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RESEARCH

Modeling the long-term vegetation dynamics of a backbarrier salt marsh in the Danish Wadden Sea

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Background: Over the past three decades, gradual eustatic sea-level rise has been considered a primary exogenous factor in the increased frequency of flooding and biological changes in several salt marshes. Under this paradigm, the potential importance of short-term events, such as ocean storminess, in coastal hydrology and ecology is underrepresented in the literature. In this study, a simulation was developed to evaluate the influence of wind waves driven by atmospheric oscillations on sedimentary and vegetation dynamics at the Skallingen salt marsh in southwestern Denmark. The model was built based on long-term data of mean sea level, sediment accretion, and plant species composition collected at the Skallingen salt marsh from 1933–2006. In the model, the submergence frequency (number yr^{-1}) was estimated as a combined function of wind-driven high water level (HWL) events (> 80 cm Danish Ordnance Datum) affected by the North Atlantic Oscillation (NAO) and changes in surface elevation (cm yr^{-1}). Vegetation dynamics were represented as transitions between successional stages controlled by flooding effects. Two types of simulations were performed: (1) baseline modeling, which assumed no effect of wind-driven sea-level change, and (2) experimental modeling, which considered both normal tidal activity and wind-driven sea-level change.

Results: Experimental modeling successfully represented the patterns of vegetation change observed in the field. It realistically simulated a retarded or retrogressive successional state dominated by early- to mid-successional species, despite a continuous increase in surface elevation at Skallingen. This situation is believed to be caused by an increase in extreme HWL events that cannot occur without meteorological ocean storms. In contrast, baseline modeling showed progressive succession towards the predominance of late-successional species, which was not the then-current state in the marsh.

Conclusions: These findings support the hypothesis that variations in the NAO index toward its positive phase have increased storminess and wind tides on the North Sea surface (especially since the 1980s). This led to an increased frequency and duration of submergence and delayed ecological succession. Researchers should therefore employ a multitemporal perspective, recognizing the importance of short-term sea-level changes nested within long-term gradual trends.

Keywords: marsh submergence, North Atlantic Oscillation, ocean storminess, sedimentation, vegetation dynamics

Introduction

Studies on salt marsh ecology and biogeography indicate that periodic seawater inundation is a fundamental stress factor that influences the distribution and dynamics of vegetation (Adam 1990; Pennings et al. 2005; Silvestri et al. 2005). Sea surface elevation dictates the frequency, depth, and duration of marsh inundation, as well as salinity, soil redox potential, and nutrient status (Davy et al. 2011; Morris et al. 2002; Suchrow and Jensen 2010). Different plant species have distinct levels of tolerance to these physical conditions. This causes their distribution to emerge as a zone along the elevation gradient. The zonal pattern of distinct plant species has been the focus of several ecological studies (Kim 2014, 2018a; Kim and Ohr 2020; Pennings et al. 2005).

Due to our rapidly warming climate, increasing attention is being paid to the future fate of salt marsh vegetation and the stability of marshes themselves (Bakker et al. 1993; Bertness et al. 2002; Feagin et al. 2010; Kim et al. 2011a;

Kirwan et al. 2010; Reed 1995). This warming trend induces the thermal expansion of oceans and the melting of polar and alpine ice, causing the mean sea level to rise along many coastlines worldwide. As long as this rise in sea level occurs at an optimal or acceptable rate over multiple decades, the marsh surface and water level are likely to readjust towards equilibrium. This equilibrium may be reached through positive feedback between biomass productivity and sediment accretion (Morris et al. 2002). However, if the rise in sea level exceeds sedimentation, the marsh will experience retarded or retrogressive succession. This is characterized by the dominance of pioneer species that are highly tolerant to the physical stresses associated with seawater inundation (Bakker et al. 1993; Kim et al. 2011b; Warren and Niering 1993).

Anomalies in several atmospheric oscillations, such as the North Atlantic Oscillation (NAO) and El Niño-Southern Oscillation, increased during the late 20th century. This caused an increase in the magnitude and frequency of meteorologically induced storms on various ocean surfaces (Bromirski et al. 2003; Güenther et al. 1997). For example, the NAO enters positive and negative phases when the pressure differences between the Icelandic low-pressure system and the Azores high-pressure system become larger and smaller than normal, respectively. During the positive phase, the Atlantic and, eventually, the North Sea often experience strong westerly gales. These gales push the ocean surface water towards the east, resulting in high-wave storm surges along the coast of northern European countries.

The Skallingen salt marsh in southwestern Denmark has been subjected to frequent wind-induced sea-level variations. In Esbjerg, a city near Skallingen (Fig. 1), an extreme water level of 4.4 m above the Danish Ordnance Datum (DNN) was recorded during past storm surges. During such an event, the entire area of the sheltered backbarrier salt marsh could be inundated with saline water for 24 hours (Bartholdy and Aagaard 2001). Bartholdy et al. (2004) found that periods of wind-induced sea-level rise, which increased the magnitude and duration of submergence, corresponded substantially to those of rapid sedimentation. Furthermore, the NAO variation accounted for a significant amount of the variation in the annual sedimentation rate between 1970 and 1999 ($R^2 = 0.63$, $p < 0.01$). This indicates a close relationship between the occurrence of wind-driven setups and the NAO index. Kim (2009) and Kim et al. (2011b) proposed that the frequency of these meteorological and hydrological phenomena influence the vegetation dynamics of salt marshes; however, both studies were hypothesis-generating and descriptive.

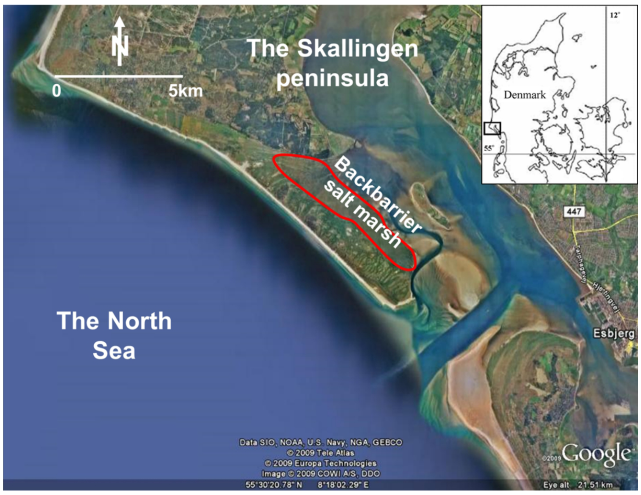

Fig. 1 The study marsh in the backbarrier side of the Skallingen peninsula.

This study evaluated the cumulative effects of short-term episodic sea-level rise events, which are driven by ocean storminess, on the dynamics of salt marsh vegetation. The main objective is to develop quantitative models to evaluate the concepts described by Kim (2009) and Kim et al. (2011b) involving the Skallingen salt marsh. Historical data on the dynamics of vegetation, sedimentation, and sea level, acquired from as far back as the 1930s were used. Simulations based on these data illustrate the impact of wind-driven sea-level change on changes in plant species composition and environmental factors. This assists in developing our understanding of the specific processes that generate these dynamics.

