E. cava*, which was found in the low intertidal zone and throughout the subtidal zone.

The annual mean biomass (g wet wt  $m^{-2}$ ) of macroalgae was 2,932.3; the highest value was recorded in spring (3,759.2) and the lowest was observed in winter (2,182.5). Fluctuations in vertical macroalgal biomass by season are shown in Fig. 3. Biomass was generally the greatest in the shallow subtidal zone and decreased with both increasing depth and intertidal height. However, biomass was higher in the mid-intertidal zone than in the low-intertidal zone during the winter and spring. This exceptional pattern was due to abrupt increases in the abundance of *S. fusiforme*, *S. thunbergii*, and *C. crassicaulis* during winter and spring (Fig. 2).

Vertical variations in percent biomass of the six functional seaweed groups are shown in Fig. 4. Thick-leathery group algae (TL) were the most abundant (70.63%), followed by jointed calcareous (JC, 12.70%), coarsely branched (CB, 9.53%), filamentous (F, 2.95%), sheeted (S, 3.90%), and crustose (C, 0.27%) form algae. The abundance percentage of the TL group was the lowest (44.44%) in the low intertidal level and increased toward both the higher intertidal and deeper subtidal sides. The JC group algae showed an opposite trend to the TL group algae. CB group algae were most abundant in the mid-intertidal level and decreased gradually toward the lower vertical level. S group algae appeared sporadically but were most abundant in the high-intertidal level. The F group algae were the highest in the subtidal level at depths of 7–12 m and then decreased toward both the upper and lower levels. Algae in the C group were rare throughout the vertical levels.

Seasonal and vertical variations in species number, diversity indices ( $H'$ ), and dominant indices ( $D$ ) are shown in Fig. 5. The seasonal  $H'$  values for all vertical levels ranged from 2.23 (autumn) to 2.80 (spring). In general, annual  $H'$  values were higher near the MLW and declined gradually toward higher and lower levels. The number of species varied both seasonally and vertically, with most high values occurring in the spring. Species number in-

**Table 1.** Seasonal variations in macroalgal species biomass (g wet wt m<sup>-2</sup>) from Marado, Jeju Island, Korea, June 2010 to May 2011

Species	Summer	Autumn	Winter	Spring	F-form
Chlorophyta					
<i>Bryopsis hypnoides</i>		+			F
<i>Derbesia tenuissima</i>			+		F
<i>Caulerpa geminata</i>	5.46	0.51	5.34	1.20	CB
<i>Cladophora japonica</i>		+			F
<i>C. meridionalis</i>	+	+			F
<i>Cladophora</i> sp.		+			F
<i>C. wrightiana</i>	153.76	118.18	69.59	48.19	F
<i>Cladophoropsis javanica</i>		+			F
<i>Codium arabicum</i>	0.81	+			CB
<i>C. fragile</i>	+				CB
<i>Boodlea coacta</i>	+	+			F
<i>Ulva compressa</i>				2.56	S
<i>U. japonica</i>	0.22		+		S
<i>U. pertusa</i>	18.40		23.07	21.49	S
Phaeophyta					
<i>Leathesia difformis</i>	+			36.89	CB
<i>Peterospongium rugosum</i>			+		CB
<i>Desmarestia tabacoides</i>				3.25	CB
<i>Dictyopteris latiuscula</i>			+	5.44	CB
<i>D. prolifera</i>	46.50	180.06	+	11.01	CB
<i>D. undulata</i>				+	CB
<i>Dictyota coriacea</i>	5.33	+		7.90	S
<i>D. dichotoma</i>	0.91	+	+	5.34	S
<i>D. friabilis</i>	0.38		+		S
<i>D. maxima</i>	3.56				S
<i>D. okamurae</i>			0.83	50.86	S
<i>Distromium decumbens</i>	2.45	1.03	+	1.17	S
<i>Spatoglossum latum</i>	3.80	+		1.38	S
<i>Zonaria diesingiana</i>	3.30	0.51			S
<i>Ralfsia expansa</i>			+		C
<i>Myagropsis myagroides</i>			8.32		TL
<i>Sargassum coreanum</i>	269.06	12.26	0.55	1.48	TL
<i>S. filicinum</i>				20.04	TL
<i>S. fulvellum</i>	0.14	8.30	5.17	130.22	TL
<i>S. fusiforme</i>	147.92	91.04	425.92	356.77	TL
<i>S. hemiphyllum</i>	2.35	4.04	31.15	0.62	TL
<i>S. horneri</i>	+	0.16	24.76	276.35	TL
<i>S. macrocarpum</i>	234.16	115.90	228.78	214.44	TL
<i>S. micracanthum</i>	5.73	26.56	49.27	46.15	TL
<i>S. nipponicum</i>	89.01	0.32	37.66	73.72	TL
<i>S. patens</i>	10.79	109.33		0.24	TL
<i>S. siliquastrum</i>	3.36	0.29	4.29	61.23	TL
<i>S. thunbergii</i>	51.80	28.78	93.81	259.35	TL
<i>S. yendoii</i>	13.99	15.03	56.05		TL
<i>S. yezoense</i>	62.46	25.35	33.71	43.86	TL
<i>Ishige foliacea</i>	3.62		0.02	0.05	CB
<i>I. okamurae</i>	143.76	136.36	29.98	28.98	TL
<i>Ecklonia cava</i>	1,325.39	951.37	558.70	1,026.67	TL
<i>Undaria pinnatifida</i>	10.30			274.56	TL
<i>Colpomenia peregrina</i>				+	CB
<i>C. sinuosa</i>	0.52			22.47	CB

