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Research Article

Vertical distribution of the salt marsh invader *Spartina alterniflora* and native halophytes on the west coast of Korea in relation to tidal regimes

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Abstract

Smooth cordgrass (*Spartina alterniflora* Loisel.), an aggressive non-native species worldwide, colonized tidal flats on the west coast of Korea in two regions differing in tidal amplitude between 1990–2004. By the time of our study in 2015, expansion had occurred both clonally and through formation of new patches, providing an opportunity to determine intertidal range, which is a key component of understanding the threat posed by *S. alterniflora* through competition with native halophytes or transformation of unstructured mudflat. At Ganghwa (5.69 m tidal range), *S. alterniflora* ranged from 3.52 to 1.34 m above Mean Sea Level (MSL). At Jindo (2.02 m tidal range), *S. alterniflora* ranged from 1.57 to -0.18 m relative to MSL. Thus, a wider absolute intertidal range was occupied by *S. alterniflora* at the megatidal vs mesotidal region, but the lower limit of *S. alterniflora* did not extend below MSL under megatidal conditions, a pattern that now appears to emerge consistently in both the native and introduced range. In both study regions, *S. alterniflora* occurred at the same elevations as other salt marsh plants, occupying an upper zone with *Phragmites australis* (non-native) and middle zone with several native species including *Suaeda japonica*. *S. alterniflora* occurred below native marsh vegetation at all sites, which would result in transformation of the extensive mudflats along the Korean coast.

Key words: saltmarsh plants, invasive species, megatidal flat, Yellow Sea, Korean coastal wetland, Ganghwa, Jindo

Introduction

Salt marshes are characterized by striking zonation of vascular plants correlated with marsh elevation (Chapman 1974; Gray 1992). Lower limits are typically defined by physical stress of salinity or waterlogging, and few plant species have adaptations that enable survival below the high tide mark. One such species is smooth cordgrass (*Spartina alterniflora*, hereafter *Spartina*), which accordingly has had transformative effects after introduction to tidal flats lacking vegetation at that zone (Strong and Ayres 2013; Ruesink 2018). *Spartina*'s intertidal distribution in its native range tends to increase with tidal amplitude, with an additional latitudinal factor appearing to restrict its upper limit (McKee and Patrick 1988). The recent invasion of *Spartina* along the west coast of Korea allows evaluation of whether these patterns of intertidal distribution persist in novel meso- and megatidal regions and overlap with native marsh.

Spartina, native to the Atlantic and Gulf coasts of America (Simenstad and Thom 1995; Blum et al. 2007), exclusively dominates low marsh habitats, followed by dense, monospecific stands of *Spartina patens* at slightly higher elevations, before reaching a suite of species in the high marsh zone (Bertness 1991). *Spartina* generally grows between Mean High Water (MHW) and Mean Low Water (MLW). However, no consistent elevation exists for zonation relative to a tidal datum due to biotic interactions, tidal inundation, and local or regional differences in other factors, such as salinity and physical disturbance (McKee and Patrick 1988).

Spartina has invaded in the western United States, Australia, New Zealand, Japan, and China, following either intentional or unintentional introduction (An et al. 2007; Maebara et al. 2020). The growth form includes colonization by seeds or fragments and subsequent clonal expansion into dense patches that ultimately fuse into meadows. Stems can accumulate sediment and/or build up rhizome mats below ground that effectively raise the level of the tidal flat. *Spartina* has a wide ecological niche, occupying sediments ranging from silt to cobble, a large latitudinal range (Mexico to Nova Scotia where native; Bruno and Kennedy 2000; Pennings and Bertness 2001), and salinity from brackish to saltwater (Nestler 1977; Field observation from Korean coast). Such high environmental tolerance may enable still wider distribution where introduced, as the realized niche is less restricted, which in turn can lead to competition with native vegetation. Additionally, genetic changes appear to have occurred in *Spartina* invading China and Japan that may enhance performance in the invaded range (Liu et al. 2020; Maebara et al. 2020).

Two regions along the west coast of Korea currently have *Spartina*. The introduction of *Spartina* was reported in 2015 (Jung et al. 2015; Kim et al. 2015). These were reported as *S. anglica* in Ganghwa and *S. alterniflora* in Jindo respectively, later revealed as *S. alterniflora* through total genomic DNA studies from these two study sites (Hong JS, unpublished data). At Ganghwa, *Spartina* is estimated to have arrived at Buno in 1990 and Dongmak in 2004. At Jindo, *Spartina* is estimated to have arrived at the local site of Namdong-ri in 2004. As of 2015, *Spartina* occupied 2,245 m^2 in Buno, 8,738 m^2 at Dongmak, and 6,263 m^2 at Namdong-ri (unpubl. Data by authors). By 2020, *Spartina* had expanded to over 40,000 m^2 of previously unvegetated tidal flat in at least eight different sites along the west coast of Korea (Jung HI, Korea Marine Environment Management Corporation, personal communication), despite substantial investment (3.5B Korean Won = US $3 million) in mechanical control efforts of plowing and mowing.

The goal of this study was to evaluate the extent of transformation of tidal mudflats on the west coast of Korea likely to occur from *Spartina*, and the extent of overlap with native marsh species. To accomplish this goal, we accurately measured the vertical distribution of *Spartina* and native halophytes at sites with different tidal regimes. We expected that the intertidal distribution of invasive *Spartina* would at least match that of the native range and potentially be wider.

Materials and methods

Study sites

Two regions on the west coast of South Korea about 400 km apart have been invaded by *Spartina* marshes. Ganghwa is located at the estuaries of the Han River near the Seoul metropolitan area. The southern coast of Ganghwa Island has a wide open-coast megatidal muddy flat with a total area of about 105 km^2 (approximately 17.5 × 6 km, Fig. 1). A large amount of sediment is supplied from the land and transported by tide and currents with the mixing of Yellow Sea seawater and freshwater from the Han River (Lee et al. 2011). The mean tidal range is about 6 m (KHOA 2017). Two sites within the Ganghwa region were known to contain *Spartina* in 2015. At the first site, Dongmak (37°35.62'N, 126°26.74'E), the upper zone consisted of small patches of reed marsh (*Phragmites australis*) and scattered other halophytes (*Triglochin maritimum* and *Schoneoplectus triqueter*). Further down, *Suaeda japonica* occurred in a dense band of 100 m width. In 2015, eleven years after its introduction in 2004, *Spartina* occurred along a 1.5 km section of coastline, with small patches, many of which had expanded and fused. At the second site, Buno (37°35.51'N, 126°27.76'E), where *Spartina* likely arrived in 1990, a large *Spartina* patch was located adjacent to the dock in a relatively enclosed area, and small patches were distributed along the coastline to the north. No native vegetation was present at this site. The second region of Korea invaded by *Spartina* is in the southwestern part of Jindo Island on the southernmost part of the west coast of Korea, where the tidal range is about 2 m (KHOA 2017). The study site, Namdong-ri (34°21.86'N, 126° 9.72'E), is a small tidal flat of about 0.029 km^2 in an enclosed bay, with an entrance just 50 m wide. The upper part of the bay is connected to a rivulet from the land. *Spartina* vegetation, which first appeared in 2004, was by 2015 composed of rather cohesive and atypical large patches. The largest *Spartina* patch was about 100 m wide. The upper zone was dominated by halophytes such as *P. australis*, *Zoysia sinica*, and *Suaeda maritima*.

