

Shore Height and Low-tide Exposure as Regulators of Intertidal Distribution Thresholds of Seagrass *Enhalus acoroides* in the Gulf of Thailand

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ABSTRACT

Understanding environmental controls on seagrass distribution is essential because inappropriate elevation selection can reduce restoration and transplantation success. This study investigated how shore height and low-tide exposure influence the distribution of *Enhalus acoroides* in the upper intertidal zone of the Gulf of Thailand. Shore height was measured at 261 stations across seven sites during 2022–2023 using a theodolite and a surveyors' rod, and expressed as height above lowest low water (cm H_LLW) based on predicted tidal levels. Aboveground biomass was estimated using a modified Rapid Visual Estimation Technique. Across shore heights of 0–120 cm H_LLW, the frequency of *E. acoroides* occurrence followed a normal distribution ($D = 0.09$, $p = 0.35$), with most observations between 40 and 80 cm H_LLW. Preferred shore-height ranges varied among sites, extending from 0 to 106 cm H_LLW. Percentage cover did not differ significantly among H_LLW intervals of 0–40 cm, 40–80 cm, 80–120 cm. However, aboveground biomass differed significantly among groups, with the highest biomass at 0–20 cm H_LLW (17.77 ± 6.75 g DW·m⁻²), where mean cover was $48.18 \pm 35.73\%$. The upper shore-height threshold of *E. acoroides* was lower in the eastern Gulf of Thailand (77 cm H_LLW) than in the southern coastal region (106 cm H_LLW) and was substantially lower than thresholds reported for the Andaman Sea. These regional and local differences were closely associated with tidal regime, low-tide level, desiccation duration, and sediment water-level drawdown. The findings provide practical guidance for restoring and transplantation intertidal *E. acoroides* meadows under changing coastal conditions associated with global warming.

Keywords: Desiccation, Lowest low water, Seagrass distribution, Shallow threshold, Tidal level

INTRODUCTION

Seagrass beds are vital components of coastal ecosystems, contributing to biodiversity maintenance, fisheries productivity, detrital export, and long-term carbon sequestration (Fourqurean *et al.*, 2012; Kanmarangkool *et al.*, 2022; Lyimo and

Hamisi, 2023). In the Indo-Pacific region, *Enhalus acoroides* is one of the most ecologically important and widely distributed seagrass species (Green and Short, 2003). Stankovic *et al.* (2021) estimated that organic carbon storage within Southeast Asian seagrass ecosystems amounted to 121.95 ± 76.11 Mg·ha⁻¹, highlighting their significance in climate regulation.

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E. acoroides meadows represent a major ecological resource in tropical coastal areas, supporting a wide range of marine fauna. The large leaves and accumulated detritus of this species provide essential food resources and shelter for many marine organisms, with particular importance for dugongs (Coles *et al.*, 1993; Hines *et al.*, 2005). The occurrence of *E. acoroides* in dugong stomach contents further underscores its ecological importance (Adulyanukosol *et al.*, 2001). Recent declines of this species have raised concern about the degradation of tropical ecosystem (Yu *et al.*, 2018). Changes in seagrass habitat structure have been shown to strongly affect associated fauna and ecosystem functioning (Coles *et al.*, 1993; Unsworth *et al.*, 2007; 2009).

Globally, seagrass ecosystems are increasingly threatened by anthropogenic activities, including increased turbidity from land-derived sedimentation (Spalding *et al.*, 2003; Orth *et al.*, 2006), plastic pollution (Balestri *et al.*, 2017), and physical disturbances such as shallow-net trawling, destructive fishing practices, boating, anchoring, and shipping (Spalding *et al.*, 2003). Collectively, these pressures have caused widespread degradation and loss of seagrass meadows worldwide (Spalding *et al.*, 2003; Grech *et al.*, 2012). However, long-term biomass changes in some intertidal seagrass systems have also been linked to natural drivers, particularly tidal cycles, daylight exposure, and high solar radiation, rather than being solely attributed to anthropogenic stressors (Unsworth *et al.*, 2012). Nevertheless, the role of tidal exposure in determining the upper intertidal distribution limit of *E. acoroides* remains insufficiently understood, particularly in relation to exposure-associated stressors such as high light intensity, elevated temperature, and desiccation (Unsworth *et al.*, 2012).

Along the Thai coastline, *E. acoroides* occurs in both the Andaman Sea and the Gulf of Thailand, where tidal regimes differ substantially. Water levels in the upper Gulf of Thailand are generally higher and more variable than in the lower Gulf, whereas the Andaman Sea exhibits more stable water levels due to a lower magnitude of water mass fluctuation (Aungsakul *et al.*, 2007). In the Andaman Sea, which has a semi-diurnal tidal regime,

E. acoroides distribution is restricted to shallow intertidal zones and is primarily controlled by shore height above the lowest low water level rather than seawater depth, with an upper distribution limit of 200 cm above the lowest low water level (Monthum *et al.*, 2023). The interaction between shore height and tidal regime influences the duration of aerial exposure during low tide, which is associated with high light intensity, elevated temperatures, and drying conditions, thereby increasing physiological stress in seagrasses. Although the upper distribution limit of *E. acoroides* has been reported for the Andaman Sea, comparable information for the Gulf of Thailand remains limited. This gap is important because tidal regimes differ between the two regions and may influence aerial exposure during low tide.

