



Short-term evolution pattern in salt marsh landscapes: the importance of physical constraints

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Abstract

Context Salt marsh landscapes at the land-sea interfaces exhibit contrasting spatiotemporal dynamics, resulting from varying physical constraints that limit new marsh establishment. The expansion of salt marsh landscapes towards the sea or their retreat towards the land is determined by patch-level changes, relying on the balance of power between the intrinsic biota traits and external physical disturbances.

Objectives Examine how marsh dynamics respond to physical constraints, and clarify the pathway from coupled physical processes involving hydrodynamic forces, sediment transport, and morphological changes to rapid patch evolution and landscape changes.

Methods We defined and distinguished four types of marsh changes based on patch proximities from

five-month drone images in two typical marsh pioneer zones of the Yangtze Estuary, China: outlying expansion, edge expansion, infilling expansion, and retreat. Hydrodynamics and sediment transport were synchronously measured and compared near the two marsh edges, and morphological changes were generated by drone-derived digital elevation models (DEMs).

Results We identified distinct seasonal patterns of net marsh expansion at the accretion-prone site, that is: Net marsh expansion started from the outlying expansion in spring, followed by edge expansion in summer and infilling expansion in autumn. However, at the erosion-prone site that experienced high bed shear stress, low sediment availability and high seaward sediment transport, we only observed limited infilling and edge expansion in spring. This suggests that the potential for long-distance patch formation beyond the initial marsh edges is diminished in areas subjected to intensive physical disturbances.

Conclusions Patch evolution dynamics in response to site-specific physical constraints drive state differentiation of salt marsh landscape changes. Consequently, the heterogeneous evolution in salt marsh landscapes should be taken into account in restoration practice.

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Introduction

Salt marshes are one of the most valuable ecosystems on the earth (de Groot et al. 2012). Ecosystem services sustained by salt marshes play key roles in human welfare, biogeochemical cycles and biodiversity conservation (Costanza et al. 1997; Kirwan and Mudd 2012; Bauer et al. 2013; Temmerman et al. 2013). Nevertheless, with the combined effect of sea level rise (Church and White 2011), decreased sediment supply (Syvitski et al. 2005; Kondolf et al. 2014;), extreme events (Woodruff et al. 2013; Vasseur et al. 2014; Hanley et al. 2020) and estuarine projects (Luan et al. 2018), salt marshes worldwide are facing threats, and their deterioration is accelerating (Kirwan and Megonigal 2013; Li et al. 2018; Schuerch et al. 2018). Thus, an in-depth understanding of salt marsh evolution is needed to incorporate interdisciplinary solutions linking land cover and environmental processes.

Time scale matters in marsh evolution. Shifts of marsh cover in pioneer zones often happen within a few months due to the short life history of marsh macrophytes (Jiang et al. 2022), and becomes an essential portion of cyclic marsh-mudflat dynamics (Bouma et al. 2016). Previous studies have made efforts to fill the gap between the annual or decadal marsh changes, and physical constraints (e.g., van Wesenbeeck et al. 2008; Wang and Temmerman 2013; van Belzen et al. 2017). However, spatially explicit short-term marsh evolution (usually within a few months) is poorly understood and limited by the resolution of data acquisitions.

Spatially scaling up amplifies the complexities of marsh development (van de Koppel et al. 2012; Folkard 2019). The equilibrium between marsh vegetation and sediment dynamics at population-community level is the prerequisite for marsh survival (Ge et al. 2019). At the landscape level, unique land covers are created as a result of spatial heterogeneities in environmental factors (Perry 2002; Moffett et al. 2012; Stein et al. 2014). Site-specific variables such as sediment supply and geomorphology may result in distinct trajectories of marsh development (Mariotti and Carr 2014; Schuerch et al. 2014; Li et al. 2021). Additionally, infrequent but abrupt disturbances (e.g., storms and peak riverine runoffs) bring uncertainties to marsh evolution (Wang et al. 2016; Leonardi et al. 2018). Therefore, it is necessary to explore how salt

marshes spatially respond to the diverse and intertwined physical constraints, as this will help in understanding the variety of salt marsh landscapes.

Dynamic salt marsh landscapes are formed through the life-history processes of pioneer species that depend on biophysical interactions, including propagule retention (Zhu et al. 2020), seedling establishment (Zhao et al. 2021c), and clonal growth (Huang et al. 2022). Yuan et al. (2020) suggested that successful colonization of pioneer species require a suitable elevation and a moderate sedimentary regime. Other studies have also emphasized the importance of bed level changes in marsh establishment (e.g., Bouma et al. 2016; Cao et al. 2018; Wiegman et al. 2018). To a large extent, hydrodynamic force and sediment supply control the local accretion-erosion shifts. Less intensive hydrodynamics and high sediment availability promote marsh expansion (Ladd et al. 2019), while erosion induced by strong hydrodynamics and low sediment supply can lead to marsh loss (Poirier et al. 2017; Willemsen et al. 2022). Given the significance of physical settings, the spatially varying external forces such as sediment dynamics and morphodynamics may make uneven effects on marsh development, and contribute to the differentiation of short-term marsh evolution patterns at the landscape scale.

Here, we aim to unravel the underlying links between short-term marsh evolution patterns and physical constraints, taking typical marsh pioneer zones in the Yangtze Estuary as the model system (Fig. 1a, b). We conducted field investigations in two marsh pioneer zones subjected to similar wind and tide conditions (the straight-line distance between the two sites is about 7 km, Fig. 1c), with drone flights and hydro-sediment measurements in the five-month survey. We compared sediment dynamics, geomorphology, and marsh changes between the two sites, and further clarified the relationships between sediment dynamics, morphodynamics, and marsh dynamics. The outcomes of the present study will shed light on spatial consequences of biophysical interactions and give implications for restoration strategies of coastal wetlands in other similar mega-delta systems.

