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The vulnerable seagrass Halophila beccarii Aschers. (Hydrocharitaceae) from Malaysia

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Halophila beccarii Aschers. is a small, vulnerable seagrass species found throughout the Indo-West Pacific. In Malaysia, its distribution is highly fragmented and faces increasing threats from human activities and natural disturbances. Although it can tolerate various ecological conditions, its limited and scattered range raises significant conservation concerns. Long-term observations and monitoring were conducted from 1996 to 2025 at numerous coastal and estuarine sites within Peninsular Malaysia, Sabah, and Sarawak. Historical data and recent field surveys were combined to assess changes in distribution, population status, and habitat conditions. Halophila beccarii, once considered rare, was found at 15 locations across various intertidal habitats, ranging from freshwater to the brackish waters of mangrove river systems, shallow coastal lagoons, marine coastal areas, and subtidal shoals. It is commonly observed at depths of 1.0 to 2.0 meters and rarely exceeds 3.0 meters during high tide. The species thrives in temperatures from 25 to 38°C and salinity levels from 0 to 32 psu. Scattered patches or monospecific meadows of H. beccarii often occur alongside other seagrasses, such as Halodule pinifolia, macroalgae, seaside grasses, or mangroves, on substrates including sand, silty sand, loam, and calcareous mud. Declines are driven by reclamation, dredging, sand mining, sedimentation, monsoonal flooding, and coastal erosion. Disturbed habitats often shift to dominance by H. pinifolia, a more resilient species. These findings highlight H. beccarii's vulnerability despite its ecological adaptability, reinforcing its current IUCN "Vulnerable" status and emphasizing the need for targeted conservation, seed bank protection, and adaptive monitoring strategies.

KEYWORDS

vulnerable seagrass, *Halophila beccarii*, coastal development, dredging, sand mining, Malaysia

1 Introduction

Seagrasses are underwater marine angiosperms from the class Monocotyledoneae. They are the only group of flowering plants (monocotyledonous angiosperms) that have successfully adapted to life in marine and estuarine environments. Unlike algae, seagrasses possess true vascular tissues, including roots, stems, and reproductive organs such as flowers and seeds, allowing them to complete their entire life cycle submerged in seawater. Seagrasses play essential ecological roles by stabilizing sediments, improving water quality, cycling nutrients, and serving as vital nursery grounds for many marine organisms (Orth et al., 2006; Duarte, 2002). Evolutionary, they are thought to have derived from terrestrial monocots that recolonized the sea approximately 100 million years ago (Les et al., 1997). Globally, about 72 species are currently recognized, distributed in tropical and temperate shallow waters (Short et al., 2007).

In Malaysia, they form patches to meadows, usually growing in shallow intertidal riverbanks, subtidal rivers, inland lagoons, and around islands. Malaysia has 17 seagrass species; Enhalus acoroides, Thalassia hemprichii, Halophila beccarii, H. decipiens, H. major, H. minor, H. ovalis, H. nipponica, H. spinulosa, H. tricostata, Cymodocea rotundata, C. serrulata, Halodule pinifolia, H. uninervis, Syringodium isoetifolium, Thalassadendron ciliatum, and Ruppia maritima (Fortes et al., 2018; Muta Harah and Japar Sidik, 2024; Che Alias et al., 2024). Of the 17 seagrass species, H. beccarii has a disconnected and scattered distribution that faces mounting threats from human activities and natural disturbances (Japar Sidik and Muta Harah, 2011a; Japar Sidik et al., 2018).

Halophila beccarii is a monoecious, i.e., with male and female flowers either on the same erect shoot or separate shoots of the same plant. Its distribution is limited, found in intertidal sand and muddy areas of Korea Island, Penang, the northern Peninsula of Malaysia (Muta Harah and Japar Sidik, 2004), as well as in muddy riverbanks of the Pendas and Johor Rivers at Kampong Pendas in southern Johor (Muta Harah, 2023). On the east coast of Peninsula Malaysia, it is in shallow intertidal sand and mud areas within inland lagoons of Pengkalan Nangka in Kelantan, Paka, Kemaman, and Telaga Simpul in Terengganu. Halophila beccarii is commonly associated with mangroves. In riverine environments, H. beccarii experiences stable salinity levels ranging from 20 to 24 psu. Conversely, lagoon habitats showed significant salinity fluctuations, ranging from low levels of 0 to 0.5 psu during the monsoon season to brackish water conditions with salinity levels between 11 and 19 psu during the dry season (Japar Sidik et al., 2018). In Sarawak, East Malaysia, H. beccarii thrives in small patches located at the forefront of mangroves on muddy substrates.