Field survey

Field surveys were conducted at Jindo and Ganghwa tidal flats in June and August 2015, respectively. Native halophytes and *Spartina* inhabited these tidal flats, including in front of the levee in both regions. To measure vertical distribution, we included all patches along each transect. Transects were established from the upper part of the tidal flat past the lower extent of any vegetation. They were 15 m wide and perpendicular to the shore, extending 300 m at Dongmak, 50 m at Buno, and 100 m at Namdong-ri. Five transects were established at Dongmak and Namdong-ri, and two at Buno. Intertidal elevation was determined at stations every 1–10 m, with closer intervals where slope condition and marsh plant presence changed (sextant-based positioning). Distance between stations was recorded, and at each station, tidal elevation was determined (Total Station, PANTAX R-300) in relation to nearby spatial reference points (National Geographic Information Institute in Korea - NGII and Korea Hydrographic and Oceanographic Agency - KHOA). We used the harmonic constants obtained from KHOA at each site to extract elevation for the following tidal datums: AHHW, MHWS, MHW, MHWN, MTR (MHW–MLW) (Table 1). We used the term Half Tide Level (HTL) to refer to the plane midway between MHW and MLW, which is similar to Mean Sea Level (McKee and Patrick 1988).

Table 1. Mean tidal range and elevations of tidal datums in each study site. Values represent the elevation above Mean Sea Level (m).

Tidal datum	Tidal datum abbreviation	Ganghwa (Dongmak, Buno)	Jindo (Namdong-ri)
Approximately Higher High Water	AHHW	4.67	1.95
Mean High Water Spring	MHWS	3.99	1.35
Mean High Water	MHW	2.85	1.01
Mean High Water Neap	MHWN	1.73	0.66
Mean Tidal Range (MHW–MLW)	MTR	5.69	2.02

Vegetation mapping and image analysis

Area of vegetation was determined from photographs at an altitude of 50 m using a drone (DJI Phantom 3) equipped with a digital camera. Prior to photography, reference points for measuring GSD (Ground Sample Distance) were arbitrarily set and their geopositions recorded. Multiple photos from the drone were combined to create a vegetation map for each 15 m-wide transect using Agisoft PhotoScan pro, an image editing software. Elevations measured in the field were adjusted to local elevation (meters above local mean sea level) and incorporated as a data layer along each transect. Based on the map, we described vegetation type, percent coverage, and distribution area per 0.1 m interval of elevation.

Comparison with global data on intertidal distribution of *Spartina alterniflora*

We found reports of *Spartina* upper and lower limits at 28 sites within the native range that differed in tidal regime, as well as seven sites outside the native range. We compiled this information to assess whether the intertidal distribution in Korea showed upper and lower limits consistent with the meso- and mega-tidal regimes along the coast.

Results

Tidal condition, profile, and vertical distribution of salt marshes

Mean tidal range (MTR) at Ganghwa was 5.69 m, more than twice that of 2.02 m in Jindo (Table 1). The slope of the tidal flat was shallowest at Dongmak (Ganghwa) (Fig. 2A, B). Namdong-ri site in Jindo was relatively steep, with high bathymetric variation in the upper tidal flat and lower parts near the tidal creek (Fig. 2C). There were tidal creeks at the end of the marsh, coinciding with the boundary of the *Spartina* vegetation (Figs 1, 2C).

Marshes including *Spartina* vegetation of Dongmak were vertically distributed from 3.63 m to 1.49 m (Δ Elevation = 2.14 m) above MSL. Those of Buno were vertically distributed from 2.70 m to 1.34 m (Δ Elevation = 1.36 m), with the upper limit restricted due to the artificial wall. Those of Namdong-ri were distributed from 1.69 m to -0.18 m (Δ Elevation = 1.87 m) (Fig. 2). Comparing tidal datums presented in Table 1 with Fig. 2, marshes at Ganghwa were distributed from below MHWS (Dongmak) or MHW (Buno) to below MHWN. However, in Namdong-ri of Jindo, marshes were distributed from below AHHW to below MSL, meaning that the marsh of Namdong-ri experienced a wider variety of tidal inundation duration than at Ganghwa.