Table 1. Continued

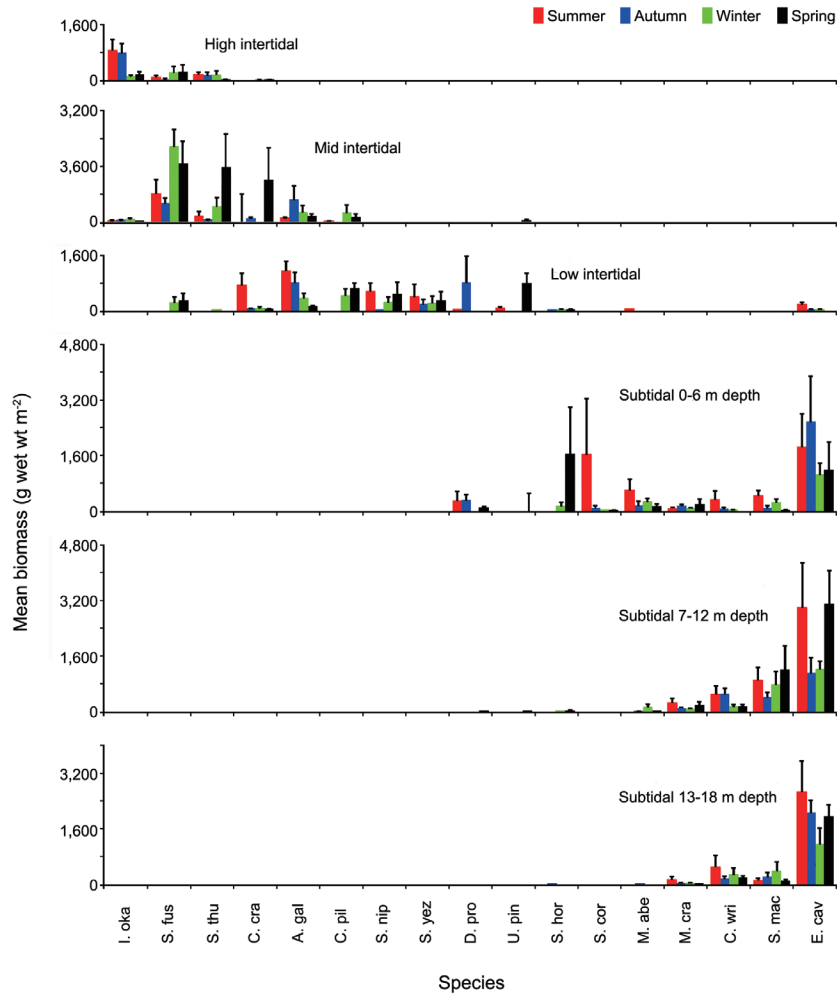
Species	Summer	Autumn	Winter	Spring	F-form
<i>Petalonia binghamiae</i>			9.72	1.91	CB
<i>Scytosiphon lomentaria</i>				27.62	S
<i>Sphacelaria</i> sp.			+		F
<i>Halopteris filicina</i>	0.76			+	F
Rhodophyta					
<i>Porphyra ishigecola</i>			0.25	+	S
<i>P. suborbiculata</i>			37.46	+	S
<i>Bonnemaisonia hamifera</i>				+	F
<i>Ptilonia okadae</i>		+			S
<i>Aglaothamnion callophyllidicola</i>		+	+	+	F
<i>Anotrichium yagii</i>		+	+	+	F
<i>Antithamnion callocladum</i>			+	+	F
<i>A. cristirhizophorum</i>			+		F
<i>A. densum</i>			+		F
<i>A. nipponicum</i>			+	+	F
<i>Balliella subcorticata</i>		+			F
<i>Campylaephora crassa</i>			+	+	F
<i>Ceramium cimbricum</i>		+			F
<i>C. flaccidum</i>			+		F
<i>C. tenerrimum</i>			+	+	F
<i>Ceramium</i> sp.				+	F
<i>Griffithsia japonica</i>		+	+	+	F
<i>G. venusta</i>			+	+	F
<i>Pleonosporrium yagii</i>			0.02	+	F
<i>Plumariella yoshikawae</i>				+	F
<i>Heterosiphonia pulchra</i>		+	+	+	F
<i>Acrosorium polyneurum</i>		+	+		S
<i>Acrosorium</i> sp.		+	+	0.96	S
<i>Erythroglousum minimum</i>		+			S
<i>Herpochondria elegans</i>			+	+	S
<i>Hypoglossum minimum</i>			+		S
<i>Schizoseris subdichotoma</i>			+		S
<i>Sorella repens</i>			+	+	S
<i>Ardissonula regularis</i>				+	F
<i>Benzaitenia yenoshimensis</i>				+	CB
<i>Chondria crassicaulis</i>	379.07	20.78	8.03	204.69	CB
<i>Chondrophycus intermedius</i>		3.26	1.15	6.41	CB
<i>Herposiphonia fissidentoides</i>			+		F
<i>H. subdisticha</i>			+	+	F
<i>Laurencia composita</i>	+	0.11			CB
<i>L. intricata</i>		0.13			CB
<i>L. nipponica</i>	13.18				CB
<i>L. okamurae</i>	0.31	0.35		5.84	CB
<i>L. pinnata</i>	+	+	+	+	CB
<i>L. venusta</i>		0.28	0.06		CB
<i>Neosiphonia elongella</i>				+	F
<i>Polysiphonia atlantica</i>		+	+	+	F
<i>Symphyocladia marchantioides</i>				+	S
<i>S. pumila</i>	+	+	+	+	S
<i>Alatocladia modesta</i>	9.67	2.15	2.42	2.78	JC
<i>Amphiroa anceps</i>	73.21	29.97	29.30	17.43	JC
<i>A. beauvoisii</i>		4.74	5.16	74.37	JC