Globally, *H. beccarii* is distributed across the Indo-West Pacific region and is widely reported from India (Untawale and Jagtap, 1977; Parthasarathy et al., 1988), Sri Lanka (Udagedara et al., 2017), Bangladesh (Billah et al., 2016; Hena et al., 2009), Malaysia (Fakhrulddin et al., 2013; Muta Harah et al., 1999; 2002), the Philippines (Liao and Geraldino, 2020), Thailand (Hiranphan et al., 2020), Myanmar (Aye et al., 2014), and Vietnam (Phan et al., 2017). It has also been recorded in the Andaman and Nicobar

Islands (Savurirajan et al., 2015) and is described as one of the earliest colonizers in mangrove succession (Parthasarathy et al., 1988, Parthasarathy et al., 1991; Jagtap, 1991). Halophila beccarii tolerates high nutrient environments and fluctuating conditions in temperature, salinity, and tidal inundation (Greve and Binzer, 2004; Fakhrulddin et al., 2013). Despite its wide ecological tolerance, its distribution remains narrow and fragmented, with the IUCN Red List Categories and Criteria Version 3.1 classifying the species as Vulnerable (IUCN, 2011; Short et al., 2011; Geng et al., 2022), while some national assessments, such as in Sri Lanka, report it as Endangered or locally extinct in parts of the Philippines (Udagedara et al., 2017; Liao and Geraldino, 2020).

This research project on the inventory of marine plants and associated organisms is part of the Intensification in Priorities Research, funded by the Ministry of Science, Technology, and Environment Malaysia, the Japan International Cooperation Agency (JICA), the Japan Society for the Promotion of Science (JSPS), and the Forest City project. The taxonomic identification of *H. beccarii* was based on the criteria established by den Hartog (1970). This paper provides a historical perspective on the discovery and distribution of *H. beccarii* in Peninsular Malaysia and Sarawak, East Malaysia, drawing on both previous and current records. The significance of *H. beccarii* seagrass areas and the habitat disruption caused by natural factors and human activities affecting *H. beccarii* are also explored.

2 Materials and methods

Observation and *in-situ* field data were collected from February 1996 to April 2025 across multiple coastal locations in Peninsular Malaysia and Sarawak. From February 1996 to January 1999, three key sites, Sungai Kemaman, Sungai Paka Lagoon, and Pengkalan Nangka Lagoon were monitored almost monthly, providing high-resolution temporal data. Other sites were visited 2–5 times during this period for exploratory or confirmatory surveys. From 2011 onwards, long-term monitoring continued for several sites where *H. beccarii* populations persisted or reappeared. These included Paka Shoal, Pengkalan Nangka Lagoon, Sungai Kemaman, Pulau Korea, and Sungai Pendas, which were revisited one to two times per year up to 2025 to track species persistence and changes in habitat. Surveys were conducted during low to lowest spring tides, when seagrass beds were naturally exposed, or through snorkeling and SCUBA diving in subtidal zones.

The roving method was employed during sampling, using a 50 cm x 50 cm quadrat, to assess community composition. When available, complete plant specimens, including leaves, rhizomes, flowers, and fruits, were collected for morphological analysis. Measurements of morphological features included leaf blade length and width, petiole, and erect stem, taken with vernier calipers, (n=30). The morphometric measurements were analyzed using SPSS Statistics ANOVA to compare between locations. Reproductive structures were examined when present, with additional measurements for pedicel, tepal, anthers, ovary, hypanthium, style, fruits, and seeds. Specimens were preserved in

two ways: (1) wet preservation in 5% formaldehyde (diluted from 37–40% commercial formalin at a 1:8 ratio with seawater), and (2) mounted as herbarium specimens following Menez et al. (1983). All site locations were recorded with handheld GPS units to document the spatial distribution of *H. beccarii*.

