Spatial Variability in Distribution, Abundance and Species Composition of the Subtidal Macroalgal Assemblages Found Along the Geumo Archipelago in the Central South Sea of Korea

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Abstract: Dense macroalgal assemblages are a common feature of the rocky subtidal habitats along the coast of Geumo Archipelago in the central South Sea of Korea, but are highly variable in space. This study addresses two questions concerning the algal assemblages: (1) how variable the distribution, abundance and species composition of the assemblages are in space, and (2) how closely the distribution, abundance and species composition of the assemblages are correlated to the spatial variation in abiotic factors. To answer these questions, we investigated 30 sites along the coast in autumn of 2003. The nonmetric multidimensional scaling analysis showed that there were strong differences in the composition and abundance of species in the assemblages among the sites. The similarity among the sites based on presence/absence data was approximately 51%, whereas the similarity based on abundance data was less than 37%, suggesting that the abundance of species contributed much to these differences. There were also strong differences in the number of species, abundance and vertical distribution of the assemblages along the coast. Multiple regression analyses revealed that the number of species, abundance and vertical distribution of the assemblages had a positive relationship with water depth, but less than 58% of total variation in these variables was explained by this abiotic factor. The results suggest that spatial (between habitats) variation is an important and consistent component of subtidal algal assemblages in Geumo Archipelago and should be explained before any differences between localities are assessed.

Key words: macroalgal assemblages, subtidal, spatial variation, abiotic factors, water depth, South Sea

1. Introduction

Variation in distribution, abundance and composition of species is an intrinsic and important component of all habitats and has been shown to occur on a variety of spatial scales (see reviews by Foster et al. 1988; Coleman 2002). Some patterns of distribution and abundance are general and show little variation in the case of smaller scales (e.g., geographic patterns; Foster et al. 1988), while other patterns are specific to particular places (Underwood and Chapman 1998; Coleman 2002). Understanding these patterns of variation and how they change in space is, therefore, important and required to fully understand the ecology of the organism or assemblages being studied.

Marine macroalgae, in particular, show great spatial variation in patterns of distribution and abundance (e.g., among local areas along a coastline; see reviews by Schiel and Foster 1986). This variation may result from physical features of their environment. Light, temperature and nutrient distribution have been implicated as causes of distributional variation among localized areas (Michanck 1979; Druehl 2000). The availability of hard substrata may impose limits on the depth distribution of algae in areas where light penetration is still sufficient for algal growth (Schiel and Foster 1986). Salinity and wave action are also correlated with differences in abundance of species between localities (Lobban and Harrison 1994).

Dense macroalgal assemblages are a characteristic of

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the rocky subtidal habitats along the coast of Geumo Archipelago in the central South Sea of Korea, but are highly variable in space. Furthermore, physical factors that affect macroalgal community structure also vary considerably between localities. Temperature shows a strong gradient along the coast largely due to the interaction between the Tsushima Warm Current and the cold shelf waters. In addition, the local-scale fluid dynamics associated with the interaction between water motion and depth also cause spatial variation in abiotic factors. For example, the fluid dynamics in the shallow nearshore area induce the routine resuspension of bottom sediments, resulting in a turbid environment with a high concentration of nutrients. Such variation in abiotic factors may affect the distribution, abundance and species composition of the algal assemblages and, thereby, result in the present distribution pattern.

This study addresses two questions concerning the subtidal algal assemblages in the central South Sea of Korea: (1) how variable the distribution, abundance and species composition of the assemblages are in space, and (2) how closely the distribution, abundance and species composition of the assemblages are correlated to the spatial variation in abiotic factors.

2. Materials and methods

Study area

This study was done at Geumo Archipelago (34° 30'N, 127° 45'E) in the central South Sea of Korea about 10 km south of Yeosu Peninsula (Fig. 1). This area is characterized by several islets separated by shallow bottom sediments (primary, muddy sand), and turbidity is generally high due to the resuspension of bottom sediments (suspended sediment, 17.0-38.0 mg · L⁻¹). The hard substrata available for algal attachment are limited to less than 10 m in depth, and are mostly composed of sandstones and conglomerate outcrops.