We hypothesize that the upper shore-height thresholds of *E. acoroides* differs between the Andaman Sea and the Gulf of Thailand due to differences in tidal regimes. The Andaman Sea experiences a semi-diurnal tidal cycle, whereas the Gulf of Thailand is dominated by a diurnal tide. These contrasting tidal patterns may influence water level fluctuations and the duration of aerial exposure during low tide, thereby affecting desiccation stress and distribution patterns. In this study, we examined shore height above the lowest low water level (H_{LLW}) in intertidal *E. acoroides* beds in the Gulf of Thailand to determine the upper shore-height threshold and related it to low-tide exposure duration. By linking shore height with tidal dynamics, this study provides baseline information for assessing exposure-related die-off risk and identifying suitable sites for restoration and transplantation of *E. acoroides* under changing coastal conditions.

MATERIALS AND METHODS

Study site

The study included seven *E. acoroides* beds in the Gulf of Thailand, selected to represent major beds with extensive spatial coverage. These sites were categorized into two regions: Kradat Island (Figure 1b) in the eastern Gulf of Thailand, and six sites in the southern Gulf of Thailand:

Hua Thanon and Nah Thum beaches on Samui Island, Nai Wok Bay on Pha Ngan Island, the east and west coasts of Tan Island, and Tharai Island (Figure 1c–1h).

Sampling stations were established along transects oriented perpendicular to the coastline. The transects were arranged parallel to one another and spaced 200 m apart. Stations were positioned at 50 m intervals along each transect and georeferenced using a handheld GPS unit (Garmin GPSMAP 64x). Transect lengths and station numbers varied according to local depth profiles.

The total surveyed area was 0.69 km² at Kradat Island (Figure 1b), 0.95 km² across Samui, Pha Ngan, and Tan islands (Figure 1c–g), and 0.10 km² at Tharai Island (Figure 1h). In total, specimens and environmental data were collected from 261 stations in 2022 and 2023.

Sampling techniques and data analysis

At each station, shore height was measured using a theodolite (Nikon AP-8) and a surveyor's rod following standard surveying procedures (Leliaert and Coppejans, 2004). The theodolite

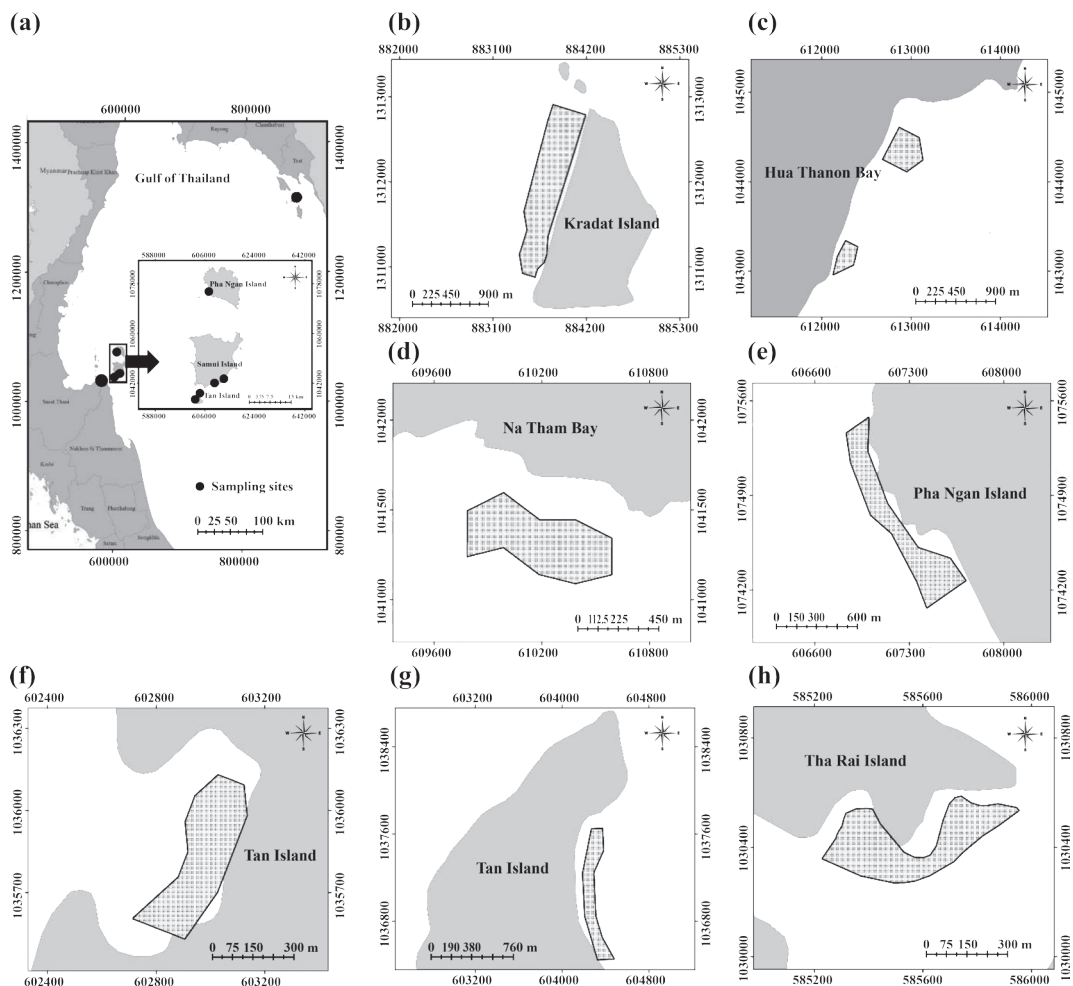


Figure 1. Intertidal seagrass study locations in Thailand: (a) sampling sites in Thailand; (b) Kradat Island; (c) Hua Thanon Bay; (d) Nah Thum Bay; (e) Nai Wok Bay; (f) west side of Tan Island; (g) east side of Tan Island; (h) Tharai Island. The pattern (▨) indicates the study area.