Environmental parameters, including temperature (°C), salinity (psu), pH, dissolved oxygen (DO, mg/L), and conductivity (μS/cm), were measured *in situ* at each site using a YSI 33 SCT meter and a YSI Professional Plus multiparameter instrument (YSI Inc., USA) for measurements collected from 2015 onward. Measurements were taken during both low and high tides, with three replicates per parameter at each station. The instruments were calibrated in the field following the manufacturer's guidelines. Salinity measurements were conducted during both the monsoon and dry seasons to account for tidal and seasonal variation. In brackish systems such as Sungai Kemaman and Pengkalan Nangka, data collection focused on detecting fluctuations caused by freshwater inflow and tidal mixing. These measurements contributed to assessing the estuarine conditions where *H. beccarii* was found.

Sediment samples were analyzed using the standard hydrometer method (English et al., 1997), and soil texture was classified based on the USDA Textural Triangle (Gerakis and Baer, 1999). Water depth was estimated using Ebb Low Water Spring (ELWS) tide charts. Disturbances at the sites (e.g., reclamation, infrastructure, breakwaters) were documented with photographs during each survey.

Changes in seagrass extent were evaluated using historical mapping (before 2011) and field surveys conducted between 2015 and 2025. The seagrass area was estimated through GPS tracking of patch boundaries during low tide and aerial imagery, when available. Losses were identified by comparing the current extent to earlier records.

3 Results

3.1 Historical overview and records of *Halophila beccarii*

Halophila beccarii was first collected in 1867 by Italian botanist Odoardo Beccari from the Bintulu River (now Bintulu), Sarawak, East Malaysia (Beccari, 1904; den Hartog, 1970). This type specimen, later described by Ascherson in 1871, laid the foundation for recognizing *H. beccarii*, commonly known as Beccari's seagrass or Ocean's Turf seagrass, as a member of the Hydrocharitaceae family. Characterized by its rosette-forming, leafy shoots and short, creeping rhizomes, the species is well-adapted to colonize unstable substrates in brackish and estuarine environments (Figure 1).

The storyline of the discovery of *H. beccarii* in Malaysia (Figure 2) starts with the first collection made by Beccari in 1867 in Sarawak, East Malaysia. In Peninsular Malaysia, subsequent records of *H. beccarii* collection were noted by den Hartog (1970) from Sungai Tebrau and Jalan Skudai, Johor, in 1965. Our surveys confirmed the species' presence along the east coast starting in 1992 at the mudflats of Sungai Kemaman, Terengganu. This was followed

by successive discoveries in 1996 at Paka Lagoon, Paka River, Paka Shoal, and Chukai, and in 1997 at Telaga Simpul. During this period, field investigations also extended to Kelantan, where *H. beccarii* was observed at Pengkalan Nangka Lagoon, Pengkalan Nangka Shoal, Kampung Baru Nelayan, and Pantai Baru Lagoon. By 1999, its distribution expanded northward in Penang, observed at Seberang Prai and Korea Island. Rediscovery in Sarawak occurred much later, with documentation in Lawas after a 141-year gap from the original Bintulu collection. In Johor, the species reappeared at Sungai Pendas in 2015 and at Tanjung Surat, Kampung Nyior by 2021 (Figure 3), where it was found in both monospecific and mixed stands with *Halophila ovalis*.

3.2 The distribution, present status, and disturbances of *Halophila beccarii* population

Halophila beccarii is mainly found along the east coast of Peninsular Malaysia, with scattered populations also along the southeast, south, and west coasts. This species has been observed in 15 areas, as shown in Figure 4. It is found as either monospecies or two species in the lagoon, subtidal island, intertidal mangrove association, intertidal sandy beach, subtidal shoal, and intertidal areas associated with coral. It occupies the middle to upper intertidal zone, shallow intertidal in the mangrove area, and intertidal mudflat in front of the mangrove.

