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Environmental and Ecological Characteristics Influencing Spatial Distribution of Halophytes in Hampyeong Bay, Korea

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ABSTRACT

During our observations of changes in halophyte distribution in Hampyeong Bay over a period of five years, we found that the distribution area showed a maintenance for *Phragmites communis* community, a tendency of gradual increase for *Zoysia sinica* community, gradual decrease for *Suaeda maritima* community, and disappearance for *Limonium tetragonum* community during the studied period. The *Phragmites communis* community stably settled in areas adjacent to land and appeared not to be significantly affected by physical factors (such as tides and waves) or disturbances caused by biological factors (such as interspecific competition). Among studied species, germination time was shown to be the fastest for *Suaeda maritima*. In addition, this species showed certain characteristics that allowed it to settle primarily in new habitats formed by sand deposition as its growth was not halted under conditions with high amounts of sand and high organic matter content. However, in areas where *Zoysia sinica* and *Suaeda maritima* resided together, the area inhabited by *Suaeda maritima* gradually decreased due to interspecific competition between the two species. This was believed to be the result of a sharp decrease in the germination of *Suaeda maritima* since May, while the germination of *Zoysia sinica* was continuously maintained, indicating that the latter had an advantage in terms of seedling competition. In the case of the *Limonium tetragonum* community, its habitat was found to have been completely destroyed because it was covered by sand. The study area was confirmed to have undergone a large change in topography as tides and waves resulted in sand deposition onto these lands. Hampyeong Bay is considered to have experienced changes in halophyte distribution related to certain complex factors, such as changes in physical habitats and changes in biological factors such as interspecific competition.

Keywords: Biodiversity, Brackish water, Salt marsh, Halophyte, Succession, Vegetation map

Introduction

Salt marshes are areas between the highest and lowest tides of the tidal range (Pigott, 1969). They are periodically affected by seawater and inhabited by vascular plants (Chapman, 1974). They serve as a buffer zone for marine and terrestrial ecosystems. They can be divided into coastal and estuarine salt marshes. Coastal salt marshes are areas where common terrestrial plants cannot grow because of high salt concentrations in the soil, which is why these areas are inhabited by plants called halophytes (Myung, 2004). Compared to inland habitats, coastal salt marshes contribute more to the preservation of national biodiversity as they are home to more species that have evolved to adapt to hostile environments (Lee & Ignaciuk, 1985). Salt marshes are known to be the most productive ecosystems among uncultivated areas because of their diverse physical, chemical, and biological environmental factors. In South Korea, large areas of salt marshes are developed on the west and southern coasts. In particular, the west coast is characterized by a great difference in sea level between high and low tides. It includes a large intertidal zone and a complex coastline, resulting in environmental conditions suitable for various halophyte species (Lee *et al*., 2019).

Halophytes can grow in areas with specific geographical requirements (Kim & Song, 1983; Lee *et al*., 2019).

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There are 62 species of halophytes belonging to 21 families, 44 genera, 57 species, four mutants, and one variety distributed throughout South Korea. Of them, 33 species are distributed in sand dunes and 29 species are distributed in salt marshes (Shim *et al*., 2009). Environmental factors that can influence the distribution of halophytes include soil salinity, duration and frequency of coastal flooding, soil texture, and groundwater level (Hong *et al*., 2015; Inoue & Washitani, 1989; Kim *et al*., 2006; Lee & Ignaciuk, 1985; Linthurst & Seneca, 1980; Ranwell, 1972). Biological factors such as interspecific competition can also influence this phenomenon (Buttery & Lambert, 1965; Grace & Wetzel, 1981). Various environmental factors can heavily influence ecological processes of halophytes and determine the distribution and succession of salt marsh communities (Disraelli & Fonda, 1979; Hinde, 1954; Snow & Vince, 1984; Stevenson, 1954; Vogl, 1966). According to previous studies, the influence of tidal movements and the rise in sea levels caused by climate change can lead to dynamic changes in the topography and coastline of South Korea's west coast (Cho *et al*., 2001; Kim & Lee, 2011). This can lead to changes in the growth environment of halophytes that inhabit the area, which can consequently affect biodiversity of the region. Because halophyte distribution patterns will change over time, it is necessary to broadly review distribution changes of halophytes and soil environment in their habitats to understand the correlation between halophytes and habitat soil environment. In addition, comprehensive data are required to understand the habitat environment of halophytes from an ecological point of view and to explain ecosystem structure and distribution characteristics of tidal flats and coastal salt marshes for conservation and management of these habitats.

Therefore, the objective of this study was to analyze environmental and ecological characteristics related to the spatial distribution of halophytes by comparing and analyzing soil factors, seedling emergence rates, and changes in existing vegetation over a five-year period from 2016 to 2020, focusing on the Hampyeong Bay located in Muan-gun, Jeollanam-do, Korea. Purposes of this study are to obtain systematic and scientific data by identifying distribution change characteristics of coastal halophyte communities and to secure important basic data that could be used for coastal wetland ecosystem conservation and management policies.

Materials and Methods

Study site

The Hampyeong Bay is located in the southern section of the West Sea of the Korean Peninsula. It is a relatively large bay with a maximum width of 12 km along the mainland and a length of 17 km, forming a semi closed environment. The entrance of the bay is located in the northwestern direction from the study site, with a maximum depth of 23 m. Thus, it is especially narrow and steep.