Materials and Methods

Study area and environmental histories

The marsh investigated in this study began to form at the beginning of the 20th century and is situated on the backbarrier side of the Skallingen peninsula in southwestern Denmark (Fig. 1) (Aagaard et al. 1995; Bartholdy et al. 2014, 2018; Nielsen 1935). This coastal area is classified as micro-tidal, as the tidal range is between ~1.7 m during spring and ~1.3 m during neap tides, with a mean of 1.5 m (Davies 1964).

This study was based on detailed long-term sea level data (Bartholdy et al. 2004), which were derived from a tidal gauge established in Esbjerg. Overall, the data show that the yearly mean sea level has risen since the 1930s (Fig. 2A). The general rate of sea-level rise from 1931–2006 was 2.3 mm yr^{-1}, but since 1976, the rate increased to 5.0 mm yr^{-1}.

To correct the high water levels (HWL) recorded in Esbjerg for the Skallingen marsh, a quadratic regression model first suggested by Bartholdy et al. (2004) was employed. This model was developed based on the differences observed between the two locations' HWL. As a result, the number of annual HWL events in the marsh increased after 1931 (Fig. 2B). Since 1931, on average, the surface eleva-

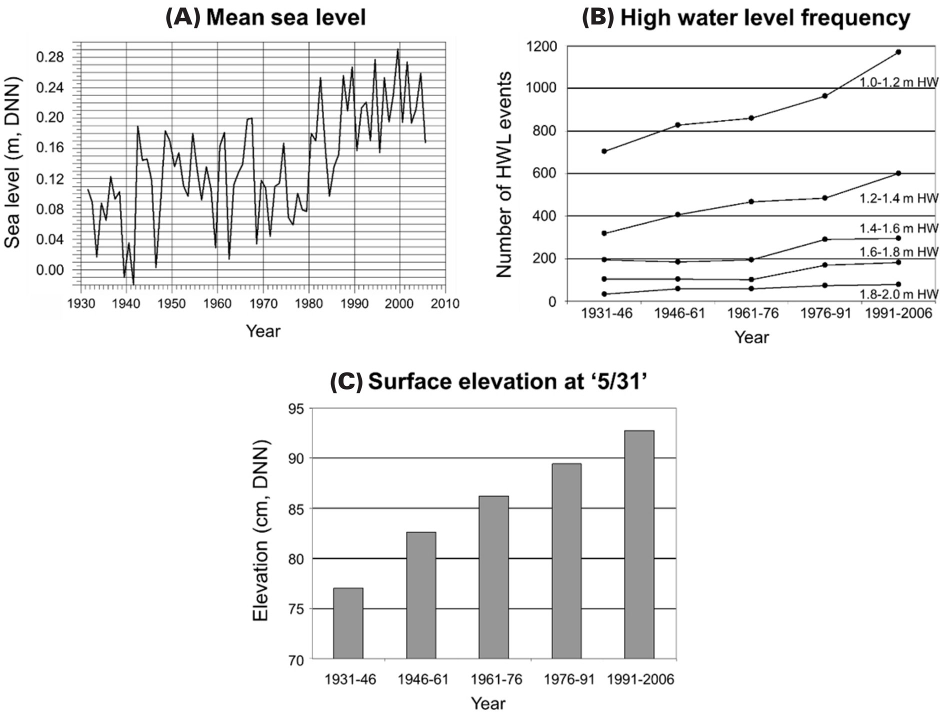

Fig. 2 Temporal variation of (A) mean sea level in meter DNN (Danish Ordnance Datum), (B) frequency of high water levels (HWL), and (C) surface accretion in cm DNN in the Skallingen salt marsh, Denmark. The mean sea level was estimated based on the annual averages from July to July. The surface elevation was based on data from the monitoring site, called "5/31" in Bartholdy et al. (2004). Adapted from the article of Kim (Texas A&M University 2009).

tion has increased by ~0.2 m (Fig. 2C). The elevation of the 0.8 m DNN was regarded as the mean surface level of the marsh (Bartholdy, personal communication). Therefore, all the HWL levels presented in Fig. 2B may induce "over-marsh" inundation.

Vegetation data and analysis

Data acquisition

Original vegetation sampling was conducted by Danish geographers in 1933 and 1949 to determine the presence of vascular plant species at 29 plots. These plots were established along three transects that were perpendicular to the coastline of the Skallingen salt marsh. During the summer of 2006, I visited the same plots to obtain the same set of data on species frequency (Kim 2009; Kim et al. 2011b). The previously surveyed locations were identified using the geographic coordinates of the three historical transects provided by Bartholdy et al. (2004).

To replicate the original sampling approach, a 2 m × 1 m rectangular quadrat was used, which was divided into 200 subdivisions of 0.1 m × 0.1 m. Ten of these subdivisions were randomly selected and the presence of vascular species in each subdivision was recorded. The frequency of each species in the rectangular quadrat ranged from 0–10. Species nomenclature follows that of Tind (2003). At each location, the frequency data were documented and the average between three quadrats was calculated (quadrats were separated by a distance of 2 m and located at 0°, 120°, and 240° azimuth). This was done to minimize any effect of having resampled a site that was slightly offset from the originally sampled location.

Classification of vegetation associations

To classify the samples into ecologically meaningful vegetation associations, hierarchical agglomerative cluster analysis was employed in tandem with indicator species analysis (McCune et al. 2002). Twenty-nine samples from each of the 3 years (1933, 1949, and 2006) were combined into one dataset to acquire a total of 87 samples. Samples were normalized to make observational units more equitable in terms of species frequency and to enhance the detection of broad compositional similarities among samples. For the cluster analysis, Ward's method (Ward 1963) was used to minimize the increase in the sum of the squares of each sample distance to the centroid of the group to which it belonged. The Euclidean squared distance was then used as a measure of dissimilarity to maximize defensibility (McCune et al. 2002). After cluster analysis, indicator species analysis was conducted to select the optimal number of vegetation associations (Dufrêne and Legendre 1997; McCune et al. 2002). Detailed explanations of the classification methods are described by Kim et al. (2011b). All statistical procedures were performed using PC-ORD Version 4.14 (MjM Software Design, Gleneden Beach, OR, USA).

Simulations

The following section presents the methods for simulating the past and future dynamics of vegetation and geomorphology in the Skallingen salt marsh based on the field data available. The objective of these models is to show a close linkage between NAO variation, dynamics of surface elevation, and submergence frequency. In addition, these simulations emphasize the significance of short-term wind-induced sea-level variation by comparing baseline and experimental models that assume the absence and presence of such meteorological events, respectively.

Conceptual model

The conceptual model consisted of two major components: physical factors and ecological succession (Fig. 3). The abiotic components were divided into three parts: sea-level variation (driven by both temporary storminess and normal tides), surface accretion, and frequency of over-marsh inundation. The variation in the NAO index influenced the total number of HWL per year, which was divided into four categories (Fig. 3A): low HWL (80–100 cm DNN), mid HWL (100–120 cm DNN), high HWL (120–140 cm DNN), and extreme HWL (> 140 cm DNN). However, for the baseline simulation, in which no wind-driven sea-level fluctuation was assumed, extreme HWL events were not included because they were not expected to occur under normal tidal conditions.