Table 1 shows the changes in distribution and area coverage before 2011 and from 2015 to 2025, highlighting significant population declines or complete losses across many sites. The largest historical populations were recorded in Kemaman (17 ha), Telaga Simpul (28 ha), Paka Shoal (43 ha), and Pengkalan Nangka Lagoon (35 ha). However, many of these sites now show significantly reduced sizes or are completely lost. For example, sites such as Chukai, Paka River, and Kampung Baru Nelayan no longer have any *H. beccarii* present. Field visits between 2011 and 2025 confirmed the ongoing decline and disappearance of *H. beccarii* meadows at several locations, while only a few sites, such as Paka Shoal, Telaga Simpul, Pengkalan Nangka Lagoon, Korea Island, and Sungai Pendas, still support small patches.

The decline results from both human and natural disturbances. Human pressures include riverbank reclamation at Chukai, mangrove clearing at Kemaman, sand mining or dredging for flood control projects at Paka Shoal (Figures 5A, B). In Pengkalan Nangka, dredging replaced muddy substrate with sand, allowing H. pinifolia to colonize the area previously occupied by H. beccarii (Figure 5C). Additionally, deepening the shoals and road construction damaged H. beccarii in parts of Pengkalan Nangka and Kg Baru Nelayan (Figure 5D). Shellfish harvesting for Ostrea sp., Meretrix meretrix, Gari elongata (Figures 5E, F), and urban development in Seberang Prai also destroy the habitat of *H. beccarii*. Natural factors such as freshwater input during monsoons, winddriven waves, and sediment movement also contribute to habitat instability in shallow estuarine areas. These findings, gathered over decades of monitoring and field visits, indicate a significant reduction in the range of H. beccarii in Malaysia.



FIGURE 1
(A) TYPE specimen of Halophila beccarii Aschers. 1871 in Neumayer, Borneo, Sarawak, in the mouth of the river Bintula, O. Beccari 11826 (=P.B. 3666) (L). The TYPE specimen photo was obtained with permission from the Rijksherbarium, Leiden, the Netherlands. (B) Dense H. beccarii forms thick growth. (C) Halophila beccarii ramets exhibit a modular arrangement. Each ramet is composed of modules, i.e., a piece of rhizome, which can be horizontal or vertical, a pair or bundle of leaves attached to the rhizome, and a root system. (D) Halophila beccarii (shown as green growth on mudflat surface, exposed during low tide) growing in brackish coastal water of the mangrove system.

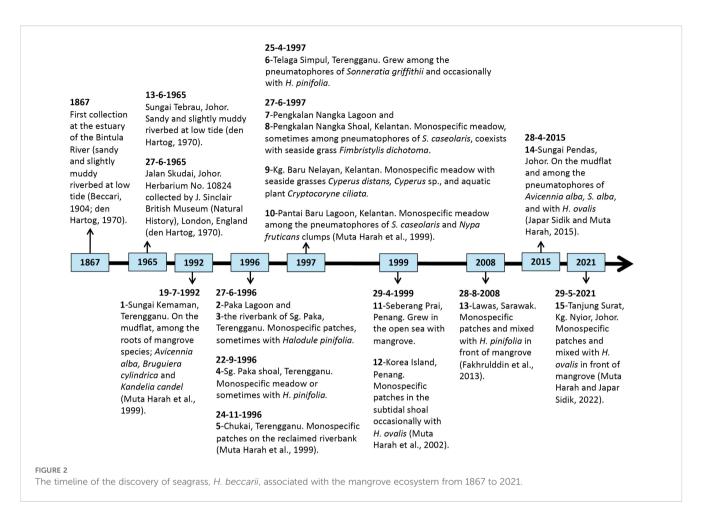
3.3 Habitat description of *Halophila* beccarii

In Peninsular Malaysia, *H. beccarii* is distributed across various shallow intertidal zones with differing environmental and substrate conditions. The species thrives in areas influenced by the northeast monsoon, including the east coast sites of Terengganu (Kemaman River, Paka Lagoon) and Kelantan (Pengkalan Nangka Lagoon), where it shows notable seasonal changes in rainfall, salinity, and water temperature.