**Table 1.** Continued

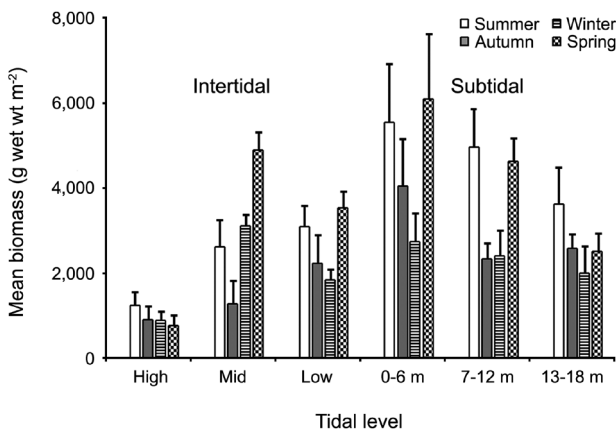
Species	Summer	Autumn	Winter	Spring	F-form
<i>A. dilatata</i>	6.96	+			JC
<i>A. ephedraea</i>		9.38	12.65	1.29	JC
<i>A. foliacea</i>		1.96	3.23	1.03	JC
<i>A. galapagensis</i>	203.58	234.82	98.05	90.74	JC
<i>A. pusilla</i>	10.26	1.03	+		JC
<i>Corallina confusa</i>	1.69	17.90	24.96	5.66	JC
<i>C. elongata</i>	3.97	+	7.58	23.62	JC
<i>C. pilulifera</i>	1.51	+	111.23	120.56	JC
<i>Jania arborescens</i>	2.57	+		0.11	JC
<i>Marginisporum aberrans</i>	95.13	26.93	60.30	19.28	JC
<i>M. crassissimum</i>	67.57	38.11	25.27	58.30	JC
<i>Synarthrophyton chejuensis</i>	+	+	+	+	C
<i>Gelidium elegans</i>			0.79	0.22	CB
<i>Acanthopeltis longiramulosa</i>	0.46	3.10		0.35	TL
<i>Acanthopeltis</i> sp.			0.21	+	TL
<i>Chondracanthus intermedius</i>	2.34	+	+	4.01	CB
<i>Caulacanthus ustulatus</i>	+		+	2.11	F
<i>Hypnea boergesenii</i>	+				CB
<i>Dudresnaya japonica</i>			+	0.78	CB
<i>Gloiopeltis furcata</i>	3.92			7.91	CB
<i>Callophyllis adhaerens</i>	+	+		0.06	CB
<i>C. crispata</i>		+			CB
<i>Callophyllis</i> sp. 1	0.15		+		CB
<i>Callophyllis</i> sp. 2	+		+	0.65	CB
<i>Kallymenia callophylloides</i>			+		CB
<i>K. crassiuscula</i>				+	CB
<i>Peyssonnelia capensis</i>	3.97	12.15	14.02	1.24	C
<i>Portieria japonica</i>	0.23			+	CB
<i>Grateloupia angusta</i>	16.08	11.56	4.83	4.29	TL
<i>Galaxaura apiculata</i>	+			0.09	JC
<i>G. falcata</i>	+				JC
<i>G. hystrix</i>		0.21			JC
<i>G. marginata</i>		+			JC
<i>Dermonema pulvinatum</i>	0.26				CB