The entrance of the bay and Hyeonhwa-ri, Hyeongyeong-myeon, Muan-gun (N 35°02′07.53″, E 126°25′07.53″) located in the center of the inner bay were selected as study areas. The area in Hyeonhwa-ri is located in the innermost part of the Hampyeong Bay with an intertidal zone width of approximately 1.5 km. It has the widest distribution of halophytes within the Hampyeong Bay and the highest appearance rate of sand dune plants and coastal halophytes. Changes of sedimentary facies in the coast are well known due to the influence of tidal current, leading to a clear portrayal of changes in halophyte distribution (Fig. 1).

Analysis of soil factors

In the period from March to October 2016–2020, pH, moisture content, organic matter content, salt concentration, electrical conductivity, and texture of soils in the study area were measured to determine soil factors in each community appearing in the Hampyeong Bay. Soil analysis was conducted on *Phragmites communis*, *Suaeda maritima*, *Zoysia sinica*, *Limonium tetragonum*, and *Artemisia fukudo*, the most representative communities.

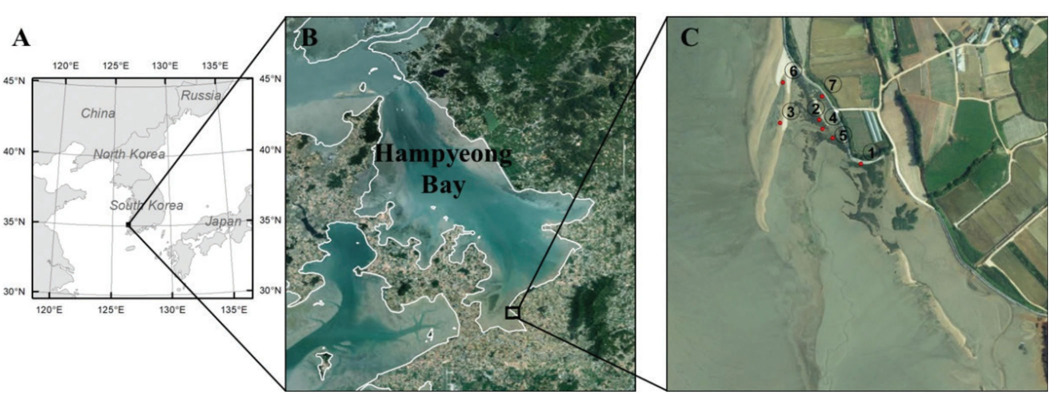

Fig. 1. Map of the study site. A: Location of the study site; B: Front view of the entire Hampyeon g Bay; C: Locations of quadrats (1–7).

For soil sampling, soils within 15 cm of depth were collected from halophyte communities at each point after removing the organic material layer to eliminate fallen leaves and foreign substances, followed by 1 cm of topsoil. Three samples were collected from each point (five quadrats) twice a month and brought to the laboratory where soil moisture contents were measured. The rest of the soil was desiccated for two weeks, sieved through 2 mm pores, and used for organic matter content measurement and subsequent soil analysis.

To calculate soil moisture, moist soil samples (10 g) collected at each site were transferred to the laboratory and immediately placed in weighing bottles, followed by measuring the weight before soil drying. After drying at 80°C in a dryer for 48 hours, soil weight was measured again and the moisture content was converted into a percentage based on the difference in soil moisture content.

Organic matter content was calculated by placing 10 g of dry soil in a crucible, heating it at 500°C for four hours in a dryer, and measuring the difference in weight to determine the amount of loss on ignition.

Soil acidity (pH), electrical conductivity (EC), and salinity were calculated by mixing 10 g of shade-dried soil with distilled water at a 1:5 (w/w) ratio, followed by shaking the mixture for 60 minutes. The mixture was then filtered through a KFP filter paper. The pH, EC, and salinity were then measured using a YSI 60 pH & temperature meter (YSI pro30).

Soil texture was determined by sieving 50 g of shade-dried soil through 2 mm, 500 μm, and 100 μm sieves. Soils with sizes ranging from 2 mm to 0.05 mm were classified as sand, while those with sizes below 0.05 mm were classified as a combination of silt and clay.

Analysis of halophyte communities

To identify the vegetation in this survey area, vascular plants were collected, categorized, and identified based on the literature (Lee, 1996). The plant list classification system used was based on the Engler system.

Halophyte community survey was conducted through a field survey. A sample block was installed in the survey area. Dominance and sociability were recorded according to the vegetation survey method reported by Braun-Blanquet (1964) for all species and constituent species that appeared within a 1 m x 1 m quadrat. A comprehensive distribution chart was prepared according to the classification of communities. Seedling emergence rate was calculated as the percentage of the population at the time of measurement to the maximum number of the year (numbers of seedlings per month/maximum numbers of seedlings of the year x 100) by measuring the number of living individuals per unit that appeared in the 1m x 1m quadrat per month after selecting a homogeneous area of five types of halophytes distributed in the salt marsh of the survey area. For the distribution and area of vegetation, orthophotos were produced using aerial photographs and unmanned aerial vehicles (Drones_Mavic pro model, DJI, Shenzhen, China) of the survey area. The existing vegetation map was produced and distribution areas for each community were calculated using the Quantum Geographic Information System (QGIS) program.