Table 2 presents the habitat characteristics, physical and chemical parameters of *H. beccarii* in various locations. This species inhabits a variety of intertidal environments, from freshwater zones during low tide to brackish waters at high tide. Environmental monitoring at key sites revealed that during the monsoon season, heavy rainfall, ranging

from 300 to over 700 mm/month, causes reduced salinity, often approaching freshwater levels, especially during low tides. Temperatures remain warm, generally between 27 and 31°C, and total suspended solids (TSS) tend to rise, indicating increased turbidity. In contrast, during the dry season, rainfall is minimal, and salinity increases significantly, with peak measurements ranging from 30 to 38 psu, depending on the site and tide phase. Despite these changes, *H. beccarii* remains present, demonstrating its ecological adaptability and wide environmental tolerance.

Environmental variability is closely related to habitat type. In mangrove riverbank and mudflat systems such as Kemaman River and Sungai Paka, *H. beccarii* coexists with mangrove pneumatophores in warm, low-salinity environments with muddy or sandy-loam substrates. In these habitats, the species is usually found at depths ranging from 0.8 to 2.5 meters below the water surface (ELWS). The



intertidal seagrass habitats are not entirely submerged but are exposed twice daily depending on the tides.

In protected coastal lagoons and estuaries, such as Pengkalan Nangka Lagoon, the species often forms pure stands or coexists with emergent freshwater species, including *Fimbristylis dichotoma* and *Cryptocoryne ciliata*. These areas exhibit fluctuating salinity levels ranging from 0 to 24 psu, warm waters with temperatures from 28 to 38°C, and sand to sandy-mud substrates.

Open shallow coastal areas, such as Telaga Simpul and Seberang Prai, have slightly higher salinity levels, ranging from 15 to 31 psu, and host H. beccarii on sandy-mud substrates at depths of 1.0 to 2.0 meters ELWS, often in association with other seagrasses like H. pinifolia. In contrast, shoals and reclaimed island habitats, including Korea Island and Paka Shoal, show evidence of colonization by H. beccarii in more disturbed or human-altered environments. Here, the species is found at greater depths of 2.7 to 3.5 meters ELWS, on calcareous or sandy mud substrates, and coexists with H. pinifolia. These areas exhibit high environmental variability, especially in salinity (13 to 32 psu) and temperature (30 to 35°C), yet still support healthy populations. The range of environmental conditions observed across these habitats demonstrates the adaptability of H. beccarii, especially in estuarine and monsoon-influenced ecosystems. This habitat-based classification, combined with seasonal environmental data, addresses reviewer concerns by showing how H. beccarii's distribution is more influenced by its tolerance to fluctuations in salinity, temperature, and turbidity than by strict environmental thresholds. Additionally, the analysis of site-specific monsoon impacts highlights the importance of considering seasonal variability and hydrodynamic protection when interpreting ecological patterns of this vulnerable seagrass species.

3.4 Life cycle of Halophila beccarii

Halophila beccarii is a small seagrass species characterized by its monoecious reproductive system and creeping rhizome with a single root per node that bears numerous root hairs. Morphometric measurement of vegetative morphology of H. beccarii from ten locations is illustrated in Table 3. The species features two protective scales: an upper transparent scale that covers the upright shoot and a lower scale that shields the rhizome. Each shoot produces 4 to 12 rosette leaves that are oblong to elliptical. Petiole lengths range from 3.36 to 17.18 mm, leaf lengths from 3.27 to 13.17 mm, and leaf widths from 0.20 to 3.14 mm across different locations in Malaysia. Leaf morphology varies across sites, likely due to local environmental factors and hydrodynamic exposure. The longest petioles were recorded at Sungai Pendas (12.52 \pm 2.38 mm), and the widest leaf blades (2.55 \pm 0.29 mm). These differences highlight H. beccarii's ability to adapt to various hydrological and sedimentation conditions,