was positioned between two adjacent transect lines. Field measurements were referenced to the predicted tidal height above the lowest low water level at the corresponding date and time of sampling. These values were then converted to shore height above the lowest low water level (H_LLW, cm) using Tide Tables: Thai Waters (A.D. 2022 and 2023). The lowest low water level represents the mean of the lowest tides recorded at a tidal station over an 18.6-year tidal cycle (Hydrographic Department, Royal Thai Navy, 2023).

The abundance of *E. acoroides* was quantified across the study sites. Total aboveground biomass was assessed using a modified Rapid Visual Estimation Technique (Mellors, 1991). In addition, the presence of *E. acoroides*, its aboveground biomass, and percentage cover were recorded at each station.

Data analyses were conducted using R software (R Development Core Team, 2020). The ggplot2 package was used for data visualization, including histograms and graphical summaries. Differences in percentage cover and aboveground biomass among H_LLW interval groups were evaluated using one-way ANOVA. Homogeneity of variance (Levene's test) was applied and Welch's ANOVA or the Kruskal–Wallis test was used as an alternative when assumptions were not met. Pairwise relationships among H_LLW, percentage cover, and aboveground biomass were examined using Pearson correlation analysis.

Predicted lowest tide data for 2022–2023 (Hydrographic Department, Royal Thai Navy, 2022; 2023) from the nearest tide stations were integrated with site-specific upper shore-height thresholds to define the threshold for the Gulf of Thailand. Upper shore-height thresholds at Kradat and Samui islands were used to estimate seagrass desiccation duration at corresponding shore heights in 2022, when the seagrass die-off crisis began. To assess long-term variability in tidal exposure, predicted lowest tide levels from 2019 to 2025 (Hydrographic Department, Royal Thai Navy, 2019–2025) were compiled and analyzed to quantify interannual differences in minimum tidal heights.

RESULTS AND DISCUSSION

E. acoroides occurred predominantly as monospecific stands across all study sites. Its abundance, expressed as aboveground biomass and percentage cover, varied along the gradient of shore height above the lowest low water level (H_LLW). Stations with higher H_LLW values were located in shallower water or exposed to air during low tide, whereas lower H_LLW corresponded to deeper areas. The frequency of *E. acoroides* occurrence across the H_LLW gradient followed a normal distribution ($D = 0.09$, $p = 0.35$; Figure 2), with most observations between 40 and 80 cm H_LLW (Table 1). Preferred shore-height ranges of *E. acoroides* varied among sites, spanning 14–77 cm H_LLW at Kradat Island, 0–78 cm at Hua Thanon Bay, 57–106 cm at Nah Thum Bay, 2–82 cm at Nai Wok Bay, 66–100 cm on the west side of Tan Island, 57–86 cm on the east side of Tan Island, and 5–59 cm at Tarai Island (Table 1). The upper shore-height threshold observed across all sites was 106 cm H_LLW.

No significant difference in percentage cover was found among H_LLW interval groups (0–40 cm, 40–80 cm, and 80–120 cm), whereas aboveground biomass showed a significant difference among the groups (Figure 3 and Table 2). However, the highest aboveground biomass occurred at 0–20 cm H_LLW (17.77 ± 6.75 g DW·m⁻²), with a mean coverage of $48.18 \pm 35.73\%$. Pearson correlation analysis showed no significant correlation between H_LLW and percentage cover ($r = 0.10$), or between H_LLW and aboveground biomass ($r = -0.23$) (Figure 4). However, percentage cover and aboveground biomass were positively correlated ($r = 0.71$).

The distribution of *E. acoroides* differed markedly between the Gulf of Thailand and the Andaman Sea. In the Gulf of Thailand, the upper shore-height threshold was 106 cm H_LLW, indicating a deeper and narrower distribution range than that reported for the Andaman Sea. In contrast, Monthum *et al.* (2023) documented an upper shore-height threshold of 220 cm H_LLW in the Andaman Sea, where *E. acoroides* occupied a broader depth range and showed a wider spatial distribution (Table 2 and Figure 5).

Table 1. Percentage cover and aboveground biomass of *Enhalus acoroides* at different shore heights above the lowest low water level (H_LLW) across the study locations.