The rate of sediment deposition per year was dependent on the total HWL frequency and surface elevation (Fig. 3B). Specifically, negative feedback exists between sedimentation and elevation because the frequency and duration of submergence should decrease as the elevation increases.

The submergence frequency for low (80–100 cm DNN), mid (100–120 cm DNN), and high (120–140 cm DNN) marsh areas was investigated (Fig. 4). Therefore, the frequency varies depending on which of these three sites is being examined and the change in the elevation of the site over time. For example, a low area with an 80 cm-elevation should experience a flooding frequency of "low HWL + mid HWL + high HWL + extreme HWL" that is equivalent to the total HWL per year. However, only high HWL and extreme HWL were considered as over-marsh inundation events for the site that was 120 cm high. In short, not all of the HWL events caused a complete submergence of the marsh elevation zone.

Ecological succession was significantly influenced by submergence frequency, which controlled the "flooding effects" (see section, Experimental simulation). Transitions among successional stages explicitly integrate the combined effects of abiotic (i.e., flooding) and biotic dynamics (i.e., competition and facilitation). As each transition was bidirectional, positive and negative values controlled by flooding effects could result in progressive and retrogressive succession, respectively (Fig. 3D). The transitions were also dependent on the density of the earlier and later stages that competed. Facilitative interactions were expressed as "maturation." Facilitation is considered an important contributor to (progressive) vegetation succession in salt marshes, where the establishment of late-successional species is often hampered by the physical stresses imposed by saline water inundation (Bertness and Shumway 1993; Emery et al. 2001; Pennings and Callaway 1992). Therefore, the biological and ecological success of late-successional species strongly depends on system maturation facilitated by ear-

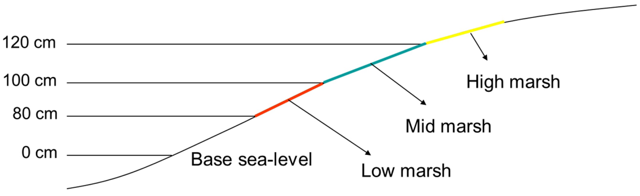

Fig. 4 Topographic profile of the study marsh with different elevation zones.

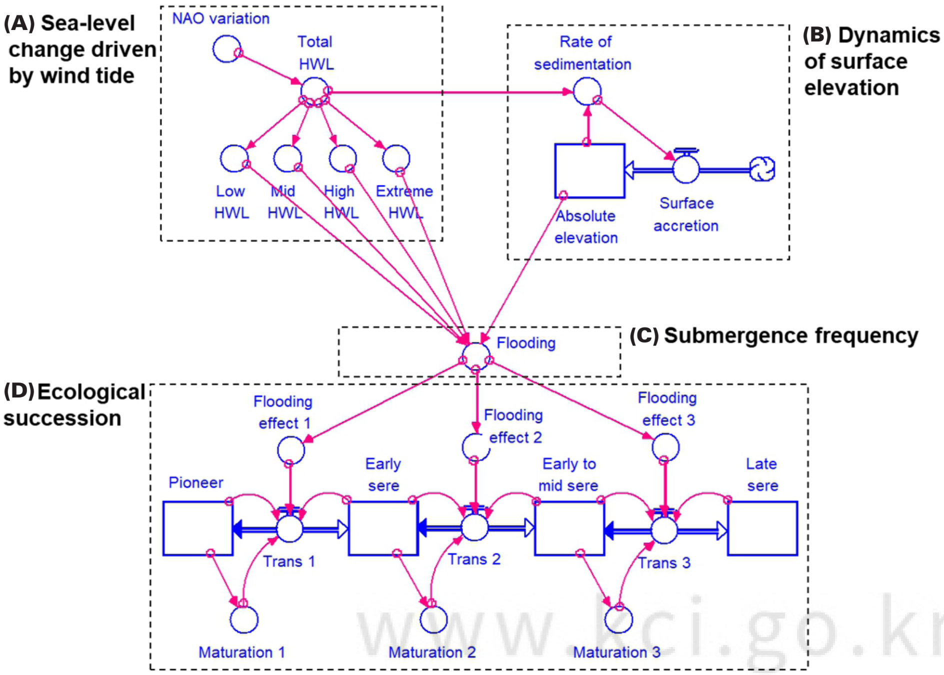

Fig. 3 Conceptual model of abiotic and biotic dynamics in the study marsh drawn using STELLA® 7.0.1. (A) Sea-level change driven by wind tide. (B) Dynamics of surface elevation. (C) Submergence frequency. (D) Ecological successin. NAO: North Atlantic Oscillation; HWL: high water level.

ly-successional species that ameliorate edaphic conditions and accumulate organic matter (Bertness et al. 1992; Kim and Phillips 2013; Srivastava and Jefferies 1995; van de Koppel et al. 2005). However, the degree or speed of maturation differs among transitions. An extended period is required for system maturation to allow for the dominance of late-successional species. This is because the growth of these perennial, tall-stature species is strongly associated with the progressive accumulation of nutrients (especially nitrogen; Olff et al. 1997; Van Wijnen and Bakker 1999).

Data

The observed and predicted data for the NAO index variation were combined. These values were derived from Bartholdy et al. (2004) and Paeth et al. (1999). The observed values ran from 1933–1999, and the predicted values encompassed the period from 2000–2050. In addition to NAO data, long-term hydrological, sedimentological, and floristic data were acquired from the Skallingen salt marsh (Kim 2009; Kim et al. 2011b).

All HWL events were recorded using a tidal gauge at Esbjerg. The levels were corrected for the study marsh using a quadratic regression model based on recent differences in HWL between Skallingen and Esbjerg (for a detailed procedure, see Bartholdy et al. 2004). After this correction, low HWL, mid HWL, high HWL, and extreme HWL explained 43, 28, 14, and 15% of the total HWL observed, respectively.

The rate of sedimentation at sites with different surface elevations was determined based on robust long-term field monitoring and simulation approaches carried out by Bartholdy et al. (2004) at the Skallingen salt marsh since the early 1930s. Analyses of sediment cores from the marsh and subsequent modeling allowed these researchers to estimate rates of surface accretion as 0.25, 0.16, and 0.07 cm yr^{-1} for low, mid, and high marsh areas, respectively.

Floristic data were acquired and analyzed as described in the previous section. The initial relative occupancy (%) of each vegetation group was determined for the three marsh sites based on the results of the hierarchical cluster analysis.

Experimental simulation

In the experimental simulation, the effects of wind-driven sea-level rise and normal tides were considered. The variables and their relationships in the conceptual model were quantified based on the data available. Using STELLA® 7.0.1, model simulations were performed at yearly intervals. The simulation results were evaluated using the observed data.