Site description

The Yangtze River flows in the length of 6379 km with a basin area of 1,800,000 km² (Dai 2021) before

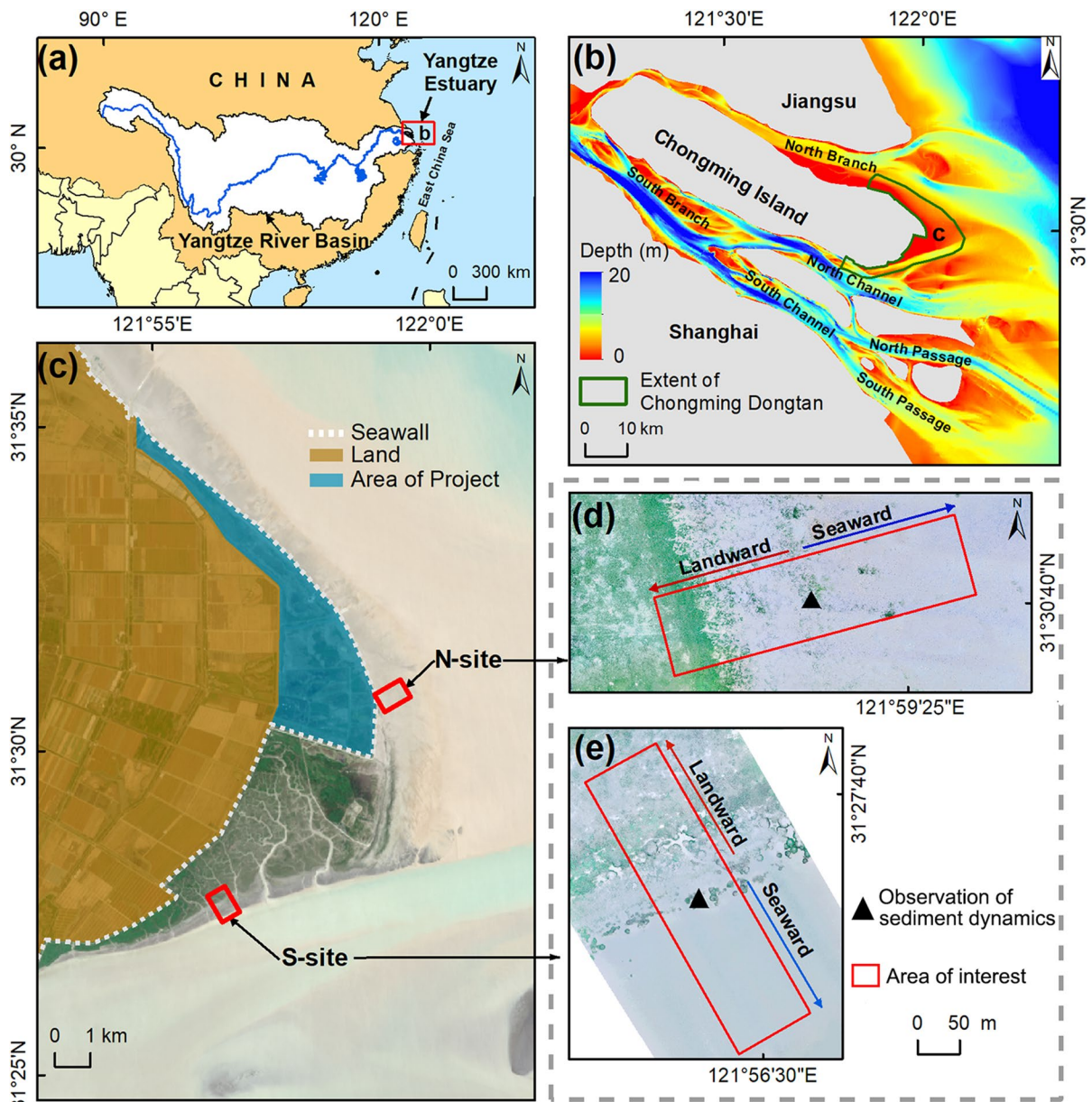


Fig. 1 Study area: (a) Extent of Yangtze River Basin and location of the Yangtze Estuary; (b) Overview of the Yangtze Estuary; (c) Satellite images of CDNR (data source: Landsat-8); (d) Drone images at N-site and (e) at S-site

entering the East China Sea (Fig. 1a). The Yangtze Estuary (Fig. 1b) is famous for bifurcated patterns and high turbidity as one of the mega estuarine systems worldwide. Due to hydraulic projects and the soil conservation policy in the Yangtze River Basin, sediment discharge into the Yangtze Estuary has started to decline since the 1970s (from $> 400 \text{ Mt yr}^{-1}$ in 1970 to 105 Mt yr^{-1} in 2019, Guo et al. 2019). The

continuously decreased fluvial sediment input has provoked concerns about the vulnerability of coastal wetlands in the Yangtze Estuary (Yang et al. 2006; Wang et al. 2014; Leonardi et al. 2021).

Chongming Dongtan National Nature Reserve (CDNR) is located at the east head of Chongming Island in the Yangtze Estuary (Fig. 1c). Astronomic tides in the region are semidiurnal with diurnal

inequality. The average tidal range is 2.5 m but can reach 3.5–4.0 m during spring tides according to the Sheshan gauging station (20 km east of CDNR, Yuan et al. 2022). Winds controlled by the subtropical monsoon prevail in the southeast in summer and the northwest in winter. Highly variable wind speed can reach 36 m s^{-1} (GSII 1996).

Two represented marsh pioneer zones were selected in CDNR, namely N-site and S-site, respectively (Fig. 1d, e). Properties of vegetation, surface sediment and water at both sites were shown in Table 1. The two sites were mainly covered by pioneer *Scirpus* communities (*Scirpus mariqueter* at N-site, and *Scirpus triqueter* at S-site). Surface sediment is muddy at N-site and sandy at S-site. Controlled by runoffs of the North Channel in the Yangtze Estuary (Fig. 1b), water salinity at S-site is lower than that at N-site. Vertical accretion at N-site has continued after the new seawall closure in 2014 (Fig. 1c, Wei et al. 2018), while erosion was found at S-site (Zhao et al. 2008; Yang et al. 2020).

Methodology

Data acquisition

Drone monitoring

The RTK-enabled drone (DJI Phantom 4-RTK, DJI, China) was equipped to take photos at N-site and S-site. The advantage of the RTK-enabled drone is its high accuracy without the need for ground control points. Four flights were executed on the following dates in 2021: 23rd April, 30th June, 31st July, and 24th September (see Table S1 for flight time). All flights used the same parameter settings, as detailed in Table S2.

Ground validation points were measured instantly after each flight using the real-time kinetics GPS units

(RTK-GPS, Hi-Target, China). Validation points for April at the N-site were unavailable due to severe weather conditions. All surveys were horizontally georeferenced in China Geodetic Coordinate System 2000 (CGCS2000) and vertically georeferenced in the local Wusong datum.