H_LLW (cm)	Locations													
	(1)		(2)		(3)		(4)		(5)		(6)		(7)	
	COV (%)	BM (g dw·m ⁻²)	COV (%)	BM (g dw·m ⁻²)	COV (%)	BM (g dw·m ⁻²)	COV (%)	BM (g dw·m ⁻²)	COV (%)	BM (g dw·m ⁻²)	COV (%)	BM (g dw·m ⁻²)	COV (%)	BM (g dw·m ⁻²)
0–20	15.00±5.00 (3)	11.60±6.86 (3)	50.00±0 (1)	19.49±0 (1)	0 (1)	0 (1)	30.00±0 (1)	15.78±0 (1)	0 (1)	0 (1)	0 (1)	0 (1)	75.00±24.08 (6)	20.57±6.02 (6)
20–40	18.44±17.62 (9)	8.66±6.38 (9)	20.00±0 (1)	7.42±0 (1)	0 (1)	0 (1)	10.00±7.07 (2)	6.50±1.31 (2)	0 (2)	0 (2)	0 (2)	0 (2)	51.15±25.50 (13)	20.75±4.44 (13)
40–60	27.75±27.62 (12)	8.20±6.01 (12)	48.33±44.45 (6)	12.94±10.46 (6)	12.66±15.04 (3)	3.30±3.35 (3)	49.16±22.34 (12)	15.27±3.08 (12)	0 (3)	0 (3)	43.33±41.63 (3)	10.83±9.07 (3)	46.25±26.03 (12)	14.47±5.54 (12)
60–80	8.50±4.94 (2)	2.55±1.64 (2)	22.50±31.75 (4)	8.47±8.14 (4)	52.85±28.70 (7)	12.83±8.31 (7)	41.66±27.72 (9)	10.67±3.61 (9)	51.85±33.32 (7)	11.73±6.16 (7)	50.22±33.77 (9)	11.65±6.84 (9)	0 (9)	0 (9)
80–100	0 (3)	0 (3)	0 (3)	0 (3)	66.66±49.32 (9)	16.86±13.04 (9)	0 (4)	0 (4)	55.00±28.61 (4)	11.85±4.39 (4)	58.75±16.52 (4)	11.25±2.79 (4)	0 (4)	0 (4)
100–120	0 (2)	0 (2)	0 (2)	0 (2)	32.50±38.89 (2)	10.56±13.39 (2)	0 (2)	0 (2)	0 (2)	0 (2)	0 (2)	0 (2)	0 (2)	0 (2)
120–140	0 (2)	0 (2)	0 (2)	0 (2)	0 (2)	0 (2)	0 (2)	0 (2)	0 (2)	0 (2)	0 (2)	0 (2)	0 (2)	0 (2)

Note: Locations are coded as follow: (1) Kradat Island, (2) Hua Thanon Bay, (3) Nah Thum Bay, (4) Nai Wok Bay, (5) west side of Tan Island, (6) east side of Tan Island, and (7) Tharai Island; COV = percent cover (%); BM = aboveground biomass (g dw·m⁻²); Values are presented as mean±SD. Number in parentheses indicate sample size (n).

Table 2. Percentage cover and aboveground biomass of *Enhalus acoroides* at different shore heights above the lowest low water level (H_LLW) in the Gulf of Thailand and the Andaman Sea.

H_LLW (cm)	Gulf of Thailand (This study)		Andaman Sea*
	COV (%)	BM (g dw·m ⁻²)	COV (%)
0–20	48.18±35.73 ^a (11)	17.77±6.75 ^a (11)	90.00±0 ^a (1)
20–40	34.84±27.14 ^a (25)	14.73±8.05 ^a (25)	80.00±0 ^a (1)
40–60	40.33±29.50 ^a (48)	11.99±6.82 ^{ab} (48)	53.33±30.55 ^a (3)
60–80	43.87±31.05 ^a (38)	10.84±6.42 ^{ab} (38)	41.66±32.69 ^a (9)
80–100	58.13±28.92 ^a (16)	12.65±6.24 ^{ab} (16)	22.70±19.61 ^b (24)
100–120	32.50±38.89 ^a (2)	10.56±13.40 ^{ab} (2)	28.00±21.21 ^b (25)
120–140	0	0	22.38±23.16 ^b (21)
140–160	0	0	13.82±15.15 ^b (17)
160–180	0	0	16.11±20.73 ^{bc} (2)
180–200	0	0	5.00±0 (1)

Note: COV = percentage cover (%); BM = aboveground biomass (g dw·m⁻²); Values are presented as mean±SD. Different lowercase letters within the same column indicate significant ($p<0.05$) difference; Numbers in parentheses indicate sample size (n); * Data for the Andaman Sea are from Monthum *et al.* (2023).

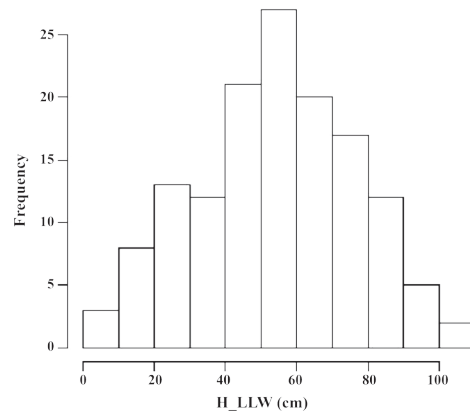


Figure 2. Frequency distribution of *Enhalus acoroides* occurrence at different shore heights above the lowest low water level (H_LLW: cm).

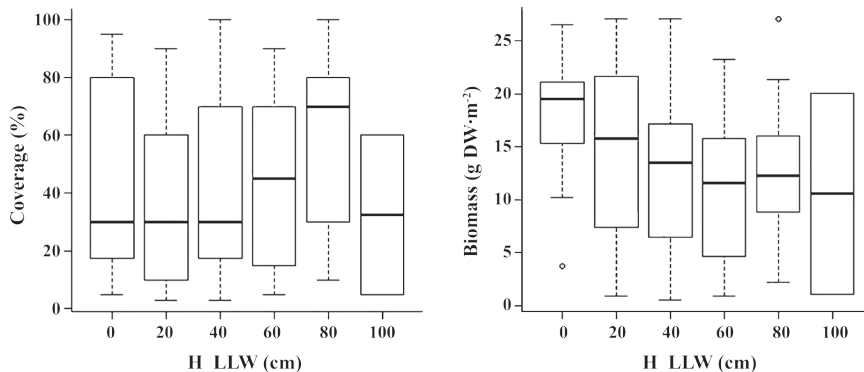


Figure 3. Boxplot showing the median values of percentage cover (a) and aboveground biomass (b) of *Enhalus acoroides* at different shore heights above the lowest low water (H_LLW: cm).