(1) NAO and sea-level variations

The annual frequency of total HWL was calculated using a combined function of the NAO index variation (1933–2050), a random variable, and an increase term, as follows:

$$\text{Total HWL} = (22.521 \times \text{NAO} + 229.76) \times \text{random}\ (0.8, 1.2) + \text{increase term} \qquad \text{Eq. (1)}$$

Through the function “random (0.8, 1.2)”, a random number was generated between 0.8 and 1.2 and multiplied to ensure that the correlation coefficient was maintained between a total HWL and NAO of 0.48 (i.e., $R^2 = 0.23$; Fig. 5A). An increase term with a slope of 1.7331 (see Fig. 5B) was added to include an increasing number of submergences over time.

(2) Rate of sedimentation

The rate of sediment accretion (cm yr^{-1}) was parameterized into the following four categories:

If ($80 \le$ absolute elevation < 100) then $0.25 + (0.25/237.3) \times (\text{total HWL} - 237.3)$

else if ($100 \le$ absolute elevation < 120) then $0.16 + (0.16/237.3) \times (\text{total HWL} - 237.3)$

else if ($120 \le$ absolute elevation < 140) then $0.07 + (0.07/237.3) \times (\text{total HWL} - 237.3)$

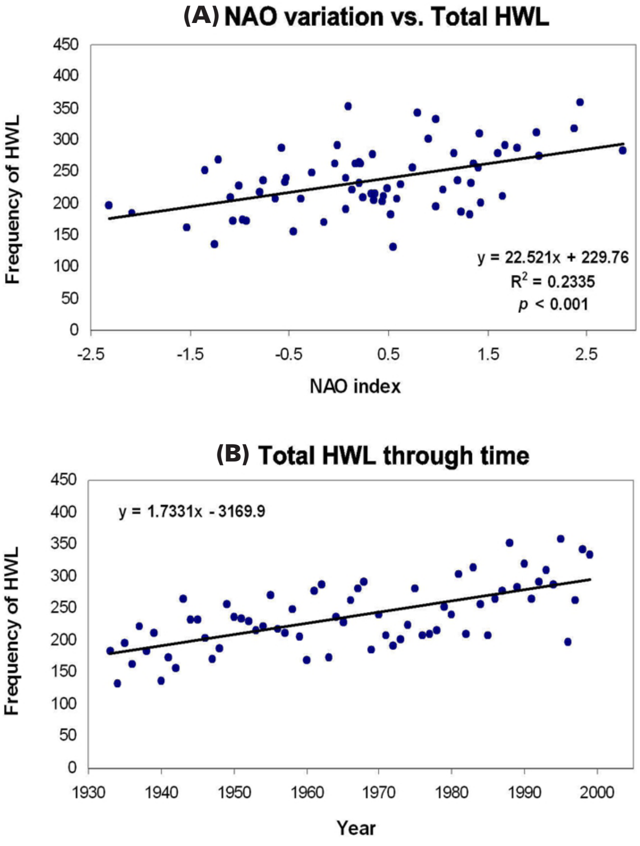

Fig. 5 Comparison of (A) the yearly North Atlantic Oscillation (NAO) variation and the frequency of total high water level (HWL) and (B) the frequency of total HWL over time.

else 0.03 + (0.03/237.3) × (total HWL – 237.3) Eq. (2)

Here, 237.3 represents the average number of HWL per year observed in the field (Kim 2009; Kim et al. 2011b, 2013a). If the total HWL exceeds this average in a certain year, the sedimentation rate increases accordingly. The constants, 0.25, 0.16, 0.07, and 0.03, were selected to ensure that a greater sedimentation rate would be obtained at lower marsh zones.

(3) Submergence frequency

The flooding frequency was classified into the following five categories:

If (absolute elevation < 80)
then low HWL + mid HWL × 1.1 + high HWL × 1.2 + extreme HWL × 1.3

else if (80 ≤ absolute elevation < 100)
then [1 – (absolute elevation – 80) × 0.05] × low HWL + mid HWL × 1.1 + high HWL × 1.2 + extreme HWL × 1.3

else if (100 ≤ absolute elevation < 120)
then [1 – (absolute elevation – 100) × 0.05] × mid HWL + high HWL × 1.1 + extreme HWL × 1.2

else if (120 ≤ absolute elevation < 140)
then [1 – (absolute elevation – 120) × 0.05] × high HWL + extreme HWL × 1.2

else extreme HWL × 1.2 Eq. (3)

For every case, a high HWL (e.g., high HWL or extreme HWL) compared to the current surface elevation was weighted because these events should result in longer and deeper submergences than usual. In this regard, the inundation frequency in the model can also be understood as submergence intensity. The above equations assume that any type of HWL is evenly distributed within the associated vertical spectrum (e.g., the vertical spectrum of a low HWL ranges from 80–100 cm). Thus, if the surface elevation was 110 cm (i.e., mid marsh) in a certain year, this site should experience a yearly frequency of 0.5 × mid HWL + high HWL × 1.1 + extreme HWL × 1.2.

(4) Flooding effects

The flooding effect was parameterized as follows (Fig. 6):

Flooding effect 1 = – (0.25/500) × flooding + 0.20
Flooding effect 2 = – (0.25/500) × flooding + 0.15
Flooding effect 3 = – (0.45/500) × flooding + 0.05 Eq. (4)

The flooding effect was assumed to be an inverse-linear function, in which the effect became positive as the frequency of inundation decreased, and negative as the frequency of submergence increased. However, this basic rule varies for different transitions among successional stages, each with different physiological traits (Kim and Ohr 2020). Of all the species assessed, pioneer species were the least sensitive to flooding events at all stages. This suggests that pioneer species benefit from frequent inundation, which restricts the biological and competitive success of late-successional species. In contrast, late-successional species were most negatively influenced by an increase in flooding events. The maximum possible inundation frequency per year was set at 500, considering the historical hydrological fluctuations at Skallingen (Bartholdy, personal communication).

(5) Transition between successional stages

The generic equation for the transitions between successional phases is as follows:

Transition$_{n\rightarrow n+1}$ = flooding effect × phase$_n$ × phase$_{n+1}$ × 0.01 + maturation$_{n\rightarrow n+1}$ Eq. (5)

System maturation for different successional stages is defined as follows:

Maturation 1 = pioneer × 0.03
Maturation 2 = early-successional × 0.02
Maturation 3 = early- to mid-successional × 0.015 Eq. (6)

The constant for maturation 3 (0.015) was the smallest

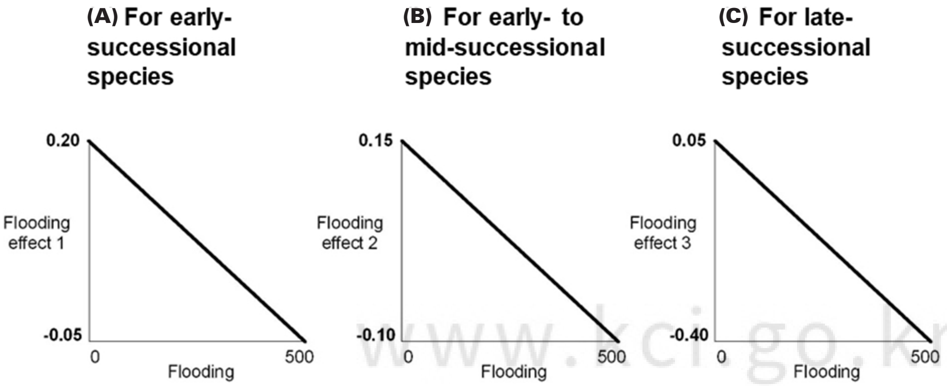

Fig. 6 Graphical representation of the functions for parameterizing flooding effects for different vegetation associations. (A) For early-successional species. (B) For early- to mid-successional species. (C) For late-successional species.

because late-successional species require a longer time for establishment than pioneer and early-successional species.