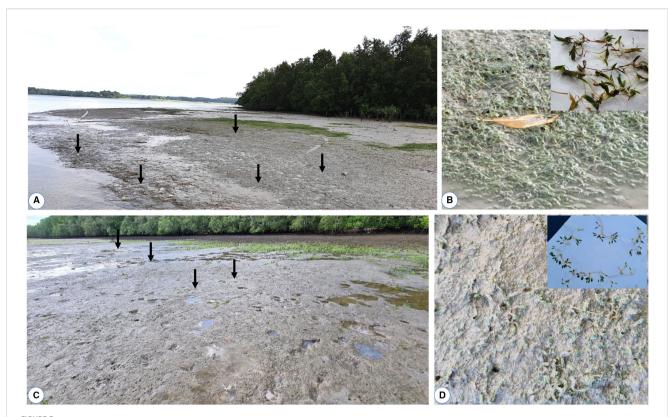
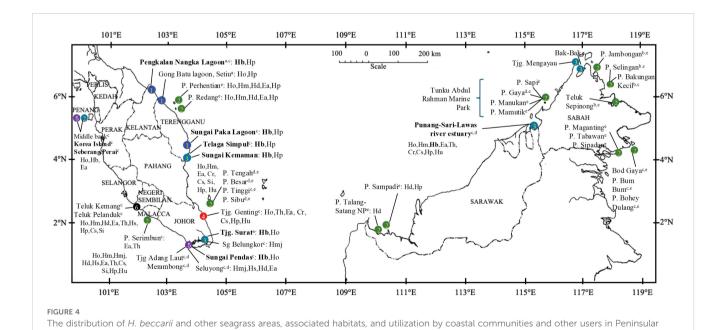


FIGURE 3

New record of *H. beccarii* in 2015 at **(A, B)** shallow intertidal, in the mangrove area of Sungai Pendas, Johor, and **(C, D)** monospecific *H. beccarii* in 2021 at an intertidal mudflat in front of mangrove Tanjung Surat, Johor.



Malaysia, Sabah, and Sarawak. 1-Lagoon, 2-subtidal island, 3-intertidal mangrove association, 4-intertidal sandy beach, 5-subtidal shoal, 6-intertidal associated with coral. Aquaculture^a, turtle sanctuary^b, traditional capture fisheries^c, dugong feeding ground^d, and marine park^e (Japar Sidik and Muta

Harah, 2011b; Muta Harah and Japar Sidik, 2024).

TABLE 1 Distribution area of Halophila beccarii in Peninsular Malaysia and Sarawak, with associated systems, area of previous and present seagrass, and identified disturbance factors.