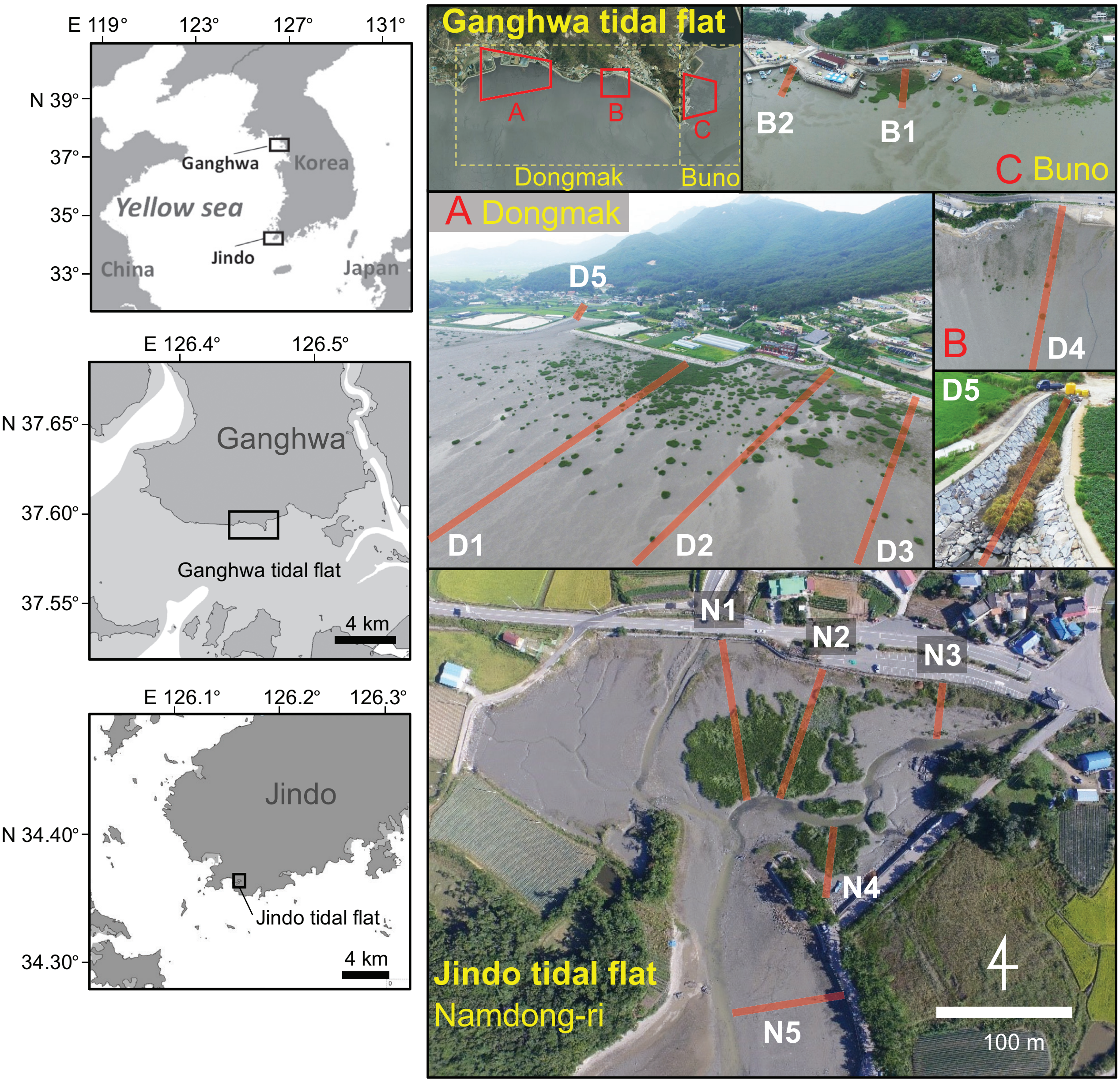

Figure 1. The study areas, Ganghwa and Jindo tidal flats located in the west coast of Korea and photographs showing the survey transects established in each sampling site in Ganghwa (Dongmak, D1–5; Buno, B1, 2) and Jindo (Namdong-ri, N1–5).

Distribution of *Spartina* marsh by drone image analysis

Dongmak and Buno, Ganghwa

The areal cover of *Spartina* vegetation on transects of Dongmak was 1,918 m^2, which was 14% of total area surveyed (Fig. 3A). Based on image analysis of the vegetation map, the coverage of *Spartina* patches here was the highest in transect D1 (28%) where the largest patch of *Spartina* occurred. The coverage of *Spartina* patches was the lowest in transect D4 (3%). The coverage increased rapidly below MHW, peaking at 2.5 m above MSL. It gradually decreased to MHWN. The mean elevation of *Spartina* marsh was 2.43 m above MSL. More than 90% of surveyed *Spartina* marshes were distributed between 2.9 m and 1.8 m. The highest patch appeared at 3.52 m while the lowest patch appeared at 1.49 m

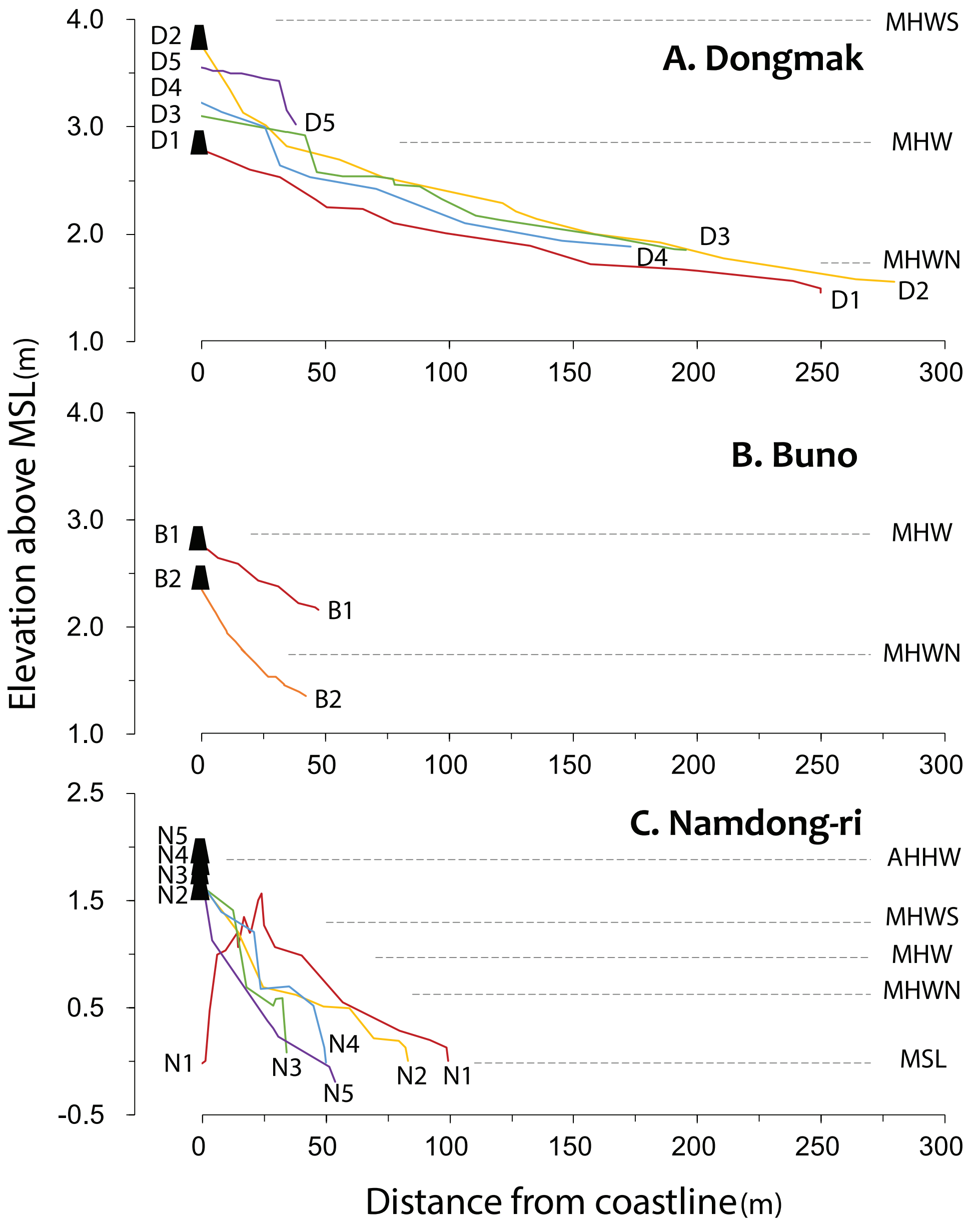

Figure 2. The transect profiles of the study site. Solid trapezoid marks indicate an artificial levee (**A** Dongmak; **B** Buno; **C** Namdong-ri).

above MSL (Fig. 3A, Table 2). Therefore, the vertical distributional range of *Spartina* patches in Dongmak was 2.03 m. The highest patch was on transect D5. Its size was small. Transect D5 included a narrow channel about 3 m wide. The channel was connected to a small stream of freshwater input (Fig. 1). The patch on D5 transect was close to MHWS. In Buno, only the *Spartina* vegetation existed. The areal cover of the marsh on transects was 634 m^2, accounting for 45% of the survey area (Fig. 3B). The mean elevation, main distributional range, and lower limit of the distribution were similar to those of the nearby Dongmak. However, the upper limit of the distribution was located lower (Fig. 3B, Table 2). Here, the highest elevation of the *Spartina* marsh was 2.70 m above MSL. Its distribution range was 1.36 m, which was narrower than that in Dongmak. However, the distribution was limited in the uppermost part due to the artificial levee (Figs 1, 2).