<i>Schizymenia dubyi</i>	0.30		+	5.05	CB
<i>Plocamium telfairiae</i>	17.71	8.93	38.81	32.10	CB
<i>Champia expansa</i>		+	+	0.19	S
<i>C. parvula</i>	0.24	+	+	3.26	CB
<i>Gloiocladia leptophylla</i>				0.06	CB
<i>G. spinulosa</i>				0.36	CB
<i>Gelidiopsis variabilis</i>	+				CB
<i>Chrysomenia wrightii</i>			+		CB
<i>Sebdenia yamadae</i>	0.15				CB
Total biomass (g wet wt m <sup>-2</sup> )	3,534.46	2,253.26	2,182.47	3,759.19	
No. of species	73	75	88	98	

F, filamentous; CB, coarsely branched; S, sheeted; C, crustose; TL, thick-leathery; JC, jointed calcareous group algae.  
+, measured below 0.01 g wet wt m<sup>-2</sup>.

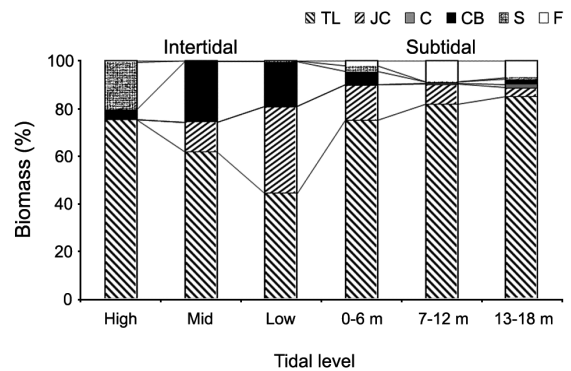




**Fig. 2.** Seasonal and vertical variation in common macroalgal mean biomass (g wet wt m<sup>-2</sup>; mean + standard error), during a year at Marado, Jeju Island. *I. oka*, *Ishige okamurai*; *S. fus*, *Sargassum fusiforme*; *S. thu*, *S. thunbergii*; *C. cra*, *Chondria crassicaulis*; *A. gal*, *Amphiroa galapagensis*; *C. pil*, *C. pilulifera*; *S. nip*, *S. nipponicum*; *S. yez*, *S. yezoense*; *D. pro*, *Dictyopterus proliferus*; *U. pin*, *Undaria pinnatifida*; *S. hor*, *S. horneri*; *S. cor*, *S. coreanum*; *M. abe*, *Marginisporum aberrans*; *M. cra*, *M. crassissimum*; *C. wri*, *Cladophora wrightiana*; *S. mac*, *S. macrocarpum*; *E. cav*, *Ecklonia cava*.



**Fig. 3.** Seasonal and vertical variations in total macroalgal biomass (g wet wt m<sup>-2</sup>; mean + standard error), during a year at Marado, Jeju Island.