Results

Soil factors

Fig. 2 shows results of the analysis of soil factors based on vegetation communities at the study site. The highest soil pH value of 6.9 was recorded for the *Limonium tetragonum* community, followed by pH of 6.8 for *Suaeda maritima* and *Artemisia fukudo* communities, 6.7 for the *Zoysia sinica* community, and 6.5 for the *Phragmites communis* community. The highest moisture content was 20.7% for the *Phragmites communis* community, followed by 14.4% for the *Zoysia sinica* community, 9.5% for the *Limonium tetragonum* community, 8.0% for the *Artemisia fukudo* community, and 7.0% for *the Suaeda maritima* community. Organic matter contents were 1.6% and 1.5% for *Phragmites communis* and *Zoysia sinica* communities, respectively, and 1.3% and 1.2% for *Limonium tetragonum* and *Artemisia fukudo* communities, respectively. The organic matter content was the lowest for the *Suaeda maritima* community at 0.6%. The *Phragmites communis* community showed the highest salinity of 10.0 ppt. Salinities of *Zoysia sinica*, *Limonium tetragonum*, *Suaeda maritima*, and *Artemisia fukudo* communities were 7.0 ppt, 4.4 ppt, 3.8 ppt, and 3.7 ppt, respecti vely. Similar to salinity results, EC was the highest for the *Phragmites communis* community, followed by those for *Zoysia sinica*, *Limonium tetragonum*, *Suaeda maritima*, and *Artemisia fukudo* communities. The highest sand content was 78.0% recorded for the *Limonium tetragonum* community, followed by 75.9% for the *Suaeda maritima* community, 72.6% for the *Artemisia fukudo* community, 71.8% for the *Zoysia sinica* community, and 68.4% for the *Phragmites communis* community.

Halophyte communities

Halophyte communities in this survey area were assessed and described using a synthesis table (Table 1) according to the table manipulation method. The *Phragmites communis* community, *Zoysia sinica* community, *Suaeda maritima* community, *Zoysia sinica-Artemisia fukudo* community, and *Artemisia fukudo* community were major dominant communities.