Algal assemblages

To examine the spatial variations in the distribution, abundance and species composition of the algal assemblages, 30 study sites were chosen in September 2003 (Fig. 1). At each site, a 50 m long transect was established perpendicular to the shore. The transect began at a depth of 1 m and ended at the depth of 9 m. The percentage of cover for all species other than crustose coralline algae was estimated at 2 m depth intervals along the transect using a 0.25 m² PVC quadrat with 25 squares, and then averaged across depths (n = 5). The vertical distribution range of the assemblages (hereafter vertical range) was determined by recording the maximum depth to which the algal species extended.

Abiotic factors

In early November 1999, abiotic factors such as temperature, salinity, suspended sediment, dissolved nitrogen, turbidity and water depth of the 30 sites were measured. At each site, water samples (n = 2) were collected at the surface and bottom water, and transported to the laboratory while in icebox storage. The amount of suspended sediment (mg · L⁻¹) was determined by measuring the material retained on a 0.45 μm pore-diameter glass-fiber filter. The materials were dried for 2 hours under 105°C, cooled under ambient air temperature, and weighed. Dissolved nitrogen (NO₃⁻, NO₂⁻, NH₄⁺) was determined using a QuikChem 8000 autoanalyzer. Temperature and salinity were measured in situ with a portable YSI-30 salinity and temperature meter.

Turbidity was expressed as the light attenuation coefficient (k). At each site, 5-min integrated measurements of photosynthetic photon flux density were performed on sea surface (Iₛ) and at 3 and 6 m depths during daytime (10:00 -14:00 h), using a 2π cosine-corrected underwater PAR sensor (LiCor LI-1400). The value of k was calculated from the Beer-Lambert expression (Iₛ = Iₒ · e⁻ᵏ𝑧), where z represents depth (m). Greater k values indicate higher turbidity.
Spatial Variability in Distribution, Abundance and Species Composition of Subtidal Macroalgal Assemblages

Water depth was measured at particular horizontal distances from the shoreline. In most of the study sites, stands of macroalgae were found within a 10 m horizontal distance from shoreline due to shallow sandy-mud flats or steep slopes along the shoreline. For this reason, water depth at all sites was measured with a 20 m line spaced 10 m apart along the shoreline by using an echo sounder on board, then corrected to the values below datum to remove tide-related variations.

Statistical analysis

All statistical analyses were done using SYSTAT 10.2 and Primer v5. To examine the spatial variability in algal assemblages, raw data were analyzed using nonmetric multidimensional scaling (nMDS) analyses. Presence/absence data were also analyzed to eliminate the influence of abundance and give equal weighting to rare species.

Principal Components Analysis (PCA) was used to reduce the six environmental variables (temperature, salinity, suspended sediment, dissolved nitrogen, turbidity and water depth) to fewer principal components and examine the relationships between the 30 sites in terms of these components (Quinn and Keough 2002). Since each of these variables was measured on different scales, PCA was done on the correlation matrix. Principal components having eigenvalues larger than 1.0 were retained, and then rotated using the varimax technique. A biplot of variable loading vectors and site scores on the principal components was also performed to reveal patterns in the data.

Multiple regression with forward variable selection was used to examine the relationship between the six environmental variables and three response variables (i.e., the number of species, abundance and vertical range of algal assemblages), since three of the six variables were found to not be normally distributed. The t statistics and their associated P values were used to assess the significance of individual b coefficients. To assess the relative importance of the independent variables in the given model the regression coefficients (b) for standardized data were calculated.

3. Results

Spatial variability of algal assemblages

The nonmetric multidimensional scaling analyses showed that there were strong differences in the composition and abundance of species in the assemblages among the 30 sites (Fig. 2). For the raw data, the similarity between the two furthest sites on the nMDS ordination plot (S17 and S29) was 5% and the mean similarity among sites was

![Figure 2](image1.png)

Fig. 2. nMDS ordinations of the 30 sites based on (a) raw data, (b) presence/absence and Bray-Curtis similarities among sites.