Measurements of hydrodynamics and sediment

Waves (RBRduo³ T.DI wave, RBR, Canada), currents (EMCM, JFE, Japan) and sediment (OBS-3A, Campbell Scientific, USA) were observed synchronously at the two marsh edges (Fig. 1b, e) in four spring tides from 8th to 10th June in 2021, with an average wind speed of 3.6 m s^{-1} (Fig. S1). All deployed sensors were placed at 15 cm above the seabed (Fig. S2). Turbidity signals recorded by OBS-3A were calibrated to suspended sediment concentration (SSC) using sediment samples near the instruments (Fig. S3).

Drone-related data processing

It took three steps in the procedure of drone-related data processing (Fig. S4): (1) Obtain orthoimages and rough point cloud; (2) Recognize marsh covers in orthoimages; (3) Modify point cloud and generate a digital elevation model (DEM). The procedure specified a spatial resolution of 10 cm. DEM products were validated against ground validating points and yielded low errors at both sites (4.34 cm at N-site and 4.60 cm at S-site, Fig. S5).

Data analysis

Spatial analysis on marsh evolution

We selected two proxies, the marsh area and the number of patches, respectively, to represent spatially explicit marsh vegetation dynamics. To elaborate,

Table 1 Properties of vegetation, sediment and water at N-site and S-site

| Items | Properties | N-site | S-site |
|------------|---|---------------------------|--------------------------|
| Vegetation | Species | <i>Scirpus mariqueter</i> | <i>Scirpus triqueter</i> |
| | Canopy height (m) | 40.26±3.81 | 53.14±6.42 |
| | Aboveground biomass (g m^{-2}) | 244.96±52.01 | 177.04±39.73 |
| Sediment | Median grain size (ave.±std., μm) | 17.48±7.75 | 43.20±4.50 |
| Water | Salinity (median/max., PSU) | 10.87/24.44 | 2.44/16.18 |

changes in the marsh area represent the extent of marsh vegetation gain or loss covering the landscape, while changes in the number of marsh patches explain how marsh vegetation patches are spatially rearranged (e.g., more clustered or more scattered).

By referencing theories and cases in urban growth (Forman 1995; Berling- Hoffhine Wilson et al. 2003; Berling-Wolff and Wu 2004; Xu et al. 2007; Liu et al. 2010), four types of marsh patch changes were defined and identified according to patch-to-patch proximities (Fig. 2): outlying expansion, edge expansion, infilling expansion and retreat.

Outlying expansion means isolated-grown patches apart from old patches. Edge expansion is defined as the growth adjacent to patch fringes. Infilling expansion refers to the new growth filling gaps inside or between old patches. Retreat is the reduction of patch area. The three marsh expansion topologies were distinguished from shared borders between newly-grown patches and existing patches, using the method proposed by Xu et al. (2007):

$$S = L_C/L \tag{1}$$

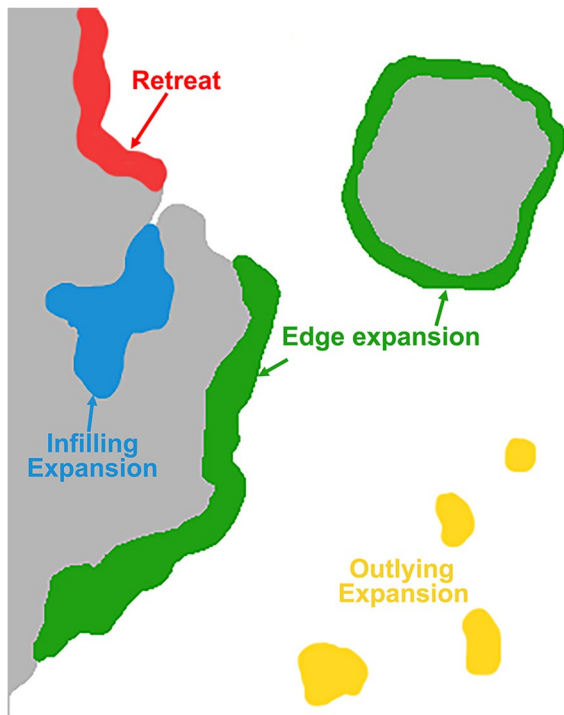


Fig. 2 Illustrations of marsh changes around the grown marshes (the gray part)

$$S = \begin{cases} = 0 & , \text{outlying expansion} \\ \in (0, 0.5) & , \text{edge expansion} \\ \in (0.5, 1] & , \text{infilling expansion} \end{cases} \tag{2}$$

where L_C is the length of the shared borders between new patches and old patches (m), L is the perimeter of new patches (m), and S is the ratio of "inherited borders" in newly grown patches.

Morphological changes

To assess the lateral propagation of tidal flats at the two sites, we used the dataset from the Sheshan gauging station to determine the mean high neap water level (MHNW) during the period from March to October 2021, with a value of 2.68 m above Wusong datum. The dynamic MHNW contour on the DEMs visually depicts the landward retreat or seaward expansion of tidal flats. Moreover, tidal flats below the MHNW were susceptible to inundation during most tides. In comparison, tidal flats above MHNW possibly would not be inundated by neap tides, thus gaining the opportunity for marsh seedlings to anchor and establish during the inundation-free period. Consequently, we computed the area of tidal flats (including both vegetated marshes and bare mudflats) above the MHNW as a proxy for potential habitats suitable for marsh establishment and growth.

We focused on vertical accretion or erosion on the tidal flats extending 200 m seaward from the initial marsh edges at both sites. To determine erosion/deposition rates, we subtracted DEMs from two neighboring months. To compare the accretion/erosion patterns between the two sites, we estimated the probability density function of monthly accretion rates over a five-month period. Additionally, we assessed elevation stability using the elevation standard deviation (STD) as a metric. This calculation followed the methodology by Xie et al. (2017), determining the STD for each spatial location over several months (specifically, in this study, four elevation values for calculating STD at each location).

Bed shear stress and sediment transport

In a calm, typhoon-free period, we collected in-situ data during four spring tides, including wave, current, and SSC measurements, which were utilized

to compute bed shear stress and sediment flux. Bed shear stress due to combined waves and currents (τ_{cw} , Pa) was estimated to quantify hydrodynamic forces (Equation S2-S12). Near-bed sediment flux per unit width within a specific duration was calculated and it was expressed as (Zhu 2017):

$$Q_s = \sum_{i=1}^n SSC_i V_i H \Delta t \quad (3)$$

where Q_s is sediment flux (kg m^{-1}), SSC is suspended sediment concentration (kg m^{-3}), V is current velocity values (m s^{-1}), Δt is the burst interval (600 s), n is the number of bursts, and H is the height of sensors above the seabed (0.15 m).