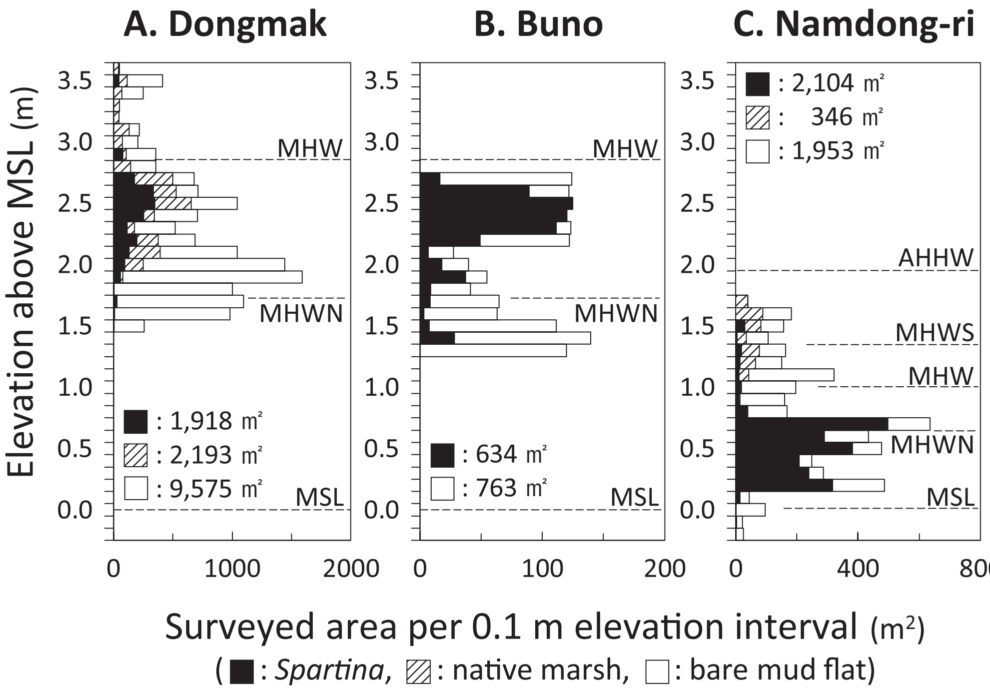

Figure 3. Vertical distribution of *Spartina* vegetation, native marsh and bare mudflat on the survey transects based on cover in aerial images. Total area estimates include the 12 belt transects surveyed. MSL: Mean Sea Level. See Table 1 for other tidal datums.

Namdong-ri, Jindo

The areal cover of *Spartina* vegetation on transects of Namdong-ri was 2,104 m², accounting for 48% of total area surveyed (Fig. 3C). The mean elevation of the *Spartina* vegetation was 0.53 m (below MHWN) (Table 2), which was lower than the mean elevation of the *Spartina* vegetation in Ganghwa above MHWN. About 90% of the *Spartina* vegetation was distributed at 0.7 m to 0.2 m, which was MHWN to near MSL (Fig. 3C). The coverage was the highest at 0.7 m but similar (65–83%) within the main distribution range. It decreased rapidly near the tidal creek at 0.2 m above MSL. This abrupt decline contrasted with Ganghwa, where *Spartina* gradually decreased at lower elevations (Fig. 3). The highest patch appeared at 1.57 m while the lowest patch appeared at -0.18 m relative to MSL (Fig. 3C, Table 2). Therefore, the vertical distributional range of *Spartina* was 1.74 m.

Native vegetation

Native vegetation was distributed from below MHWS to near MHWN in Dongmak and from below AHHW to MHWN in Namdong-ri (Fig. 4). Common reed, *P. australis*, was the highest vegetation in both regions. It was distributed below MHWS in Dongmak and below AHHW in Namdong-ri. Below the reed marsh, *T. maritimum*, *S. triqueter*, and *S. japonica* were distributed in Dongmak. *Z. sinica* and *S. maritima* were distributed in Jindo in order of elevation from high to low. In both regions, *Spartina* patches occurred throughout the elevational range of *P. australis*. In addition, *Spartina* occurred below all other vegetation in both regions. Therefore, vertical distribution ranges of *Spartina* were much larger than those of all native salt marshes surveyed. In terms of the *Spartina* invasion within the transect, *Spartina* marsh occupied 47% of the total area of marsh plants in

Table 2. Summary of the vertical distribution of *Spartina* marsh in study sites. Values represent the elevation above Mean Sea Level (m).

Locality	Ganghwa		Jindo
Site	Dongmak	Buno	Namdong-ri
Upper limit	3.52	2.70	1.57
Mean elevation	2.43±0.31	2.30±0.31	0.53±0.26
Lower limit	1.49	1.34	-0.18
Growth Range	2.03	1.36	1.74

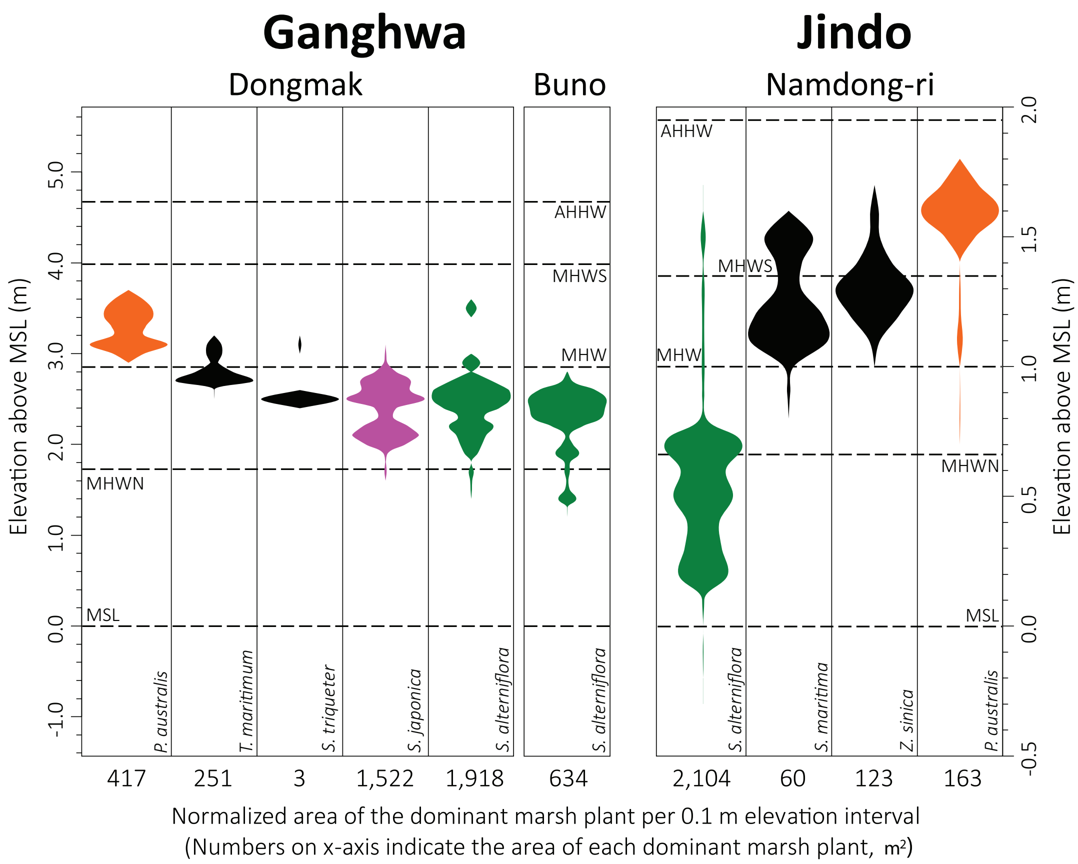

Figure 4. The vertical distribution of dominant marsh plants in study sites, as relative cover across elevations for each species. Total area differs across species and is shown below x-axis. MSL: Mean Sea Level. See Table 1 for other tidal datums.