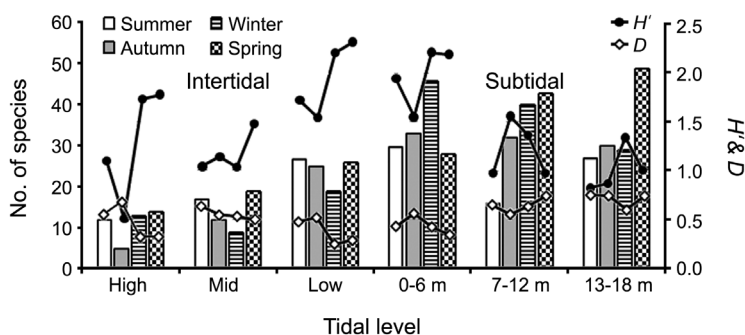


**Fig. 4.** Vertical variation in macroalgal biomass by functional group, during a year at Marado, Jeju Island. TL, thick-leathery; JC, jointed calcareous; C, crustose; CB, coarsely branched; S, sheeted; F, filamentous.

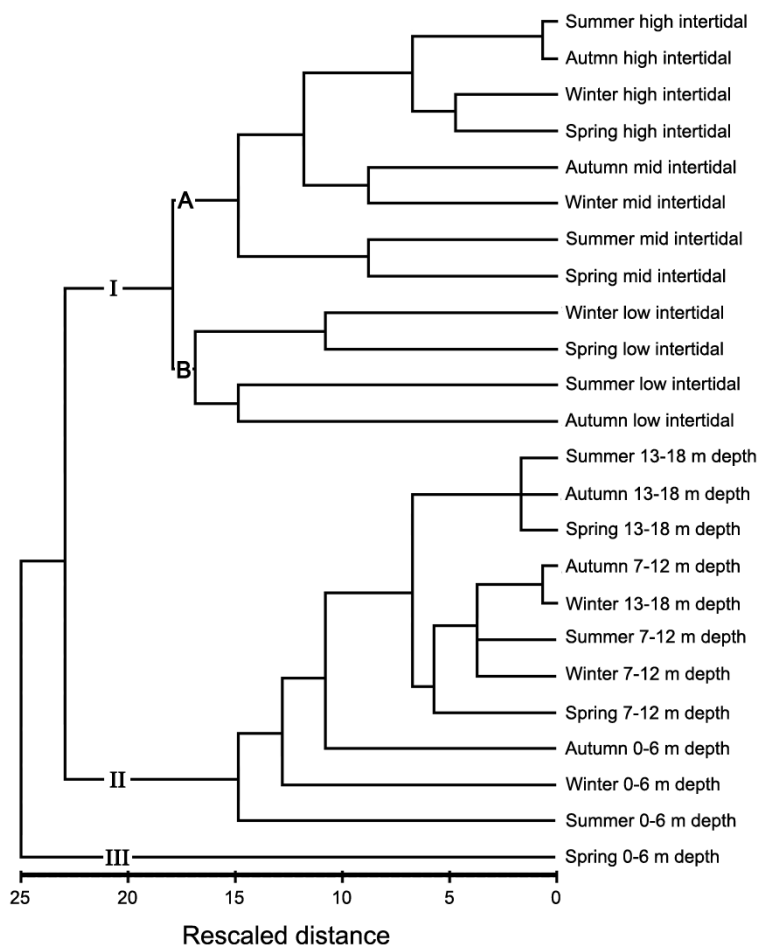
creased toward the lower tidal level in the intertidal zone. However, species number in the subtidal zone was very similar among vertical levels annually (66 at 0-6 m; 68 at 7-12 m; 69 at 13-18 m depth). No seasonal or vertical trends were observed.

Fig. 6 presents a cluster analysis dendrogram based on

similarities in macroalgal species abundances. The data were clearly divided into three groups representing the intertidal zone (I), most of the subtidal zone (II), and the shallow subtidal (0-6 m depth level) in spring (III). The trends in similarity distances varied with position on the shore: there were weak trends observed around MLW (low



**Fig. 5.** Seasonal and vertical variations in species number, diversity index ( $H'$ , black dot), and dominant index ( $D$ , white squares) from the sites investigated on Marado.



**Fig. 6.** Cluster analysis dendrogram based on the similarity of macroalgal species abundance on Marado.



intertidal and 0-6 m depth levels). Group I was divided into subgroups A and B. Subgroup A commonly contained relatively higher biomass levels of *S. fusiforme*, *S. thunbergii*, and *I. okamurae*, whereas subgroup B included *A. galapagensis*, *C. crassicaulis*, and *S. yezoense*. Group II was dominated by *E. cava* and commonly included *S. macrocarpum*. Group III only included a narrow range of the subtidal zone (0-6 m depth level) in spring; the dominant species was *S. horneri* and the subdominant species were *E. cava* and *Sargassum fulvellum*.