It assumed that sediment transport at the bottom 15 cm of the water column is landward in flooding stages and seaward in ebbing stages. Net sediment flux per tide was calculated as follows (Yang et al. 2020):

$$Q_{s-net} = Q_{s-flood} - Q_{s-ebb} \quad (4)$$

where Q_{net} is net sediment flux per tide ($\text{kg m}^{-1} \text{ tide}^{-1}$) and positive in the landward direction, $Q_{s-flood}$ and Q_{s-ebb} refer to the sediment flux of flooding tides and ebbing tides, respectively.

Results

Spatiotemporal characteristics of salt marsh changes

Marshes at N-site expanded seaward, whereas those at S-site migrated landward during the surveyed five months (Fig. 3a). The marsh area at N-site grew from 4900 m^2 in April to 16,121 m^2 in September with a gradually compacted spatial structure over five months, while the marsh area at S-site decreased from 11,781 to 10,458 m^2 during the same period (Fig. 3b, c). At the stage of *Scirpus* establishment in spring (T1, from April to June), the number of patches at N-site increased explosively from 17 to 2874 but only 45 to 50 at S-site. Scattered patches at N-site quickly merged in summer (T2, from June to July) and contributed the greatest amount to marsh growth even though typhoon In-Fa attacked at the end of July (Fig. S6). Marshes at S-site began to shrink at the rate of 569 $\text{m}^2 \text{ month}^{-1}$ after typhoon In-Fa, resulting in an increased number of patches (from 50 to 148) due to fragmentation. Although the marsh area

at both sites decreased from summer to autumn (T3, July to September), marsh loss at S-site was 2.4 times quicker than that at N-site.

Distinctly different patch-level marsh changes were evident at the two sites (Fig. 3d). At N-site, marshes exhibited varying patterns of expansion throughout seasons, that was: from outlying expansion in spring (T1), to edge expansion in summer (T2), and to infilling expansion in autumn (T3). Conversely, the dominant pattern at the S-site shifted from infilling and edge expansion in spring (T1) to subsequent retreat following the impact of typhoons (T2 and T3).

Lateral propagation and vertical accretion-erosion of tidal flats

Tidal flats at S-site experienced obvious landward retreat, while N-site maintained more laterally stable tidal flats, as evidenced by the movement of MHNW at both sites (Fig. 4a). Similarly, the area of tidal flats above MHNW remained relatively stable at N-site but decreased at a rate of 1058 $\text{m}^2 \text{ month}^{-1}$ at S-site (Fig. 4b). These observations highlight that N-site provides a larger and more stable space along the sea-to-land gradient with a low inundation frequency, which is conducive to marsh survival, compared to S-site. Comparatively, S-site had narrow space for new marsh establishment beyond the initial marsh edge and this limited space was vulnerable to erosion.

S-site was generally more prone to erosion than N-site (Fig. 4c). Both sedimentary regimes were erosion-dominant because of typhoons but N-site was more prone to accretion. The erosion rate with the peak possibility was around 1.4 cm month^{-1} at N-site and approximately 7.5 cm month^{-1} at S-site. Besides, high elevation variabilities represented by elevation STD further explained that bed level at S-site was unstable (Fig. 4d). In summary, S-site experienced much more intensive erosion and variable bed level changes compared to N-site. These differences may be attributed to site-specific hydrodynamics and sediment availability.

Hydrodynamics and sediment transport near marsh edges

Marsh edges at S-site experienced stronger hydrodynamics and lower sediment availability than N-site (Fig. 5a-e). Among the observed four tides, maximum water depth (h), maximum significant wave

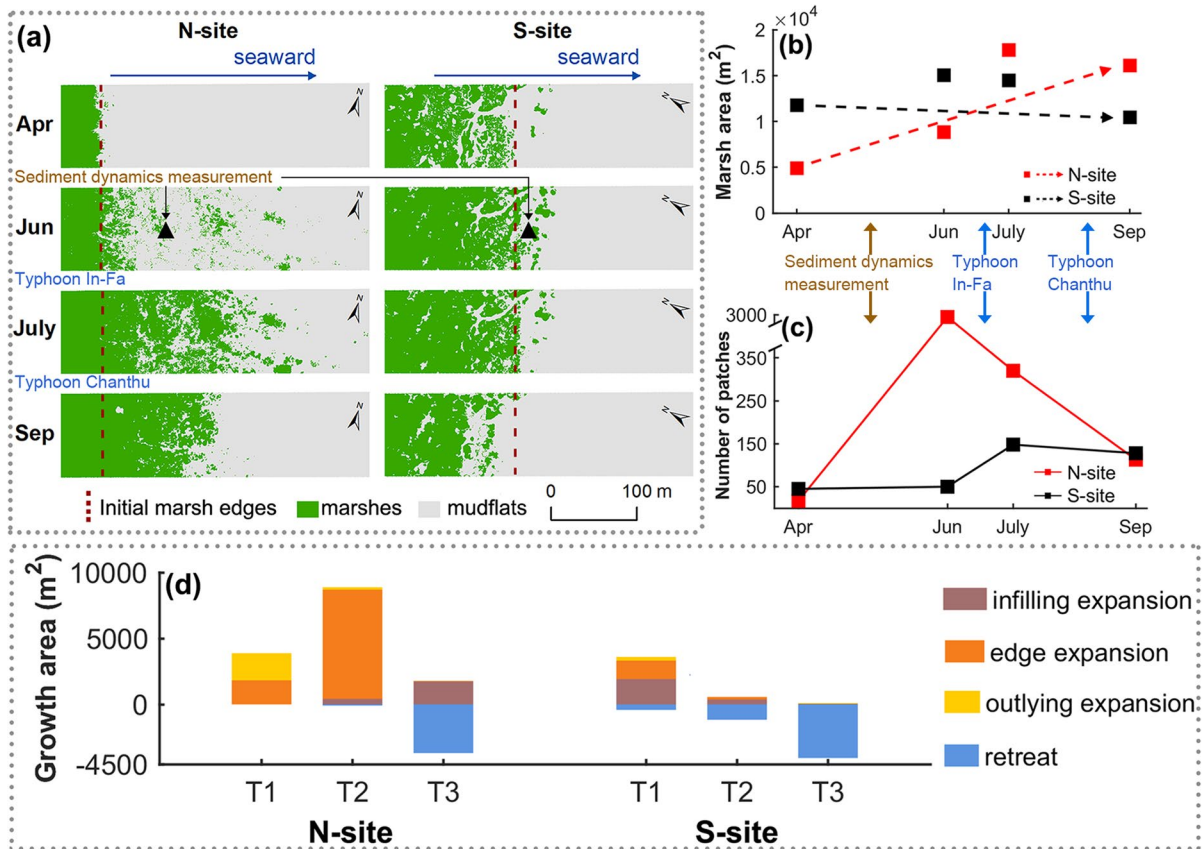


Fig. 3 Salt marsh changes at N-site and S-site: (a) Marsh cover; (b) Marsh area; (c) Number of patches; and (d) The growth area belonging to different change types in different