Dongmak and 86% in Namdong-ri (Fig. 3). Invasion of *Spartina* into the zone of *P. australis* was clearly observed in D2 and D5 of Dongmak and N3 of Namdong-ri. In transect D2 of Dongmak, small patches of *Spartina* were attached to the edge of the *P. australis* marsh (Fig. 5). However, in D5, patches of *Spartina* and *P. australis* of similar sizes were attached. Between AHHW and MHW of N3 in Namdong-ri, *Spartina* patches existed inside *P. australis* patch as well as *S. maritima* (Fig. 5). Native vegetation was not distributed below MHWN, the main distribution range of the *Spartina* in Namdong-ri (Fig. 4). Therefore, *Spartina* of Namdong-ri existed alone in their main distribution range. On the other hand, the main distributional range of *Spartina* at Dongmak, MHW and MHWN, overlapped that of *S. japonica* (Fig. 4), a halophyte at the lower edge of native marsh. For that reason, most patches of *Spartina* in Dongmak were found in the *S. japonica* marsh.

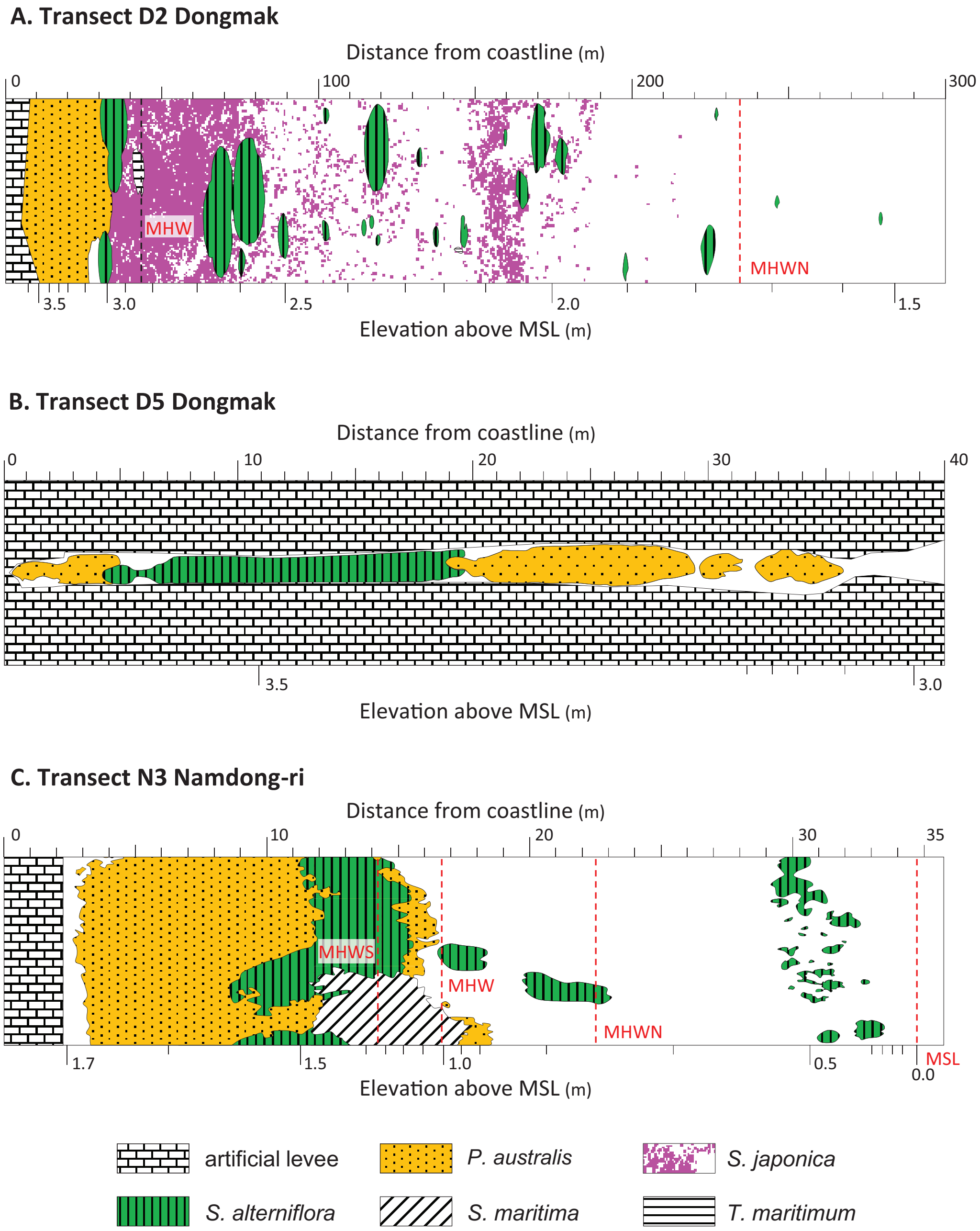

Figure 5. The maps of distribution of saltmarsh vegetation in transect D2 (**A**) and D5 (**B**) in Dongmak and N3 (**C**) in Namdong-ri. The transect D5 was between MHWS and MHW. See Table 1 for tidal datums.

Comparison with global data on intertidal distribution of *Spartina alterniflora*

The intertidal elevations occupied by *Spartina* in 2015 at three sites in Korea were consistent with reports elsewhere in its native and non-native range, once accounting for tidal regime (Fig. 6). In much of the native range of *Spartina*, vertical distribution increases directly with tidal amplitude. However, above a tidal range of 3 m, the lower limit of *Spartina* rises approximately in parallel with the upper limit (Fig. 7). Meso-tidal and mega-tidal Korean sites thus showed primarily a shift upwards in *Spartina* as tidal range increased.