		Latitude (N) and		Area	a (ha)	Disturbar	nce	
No.	State/ location	longitude (E)	Associated system	Before 2011	Present	Human	Natural	
Johor								
1	Sg. Pendas	1°C 22' 30.5" N 103°C 38' 20.5" E	Submerge mangrove riverbanks during normal high tides.		0.5	Human habitation	Waves, causing erosion	
2	Tanjung Surat, Kg. Nyior	1°C 28' 6.3" N 104°C 2' 41.3" E	On mud flat in front of mangrove, submerge during high tide.	-	0.5	Human habitation, sand mining	Wind-blown waves	
Teren	gganu							
3	Kemaman river	4°C 13' 52.3" N 103°C 26' 17.0" E	Riverbank with mangrove.	17	1	Mangrove clearing	Freshwater, wind-blown waves, shifting of sand during north-east monsoon	
4	Chukai	4°C 14' 00.0" N 103°C 25' 38.9" E	Reclaimed riverbank.	33	Lost	Reclaimed riverbank	Wind-blown waves, shifting of sand during north-east monsoon	
5	Telaga Simpul	4°C 14' 37.4" N 103°C 27' 11.2" E	Open shallow coast.	28	3	Sand mining for shoreline stabilization against the north-east monsoon, digging activities for polychaetas	Wind-blown waves, shifting of sand during the north-east monsoon	
6	Paka Lagoon	4°C 38' 45.6" N 103°C 26' 15.2" E	Coastal lagoon.	4.7	Lost	Transportation avenues, pull net, sand dredging and mining for flood control	Freshwater, wind-blown waves, shifting of sand during north-east monsoon	
7	Paka River	4°C 38' 37.8" N 103°C 26' 15.2" E	Riverbank with mangrove.	1.5	Lost	Sand dredging and mining for flood control	Freshwater, wind-blown waves, shifting of sand during north-east monsoon	
8	Paka Shoal	4°C 38' 46.9" N 103°C 26' 24.9" E	Submerged shoal is occasionally exposed during the lowest spring tide.	43	3	Transportation avenues, pull net, sand dredging and mining for flood control	Freshwater, wind-blown waves, shifting of sand during north-east monsoon	
Kelant	an							
9	Pengkalan Nangka Lagoon	6°C 12' 27.5" N 102°C 08' 40.5" E	Coastal lagoon.	35	3	Pull net, digging activities for the collection of <i>Gari</i>	Freshwater from rain during the north-east	
10	Pengkalan Nangka Shoal	6°C 12' 28.3" N 102°C 08' 49.9" E	Submerged shoal is occasionally exposed during the lowest spring tide.	5	Lost	elongata (Hiatula sordida) Meretrix meretrix, sand dredging and mining for flood controls and land- based development	monsoon. Competition among seagrass (Halodule pinifolia invasion to the Halophila beccarii area)	
11	Kg. Baru Nelayan	6°C 12' 13.5" N 102°C 09' 11.5" E	Coastal lagoon with mangroves and mudflat.	27	Lost	Sand dredging and mining for flood controls and land-based development	Freshwater from rain during the north-east monsoon	
12	Pantai Baru lagoon	6°C 13' 0.4" N 102°C 12' 0.15" E	Coastal lagoon with mangrove.	20	nd	-	-	

Wind-blown waves, shifting of sand during Wind-blown waves, shifting of sand and erosion during southwest monsoon. nonsoon Disturbance Digging activities for the collection of (Meretrix Digging activities for the collection of Meretrix Land reclamation for bridge development meretrix and Siliqua patula) 0.5 0.5 pq Area (ha) Before 2011 0.5 0.5 0.5 Associated system Open shallow coastal area Man-made island - subwith mangrove and Mudflat in front of tidal fringe. mangrove. mudflat. -atitude (N) and 5°C 21' 14.0" N 100°C 23' 18.0" E ongitude (E) 100°C 19' 08.4" E 115°C 24.394' E 5°C 21' 14.3" N 4°C 57.195' N Punang Sari-Lawas River State/location Seberang Prai Korea island estuary Sarawak Penang 9. 13 14 15

Continued

especially in highly dynamic coastal and intertidal zones. The male flowers arise sub-terminally from short lateral branches within the rosette and have three pale brown tepals (1.82–2.91 mm \times 0.55–2.18 mm) and three anthers (1.00–2.30 mm long). Female flowers emerge laterally, consisting of an ovoid ovary (0.55–1.82 mm \times 0.18–0.86 mm) and 2–3 styles that can reach up to 13.01 mm in length. Typically, one fruit is produced per reproductive shoot, and it is ellipsoid to ovoid in shape, transparent, and contains 1 to 7 seeds. Each seed is globose, reticulate, and reddish-brown, measuring 0.64–1.40 mm \times 0.45–1.09 mm.

Field observations and seedling studies reveal that H. beccarii exhibits both annual and perennial life cycles, which are affected by local hydrology and climate. At dynamic, monsoon-driven sites like Pengkalan Nangka Lagoon, Kelantan, and Paka Shoal, Terengganu, H. beccarii functions as an annual species, as illustrated in Figure 6. Plant cover completely disappears during the northeast monsoon from November to January, entering dormancy. Recolonization begins in February with seed germination (Figure 6A). The germinating seeds (Figure 6B) develop into seedlings (Figures 6C, D) from March to April, forming a network of rhizomes. Juvenile plants (Figure 6E) continue vegetative propagation, growing into mature plants that produce male (Figure 6F), female (Figure 6G) flowers, fruit (Figure 6H) and seeds (Figure 6I) from April to September. Between October and November, plant density decreases again, signaling another dormancy phase. From December to January, the meadow recolonizes through the germination of seeds and seedlings, ensuring its continued presence in the natural environment.