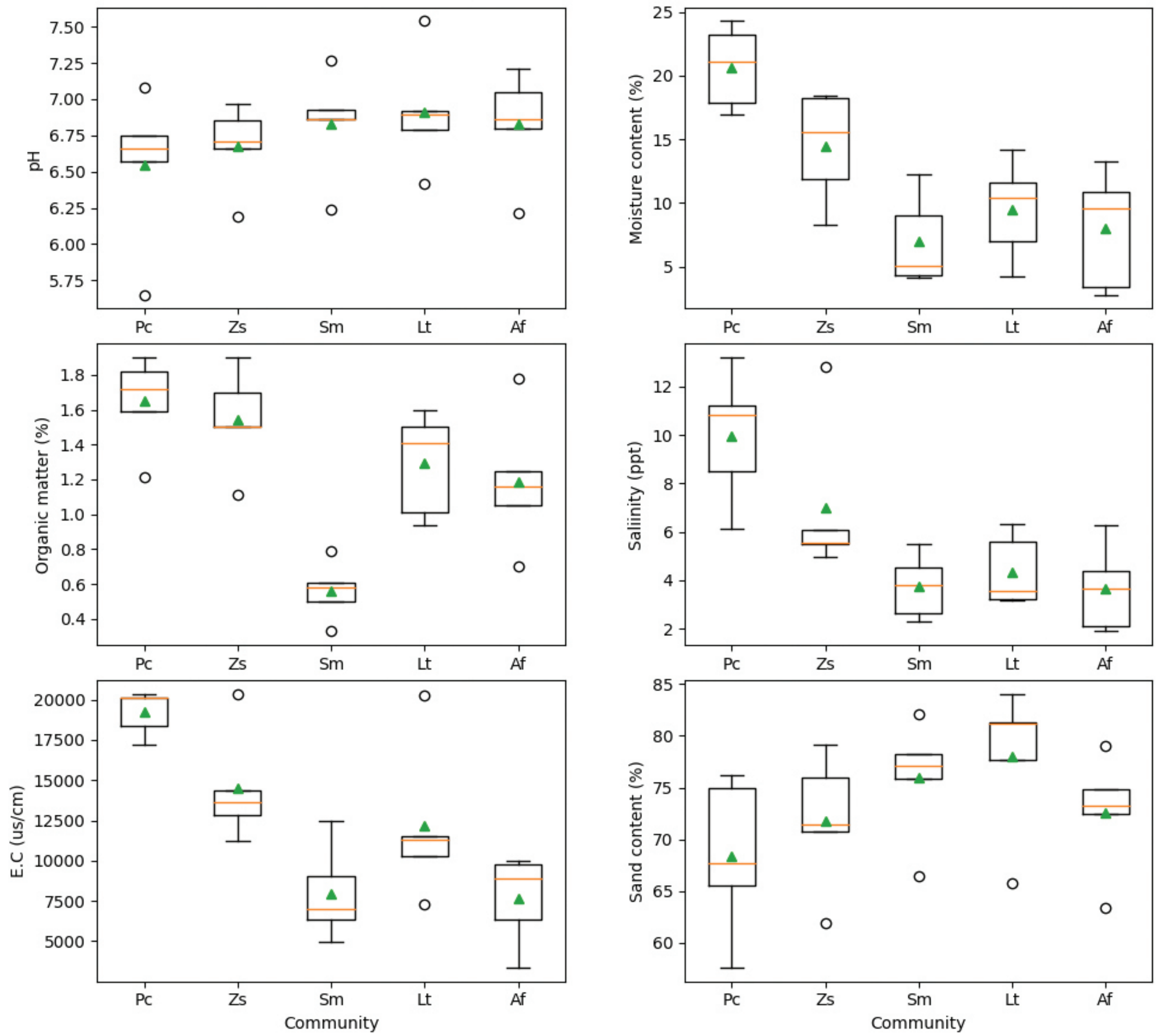

Fig. 2. Physicochemical characteristics of soil by vegetation community in Hampyeong Bay, Korea (average values from 2016 to 2020). Pc: *Phragmites communis*, Zs: *Zoysia sinica*, Sm: *Suaeda maritima*, Lt: *Limonium tetragonum*, Af: *Artemisia fukudo*.

In 2016, plants in the *Phragmites communis* community had a height range of 106–269 cm, a cover rate of 95%, and an average number of species of 1.0. In 2020, these plants had a height range of 155–220 cm, a cover rate of 100%, and an average number of species of 1.0. This community was developed on the edge of the coast where freshwater was available near the coastal embankment.

In 2016, plants in the *Zoysia sinica* community had a height range of 8–32 cm, a cover rate of 80%, and an average number of species of 2.0. Species that appeared in this community were *Zoysia sinica*, *Suaeda maritima*, *Artemisia fukudo*, *Limonium tetragonum*, and *Atriplex gmelinii*. In 2020, these plants had a height range of 15.5 cm to 23.5 cm, a cover rate was 70%, and an average number of species of 2.3. Species that appeared in this community were *Suaeda maritima*, *Salsola komarovii*, and *Salicornia europaea*.

In 2016, plants in the *Suaeda maritima* community had a height range of 4–18 cm, a cover rate of 80%, and an average number of species of 2.5. Species that appeared in this community were *Suaeda maritima*, *Zoysia sinica*, *Artemisia fukudo*, *Limonium tetragonum*, *Suaeda glauca*, and *Salicornia europaea*. In 2020, these plants had an average height range of 8.8 cm to 15 cm, a cover rate was 90%, and the average number of species of 2.3. Species that

Table 1. Synthesis table of halophyte communities in the Hampyeong Bay, Korea

Community type*	1	1	2	2	3	3	4	4	5	5	6	6	7	7
Year	16	20	16	20	16	20	16	20	16	20	16	20	16	20
Average number of species	1.0	1.0	2.0	2.3	2.5	2.3	2.3	3.0	1.3	1.3	1.0	·	1.5	·
Differential species of community														
Phragmites communis	5.5	5.5	·	·	·	·	·	·	·	·	·	·	·	·
Zoysia sinica	·	·	5.5	4.4	1.1	·	3.3	2.2	1.1	1.1	·	·	+	·
Suaeda maritima	·	·	2.2	+	5.5	4.4	+	·	+	+	+	·	·	·
Zoysia sinica-Artemisia fukudo	·	·	·	·	·	·	4.4	4.4	·		·	·	·	·
Artemisia fukudo	·	·	1.1	1.1	+	+	2.2	1.1	3.3	4.4		·	·	·
Limonium tetragonum	·	·	+	·	+	·	+	·	·	·	3.3	·	·	·
Suaeda glauca	·	·	·	·	+	·	·	·	·	·	·	·	2.2	·
Companions														
Atriplex gmelinii	·	·	+	·	·	·	·	·	·	·	·	·	+	·
Salicornia herbacea	·	·	·	+	·	·	·	·	·	·	·	·	·	·
Salsola komarovii	·	·	·	+			·	·	·	·	·	·	·	·

*1: *Phragmites communis* Community, 2: *Zoysia sinica* Community, 3: *Suaeda maritima* Community, 4: *Zoysia sinica-Artemisia fukudo* Community, 5: *Artemisia fukudo* Community, 6: *Limonium tetragonum* Community, 7: *Suaeda glauca* Community.

appeared in this community in 2020 were *Suaeda maritima* and *Artemisia fukudo*. The distribution area of this community was centered around areas where sand was deposited along the coast. This community was determined to be a community of coastal salt marsh halophytes that develops around sand dunes formed along the coast.

In 2016, plants in the *Zoysia sinica-Artemisia fukudo* community had a height range of 8–65 cm, a cover rate of 70%, and an average number of species of 2.3. Species that appeared in this community were *Zoysia sinica*, *Suaeda maritima*, and *Limonium tetragonum*. In 2020, these plants had an average height range of 13.1 cm to 19.6 cm, a cover rate was 70%, and an average number of species of 3.0. Species that appeared in this community in 2020 were *Zoysia sinica* and *Artemisia fukudo*. This community was developed around areas where sand marshes were formed along the coast.

In 2016, plants in the *Artemisia fukudo* community had a height range of 23–47 cm, a cover rate of 50%, and an average number of species of 1.5. Species that appeared in this community were *Artemisia fukudo*, *Zoysia sinica*, and *Suaeda maritima*. In 2020, these plants had an average height range of 14.9 cm to 21.3 cm, a cover rate of 80%, and an average number of species of 1.3. Species that appeared in this community in 2020 were *Artemisia fukudo*, *Zoysia sinica*, and *Suaeda maritima*. This community was developed around areas where sand marshes were formed along the coast.