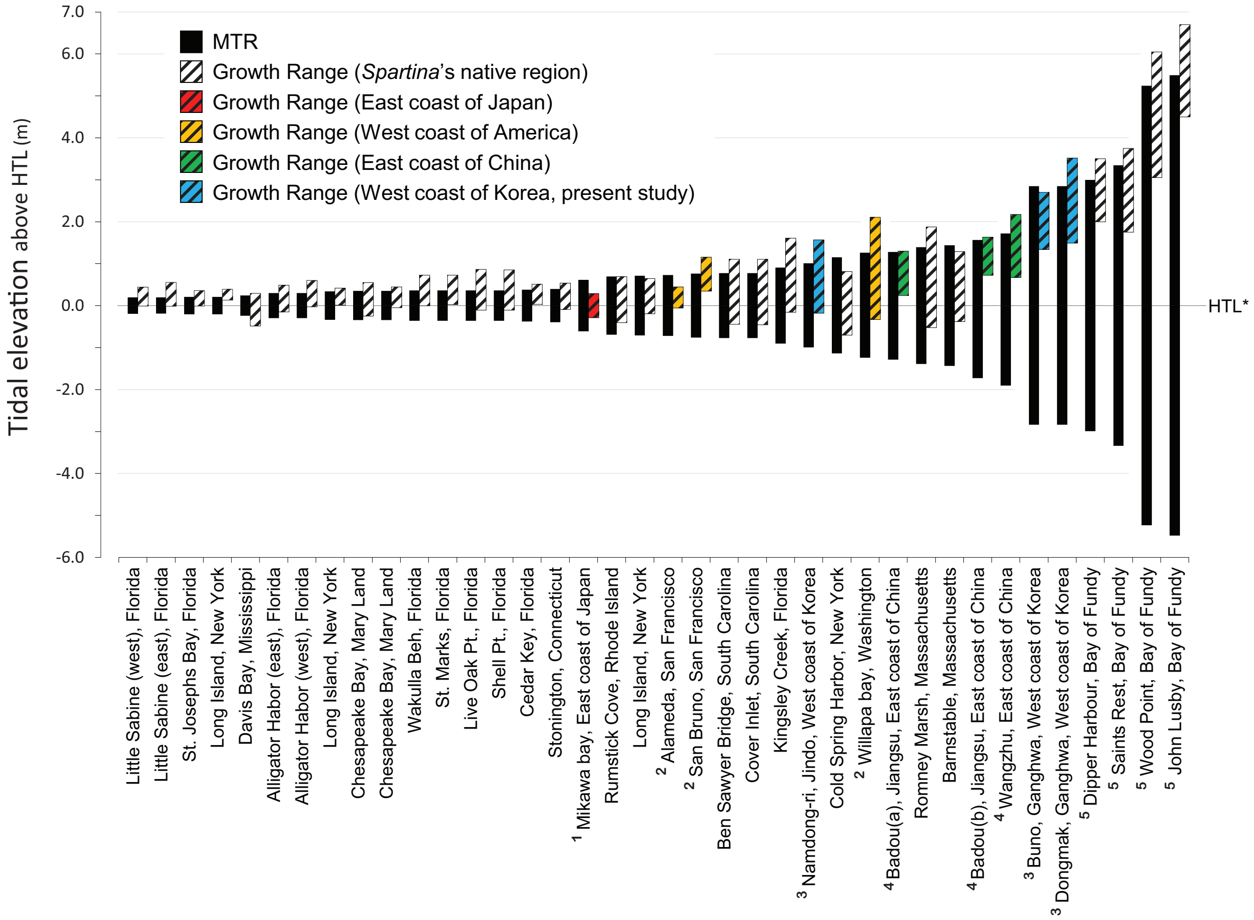

Figure 6. The elevational range of growth of *Spartina alterniflora* at locations along the east coast of America, San Francisco, east coast of China, east coast of Japan and the west coast of Korea, modified from McKee and Patrick (1988). 1: Kimura et al. 2016, 2: Callaway and Josselyn 1992, 3: present study, 4: Zhang et al. 2004, 5: Byers and Chmura 2007. HTL: Half Tide Level

Discussion

Vertical distribution range of *Spartina* in the study area

Spartina's main distributional range and elevation can vary regionally. In their native regions, *Spartina* grows principally in between MHW and MLW (McKee and Patrick 1988; Bertness 1991), except shifted higher under macrotidal conditions in the Bay of Fundy (Byers and Chmura 2007). In invaded sites in Willapa Bay, US west coast, distribution was reported from MHHW to about 1 m above MLLW (Sayce 1988). In China, *Spartina* can grow between MHW and MSL on Jiangsu tidal flat of Yangtze River Estuary, where *Spartina* was planted in 1979 to promote conversion of tidal flats into dry land (Zhang et al. 2004; An et al. 2007; Meng et al. 2020). Our study showed that the *Spartina* marshes were mainly distributed between MHW and MSL. Thus, *Spartina* is located for the moment similar to vertical ranges where native and where introduced in the Yangtze Estuary.

Spartina alterniflora is well known as an estuarine species. It has a wide variety of temperature and salinity ranges, occupying substrates from cobble to sand and mud flat (Nestler 1977; Bruno and Kennedy 2000). These wide ecological niches may allow *Spartina* to occur beyond their general distributional ranges. In fact, we observed that marginal ranges of *Spartina* in both regions were much wider than its main distributional ranges. Its patches were found even in the freshwater stream on the very upper intertidal area.

McKee and Patrick (1988) compiled vertical distributions of *Spartina* in the Atlantic and Gulf coast of America (Fig. 6). Its distribution in Jindo was measured with an upper limit between AHHW and MHWS, and lower limit below MSL. In the present study, the upper limit of the *Spartina*'s natural distribution in Jindo could not be measured due to the artificial levee. Nonetheless, compared to data from McKee and Patrick (1988), the distribution at Jindo appears similar in both *Spartina* distribution and tidal amplitudes to Kingsley Creek, Florida (Fig. 6). In Ganghwa, however, the upper limit of the distribution was between MHWS and MHW and the lower limit was close to MHWN, which was 1.34 m above MSL, and the regional comparisons for vertical distribution of *Spartina* showed a distribution rather at the upper part of the tidal elevation (Fig. 6). According to Fig. 6, our results look similar to Dipper Harbor and Saints Rest in the Bay of Fundy, Canada in native regions, and Badou and Wangzhu in East coast of China among invaded regions (Zhang et al. 2004; Byers and Chmura 2007), both of which have large tidal amplitude. The upper limit of the distribution was close to or above MHW, which is a typical upper limit across studies regardless of tidal amplitude. However, under meso- and mega-tidal regimes, the lower limit tends to shift well above MTL (Fig. 6). This pattern of vertical shift is different from what was previously reported for the native range on the east coast of United States, where elevational range increased in response to greater tidal amplitudes as *Spartina* extended both upper and lower boundaries (McKee and Patrick 1988) (Fig. 7). The lack of ability of *Spartina* to grow below MSL under mega-tidal conditions suggests that something other than inundation of the sediment is limiting. Mega-tidal conditions expose *Spartina* to extended periods of leaf inundation under low light that could be lethal. Many marsh plants survive waterlogging by actively moving oxygen to below-ground tissues, whereas inundation of leaves limits gas exchange and therefore can result in rapid and severe rhizome anoxia, particularly at night (Winkel et al. 2011).