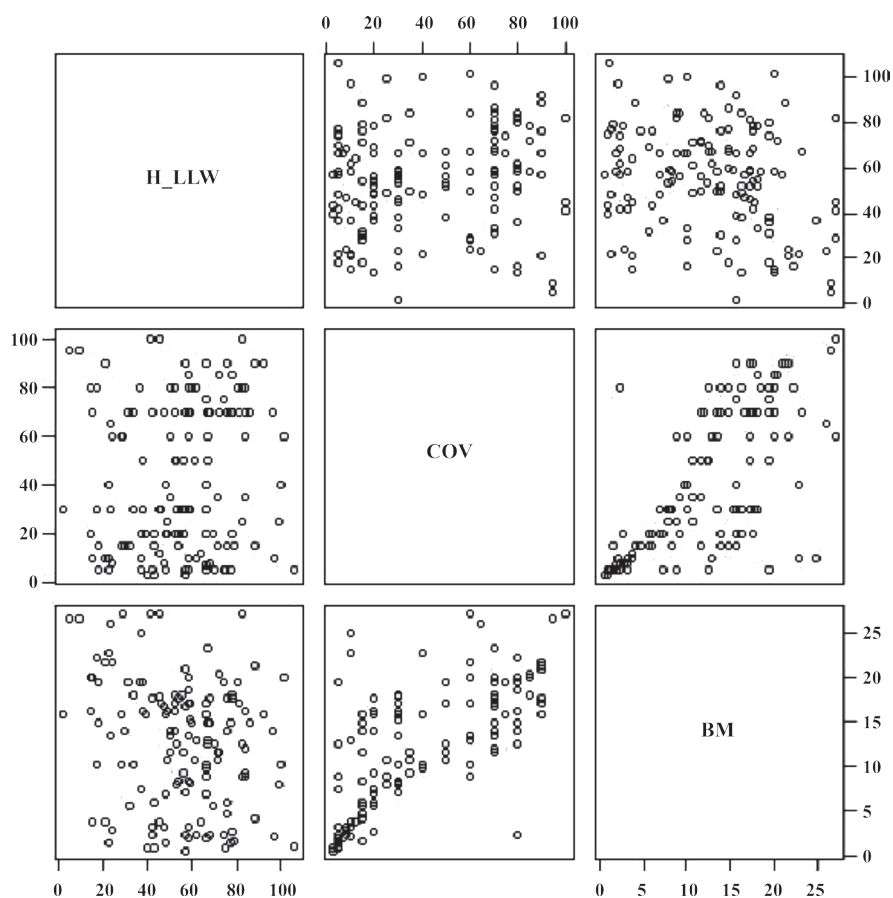


Figure 4. Scatterplot matrix showing pairwise relationships among percentage cover (COV), aboveground biomass (BM), and shore height above the lowest low water level (H_LLW) for *Enhalus acoroides*.

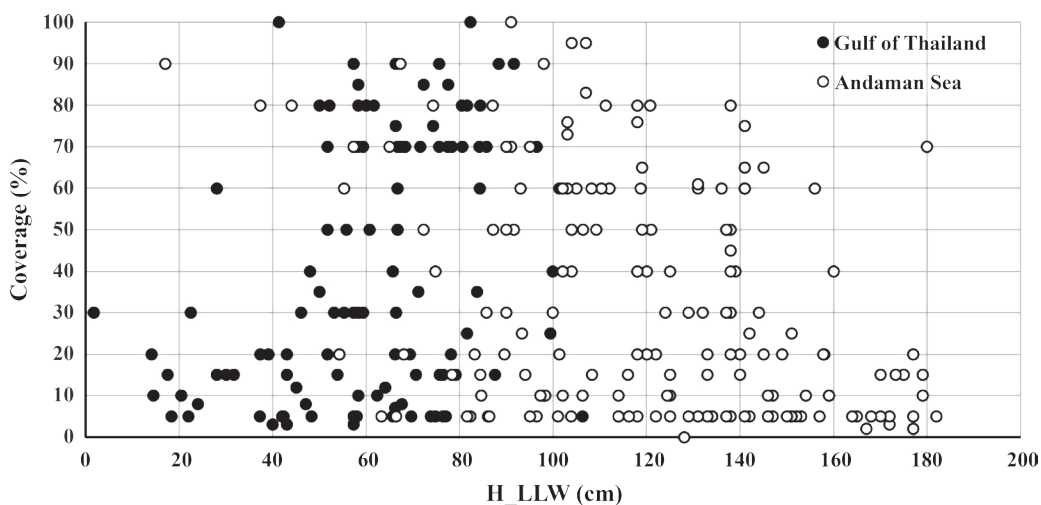


Figure 5. *Enhalus acoroides* percentage cover at different shore heights above the lowest low water level (H_LLW) in the Gulf of Thailand and the Andaman Sea. Data for the Andaman Sea were obtained from Monthum *et al.* (2023).