![Figure 3](image2.png)

Fig. 3. Spatial variations in the (a) number of species, (b) abundance and (c) vertical range of the 30 sites.
37.5%. For the presence/absence data, the similarity between the two furthest sites (S16 and S29) was 10% and the mean similarity among sites was less than 51.4%. These suggested that the abundance of species contributed much to these differences.

There were also strong differences in the number of species, abundance and vertical range of algal assemblages among sites (Fig. 3). The number of species ranged between 6 and 15 species and the highest value was found at the sites S5 and S7. The mean bottom cover ranged from 21.4 to 71.8% and the highest value was found at the site S11. The vertical ranges of the assemblages ranged between 3 and 9 m.

Abiotic factors

The spatial variation in abiotic factors at the 30 sites is shown in Fig. 4. The sites at the eastern part of Geumodo (S24-S30) showed significantly higher values in water temperature than the rest of the sites (Paired t-test: $t = 8.21$, $P = 0.0001$, $df = 12$). In contrast, suspended sediment and turbidity at the sites S24-S30 were significantly lower than those found at the remaining sites (Paired t-test, suspended sediment: $t = -5.34$, $P = 0.0007$, $df = 8$; turbidity: $t = -6.33$, $P = 0.0000$, $df = 27$). The differences in salinity, nitrogen and water depth between the two areas were not significant (Paired t-test, $P > 0.05$), but these abiotic factors also strongly varied from one another.

Correlation between algal assemblages and abiotic factors

Two principal components had eigenvalues greater than 1.0 and explained over 62% of the total variance (Table 1). Component loadings (simple correlations between the components and the original variables) showed that temperature,
Table 1. Principal Components Analysis. Values express variable loadings (correlations) for each principal component. Two principal components having eigenvalues larger than 1.0 were retained, and were then rotated using the varimax technique.

<table>
<thead>
<tr>
<th>Variables</th>
<th>Unrotated Component 1</th>
<th>Component 2</th>
<th>Rotated Component 1</th>
<th>Component 2</th>
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</thead>
<tbody>
<tr>
<td>Temperature</td>
<td>0.872</td>
<td>-0.038</td>
<td>-0.866</td>
<td>0.106</td>
</tr>
<tr>
<td>Salinity</td>
<td>0.067</td>
<td>0.801</td>
<td>0.066</td>
<td>0.801</td>
</tr>
<tr>
<td>Nitrogen</td>
<td>0.285</td>
<td>0.705</td>
<td>-0.165</td>
<td>0.742</td>
</tr>
<tr>
<td>Suspended sediment</td>
<td>-0.820</td>
<td>0.092</td>
<td>0.824</td>
<td>-0.044</td>
</tr>
<tr>
<td>Turbidity ($k$)</td>
<td>-0.782</td>
<td>0.143</td>
<td>0.795</td>
<td>0.012</td>
</tr>
<tr>
<td>Water depth</td>
<td>-0.659</td>
<td>0.052</td>
<td>0.659</td>
<td>-0.057</td>
</tr>
<tr>
<td>Variance explained</td>
<td>2.565</td>
<td>1.171</td>
<td>2.527</td>
<td>1.209</td>
</tr>
<tr>
<td>% of total variance explained</td>
<td>42.7</td>
<td>19.5</td>
<td>42.1</td>
<td>20.1</td>
</tr>
</tbody>
</table>

Fig. 5. Principal Component Analysis. A biplot of variable loading vectors and site scores related to the two principal components.

suspended sediment, turbidity and water depth correlated highest with component 1, and salinity and nitrogen correlated with component 2. Varimax rotation resulted in different structures for both component 1 and 2, but the loadings of each variable on each rotated component were easier to interpret. Component 1 represented a strong contrast among temperature, suspended sediment and turbidity.