This relationship between MTR and the lower limit of marshes has been observed in marsh vegetation more generally. Balke et al. (2016) found that, based on the data set of global marshes, the elevation of the marsh edge relative to MHW is negatively correlated to tidal range with a logarithmic curve. Therefore, they concluded that the potential salt marsh area between the pioneer (lower edge) vegetation elevation and MHW does not proportionally increase with tidal range. The lack of consistency of the lower limit in terms of tidal datums could be due to factors that determine the growth range of salt marsh plants, including flooding and drainage patterns (Mahall and Park 1976; Mendelssohn and Seneca 1980; Armstrong et al. 1985), salinity and freshwater input (Nestler 1977; Niering and Warren 1980; Webb 1983; Zedler 1986; Zedler et al. 1986), soil type and its soil oxidation-reduction (Gray and Bunce 1972; Howes et al. 1981; Mendelssohn et al. 1981), nutrient levels (Valiela and Teal 1974; Osgood and Zieman 1993), physical disturbance (Miller and Egler 1950; Redfield 1972; Bertness and Ellison 1987), and interspecific competition (Pielou and Routledge 1976; Bertness and Ellison 1987). In most studies, information on these factors is limited for comparisons between geographically different marshes. Therefore, it is difficult to predict the growth range of *Spartina* based on tidal conditions only. Nonetheless, the present study showed that the *Spartina* marsh distribution of the study sites seems quite close to the predictable elevation of the lower limit in Jindo and Ganghwa tidal condition (Fig. 7). Since 2016 of our study year, most of the *Spartina* marshes

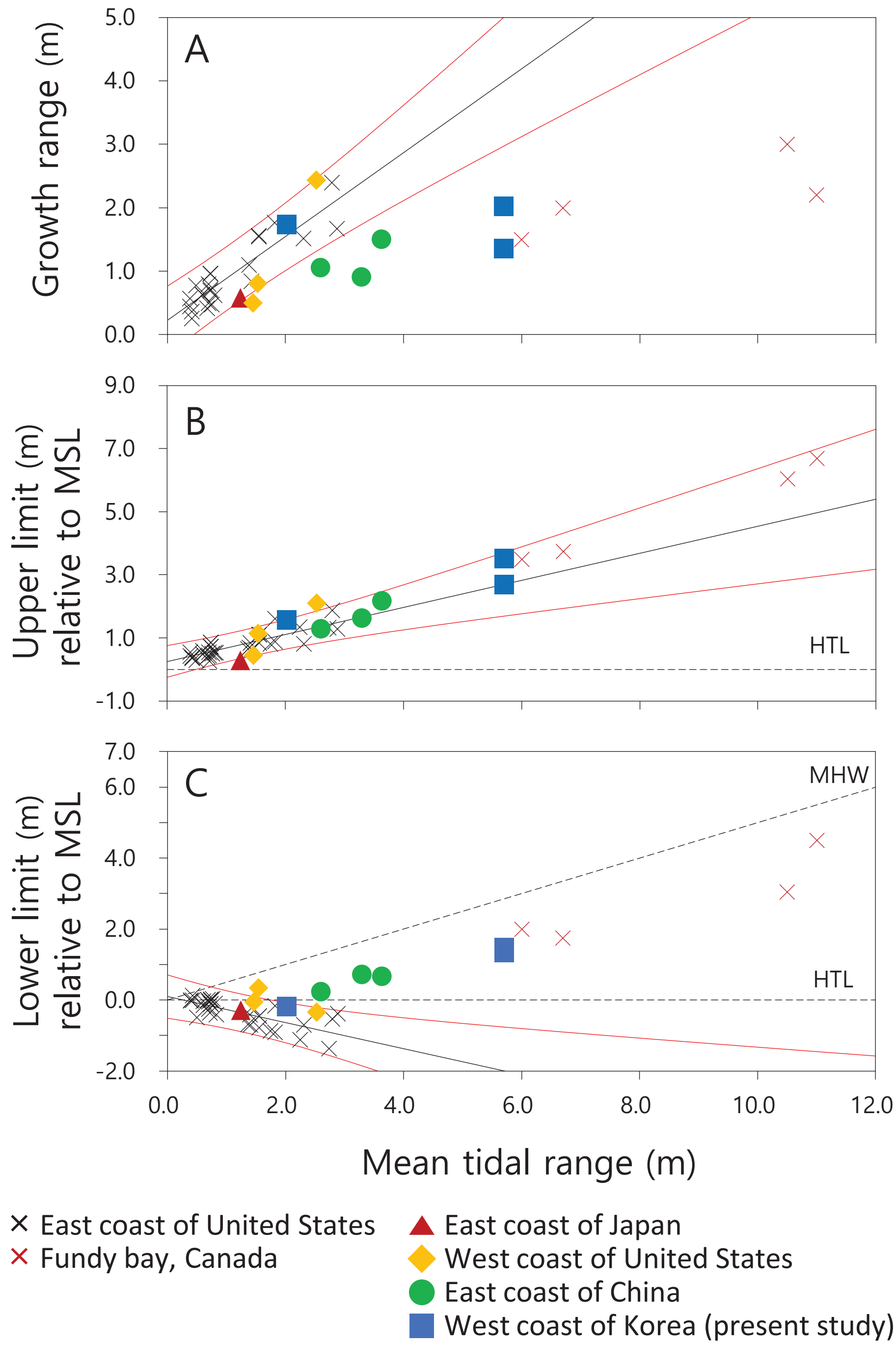

Figure 7. Relationship between mean tidal range and the growth range (**A**), upper limit (**B**) and lower limit (**C**) of occurrence of *Spartina alterniflora* relative to Half Tide Level. The trend line from McKee and Patrick (1988) and 95% Prediction Interval were fitted only to the east coast of United States.

in Jindo and Buno were removed by plowing and mowing, but in Dongmak, *Spartina* patches have been treated primarily on the upper rather than lower tidal flat (KNPS 2016; MOF 2021). Interestingly, the recent satellite imagery (Google Earth 2020, photo provided by Maxar Technologies in 2020) showed that the lowest patches did not spread any more towards the lower elevation than the survey period in 2015. It appears that Dongmak *Spartina* marsh had already reached the lowest possible elevation in 2015. Indeed, it has only been about ten years since

Spartina was introduced in Dongmak and Namdong-ri. Therefore, its spread is extremely rapid. However, it should be noted that the *Spartina* vegetation of Buno area had a lag phase for a decade after introduction (unpubl. Data by authors), suggesting that the spread of *Spartina* marsh is not always continuous but also locally different as well.

Local and regional comparisons

We observed local differences in patch shapes and their vertical distributions, showing many small scattered, round patches in the broadly open tidal flat of Ganghwa area, but rather cohesive and oblong patches in the enclosed bay of Jindo site (Fig. 1, Table 3). Therefore, *Spartina* showed horizontally expanded round patches along the shoreline in Ganghwa tidal flat, but developed atypically, near tidal creeks in a small, enclosed bay in Jindo. Further, Ganghwa site has a gentler slope, a wider and more open tidal flat with a larger tidal range, while Jindo has a relatively steeper slope, a narrower and more enclosed tidal flat with a smaller tidal range. These conditions might also have led to the similar development of patches in two sites of Ganghwa, even though the *Spartina* was introduced at different times, whereas Dongmak and Namdong-ri developed differently even though *Spartina* was introduced almost at the same time in both sites (Table 3, Fig. 4). Consequently, we think that tidal conditions might have determined the vertical distribution of *Spartina* in two study areas, but also topographical differences at the same time may be an important factor to take into consideration in the spatial distribution and form of the *Spartina* patches.

Table 3. Environmental characteristics and vertical distribution in two study localities invaded by *Spartina alterniflora* in Korea.