The upper shore-height thresholds of *E. acoroides* in the Gulf of Thailand and the Andaman Sea were compared with predicted low-tide levels from tidal stations located near the respective study areas. For the Gulf of Thailand, predicted tidal data from stations near Kradat Island and Samui Island were used as representative records. For the Andaman Sea, predicted tidal data from Trang Province, located near the study sites reported by Monthum *et al.* (2023), were used.

During low tide, *E. acoroides* occurring between the upper shore-height threshold and the lowest tide level is exposed to air. In the Andaman Sea, the upper shore-height threshold is substantially higher relative to the low-tide level, suggesting a wider vertical distribution range under relatively stable tidal conditions. Tidal levels in the Andaman Sea are more stable than in the Gulf of Thailand, reflecting less fluctuation in water mass (Aungsakul *et al.*, 2007). The upper shore-height threshold in the Gulf of Thailand was closer to the predicted low-tide level than that in the Andaman Sea (Figure 6), suggesting that *E. acoroides* in the Gulf of Thailand is generally less affected by low-tide exposure. However, in contrast to this pattern, extensive seagrass mortality was observed at Kradat Island in the Gulf of Thailand during late 2022 and 2023, which was attributed to prolonged daytime desiccation associated with drought and overheating conditions (DMCR, 2023) (Figure 7a).

Prolonged tidal exposure can impose multiple stressors on seagrasses, including desiccation, thermal stress, and high-light exposure, leading to both morphological and physiological damage. High solar irradiance may exacerbate stress through photodamage, as excess light promotes the formation of reactive oxygen that impair the photosynthetic apparatus (Ralph and Burchett, 1995; Björk *et al.*, 1999; Ort, 2001). Although *E. acoroides* exhibits relatively high resistance to desiccation due to its thick, waxy leaves that limit water loss, this morphology may paradoxically increase vulnerability during extreme low-tide events, as leaf bases can remain partially elevated above the substrate (Björk *et al.*, 1999). Experimental evidence shows that *E. acoroides* leaves can lose up to 75% of their water content within approximately 65 min at 32 °C, resulting in severe reductions in photosynthetic performance (Jiang *et al.*, 2014). Desiccation damage is further intensified by hypersaline stress caused by evaporative water loss (Che *et al.*, 2023).

In contrast, although the upper shore-height threshold in the Andaman Sea occurs at higher shore elevations and spans a wider vertical range relative to low-tide levels, seagrass beds in this region are more strongly influenced by herbivore grazing than by low-tide desiccation stress (DMCR, 2023). In addition to tidal amplitude, the timing of low tide plays a critical role. In the

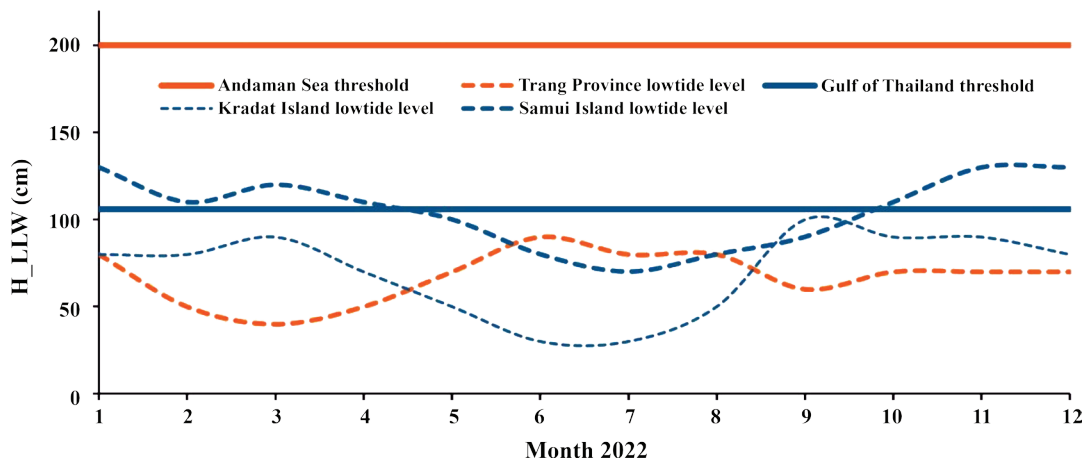


Figure 6. Monthly predicted low-tide levels and upper shore-height thresholds of *Enhalus acoroides* in the Gulf of Thailand and the Andaman Sea in 2022. The upper shore-height threshold for the Andaman Sea was obtained from Monthum *et al.* (2023).

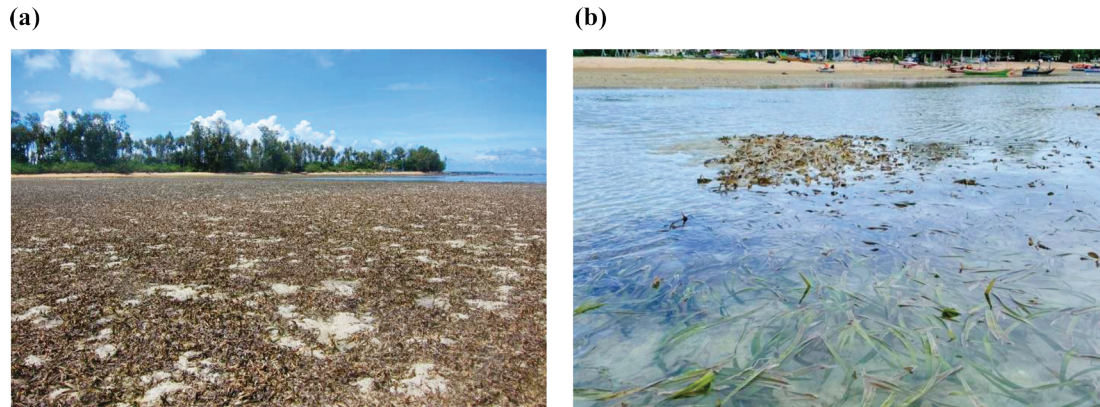


Figure 7. *Enhalus acoroides* during low tide at (a) Kradat Island and (b) Samui Island in 2022.