Baseline simulation

To investigate whether wind-driven, short-term sea-level rise plays a significant role in both ecological and sedimentological dynamics in salt marshes, a baseline simulation was run. In addition to the experimental simulation above, which considered both wind-driven sea-level changes and normal tides, a baseline simulation was conducted assuming no such meteorological variations. This baseline simulation did not include extreme HWL (> 140 cm DNN) in the total HWL because such events were unlikely to occur without a wind-driven sea surface setup.

Accordingly, the average frequency of the total HWL became 183 per year (cf. it was originally 237 when wind-driven setup was considered). However, this frequency was further reduced because a portion of the 183 occurrences observed in the field may have benefited from meteorological influences. It was assumed that 80% of these occurrences (146) were induced by normal tidal currents. The baseline simulation was therefore designated as a constant frequency of 146, because the increasing total HWL frequency observed in recent years was caused by wind-driven sea-level rise. All the other conditions included in the baseline simulation were the same as those defined for the experimental simulations.

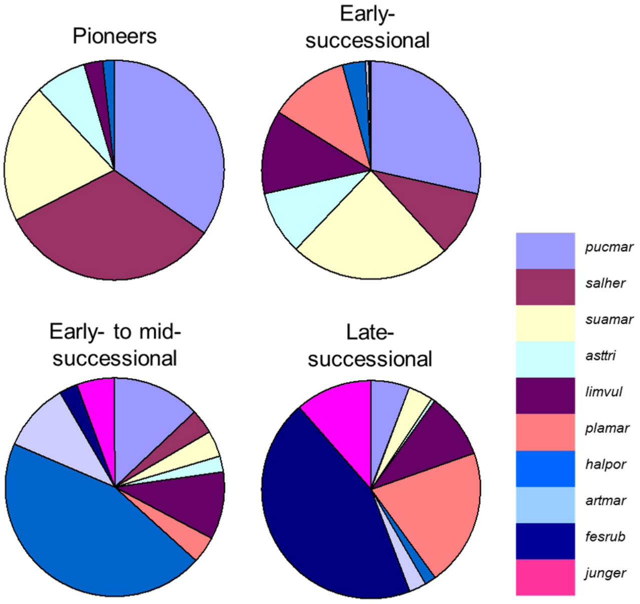

Fig. 7 Relative abundance of each species in the four groups classified (*pucmar–Puccinellia maritima* (Hudson) Parl., *salher–Salicornia herbacea* L., *suamar–Suaeda maritima* L., *asttri–Aster tripolium* L., *limvul–Limonium vulgare* Mill. and L. humlie Mill., *plamar–Plantago maritima* L., *halpor–Halimione portulacoides* (L.) Aellen, *artmar–Artemisia maritima* L., *fesrub–Festuca rubra* L., *junger–Juncus gerardii* Loisel.).

Results

Vegetation associations and dynamics

Cluster analysis identified four distinct vegetation groups: pioneer, early-successional, early- to mid-successional, and late-successional (Fig. 7). The first association showed a high frequency of *Puccinellia maritima*, *Salicornia herbacea*, and *Suaeda maritima*, typical of a pioneer community in the low salt marshes of the Wadden Sea (Westhoff 1987). The second association indicated some level of progressive succession from the pioneer stage, given the drastic decrease in *S. herbacea* and significant increase in *Limonium vulgare* and *Plantago maritima*. However, this group still represents an early-successional phase owing to the lingering presence of *P. maritima* and *S. maritima*. The third association was dominated by *Halimione portulacoides*, presumably because of its well-known competitive ability and ecophysiological advantages, e.g., its tolerance to frequent inundation and high salinity (Jensen 1985); whereas the presence of other species was extremely low. Based on previous observations (e.g., Bakker et al. 1993; Beeftink 1987; Erchinger 1985; Westhoff 1987), this community was considered to be an early- to mid-successional phase of salt marsh vegetation. The fourth vegetation association was *Festuca*-dominated with an increase in *Juncus gerardii*. This group has often been found in the high-lying areas of many Wadden Sea marshes, representing a late-successional stage (Bakker et al. 1993; Roozen and Westhoff 1985).

In 1933, the Skallingen salt marsh was dominated by pioneering vegetation groups (17 of 29 samples; Fig. 8A). In

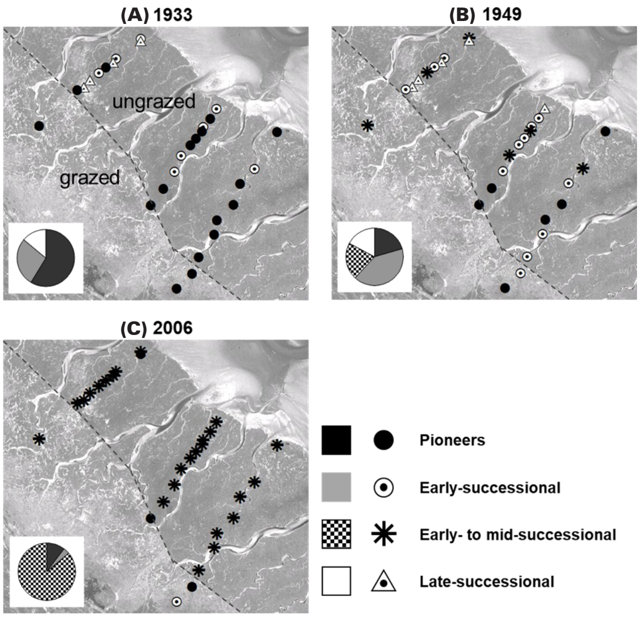

Fig. 8 Temporal dynamics of vegetation associations in the Skallingen salt marsh. (A) 1933, (B) 1949, (C) 2006. The horizontal length of each photo (taken in 1995) equals about 1.3 km in the real field. The dotted lines represent the boundary (electric fence) between the zone used for cattle grazing and the zone ungrazed.

the next 16 years, the pioneer species decreased in abundance (from 17 samples to 6; Fig. 8B), and early-successional associations became the most frequent (12 samples of 29). Notably, the six plots exhibited a high abundance of late-successional plants. In 2006, a majority of the samples (25 of 29) were dominated by *H. portulacoides*, an early- to mid-successional species (Fig. 8C). There were no late-successional plots in the contemporary period. Overall, even after 100 years of salt marsh development, with a continuously increasing surface elevation (Fig. 2C), a majority of the marsh was still not late-successional. The ecosystem has undergone some degree of retrogressive succession (the disappearance of late-successional communities since 1949) and is currently in a retarded successional state (Kim 2009; Kim et al. 2011b).