The *Limonium tetragonum* community only appeared in 2016. Plants in this community had an average height of 10–29 cm, a cover rate of 30%, and an average number of species of 1.0. Its companion species was *Suaeda maritima*. This community appeared around areas where sand marshes were formed along the coast. Furthermore, this community of halophytes distributed in brackish water salt marshes formed sloppy communities on low and high tide level lines of the deposited sandy soil.

The *Suaeda glauca* community only appeared in 2016. Plants in this community had an average plant height of 16–52 cm, a cover rate was 20%, and an average number of species of 1.5. Its companion species were *Zoysia sinica* and *Atriplex gmelinii*. This community was centered around the dry terrain on the edge of the coastal embankment. Furthermore, this community of halophytes distributed in coastal salt marshes developed around dry habitats on the lower bank of the coastline (where desalinization proceeded from the upper area of the high-water line) and on the lower section of the embankment.

Germination rates

According to monthly investigations of germination rates of dominant halophyte species in the Hampyeong Bay in the period of 2016–2020, *Suaeda maritima* and *Artemisia fukudo* had the highest germination rates in May (91.8% and 88.1%, respectively), *Zoysia sinica* and *Phragmites communis* had the highest germination rates in June (92.1% and 88.5%, respectively), and *Limonium tetragonum* had the highest germination rate in July (84.4%) (Fig. 3). *Suaeda maritima* and *Artemisia fukudo* had a rather early germination period. The tendency to decline was greater in *Suaeda maritima* than in *Artemisia fukudo*. *Phragmites communis*, *Zoysia sinica*, and *Limonium tetragonum* as perennial plants were found to proceed with later germination than *Suaeda maritima* and *Artemisia fukudo* known as biennial plants.

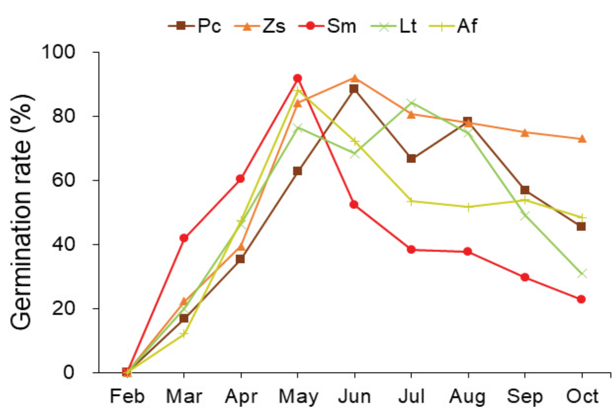

Fig. 3. Monthly changes in germination rates of halophytes (average values for the period of 2016–2020). Pc: Phragmites communis; Zs: *Zoysia sinica*; Sm: *Suaeda maritima*; Lt: *Limonium tetragonum*; Af: *Artemisia fukudo*.

Changes in vegetation

In 2016, our vegetation survey covered the distribution of seven communities: *Phragmites communis*, *Zoysia sinica*, *Zoysia sinica-Artemisia fukudo*, *Limonium tetragonum*, *Suaeda glauca*, *Artemisia fukudo*, and *Suaeda maritima*. The Suaeda maritima community was the most widely distributed one, accounting for 43.3% (6,128.5 m^2) of the total vegetation area (Table 2). In 2017, 284.0 m^2 (2.0% of the total vegetation area) of the *Suaeda maritima-Limonium tetragonum* community was newly formed in or near the *Suaeda maritima* community. Other communities showed no significant changes in their distribution areas. In 2018, the narrowly distributed *Suaeda glauca* community (36.9 m^2) disappeared, while the area covered by *Zoysia sinica* community, which accounted for 20% of the total vegetation area in 2016–2017, increased to 4,619.3 m^2 (36.9%) in 2018 (Fig. 4).

The *Suaeda maritima* community accounted for 42.5% (6,128.5 m^2) of the total vegetation area in 2017. However, the area covered by this community decreased dramatically to 23.6% (2,949.9 m^2) of the total vegetation area in 2018. The area covered by this community was partially increased in the sand-deposited terrain adjacent to seawater in the northern part of the study site. However, it was decreased significantly in the southern part of the study site. It also decreased in areas where it competed with the *Zoysia sinica* community.

In 2019, the area covered by the *Suaeda maritima* community that was distributed around the *Zoysia sinica* community was gradually decreased. The area adjacent to seawater on the northern part of the study site was also largely decreased. Although the coverage area by the *Suaeda maritima* community was further reduced in areas where it competed with the *Zoysia sinica* community, its coverage area on the southern part of the study site was actually increased.