Andaman Sea, low tides typically occur during early morning and late afternoon, limiting exposure during peak solar irradiance. In contrast, low tide in the Gulf of Thailand often coincides with midday hours, increasing the likelihood of prolonged exposure to high light intensity and elevated temperatures, thereby intensifying desiccation stress.

In 2022, widespread die-off of *E. acoroides* was reported at Kradat Island, whereas populations at Samui Island remained largely intact (DMCR, 2023). The upper shore-height thresholds of *E. acoroides* at Kradat Island (77 cm H_{LLW})

and Samui Island (106 cm H_{LLW}) were used to estimate daytime desiccation periods based on predicted low-tide levels. *E. acoroides* occurring between the upper shore-height threshold and the predicted low-tide level experienced aerial exposure only during a six-month period (April–September). At Samui Island, the longest cumulative daytime desiccation occurred in July (180 h), with a total of 459 h in 2022. In contrast, Kradat Island experienced a substantially shorter maximum monthly desiccation period (56 h in June) and a total of 142 h for the year (Figure 8). Despite the shorter duration of aerial exposure at Kradat

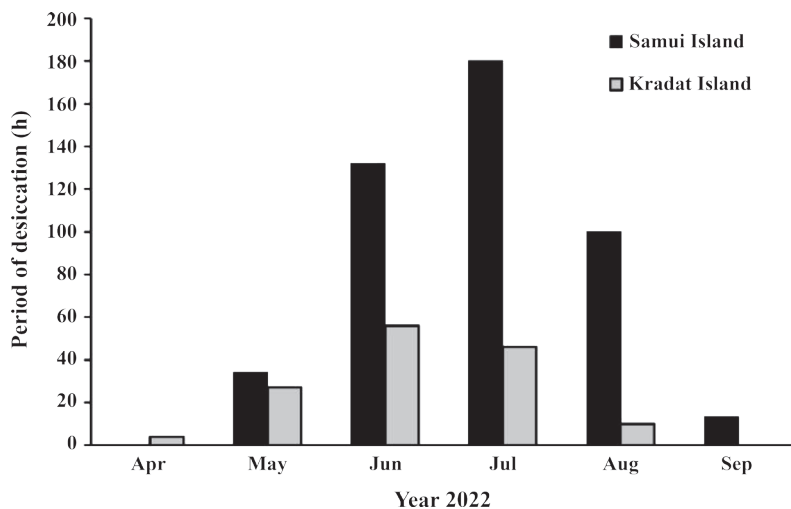


Figure 8. Monthly daytime desiccation duration of *Enhalus acoroides* at Kradat Island and Samui Island from April to September 2022.

Island, extensive seagrass mortality occurred there, indicating that *E. acoroides* die-off was not driven solely by cumulative desiccation time. Instead, the mortality event was likely associated with the coincidence of low tides with peak daytime solar irradiance, elevated temperatures, and prolonged drought conditions, which intensified desiccation stress beyond tolerance thresholds. This suggests that the timing and intensity of exposure, rather than exposure duration alone, play a critical role in triggering large-scale *E. acoroides* die-off.

Within the Gulf of Thailand, Aungsakul *et al.* (2007) reported that water levels in the upper region are higher and more variable than those in the lower region. In this study, Kradat Island is located in the upper eastern Gulf of Thailand, whereas Samui Island is in the lower region. Consistent with this pattern, the predicted low-tide level at Kradat Island was lower than that at Samui Island (Figure 6). To further clarify the influence of low-tide exposure on *E. acoroides* in the Gulf

of Thailand, seven years of predicted tidal data (2019–2025) were examined and compared with the upper shore-height thresholds identified at each study site (Figure 9). At Kradat Island and Samui Island, predicted low-tide levels during 2019–2021 were relatively moderate, reaching approximately 40 cm and 80 cm H_LLW, respectively. From 2022 onward, however, minimum low-tide levels declined markedly at both sites. At Samui Island, where the upper shore-height threshold of *E. acoroides* is 106 cm H_LLW, the lowest predicted tide (70 cm H_LLW) resulted in water levels approximately 36 cm below the sediment surface. In contrast, at Kradat Island, where the upper shore-height threshold is lower (77 cm H_LLW), the minimum predicted tide (30 cm H_LLW) exposed the sediment to a greater extent, with water levels dropping approximately 47 cm below the sediment surface.