periods. T1, T2 and T3 refer to the time interval from April to June, June to July and July to September, respectively

height (H_s) and mean flow velocity (V) at S-site were significantly 2.9, 3.6 and 1.8 times greater than those at N-site (Fig. 5a-c, $p < 0.01$, pairwise t -test), respectively. Intensive wave and current acted as significantly greater bed shear stress (τ_{cw}) at S-site (tide-averaged, 0.29 ± 0.06 Pa), while 0.20 ± 0.03 Pa at N-site (Fig. 5d, $p = 0.04$, two-sample t -test). Unlike differences in hydrodynamics between the two sites, SSC at S-site was significantly lower than that at N-site (tide-averaged, 3.22 ± 0.19 kg m⁻³ at S-site and 4.07 ± 0.28 kg m⁻³ at N-site, Fig. 5e, $p < 0.01$, pairwise t -test).

Sediment flux (Q_s) expressed that S-site had a higher magnitude of seaward-dominated sediment transport than N-site, within the range from -68.89 to 22.56 kg m⁻¹ tide⁻¹ at N-site and -187.20 to -67.19 kg m⁻¹ tide⁻¹ at S-site (Fig. 5f). The results proved that high τ_{cw} and low SSC significantly promoted seaward sediment

transport ($R^2 = 0.53$, $p = 0.04$ for the former, Fig. 5g; $R^2 = 0.75$, $p < 0.01$ for the latter, Fig. 5h). This implied that marsh edges with high bed shear stress plus low sediment availability (e.g., S-site in the study) would potentially be prone to being eroded due to weak sediment retention capacity.

Discussion

The present study aims to investigate how different physical constraints, including sediment dynamics and morphodynamics, influence seasonal marsh dynamics. This investigation was carried out by comparing two typical marsh pioneer zones in the Yangtze Estuary, China. Evidence from drone-based images reveals that all three types of the patch-level marsh expansion (outlying, edge, and infilling) were

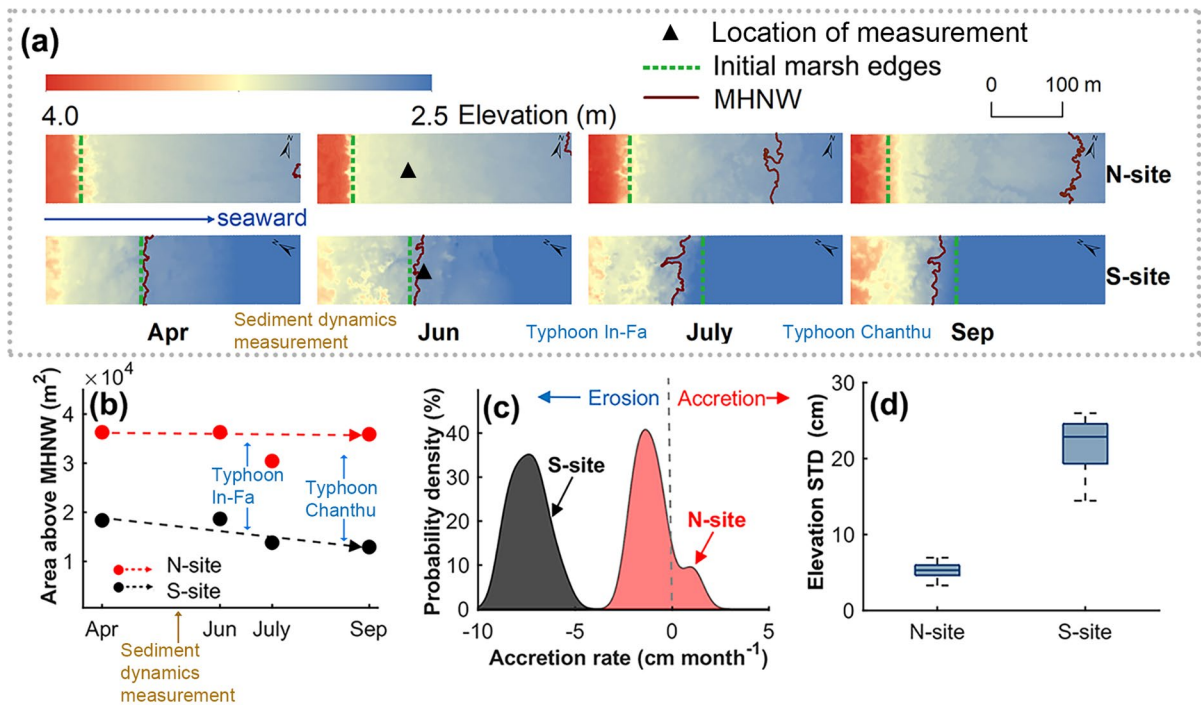


Fig. 4 Morphological changes at N-site and S-site: **(a)** Elevation distribution; **(b)** Change of area above MHNW; **(c)** Estimated probability density of accretion rate the 200-m seaward tidal flats beyond the initial marsh edge; and **(d)** Standard deviation

among the four DEMs on the 200-m seaward tidal flats beyond the initial marsh edge. MHNW: mean high neap water level; STD: standard deviation

observed in the expanding marsh system (N-site). In contrast, in the retreating marsh system (S-site), only distance-limited infilling and edge expansion were evident. This finding underscores the significance of patch level marsh changes in sustaining and accelerating seasonal net marsh expansion, which is tightly associated with site-specific sediment dynamics and morphodynamics.