## DISCUSSION

Lee and Lee (1982) documented the dominant species distributed along each vertical level in the intertidal zone of Jeju Island through seasonal investigations. Species included *I. okamurae*, *S. fusiforme*, *S. thunbergii*, and *Caulacanthus ustulatus* in the high intertidal zone; *Ulva pertusa*, *Colpomenia sinuosa*, and *C. pilulifera* in the mid-intertidal zone; and *Sargassum hemiphyllum*, *Sargassum* spp., and *E. cava* in the low intertidal zone. Table 2 compares the vertical distribution patterns of macroalgal communities that were documented in this study with previous data that were collected 30 years ago from Jeju Island, as well as recent data from other sites on the Korean peninsula. Comparison of our data and the data from the Buphwan site (Lee and Lee 1982) revealed very similar zonation patterns in the intertidal zone macroalgal communities (Table 2, Fig. 2). Moreover, these zonation patterns matched recent data from the Udo coast of Jeju Island (Kang et al. 2011). The present results indicate that the vertical distribution of dominant species on Jeju Island have been maintained for the last 30 years. Clear differences were observed in the composition of dominant macroalgal species and vertical distribution when compared with other sites along the Korean peninsula. Communities at Jusamdo in the Yellow Sea are characterized by *Desmarestia ligulata* at subtidal depths of 5 m and vertically broad distributions of *S. thunbergii* (Heo et al. 2011); Daejin communities in the East Sea are marked by *Symphyocladia latiuscula* and *Phyllospadix japonicus* (Shin et al. 2011). These differences were probably due to several factors particular to each local region, such as annual mean sea surface temperature, difference in tidal level, latitude, hydrodynamics, topography, or turbidity (Chung et al. 1998, Kim et al. 1998, Lee et al. 1998, Stewart and Carpenter 2003, Kang et al. 2011). Two species, *S. latiuscula* and *D. ligulata*, that appear to be dominant species on Daejin in the East Sea and Jusamdo in the Yel-

low Sea respectively, are rare on the coast of Jeju Island. *S. latiuscula* is distributed in the temperate to polar region (Guiry and Guiry 2012) but it does not form communities and is difficult to find on the coast of Jeju Island (Lee 1974, Choi et al. 2006). No data are available regarding the existence of *D. ligulata* on the coast of Jeju Island.

Kang et al. (2011) reported that macroalgae in the high and mid-levels of the intertidal zone are dominated by desiccation-resistant species, whereas deeper subtidal zones are dominated by kelp with a wider surface area. In addition, dominant species near the sea surface (low intertidal to shallow subtidal zone) vary with the degree of wave action. Their results correspond well with the results of our study (Figs 2 & 3). Zonation patterns in macroalgal community composition (Fig. 2) in the intertidal zone seemed to be strongly influenced by desiccation stress toward the upper extreme and by wave stress toward the lower extreme. We observed communities of dried *Ishige* spp., *Porphyra* spp. and *Gloiopeltis* spp. in the high intertidal level during the low tide that regained their vitality after becoming resubmerged again. Some reports indicate that the extent of recovery of photosynthesis after drought determines the vertical position of intertidal macroalgae (Dring and Brown 1982, Lipkin et al. 1993, Ji and Tanaka 2002). Most dominant macroalgal species in the mid- to low intertidal assemblages consisted of turf (CB and JC) or mat (TL) form algae (Figs 2 & 4). TL algal species were not usually found forming a mat-like colony (Table 1), except dominant algae in the mid- to low intertidal level such as *S. fusiforme*, *S. hemiphyllum*, *S. nipponicum*, and *S. yezoense* (Fig. 2). Turf or mat-forming macroalgae can effectively defend themselves against wave action and desiccation stress by folding each other, simple forms, and tough and protractile thallus (Hay 1981, Prathep 2005, Nishihara and Terada 2010, Nishihara et al. 2011). *S. thunbergii*, which constituted a large portion of the high and mid-intertidal assemblage, can effectively resist desiccation by retaining water among the numerous small leaves that surround its branches and by folding onto other individuals as well as being protected from wave action by its tough branches and cylindrical outline. The macroalgae in the subtidal zone of Marado also showed zonation patterns towards lower levels, but there was no obvious belt, as observed in the intertidal zone. A large portion of the shallow subtidal (0-6 m depth) assemblage consisted of the TL, JC, and CB groups (Figs 2 & 4). However, *Sargassum* spp. at this level were solitary, not mat forming, and finely branched, unlike those in the mid- and low intertidal zones. *E. cava*, the major TL species below the 6 m depth in the subtidal zone, is