A biplot of variable loading vectors and site scores on the two principal components is shown in Fig. 5. The component scores for each site show that sites at the eastern side of Geumodo (S24, 25, 26, 29 and 30) stood out from the sites at the western side of Geumodo (S1, 2, 4, 5, 6 and 7), particularly along component 1. The variable loadings on component 1 show that S24, 25, 26, 29 and 30 were in the opposite direction of the vector for suspended sediment, but were in the same direction of the vector for temperature. Thus, these were sites with low suspended sediment and high temperature. In contrast, S1, 2, 4, 5, 6 and 7 were in the opposite direction of the vector for temperature, but were in the same direction of the vector for suspended sediment. Thus, these were sites with low temperature and suspended sediment.

The relationships between the number of species, abundance and vertical range of the assemblages and abiotic factors were also examined using a multiple regression with forward variable selection (Table 2). In any case, none of the tolerances were lower than 0.2, suggesting that collinearity may not be a serious issue for data sets. In the number of species, about 52% of the variation ($r^2 = 0.522$) can be explained by this combination of predictors. The number of species had significant positive partial regression slopes against salinity and water depth and a significant negative partial regression slope against nitrogen. Values of the standard coefficient, however, indicate that water depth was more important than salinity and nitrogen in determining the number of species. In the abundance and vertical range, more than 49% of the variation (abundance: $r^2 = 0.495$, vertical range: $r^2 = 0.518$) can be explained by the combination of predictors. There was a significant positive partial regression slope for the abundance and vertical range against water depth.

4. Discussion

The results of this study reflect the great spatial variability in algal assemblages. Although the average distance between sites was less than 1 km, the distribution, abundance and species composition of algal assemblages were strongly at odds between the various sites. Not surprisingly, spatial variation appears to be a general pattern among algal assemblages along temperate rocky shores around the world (Schiel
Table 2. Multiple regression analysis models relating the number of species, abundance and vertical range of algal assemblages at the 30 sites to the six abiotic factors. Only variables with significant \( t \)-statistics are shown. Dependent variable: Number of species, \( N = 30, r^2 = 0.522 \), adj. \( r^2 = 0.397 \), SE of estimate = 2.249; Abundance, \( N = 30, r^2 = 0.495 \), adj. \( r^2 = 0.363 \), SE of estimate = 10.334; Vertical range, \( N = 30, r^2 = 0.518 \), adj. \( r^2 = 0.392 \), SE of estimate = 1.306.

<table>
<thead>
<tr>
<th>Variables</th>
<th>Estimate</th>
<th>Std Error</th>
<th>Std Coef</th>
<th>Tolerance</th>
<th>( t )</th>
<th>( P )</th>
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<td>Number of species</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
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<tr>
<td>Salinity</td>
<td>6.695</td>
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<td>0.386</td>
<td>0.856</td>
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<td>Nitrogen</td>
<td>-1.203</td>
<td>0.544</td>
<td>-0.359</td>
<td>0.788</td>
<td>-2.211</td>
<td>0.037</td>
</tr>
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<td>Water depth</td>
<td>0.495</td>
<td>0.151</td>
<td>0.570</td>
<td>0.682</td>
<td>3.266</td>
<td>0.003</td>
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<td></td>
</tr>
<tr>
<td>Source</td>
<td>SS</td>
<td>df</td>
<td>MS</td>
<td>F-ratio</td>
<td>( P )</td>
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<td>23</td>
<td>5.1</td>
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<td></td>
<td></td>
<td></td>
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</tr>
<tr>
<td>Water depth</td>
<td>2.235</td>
<td>0.696</td>
<td>0.576</td>
<td>0.682</td>
<td>3.211</td>
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<tr>
<td>Source</td>
<td>SS</td>
<td>df</td>
<td>MS</td>
<td>F-ratio</td>
<td>( P )</td>
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<tr>
<td>Regression</td>
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<td>6</td>
<td>400.9</td>
<td>3.75</td>
<td>0.009</td>
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<td>Residual</td>
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<td>23</td>
<td>106.8</td>
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<tr>
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<tr>
<td>Water depth</td>
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<td>0.088</td>
<td>0.734</td>
<td>0.682</td>
<td>4.189</td>
<td>0.000</td>
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<td>df</td>
<td>MS</td>
<td>F-ratio</td>
<td>( P )</td>
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<td>39.2</td>
<td>23</td>
<td>1.7</td>
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</table>

and Foster 1986), and can occur within a given habitat (Coleman 2002; Foster 1990; Underwood and Chapman 1998).