The shaping role of physical constraints in salt marsh establishment

Our results expressed that high bed shear stress plus low SSC decreased sediment retention capacity (Fig. 5g, h) and thus potentially accelerated vertical erosion near marsh edges. Theoretically, a high flow velocity can carry more sediment than a low one (Winterwerp, 2001). Low SSC can activate sediment resuspension by τ_{cw} -induced erosion to compensate the deficit in mass balance (Zhang et al. 2009; Deb Nath and Chaudhuri 2011). In addition, an increased sandy portion of surface sediment could weaken

sediment resistance to erosion by decreasing critical shear stress for erosion (τ_{ce}) (Panagiotopoulos et al. 1997). High τ_{cw} (Fig. 5d), low SSC (Fig. 5e), and sandy surface sediment (Table 1) at S-site increased erosion risks by increasing hydrodynamic forces and decreasing sediment erodibility. It was reasonable to infer that the bed level at S-site was more prone to being eroded and less stable than N-site from the four-tide observations, and the five-month morphological changes solidly evidenced this hypothesis (Fig. 4).

Strong hydrodynamics and unstable bed levels are effective signatures of physical disturbances to marsh establishment. Recent studies have revealed that the floatation of post-germinated seedlings promoted the onset of *Scirpus* quick dispersal (Zhao et al. 2021b; Jiang et al. 2022). The mechanism explained large-scale outlying expansion beyond existing marshes from April to June at N-site (Fig. 3d). Contrastingly, the limited outlying expansion at S-site (Fig. 3d) showed that a clear way from seedling floatation to the successful establishment depends on site-specific conditions. Physical disturbances induced by bed

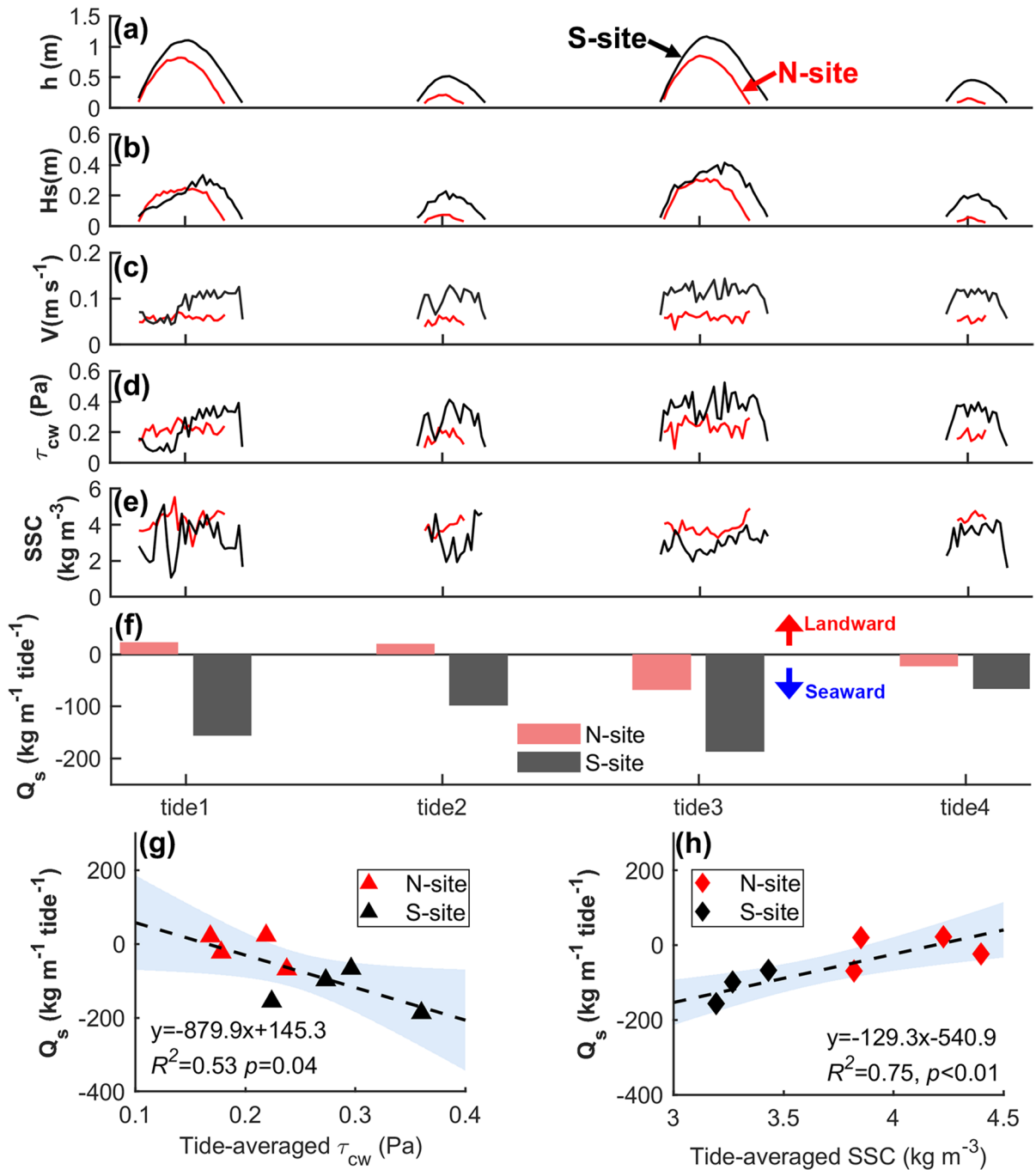


Fig. 5 Comparisons of sediment dynamics between the two marsh edges: **(a)** Water depth (h); **(b)** Significant wave height (H_s); **(c)** Values of flow velocity (V); **(d)** Bed shear stress due to combined wave-current actions (τ_{cw}); **(e)** Suspended sediment concentration (SSC); **(f)** Net sediment flux in four tides

(Q_s); **(g)** Relationships between Q_s and tide-averaged τ_{cw} ; and **(h)** Relationships between Q_s and tide-averaged SSC. All statistical analysis was finished with the significance level $\alpha = 0.05$

shear stress and consequent bed level changes would act as the force on seedlings at multiple stages, such as seedling settlement (Zhang et al. 2022), seedling anchoring (Zhao et al. 2021c), and seedling growth (Bouma et al. 2009), which facilitated seedling dislodgement and hampered its establishment. It would be challenging for seedling establishment in an environment with low SSC and activated resuspension by high bed shear stress (e.g., S-site in the study).