**Table 2.** Comparisons of the vertical distribution patterns of representative macroalgal communities among this and previous studies

	Marado <sup>a</sup> This study	Buphwan, Jeju <sup>b</sup> Lee and Lee (1986)	Udo, Jeju <sup>a</sup> Kang et al. (2011)	Jusamdo, Yellow sea <sup>c</sup> Heo et al. (2011)	Daejin, East sea <sup>b</sup> Shin et al. (2011)
<b>Intertidal level</b>	<b>High</b> <i>Ishige okamuratae</i> , <i>Sargassum fusiforme</i> , <i>Sargassum thunbergii</i>	<i>S. fusiforme</i> , <i>S. thunbergii</i> , <i>C. pilulifera</i>	<i>I. okamuratae</i> , <i>S. thunbergii</i> , <i>S. fusiforme</i>	<i>S. thunbergii</i>	<i>C. pilulifera</i> , <i>Sargassum</i> spp., <i>Grateloupia elliptica</i> , <i>S. fusiforme</i> , <i>Symphyclocladia latiuscula</i> , <i>Dicyota dichotoma</i> , Melobesioidean algae, <i>C. crassicaulis</i> , <i>Acrosorium polyneurum</i>
<b>Mid</b>	<i>S. fusiforme</i> , <i>S. thunbergii</i> , <i>Chondria crassicaulis</i> , <i>Amphiroa galapagensis</i> , <i>Corallina pilulifera</i>	<i>C. pilulifera</i> , <i>S. fusiforme</i> , <i>Ulva conglobata</i> , <i>Sargassum</i> spp.	<i>S. fusiforme</i> , <i>S. thunbergii</i> , <i>I. okamuratae</i> , <i>C. crassicaulis</i> , <i>Chondracanthus tenellus</i>	<i>S. thunbergii</i> , <i>Ulva pertusa</i>	
<b>Low</b>	<i>A. galapagensis</i> , <i>C. pilulifera</i> , <i>Sargassum yezoense</i> , <i>Sargassum nipponicum</i> , <i>Ecklonia cava</i>	<i>Sargassum</i> spp., <i>E. cava</i> , <i>Diclyopteris prolifera</i> , <i>Undaria pinnatifida</i>	<i>Sargassum hemiphylum</i> , <i>C. tenellus</i> , <i>C. pilulifera</i> , <i>Chondrophycus intermedium</i> , <i>C. crassicaulis</i>	<i>S. thunbergii</i> , <i>S. fusiforme</i>	
<b>Subtidal depth</b>	<b>0-6 m</b> <i>E. cava</i> , <i>Sargassum horneri</i> , <i>Sargassum coreanum</i> , <i>Sargassum macrocarpum</i> , <i>Undaria pinnatifida</i>	<b>1-3 m</b> <i>E. cava</i> , <i>U. pinnatifida</i> , <i>Plocamium telfairiae</i> , <i>Gelidium elegans</i> , <i>S. coreanum</i>	<b>1 m</b> <i>S. thunbergii</i> , <i>S. fusiforme</i>	<b>1 m</b> <i>Sargassum</i> spp., <i>S. latiuscula</i> , <i>Phyllospadix japonicus</i> , <i>Grateloupia cornea</i> , Melobesioidean algae	
	<b>7-12 m</b> <i>E. cava</i> , <i>S. macrocarpum</i> , <i>Cladophora wrightiana</i> , <i>Marginisporum</i> spp.	<b>4-6 m</b> <i>E. cava</i> , <i>S. horneri</i> , <i>D. prolifera</i> , <i>S. macrocarpum</i> , <i>Diclyopteris latiuscula</i>	<b>5 m</b> <i>Desmaresia ligulata</i> , <i>Gracilaria textorii</i> , <i>U. pertusa</i>	<b>5 m</b> Melobesioidean algae, <i>Sargassum</i> spp., <i>P. japonicus</i> , <i>Codium arabicum</i>	
	<b>13-18 m</b> <i>E. cava</i> , <i>S. macrocarpum</i> , <i>C. wrightiana</i> , <i>Marginisporum</i> spp.	<b>7-9 m</b> <i>E. cava</i> , <i>S. macrocarpum</i> , <i>S. horneri</i> , <i>C. wrightiana</i> , <i>Amphiroa anceps</i>		<b>10 m</b> Melobesioidean algae, <i>P. japonicus</i> , <i>Sargassum</i> spp.	