In 2020, areas covered by the *Suaeda maritima* community on the southern part of the study site were decreased, while these areas on the northern part were increased, resulting in a slight overall increase in the total area covered by this community. In the case of *Limonium*

Table 2. Area and ratio of vegetation in the study site of Hampyeong Bay (2016 – 2020)

Vegetation*	2016		2017		2018		2019		2020	
	Area (m^2)	Ratio (%)	Area (m^2)	Ratio (%)	Area (m^2)	Ratio (%)	Area (m^2)	Ratio (%)	Area (m^2)	Ratio (%)
Pc	3,092.3	21.8	3,092.3	21.4	2,532.3	20.2	2,825.6	22.3	2,926.5	22.1
Zs	3,024.1	21.4	3,024.1	20.9	4,619.3	36.9	4,696.7	37.0	5,276.2	39.8
Sm	6,128.5	43.3	6,128.5	42.5	2,949.9	23.6	2,439.0	19.2	3,182.4	24.0
Sm-Lt	0.0	0.0	284.0	2.0	272.9	2.2	887.3	7.0	199.6	1.5
Sm-Af	0.0	0.0	0.0	0.0	0.0	0.0	143.7	1.1	222.5	1.7
Zs-Af	1,479.1	10.5	1,479.1	10.2	1,057.5	8.4	798.0	6.3	812.7	6.1
Zs-Sm	0.0	0.0	0.0	0.0	170.5	1.4	34.1	0.3	0.0	0.0
Zs-Lt	0.0	0.0	0.0	0.0	229.1	1.8	236.5	1.9	0.0	0.0
Af	298.1	2.1	298.1	2.1	602.5	4.8	572.4	4.5	623.0	4.7
Lt	93.8	0.7	93.8	0.6	80.9	0.6	43.9	0.3	0.0	0.0
Sg	36.9	0.3	36.9	0.3	0.0	0.0	0.0	0.0	0.0	0.0
Total	14,152.8	100.0	14,436.8	100.0	12,514.9	100.0	12,677.3	100.0	13,242.9	100.0

* Pc: *Phragmites communis*, Zs: *Zoysia sinica*, Zs-Af: *Zoysia sinica-Artemisia fukudo*, Zs-Sm: *Zoysia sinica-Suaeda maritima*, Zs-Lt: *Zoysia sinica-Limonium tetragonum*, Sm: *Suaeda maritima*, Sm-Lt: *Suaeda maritima-Limonium tetragonum*, Sm-Af: *Suaeda maritima-Artemisia fukudo*, Af: *Artemisia fukudo*, Lt: *Limonium tetragonum*, Sg: *Suaeda glauca*.

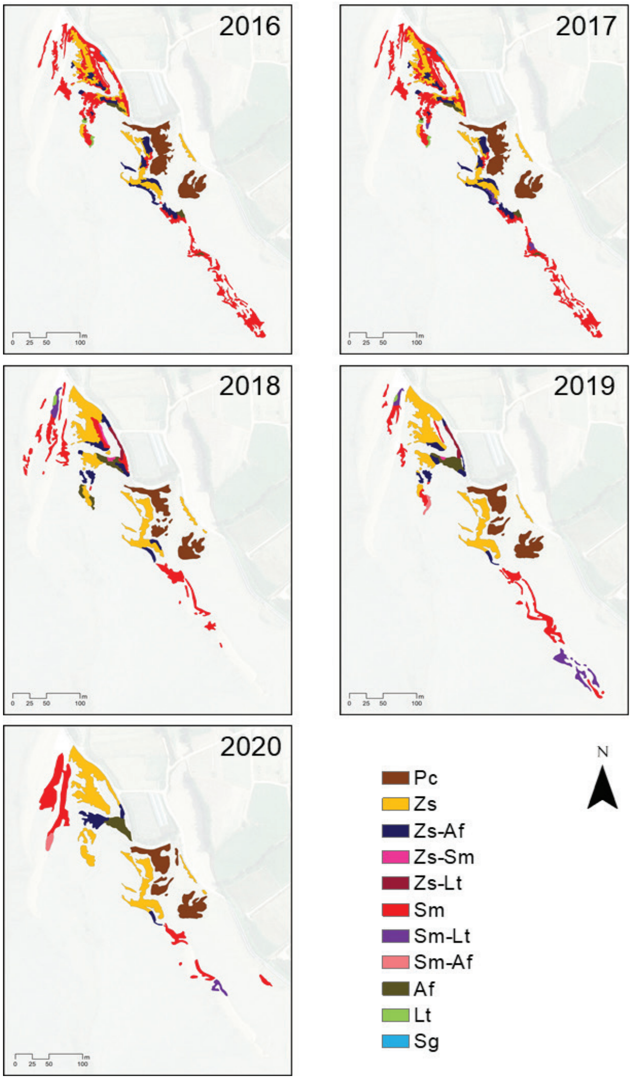

Fig. 4. Changes in vegetation coverage at the study site of Hampyeong Bay (2016–2020). Pc: *Suaeda maritima Limonium tetragonum*; Zs: *Zoysia sinica*; Zs-Af: *Zoysia sinica-Artemisia fukudo*; Zs-Sm: *Zoysia sinica-Suaeda maritima*; Zs-Lt: *Zoysia sinica-Limonium tetragonum*; Sm: *Suaeda maritima*; Sm-Lt: *Suaeda maritima-Limonium tetragonum*; Sm-Af: *Suaeda maritima-Artemisia fukudo*; Af: *Artemisia fukudo*; Lt: *Limonium tetragonum*; Sg: *Suaeda glauca*.

tetragonum community, which was distributed in small areas, sand spits were found to have expanded twice, leading to destruction of this community. The covering area of this community that was found to have expanded on the southern part of the study site was also confirmed to be destroyed as a consequence of this expansion (Fig. 5).