From the perspectives of landscape changes, we found marsh expansion at the two sites occurred within different spatial extents, as proven by the distance between the initial marsh edge and MNHW (Fig. 4a), also tidal flat area above MNHW (Fig. 4b). Elevations determine the spatial extent of marsh expansion by opening the first "windows of opportunity" (Balke et al. 2014; Hu et al. 2015b; Fivash et al. 2021). Low elevations that result in high inundation frequency lead to seedling death due to physiological stress (Cui et al. 2020; Xue et al. 2020). Sufficient habitats with moderate inundation frequency at N-site helped accommodate new scattered patches, while new marshes at S-site would enlarge in size by merging into the existing ones in the narrow space above MNHW.

Our field-based study gives empirical insights into the shaping role of physical constraints at the site-scale marsh pattern dynamics (Fig. 6a, b). It underlines two key variables: i) disturbance induced by bed shear stress and SSC, and ii) elevation-dependent spatial extent for expansion. Marsh pioneer species tend to select adaptive reproduction strategies to enhance survival in highly disturbed environments (Friess et al. 2012). Unsuitable physical disturbances decrease the possibility of success in sexual reproductions. To increase the population, asexual reproductions with high survival rates (e.g., Minden et al. 2012; Hu et al. 2015a; Silliman et al. 2015) would therefore take over, reducing the effective distance of species spread (Belzile et al. 2010; Liu et al. 2014). This informs that the distance-limited marsh expansion (e.g., infilling and edge expansion) is dominant at the seriously disturbed sites with high bed shear stress, low SSC, sediment resuspension, and bed erosion (Fig. 6b). Moreover, we supported the view that long-distance outlying expansion is more likely to occur at sites with large spatial extent that is sufficiently high in the tidal frame (Fig. 6a). The varying spatial extent often leads to changing biological

responses in landscapes (Holland et al. 2004; Miguet et al. 2016; Martin 2018). At sites with limited spatial extent, such as the S-site in this study, large-scale outlying expansion beyond the initial marsh edges becomes challenging due to the narrow potential habitats available for marsh establishment. In all, the spatially explicit marsh establishment was the consequence of trade-offs among physical disturbance, spatial extent and reproductive traits of marsh pioneer species.

Short-term marsh evolution: a temporal relay racing with opportunities and risks

The distinctly different spatial paradigms of marsh changes between the two sites highlight the significance of outlying expansion, particularly in sustaining salt marshes during storms. Scattered patches at N-site quickly grew through edge expansion (Fig. 3c) and became spatially compact (Fig. 3b), while sparse new patches at S-site were insufficient to support large-scale edge expansion and disappeared during typhoon In-Fa (Fig. 3a). At the patch level, high temperatures in summer steer clonal growth with dense tillers in salt marshes (Nieva et al. 2005). When scaling up to the site level, multiple patches of *Scirpus* tend to coalesce rather than collision (Zhao et al. 2021a). The number of previously established patches contributes to a homogeneous state of marsh cover, enhancing system resilience (Holling 1973) by setting the origin of edge expansion and invoking intraspecific positive feedback (Duggan-Edwards et al. 2020; Huang et al. 2022).

We represented the "relay-racing" spatial processes mentioned above using a conceptual diagram based on our results (Fig. 6c). It simplified marsh growing periods into three stages: establishment (stage I), growth (stage II), and recovery from abrupt events (stage III). Successful establishment at stage I does not immediately promote marsh growth but occupies blank ecological niches through outlying-expansion patches. These dense small patches expand around patch edges at stage II and substantially accelerate marsh growth. If marsh growth at stage II exceeds the threshold during extreme events, the grown marsh patches can persist into stage III (State A in Fig. 6); otherwise, marsh patches may begin to retreat (State B in Fig. 6). As a result, successive effects of landscape configuration settings in marsh establishment and landscape