Coleman (2002) said that it is extremely important to identify the scales of variation in any assemblages, particularly in the detection of environmental impacts. If small-scale variation goes undetected, differences due to impacts may be confused with differences resulting from natural spatial variability (Morrissey et al. 1992; Underwood 1993; Chapman et al. 1995). From the earliest underwater observations a number of studies have given an estimate of the distribution and abundance of Korean algae within certain depths (e.g., Koh and Sung 1983) or along depth gradients (e.g., Sohn et al. 1983; Nam 1986; Chung et al. 1991; Kang et al. 1993; Kim and Lee 1995), but these studies did not sufficiently assess variation between localized sites to determine how much can be ascribed to smaller scale habitat differences. In this regard, our study will provide a framework within which the scales of variation can be examined experimentally.

The algal assemblages investigated had a strong positive relationship with water depth, indicating that this abiotic factor can assume a much greater share of the responsibility for the variation in the number of species, abundance and vertical distribution of algal assemblages than other abiotic factors such as temperature, salinity, nitrogen, suspended sediment and turbidity. Several authors have suggested that water depth is highly correlated with the local-scale variation in the distribution and abundance of subtidal algal assemblages (Shepherd and Womersley 1970, 1971; Schiel and Foster 1986). For example, Shepherd and Womersley (1971) reported that in Australian clear subtidal areas three zones were evident on rough shores but on the sheltered lee shores the uppermost zone was very restricted and the lowermost zone did not occur due to the limited water depth, thereby reducing the number of species and vertical distribution range of algal assemblages. However, it has never been reported that water depth can influence the distribution and abundance of algal assemblages in turbid waters where the hard substrata available for algal attachment are limited to depths of less than 10 m due to shallow mud flats.
Although the multiple regression analyses showed that about 50% of variation in the number of species, abundance and vertical distribution range of the algal assemblages can be explained by the combination of predictors (i.e., temperature, salinity, nitrogen, suspended sediment, turbidity and water depth), the remaining 50% of variation cases remains unexplained by the combination of the predictors and this indicates that other factors may influence the algal assemblages. One possible factor is water movement as shown in Kain (1979) and Dayton et al. (1984). From the qualitative surveys on water motion of the 30 sites, we also observed that there was a strong variation in water motion between sites (R.S. Kang unpubl. data). In addition to water motion, the spatial variation in pre-recruitment processes such as the dispersal and availability of propagules (Deysher and Norton 1982), recruitment itself (Santelices 1990) or post-recruitment processes such as grazing (Neushul et al. 1976) and competition (Lubchenco 1980; Kang et al. 2004) may also be important in determining the present distribution patterns.

The total number of species of the algal assemblages ranged between 6 and 15. Presumably, this poor diversity may result from the limitation of hard substrata (< 10 m) and high turbidity. High concentration of suspended sediment in shallow coastal regions is commonly associated with the disturbance of bottom sediment by surface gravity waves (Booth et al. 2000), and bottom sediment resuspension also results in the reduction of water clarity (Diehl 2002). Similarly, we observed that the overall suspended sediment and turbidity in the study area were very high due to bottom sediment resuspension (Fig. 3). The process associated with bottom sediment resuspension influences propagules settlement of seaweeds in various ways. Arakawa and Matsuika (1990) reported that ca. 40% of spores released from kelp Ecklonia cava and Undaria pinnatifida were attached to suspended sediment (4 mg/l in concentration) and thus spore settlement was largely reduced by the effect of suspended sediment. Deviny and Volse (1978), Norton (1978) and Arakawa and Matsuika (1992) also reported that sediment deposition interfered with attachment of kelp spores.

In summary, spatial (between habitats) variation is an important and consistent component of subtidal algal assemblages along the Geumo Archipelago in the central South Sea of Korea. Although the study area is very turbid and the availability of hard substratum is limited to depths of less than 10 m, water depth is an abiotic factor that can explain much of the spatial variation in the number of species, abundance and vertical distribution of the assemblages.

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