Discussion

According to our observations of changes in halophyte vegetation in the study site over a five-year period, the area covered by the *Phragmites communis* community remained stable, the area covered by the *Zoysia sinica* community was gradually increased, while the area covered by the *Suaeda maritima* community was gradually decreased. In the meantime, narrowly distributed *Limonium tetragonum* and *Suaeda glauca* communities disappeared. Even in this short study period of five years, vegetation in the Hampyeong Bay salt marsh underwent significant changes.

The *Phragmites communis* community was distributed around the edge of the coastal line adjacent to land. According to Jang *et al*. (2013), the physicochemical soil environment of reed-dwelling areas has a combination of mud, silt, and clay with high moisture content, high soil salt concentration, and high organic matter content. In the present study, soil salinity was found to be the highest for the *Phragmites communis* community, which seemed to be related to soil texture characteristics. When the sand content in the soil is high, soil desalinization often occurs due to freshwater inflow or precipitation from the ground. However, when soil silt or clay content is high, it can have a contrasting effect with a poor drainage, resulting in high salt concentrations (Lee *et al*., 2009).

The *Suaeda maritima* community was distributed around sand spits where sand was deposited due to frequent disturbances caused by external physical factors such as typhoons and waves, rather than having distribution in coastal areas adjacent to land where its primary settlement would be difficult because *Phragmites communis* and *Zoysia sinica* communities were already dominant in these areas. Although the development of main roots in early stages of plant growth was slow, the development of lateral roots progressed rapidly with a tendency to maintain stable settling in unstable subsoil environments after April (Lee, 2005). The present study also showed an average germination rate of 91.8% for *Suaeda maritima* in May. This species was discovered to be the fastest-germinating species among all plant species in the area. In the same coastal salt marsh, species with earlier germination periods have an advantage during interspecific competition (Fischer & Miles, 1973; Ross & Harper, 1972). In the present study, *Suaeda maritima* appeared earlier than other plant species, including *Zoysia sinica* and *Artemisia fukudo*, which was why it was able to occupy the area earlier, providing it an advantage for growth and development. This implied an ecological significance of prematurely settling in the habitat (Harper, 1977; Mack & Harper, 1977). In addition, our analysis of soil factors in areas inhabited by *Suaeda maritima* showed the lowest organic matter and soil moisture contents, sug-

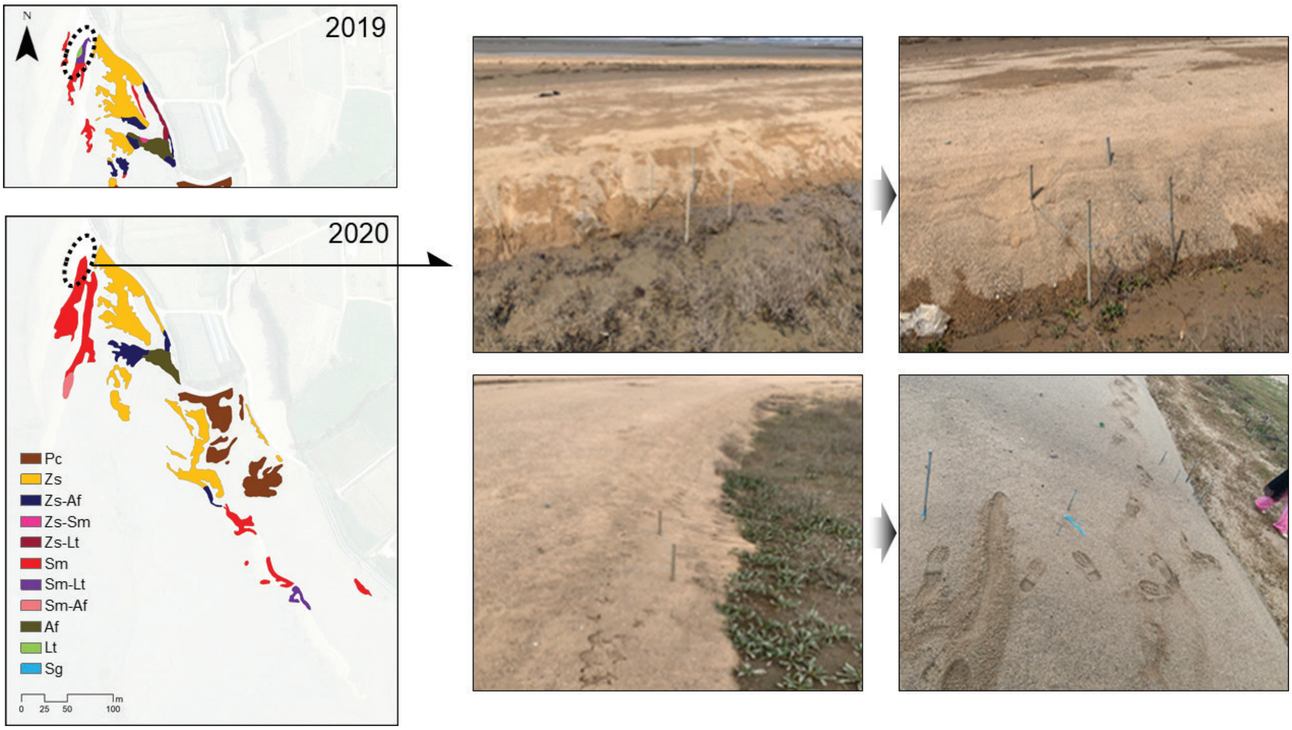

Fig. 5. Photograph showing the loss of *Limonium tetragonum* (Lt) communities due to two consecutive expansions of sand spits. Pc: *Phragmites communis*; Zs: *Zoysia sinica*; Zs-Af: *Zoysia sinica-Artemisia fukudo*; Zs-Sm: *Zoysia sinica-Suaeda maritima*; Zs-Lt: *Zoysia sinica-Limonium tetragonum*; Sm: *Suaeda maritima*; Sm-Lt: *Suaeda maritima-Limonium tetragonum*; Sm-Af: *Suaeda maritima-Artemisia fukudo*; Af: *Artemisia fukudo*; Lt: *Limonium tetragonum*; Sg: *Suaeda glauca*.