Table 1 Initial relative occupancies (%) of each vegetation association at different sites in 1933

Habitat type	Low marsh	Mid marsh	High marsh
Pioneers (%)	70	25	2
Early-successional (%)	25	60	3
Early- to mid-successional (%)	3	10	25
Late-successional (%)	2	5	70

Simulation modeling

Table 1 shows the initial relative frequencies (%) of the four vegetation groups in 1933. The frequency values were determined basically by the observed proportion of each group at Skallingen, but there were slight modifications of the original values. In the low-marsh zone, for example, the observed frequency of the late-successional group was actually 13.79%. Given that the marsh was still very young in the early 1930s, however, the value was considered too high and I reduced it to 2%. For the same reason, the early- to mid-successional group was not observed in 1933, but I set its initial frequency at 3%. The study simulation involved a random variable of the abiotic factors. Hence, 10 simulations were conducted, and the resultant values were an average of these.

Abiotic dynamics

Closely linked dynamic processes were observed among the environmental factors. First, the number of simulated inundation occurrences gradually increased over time (Fig. 9A).

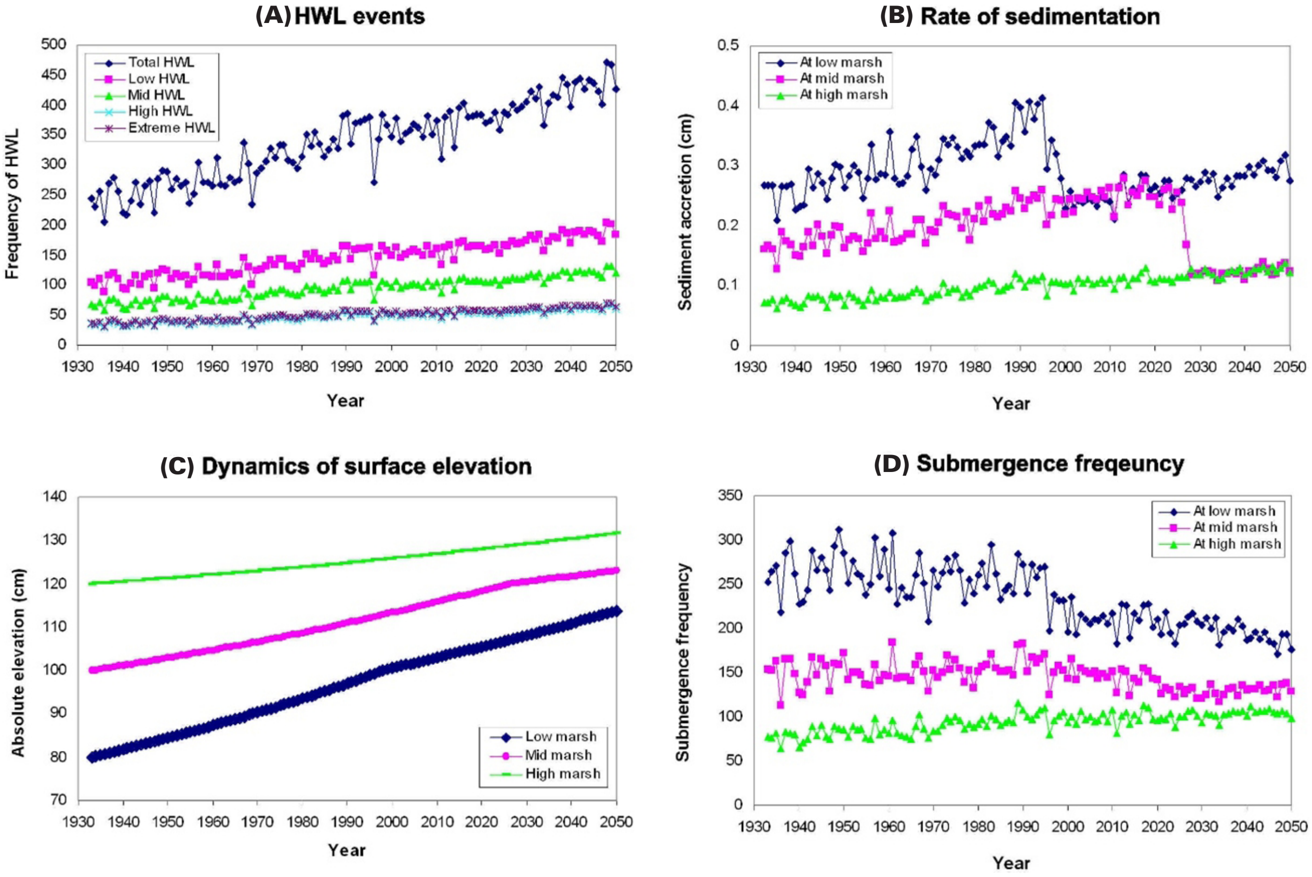

Fig. 9 Simulated (A) frequency of high water level (HWL) events per year from 1933 to 2050, (B) rates of sediment deposition, (C) dynamics of the absolute elevation, and (D) frequency of over-marsh flooding. Each value was acquired by averaging the results of 10 multiple simulations. Note that sites began as one of the low, mid, and high marshes, but owing to surface accretion over time, each could belong to a different vertical category at any particular temporal point. For example, the site that was initially a low marsh ended as a mid marsh in the simulation.

The sediment deposition rate also increased during the simulation (Fig. 9B). The degree of such an increase was the highest at the low marsh, intermediate at the mid marsh, and the lowest at the high marsh sites. However, there are significant drops in the rate of the low- and mid-areas in 1995 and 2025, respectively. Correspondingly, the increasing trend for the surface elevation slowed at these times (Fig. 9C). The differences in the initial surface elevation among the three sites gradually decreased over time. The annual number of over-marsh flooding events varied among the three sites (Fig. 9D). Decreasing and increasing patterns in the submergence frequency were observed in the low and high marshes, respectively. At the mid-elevation site, the inundation frequency was almost constant during the simulated period.