Locality	Ganghwa (Dongmak / Buno)	Jindo (Namdong-ri)
Mean Tidal Range	5.69 m	2.02 m
Type of tidal flat	opened	enclosed bay
Size of the study area	4.7 km^2 / 1.1km^2	0.03 km^2
Slope of the tidal flat	gentle	steep and undulated
Introduction time estimated (unpubl. Data by authors)	2004 / 1990	2004
Invaded area by *Spartina* marshes as of 2015	8,738 m^2 / 2,245 m^2	6,263 m^2
Vegetation type	many round patches, scattered	atypical, fused
Main distributional range	MHW–MHWN	MHWN–MSL
Growth range in tidal level (maximum–minimum)	below MHWS –below MHWN	below AHHW –below MSL

Competition with native salt marsh vegetation

Our results showed that *Spartina* had a potential to grow in any elevation used by native halophytes on the west coast of Korea. This means that the environmental plasticity of *Spartina* associated with immersion time is greater than those of other native halophytes. Competitive vegetation can set the upper limit of *S. alterniflora*, given that it is displaced by congeneric *S. patens* in its native areas of the Eastern U.S. (Bertness 1991). In addition to *S. patens*, common reed marsh *P. australis* is also known to compete with *S. alterniflora* as an invasive species in *Spartina*'s native habitat (Bertness et al. 2002; Vasquez et al. 2006).

An open question is the extent to which *Spartina* will replace or coexist with native marsh vegetation, given that *Spartina* spans its full vertical range (Fig. 4). For instance, non-native *Spartina anglica* along the Wadden Sea coast in Europe was thought to be in a phase of population increase associated with rising water temperatures (Loebl et al. 2006), with possible ecosystem-level harm. However, it may instead be the case that *S. alterniflora* allows sediment accretion to keep pace with climate-driven sea level rise in a manner promoting local diversity (Granse et al. 2021).

In Ganghwa and Jindo sites, reed marsh and *Spartina* vegetation were found at the same elevation with spatial competition observed in the upper part of the tidal flat (Fig. 5). This phenomenon holds true for the Chinese example of Yangtze River estuary, where *Spartina* has invaded, driving away two native plants, *P. australis* and *S. mariqueter* (Chen et al. 2004; Li et al. 2009).

On the other hand, in the middle part of the tidal flat below MHW in Dongmak, salt marsh has been originally dominated by monospecific *S. japonica* (Lee et al. 2006), which is a representative low marsh plant in the west coast of Korean peninsula. Bang et al. (2018) studied the distribution of salt marshes in a Siheung tidal flat (37°23'40"N, 126°46'05"E), located about 35 km from the present study site, showing a clear zonation along elevational gradients. Their study area is characterized by deep channels having a thalweg of about 5–6m below the surrounding intertidal surfaces (Wells et al. 1990). The mean tidal range in Siheung tidal flat is 5.57 m, while the vertical distribution of salt marsh plants ranges from 2.4 to 4.2 m above MSL. Four community types occurred in the marsh; (1) *Suaeda glauca*, *Z. sinica*, and *P. australis* at high elevation, (2) *Phacelurus latifolius* at mid-high elevation, (3) *S. japonica* at low elevation, (4) *Carex scabrifolia* at mid-high elevation. At Dongmak in our study, *S. japonica* occurred primarily from 2.0 to 2.9 m above MSL, whereas its distribution at Siheung was 2.4–4.2 m above MSL with a peak biomass in the elevation between 3.6 m and 3.9 m. *S. japonica* may be restricted from lower elevations at Siheung tidal flat because the channel flank is unconsolidated fluid-like mud of up to 1 m thickness and dropped sharply (more than 30° slope) to a flat. *Suaeda* marshes often harbor high macrobenthic biodiversity including two locally abundant crabs *Macrophthalmus* (*Mareotis*) *japonicus* and *Cleistostoma dilatatum* also found in the bare mud flat in Ganghwa Island (Lee et al. 2016). However, *Suaeda* habitat on the bare mud flat is gradually reduced by the invasion of this exotic plant *Spartina* (Fig. 5). This effect has also been reported in the Chinese coast, showing that *Spartina* has restricted the distribution of *Suaeda* spp. and dominated bare mud flats (Wan et al. 2009; Meng et al. 2020). Therefore, we can expect that *S. japonica* vegetation will be replaced by *Spartina* marsh, and this competitive displacement could also apply to other surrounding native salt marshes such as *T. maritimum* and *S. triqueter* (Figs 4, 5). This displacement can also be predicted for native marsh plants such as *S. maritima* and *Z. sinica* in Jindo tidal flat.

Ecological implications from the introduction of invasive species in Korean coast

The smooth cordgrass *S. alterniflora* with high invasiveness is highly opportunistic and competitive with wide ecological niches. Dispersal pattern and expansion rate of this invasive species appear often inconsistent after the introduction in the recipient waters. However, once their habitat requirements are provided, populations grow rapidly and exponentially.

As of 2020, despite investments in mechanical control of more than US$3 million over 6 years, *Spartina* continued to expand in Korea. In the US, successful control of widespread (3600 solid ha across 27,000 ha of intertidal area) *Spartina* meadows in Willapa Bay was achieved once an effective herbicide was identified (Major et al. 2003; Knott et al. 2013; Patten et al. 2017).

Worldwide, *Spartina* has become a dominant part of tidal flats where it has invaded, which is likely to occur on Korean tidal flats around Ganghwa and Jindo Islands. Recently, in Chinese coasts, the native intertidal halophyte *Suaeda* spp. and even dwarf eelgrass *Zostera japonica* have been degraded significantly by *Spartina* invasion in the Yellow River Delta. *Spartina* marsh competes with native plants, threatens native ecosystems and coastal aquaculture, and causes local biodiversity to decline (He et al. 2007; Wan et al. 2009; Wan et al. 2014; Liu et al. 2018; Meng et al. 2020; Yue et al. 2021).

We also vividly witnessed this competitive effect and rapid expansion of the *Spartina* invasion on native halophytes in Korean intertidal wetlands (unpubl. Data by authors). In addition, this invasive *Spartina* greatly alters the rates and pathways of organic carbon oxidation and associated microbial communities (An et al. 2020), but also increases belowground biomass and decreases macrofaunal density and diversity in the same study area of Ganghwa intertidal Wetland located at the Han River Estuary, Korea (Shin et al. 2022).

As *Spartina* increased at Dongmak from 2010 to 2015, *Suaeda japonica* marsh decreased its area from 99,229 m^2 to 64,986 m^2. This locally important and dominant native halophyte harbors the highest diversity in macrofauna among habitat types on these tidal flats (Lee et al. 2016; Shin et al. 2022). In addition, bare mudflat-based traditional fishing activities associated with previous local habitats will also be excluded by *Spartina* invasion.

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Authors' contributions

Sungtae Kim: Research Conceptualization, Sample design and Methodology, Investigation and Data collection, Data analysis and Interpretation, Resources, Writing- Original Draft, Visualization.

Jae-Sang Hong: Research Conceptualization, Sample design and Methodology, Investigation and Data collection, Data analysis and Interpretation, Resources, Writing- Original Draft and Review, Visualization, Funding provision

Cheol Yu: Investigation and Data collection, Writing, Resources.

Jennifer Ruesink: Research Conceptualization, Sample design and Methodology, Writing- Review & Editing, Visualization.

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