gesting that this species could grow under unfavorable conditions with low levels of nutrients and moisture. Therefore, compared to other plants, it has a higher chance of early settlement in coastal salt marshes.

In contrast, in areas where *Zoysia sinica* and *Suaeda maritima* were distributed together, the area covered by *Suaeda maritima* was gradually decreased due to competition between these two species. This seemed to be the result of difference in germination durability between them. The germination rate of *Suaeda maritima* decreased dramatically after May (91.8%) (June: 52.3%, July: 38.3%). However, the germinate rate of *Zoysia sinica* showed a slow decline (84.4% in May, 92.1% in June, and 80.7% in July). Therefore, if these two species were in a competitive relationship, habitat expansion would be difficult for *Suaeda maritima* due to continuous competition between their seedlings.

Aerial photographs taken prior to this study showed that sand spits on the northern part of the study site had gradually expanded (Fig. 6). This indicated that the sand transported by tides had been continuously deposited, leading to an increase in the area inhabitable by plants (Boyd *et al*., 1992). In particular, *Suaeda maritima*, which has adapted to early growth in coastal salt marshes, is expected to be the first one to settle in this area in the future. Contrarily, due to the influence of waves caused by strong winds such as typhoons, sand can cover the habitat of plants that are already growing here. Thus, these plants could be destroyed. Such phenomenon seemed to have occurred for the *Limonium tetragonum* community, which was narrowly distributed. Therefore, it can be concluded that tides and waves in coastal salt marshes are important factors influencing the environment for halophyte growth.

Conflict of Interest

The authors declare that they have no competing interests.

Acknowledgments

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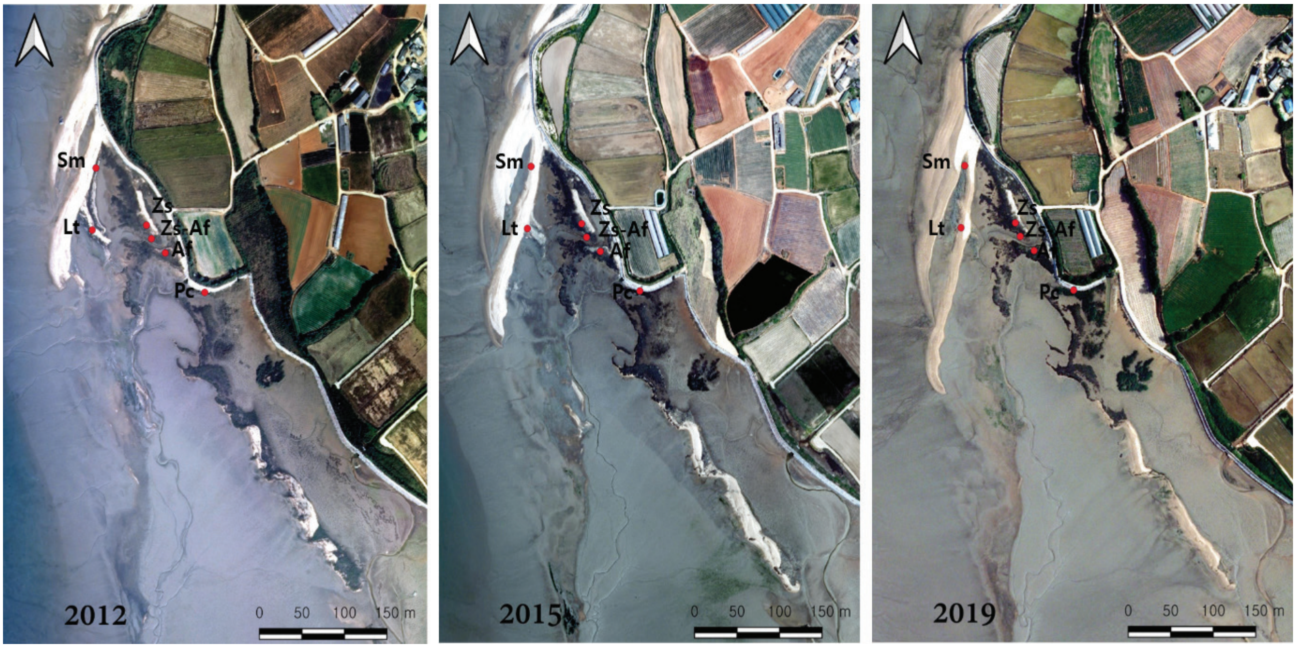

Fig. 6. Observed topographic changes of coastal areas on aerial photographs from the past to the present (2012, 2015, and 2019). The sand spit on the northern side of the site is gradually expanding.

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