These results suggest that extreme low-tide events may affect not only aboveground tissues but also belowground biomass by increasing

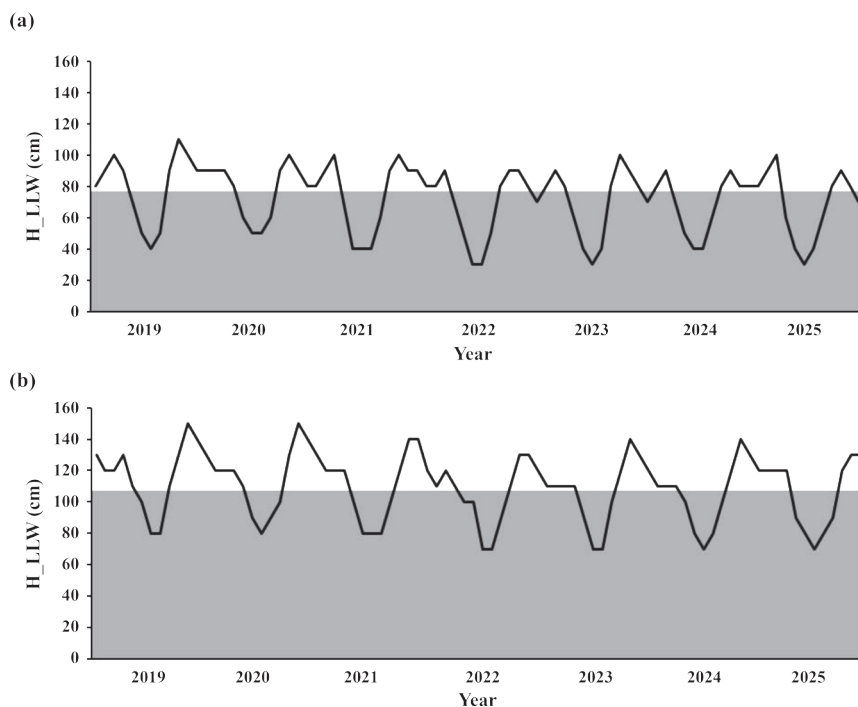


Figure 9. Predict low-tide levels above the lowest low water level (LLW, cm) at (a) Kradat Island and (b) Samui Island. The grey area indicates the vertical distribution range of *Enhalus acoroides* up to its upper shore-height threshold.

sediment drying and exposing roots and rhizomes to desiccation stress. In intertidal environments, even small differences in residual water depth can critically determine seagrass survival, highlighting the sensitivity of *E. acoroides* meadows to intensified low-tide conditions. *E. acoroides* exhibited sharp contrasts between die-off and survival across small differences in shore height (Figure 7b), further highlighting its sensitivity to subtle changes in tidal exposure.

Aerial exposure during low tide strongly constrains the upper intertidal distribution of tropical seagrasses. Leuschner *et al.* (1998) showed that seagrass leaves exposed to air for 5 h during low tide lost up to 50% of their water content, with dehydration increasing rapidly with distance from the water line. Intertidal environments are routinely subjected to both intense solar radiation and air exposure, inducing combined thermal and desiccation stress (Lan *et al.*, 2005). Consequently, seagrasses at higher intertidal elevations experience greater desiccation damage than those growing lower on the shore (Boese *et al.*, 2003). Although short-term air exposure may transiently enhance photosynthesis by reducing resistance to CO₂ diffusion (Beer and Rehnberg, 1997), desiccation constitutes a more acute stress than elevated temperature alone, particularly for upper intertidal species (Seddon and Cheshire, 2001; Shafer *et al.*, 2007).

Thermal stress further amplifies desiccation impacts. Temperatures near 40 °C represent a critical physiological threshold for seagrasses, while exposure to 43 °C causes complete mortality within days (Collier and Waycott, 2014). Repeated daytime low-tide temperature spikes of 35–43 °C can impair photosynthesis and reduce growth when sustained over consecutive days (Collier and Waycott, 2014), even though extreme low-tide exposure is typically short-lived due to tidal variability (Anthony and Kerswell, 2007). Elevated temperature also increases belowground respiration, leading to oxygen depletion and sulfide accumulation in sediments, which are toxic to seagrasses (Carlson *et al.*, 1994; Koch *et al.*, 2007). Desiccation-induced declines in root oxygen release further exacerbate

sulfide stress (Lamers *et al.*, 2013). Together, these processes define an optimal intertidal elevation or upper shore-height threshold that balances light availability and desiccation risk, which varies with tidal regime and local environmental conditions (Wang *et al.*, 2024). In tropical regions, this vulnerability is heightened because daytime low tides can elevate intertidal water temperatures to 40–44 °C (George, 2019), increasing the likelihood of climate-driven seagrass loss.

CONCLUSIONS

This study demonstrates that shore height above the lowest low water level is a key factor governing the upper intertidal distribution of *Enhalus acoroides* in the Gulf of Thailand. The upper shore-height threshold in the eastern region (Kradat Island; 77 cm H_{LLW}) was lower than that in the southern region (Samui Island; 106 cm H_{LLW}), and both were markedly lower than thresholds reported for the Andaman Sea, reflecting regional differences in tidal regimes. Within the Gulf of Thailand, spatial variation in upper shore-height thresholds was closely linked to local low-tide levels, which control both the duration of aerial exposure and the extent of water-level drawdown below the sediment surface.

These findings provide a practical framework for restoration planning by integrating predicted tidal data with site-specific shore height measurements. For transplantation, sites should be selected where shore height is lower than the regional upper shore-height threshold to minimize desiccation stress and subsurface water loss. Under increasing tidal variability associated with climate change, comparing shore height with predicted low-tide levels and threshold values can also support early identification of die-off risk areas. Overall, our results highlight shore height relative to tidal exposure as a critical determinant of *E. acoroides* persistence and offer a robust basis for monitoring, climate-adaptive conservation, and management of intertidal seagrass meadows under changing coastal conditions.

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