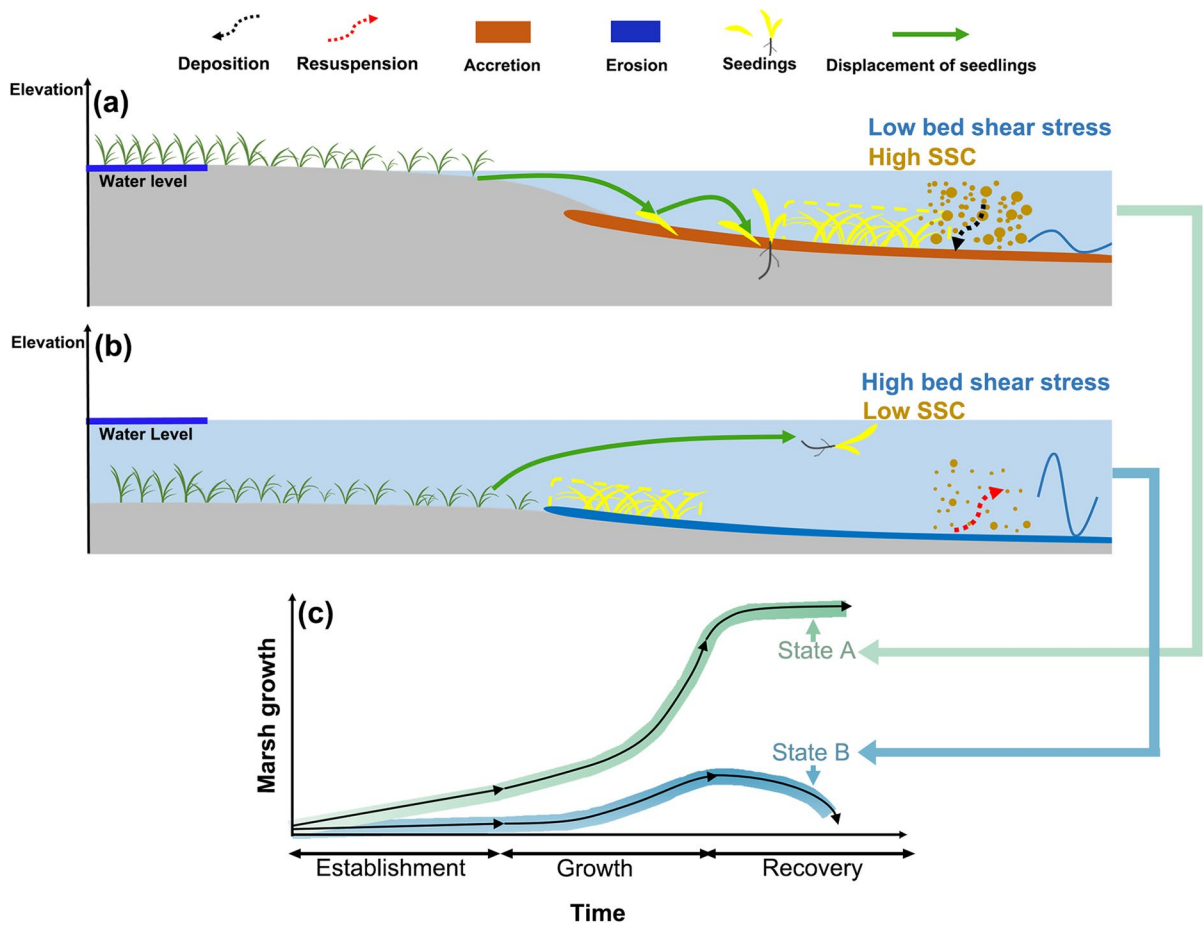


Fig. 6 Conceptual diagrams of different marsh establishment and marsh growth under varying physical conditions: **(a)** Seedling establishment at sites with low bed shear stress, high SSC and large spatial extent; **(b)** Seedling establishment at sites

with high bed shear stress, low SSC and narrow spatial extent; **(c)** Different states of short-term marsh evolution, where state A represented net seasonal marsh expansion and state B represented the net seasonal marsh shrink

composition changes in marsh growth finally shape the state of short-term marsh evolution and eventually influence the long-term pattern at inter-annual scale. The former is indispensable and heavily dependent on the magnitude of physical constraints.

It is important to note that opportunities and risks coexist in marsh establishment due to the intrinsic temporal variability of physical forces (Hu et al. 2021; van Belzen et al. 2022). Organism tolerance is enhanced by episodic low disturbances within specific temporally varying cycles. For example, adequate inundation-free periods help stabilize seedlings by forming forked roots (Jiang et al. 2022). Conversely, instantaneous peak hydrodynamics might lift seedlings

off and lead to failures of marsh colonization on mudflats (Poppema et al. 2019). A similar occasion-related mechanism also comes into play when facing typhoon events. The timing, strength and track of typhoons are uncertain (Sobel Adam et al. 2016; Lanzante 2019). Once the population size exceeds the tipping point for maintaining a stable state (Didham et al. 2005; Dakos et al. 2019), the opportunity for marsh survival can be created before typhoons. However, insufficient marsh growth might open "windows of risk" while encountering the "unknown" typhoon (e.g., S-site in the study). Therefore, subtle shifts between opportunities and risks in biophysical processes would facilitate formation of various salt marsh landscapes.

Decreased sediment challenges salt marsh conservation, spanning from monthly or seasonal (Lacy et al. 2020) to annual and decadal (Li et al. 2021) scale. Our results illustrated that low SSC hampers sediment retention near marsh edges (Fig. 5h) and shapes an erosion-prone sedimentary regime (Fig. 4c). Morphological responses to on-shore sediment supply determine the dynamic habitat size for marsh growth by elevating mudflats (Donatelli et al. 2018; Ladd et al. 2019). Sediment starving induces gradual shifts from accretion to erosion and threatens the safety of coastal wetlands by enlarging the drowned areas in mega-delta systems, such as the Yangtze (Yang et al. 2011; van Maren et al. 2013), the Mississippi (Jankowski et al. 2017; Sanks et al. 2020), and the Nile (Alfy Morcos 1995). Global sediment deficits might undermine the positive effect of marsh development and put it at a persistent risk.

Implications for restoration

It is a necessary step to convert risks into opportunities for the success in the practice of salt marsh restoration. We agree with previous studies emphasizing crucial window periods of salt marsh establishment in spring (Hu et al. 2015b; Fivash et al. 2021; Ning et al. 2020). Additionally, we further figured out that marshes should expand as soon as possible in spring to withstand subsequent typhoons in summer. Specific artificial assists can help organisms in coping with physical stress by optimizing their habitats. Auxiliary structures at the patch level, such as mesh bags to reduce loss of sowed seeds (Vanderklift et al. 2020) and mimics to strengthen stems (Temminck et al. 2020) can enhance individual survival. Expanding spatial extent at the site level can be achieved by elevating tidal platforms in front of salt marsh edges with dredged materials (Wiegman et al. 2018; Baptist et al. 2019) in case of insufficient accretions. Bio-based infrastructures on mudflats, such as oyster beds (Chowdhury et al. 2019), can dissipate wave energy, thus accelerating marsh establishment and delivering multiple ecological functions (Dafforn et al. 2015; Gittman et al. 2016).

The findings of this study highlight the significance of site-specific properties in salt marsh evolution. This is highly relevant to design strategies for restoration projects. Choosing the appropriate restoration site can reduce unnecessary costs by harnessing

"power from nature" (Cheong et al. 2013; Kumar et al. 2021). Marsh expansion in the accretion-prone site (e.g., N-site in this study) tends to be spatially significant and inherently resilient, primarily due to the robust performance of seedling survival in an accreting environment (Cao et al. 2018). Conversely, the erosion-prone sites (e.g., S-site in this study) are more likely to experience limited seaward marsh expansion and landward marsh migration. Hence, applying uniform measures for marsh restoration at the landscape scale may not be appropriate, even when dealing with the same estuarine system and similar wind exposures. It is advisable to prioritize investments in vulnerable marshes at erosion-prone sites.

Conclusion

The present study has demonstrated that physical constraints drive state differentiations in short-term marsh evolution at the landscape scale. We recognized that the seasonal net marsh expansion started from outlying expansion in spring, followed by edge expansion in summer, and infilling expansion in autumn. In contrast, only distance-limited infilling and edge expansion can be observed when the marsh is in a net seasonal retreat. This finding, combined with comparisons of hydrodynamics, sediment transport, and morphological changes, demonstrates that site-specific physical constraints drive variations in the state of short-term marsh evolution. Marsh development faces significant challenges in seizing fleeting opportunities and mitigating uncertain risks during extreme events and sediment decline. As a result, we propose that prioritizing the restoration of the erosion-prone sites should be the primary focus at the landscape scale. This information would contribute to the increased knowledge of coastal management strategies, especially for other similar mega-delta systems.

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Data availability The datasets generated or analyzed during the current study are available from the corresponding author on reasonable request.

Declarations

Competing interests The authors have no relevant financial or non-financial interests to disclose.

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