<sup>a</sup>biomass, <sup>b</sup>importance, <sup>c</sup>coverage value: criterions for the estimation of representative macroalgal communities.

comprised of finger-like holdfasts, a single solid stipe, and large leathery blades. These morphological distribution patterns in the subtidal zone seem to be the result of the water motion gradient (Stewart and Carpenter 2003, Fowler-Walker et al. 2006). The ratio of filamentous algae increased toward the deep water caused by *C. wrightiana* (Fig. 4). Yokohama et al. (1977) mentioned that *C. wrightiana* is a deep-water species and that the occurrence of siphonaxanthin seems to emphasize its ecological importance.

The general patterns of abundance, diversity, and community dynamic in the macroalgal assemblages among shore levels and along depth gradients are represented by an increase from the high intertidal zone seaward and a decrease with depth in the subtidal zone (Garrahou et al. 2002, Balata et al. 2006, Konar et al. 2009). Similarly, we found that macroalgal biomass and diversity index values ( $H'$ ) were generally higher in the shallow subtidal zone and decreased with both increasing subtidal depth and intertidal height, although these patterns varied with season (Figs 3 & 5). However, vertical species diversity (species number) did not show a general distribution pattern (Fig. 5). In particular, annual species number was remarkably similar (from 66 species in 0-6 m to 69 in 13-18 m depth, data not shown) among the subtidal levels, although  $H'$  in the shallow areas was higher than that in deeper water. These inverse relationships between species diversity (number) and  $H'$  in the subtidal zone might be caused by excessive domination by a few species in deeper areas. Large numbers of small ephemeral species were observed in deeper areas at our study sites, such as *Aglaothamnion callophyllidicola*, *Anotrichium yagii*, *Antithamnion* spp., *Griffithsia* spp., *Herpochondria elegans*, *Sorella repens*, and *Symphyclocladia pumila*, but the communities were dominated by a few large species, such as *E. cava* and *S. macrocarpum*. Balata and Piazzzi (2008) also documented exceptional patterns in macroalgal species number between shallow and deep habitats in the north-western Mediterranean Sea. The community dynamics of a macroalgal assemblage also decreases with depth (Garrahou et al. 2002, Konar et al. 2009). The higher  $H'$  and lower  $D$  values near the MLW indirectly reflect not only the large number of species, but also the dynamic variance in the assemblage, including changing abundance, elimination, and ingression of macroalgal species (Figs 2 & 5). The lower  $H'$  values in the high-to mid-intertidal zones and deep water might be the result of extreme stress from desiccation and physically stable conditions, respectively. This is reflected in the dendrogram from our cluster analysis (Fig. 6). The lower similarity between

macroalgal assemblages near the MLW indicates that the macroalgal assemblages changed dramatically with season closer to the MLW, whereas assemblages in the higher intertidal and deeper subtidal zones were more stable. Kang et al. (2011) also noted that seasonal variations in macroalgal assemblages near the MLW are more dynamic than those in assemblages in the deeper subtidal or higher intertidal zones. In many studies of the effects of wave exposure on macroalgal communities, intermediate levels of water motion enhance diversity and abundance of seaweeds by accelerating nutrient and gas exchange (Prathey 2005, Nishihara and Terada 2010).

In summary, our intensive study of macroalgal assemblages on the Marado coast provided great insights into the distribution pattern of macroalgal assemblages in unpolluted marine areas of Jeju Island. Our results also suggested that water motion in addition to tides and light penetration gradients is the major factor affecting the vertical distribution pattern in macroalgal assemblages. This information on macroalgal assemblage patterns from an uncontaminated marine area provides vital evidence for establishing effective management strategies to restore macroalgae by selecting area, season, and depth.

## ACKNOWLEDGEMENTS

We thank Mr. E. G. Han, Mr. H. W. Lee, Mr. Y. H. Ko and Miss M. Y. Yang for collecting the Marado samples. This study was supported by a National Research Foundation of Korea Grant, funded by the Korean government (2011-0003792).

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