Biotic dynamics

In general, both the baseline and experimental simulations clearly show a gradual replacement of species by others over time (Fig. 10). However, successional patterns were

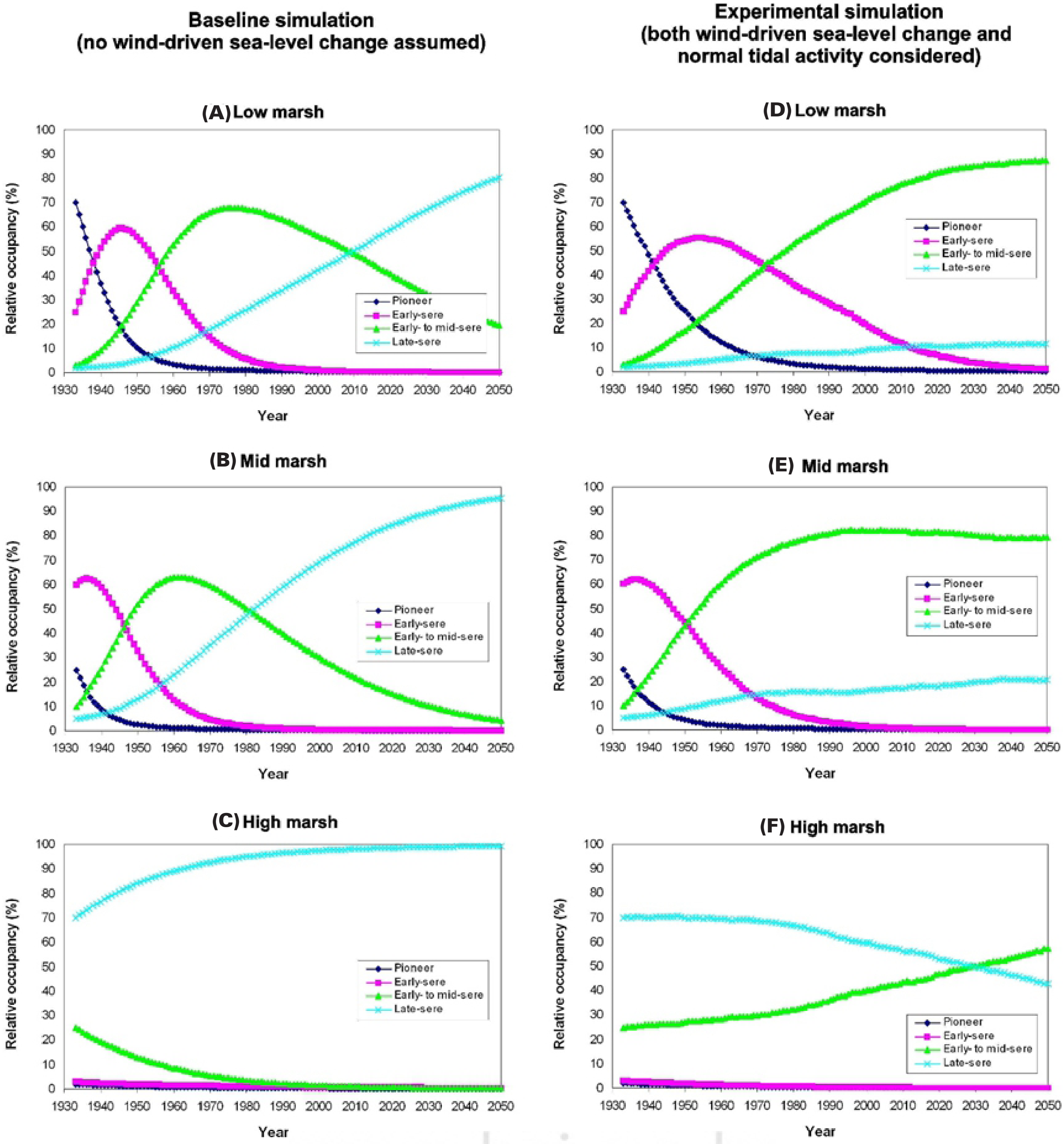

Fig. 10 Comparison of (A–C) baseline and (D–F) experimental simulations for ecological succession. Each value was acquired by averaging the results of 10 multiple simulations.

significantly different regarding the surface elevations evaluated and dependent on whether a wind-driven sea-level setup was considered. In both simulations, the dominance of pioneer and early-successional species in the low marshes was maintained for a relatively long time compared to the mid- and high-elevation sites. However, the performance of these species is poor at high altitudes.

The difference between the baseline and experimental simulation results was the most notable with respect to the dominance of the late-successional association. Such dominance was clearly observed when using the baseline simulation regardless of the surface elevation, with the fastest speed at high sites. Due to this dominance, the temporal range in which the other three successional stages dominated was narrower than that produced by the experimental simulations. In contrast, the relative occupancy of the late-successional group was suppressed in the experimental model because of the dominance of early- to mid-successional associations over time. Even in the high marsh, a conversion of dominance from late-successional to early- and mid-successional was predicted at a very late stage in the simulation (~2030).

Discussion

Model evaluation

Abiotic dynamics

The simulation results reflect the actual patterns and processes observed in the Skallingen salt marsh well. First, the increasing pattern of the simulated total HWL events over time (Fig. 9A) was similar to that of the observed events from 1933–1999 (Fig. 2B). A significant positive correlation was observed between the two variables (Pearson's $r = 0.76$, $p < 0.01$).

Second, the projected rates of sediment accretion were relatively accurate, as these rates gradually increased over time (Fig. 9B) in response to the increase in HWL events annually. As expected, the low marsh showed the highest rate of accretion, owing to its longest and deepest submergence regime. Additionally, the high-altitude site experienced the slowest sediment deposition because of its low frequency and intensity of seawater inundation. During parameterization, a decrease in the sedimentation rate was expected to occur when a tested site changed elevation categories after an increase in the surface elevation (Eq. 2). This was demonstrated in the low and mid marshes around the end of the 20th century and by 2030, respectively. However, it is also recognized that the two drops in sedimentation rate are so abrupt that they may be regarded as an exaggeration of the true sedimentation rate.

Third, the simulated dynamics of the surface elevation corresponded well with those observed in the field. Jacobsen (1958) measured the clay thickness at several locations in the Skallingen salt marsh in 1949. Bartholdy (2008) revisited these sites in 1999 and 2007 to collect the same sedimentological data and conduct topographic surveys. Based on the difference in clay thickness between these three periods (1949, 1999, and 2007), Bartholdy (2008) estimated the past and current absolute elevations at each location. Two of these monitored locations had surface elevations of 85.83 cm and 102.43 cm in 1949. These values are very similar to those simulated by the model for the low (84.17 cm) and mid (102.68 cm) marshes in the same year (Table 2 and Fig. 9C). These similarities in surface elevation were maintained in 1999 and 2007 (Table 2). However, the simulated dynamics of the surface elevation for a high marsh could not be evaluated because of the lack of relevant data in Jacobsen's (1958) and Bartholdy's (2008) studies.

Finally, variations in submergence frequency represent different histories of surface dynamics among the three elevation zones. Although the frequency of the total HWL itself has constantly increased since 1933 (Fig. 9A), the actual frequency of submergence in the low marsh has decreased significantly because of the high sedimentation rate and the subsequent rapid increase in its surface elevation (Fig. 9D). Despite continuous sedimentation at the high site, the rate of surface accretion was not sufficiently high for the elevation to keep up with the increasing frequency of high and extreme HWL events. No objective field dataset exists to validate the modeled hydrological dynamics at various locations. However, given that the simulation results for changes in surface elevation (Fig. 9C) are a sound reflection of reality, it is believed that these simulated flooding dynamics can be useful for further simulations of ecological succession (see next section, Biotic dynamics).

In summary, a convergence of environmental patterns

Table 2 Comparison of simulated and observed dynamics in surface elevation

Habitat type	Low marsh		Mid marsh		High marsh	
	Modeled	Observed	Modeled	Observed	Modeled	Observed
1949 (cm)	84.17	85.83	102.68	102.43	121.17	-
1999 (cm)	100.29	99.07	113.10	112.27	125.71	-
2007 (cm)	102.20	101.00	115.07	115.00	126.55	-

The elevation values displayed in the table for the year 1949 were measured by Jacobsen (1958). The observed elevations in 1999 and 2007 were provided by Bartholdy (2008). There were no field data available to evaluate the model predictions for high marsh.
-, not applicable.

and processes were observed in the simulation model presented for the Skallingen salt marsh. Specifically, the difference in the initial surface elevations of the three marsh locations decreased significantly due to the variable rates of sediment accretion (Fig. 9B, C). Of note, the frequencies of over-marsh flooding at the three sites became increasingly similar over time (Fig. 9D). Such increasing similarities in abiotic parameters can produce homogeneous or simple vegetation patterns over time.

Biotic dynamics

When conducting the baseline simulation, an issue arose as to which percentage of annual total HWL was considered to occur due to normal tidal activities alone (see section, Baseline simulation). I selected 80% to obtain the results presented in Fig. 10A-C. In an attempt to perform sensitivity analyses, various percentages (60, 70, and 90%) were tested; however, significantly different results were not obtained.

Considering that the salt marsh ecosystem was young in 1933, it was assumed that most of the ecosystem fell into an elevation range of between 80 and 100 cm DNN (Bartholdy et al. 2004). Therefore, floristic data (Fig. 8) can be used to evaluate successional dynamics in low marshes (Fig. 10D). At first glance, there were significant discrepancies between the modeled and observed occupancies (%) of each vegetation association in the low area (Table 3). However, a few important considerations exist that demonstrate that the simulation results for ecological succession are an acceptable representation of reality. First, the model successfully embodied the dominance of early- to mid-successional species (*H. portulacoides*) in 2006. This is encouraging because the focus was to investigate the contemporary stage of retarded succession, in which the dominance of late-successional species is suppressed by both frequent submergence and dominance by early- to mid-successional plants.

Second, a significant difference between the simulated and observed values for both the pioneer and late-successional association was anticipated. For this study, the initial occupancy was set at 2% for the late-successional group; however, a much higher percentage (13.79%) was observed in the field in 1933. This setting led to an increase in the initial percentage of pioneer communities (70%), which was higher than the true observed percentage (58.62%). This was intentional because the presence of late-successional groups at some locations in 1933 was not caused by continuous sedimentation. It was caused by the presence of local mounds, with high surface elevations of ~120 cm DNN that had already existed at Skallingen before the initial development of the marsh surface (Bartholdy et al. 2004). The elevation of these mounds was exceptionally high in the early 20th century, which was unexpected under normal environmental conditions.

Third, the observed occupancy of the pioneers in 2006 (10.34%) would have been lower or more similar to the simulated occupancy (0.90%) if there had been no livestock grazing and tidal creek effects (Fig. 8). In salt marshes, many pioneer species, especially *P. maritima*, are more grazing-tolerant than other late-successional individuals (Jensen 1985; Ranwell 1972; Westhoff 1987). Moreover, the lateral migration of tidal creeks can expose portions of the marsh platform to the direct influence of saline water (Adam 1990; Kim 2012, 2018b; Kim et al. 2012, 2013b). These factors, although not included in the current simulations, explain why a significant percentage of pioneers still existed after long-term salt marsh development, even in 2006.

Implications of the experimental model

The simulation presented in this research helped to answer the fundamental question of whether wind-driven, short-term sea level rise plays a significant role in the ecological dynamics of a salt marsh (cf. Kim et al. 2013a). A comparison of the baseline and experimental models clearly indicates that the presence of such meteorological events is essential for realizing retarded progressive succession, which was the overall situation at the Skallingen salt marsh in 2006.

The baseline simulation showed progressive successional dynamics from the pioneering to late stages. This pattern corresponds to the conventional expectations in coastal ecology and biogeography. Traditionally, succession in salt marshes has been associated with positive feedback, in which the presence of vegetation increases sedimentation, which, in turn, facilitates plant growth owing to lowered tidal inundation, salt stress, and edaphic amelioration (Bertness et al. 1992; Kim and Lee 2022; Srivastava and Jefferies 1995; van de Koppel et al. 2005). As sedimentation and elevation increase, this feedback process facilitates the establishment and growth of late-successional species by further reducing the physical stress associated with regular seawater inundation. Under the assumption of positive

Table 3 Comparison of simulated and observed dynamics in species composition

Habitat type	Pioneer		Early-sere		Early- to mid-sere		Late-sere	
	Modeled	Observed	Modeled	Observed	Modeled	Observed	Modeled	Observed
1933 (%)	70.00	58.62	25.00	27.59	3.00	0.00	2.00	13.79
1949 (%)	26.48	20.69	54.00	41.38	16.17	20.69	3.34	17.24
2006 (%)	0.90	10.34	14.40	3.45	75.02	86.21	9.68	0.00

feedback, the temporal range in which early-successional plants dominate becomes narrower owing to their facilitation and establishment of late-successional species. However, the conventional concept of positive feedback and consequent progressive succession embodied by the baseline simulation were not in accordance with the true events that occurred at the Skallingen salt marsh.

Responding to the convergent dynamics of physical factors (Fig. 9), the experimental simulation produced a simple ecological pattern in which early- to mid-successional associations (especially, *H. portulacoides*) predominated the low and mid marshes over time and, eventually, even the high site from 2030. The modeled inundation regime influenced by ocean storminess represents a level at which pioneers and early-successional species are outcompeted by this dominant group, and late-successional plants cannot tolerate it. Site-specific floristic variations driven by the considerable spatial heterogeneity in Skallingen were not the focus of the model. The model is useful because it successfully simulates the overall dominance of early- to mid-successional plants (i.e., *H. portulacoides*), which indicates the considerable influence of meteorological tides.

Conclusions

This study demonstrated that various ecological and environmental processes operate at different temporal scales (Csillag et al. 2000; Delcourt et al. 1982; Levin 1992; Whittaker et al. 2001). Based on these results, the importance of understanding the multiscale nature of these processes from a hierarchical perspective was addressed (Allen and Starr 1982; O'Neill et al. 1986; Park et al. 2012). The large-scale overall vegetation pattern was shown to be shaped by the interplay of hydrological and sedimentological processes in the study marsh over an extended period of time. This study addresses the importance of short-term wind-driven variations nested within long-term trends. Furthermore, sea-level variations at these different time scales are not necessarily mutually exclusive but combine to drive major vegetation dynamics over decades. It is important to emphasize the need for this holistic approach in future investigations of salt marsh ecology and biogeography (e.g., Kim 2019; Kim et al. 2010, 2016).

Abbreviations

HWL: High water level.
NAO: North Atlantic Oscillation.
DNN: Danish Ordnance Datum.

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Availability of data and materials

The data sets analyzed in the present paper are available upon request from the author.

Ethics approval and consent to participate

Not applicable.

Consent for publication

Not applicable.

Competing interests

The author declares no competing interests.

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