Conversely, at more stable estuarine sites such as Sungai Kemaman (Terengganu), *H. beccarii* exhibits perennial traits, with populations existing year-round. Flowering and fruiting activities were observed almost every month except June for male flowers and May–June for female flowers. This persistence suggests a more stable and resilient population structure, supported by both vegetative spread and seed production. This dual strategy, perennial in stable estuarine habitats and annual in monsoon-affected shoals, reflects *H. beccarii's* ecological flexibility. It allows the species to survive disturbances such as sediment shifts, freshwater influx, and seasonal dieback, although its long-term survival remains vulnerable to increased human activity and habitat deterioration.

4 Discussions

4.1 Distribution, habitat, and disturbances of vulnerable *Halophila beccarii*

Halophila beccarii is currently listed as Vulnerable under the IUCN Red List Categories and Criteria Version 3.1 (Short et al., 2011; IUCN, 2012), with an estimated global distribution of less than 2,000 km² (Geng et al., 2022; Chen et al., 2024). Although den Hartog (1970) described it as rare yet widely distributed across the Indo-West Pacific, recent evidence suggests its range has contracted significantly. The species is still reported in India (Jagtap and Untawale, 1981; Untawale and Jagtap, 1977; Jagtap, 1991; Parthasarathy et al., 1991), Thailand (Poovachiranon et al., 1994),



Disturbances to *H. beccarii* ecosystems. (A) flood barrier construction, (B) ground view of *H. beccarii* meadow with flood sand barrier (arrow) at Paka Shoal, (C) *H. beccarii* growing separately from *Halodule pinifolia* after dredging replaced muddy substrate with sand, (D) sand dredging to deepen the shoals and road construction caused damage to *H. beccarii* in parts of Pengkalan Nangka and Kg Baru Nelayan. Shellfish digging (E) *Ostrea* sp., (F) *Meretrix meretrix*, and *Gari elongata* at Pengkalan Nangka also destroyed the *H. beccarii*.

Vietnam (Van Tien, 1998), and Hong Kong (Hodgkiss and Morton, 1978), but it has been declared locally extinct in the Philippines (Liao and Geraldino, 2020) and Endangered in Sri Lanka (Udagedara et al., 2017). Notably, the first record from Bangladesh was recently confirmed in the Andharmanik River estuary (Haque et al., 2024), extending the known distribution along the Bay of Bengal.

In Malaysia, H. beccarii shows a patchy and declining distribution, with recent occurrences primarily along the east coast and limited observations on the west coast. It tolerates a wide range of salinity (0-32 psu) and temperature ranges (25-38 ° C), thriving in substrates ranging from sandy mud, silty clay, and calcareous substrates. Its physiological flexibility allows it to inhabit estuarine environments, where it coexists with seagrasses such as Halophila ovalis and Halodule pinifolia, macroalgae like Ulva intestinalis, and emergent species like Fimbristylis dichotoma and Cryptocoryne ciliata (den Hartog, 1970; Abhijith et al., 2019). However, despite this flexibility, H. beccarii typically persists only as scattered patches or monospecific meadows, indicating ecological vulnerability when disturbed. Experimental studies confirm its salinity tolerance in Malaysian estuaries (Fakhrulddin et al., 2019), but regional evidence shows limited resilience: low clonal diversity in Vietnam (Phan et al., 2017), strong habitat specialization in Hainan (Geng et al., 2022), and small, recently reported intertidal populations in Bangladesh (Haque et al., 2024).

Monsoonal flooding, coastal erosion, and activities such as land reclamation and pollution directly threaten its population stability. For example, severe flooding in Paka Shoal in 2014 resulted in the complete loss of seagrass due to sediment burial (Japar Sidik et al., 2018; Hossain et al., 2015). A recent visit to Pengkalan Nangka Lagoon reveals that,

following the 2024 flooding event, the *H. beccarii* area has decreased. Seasonal changes in salinity and turbidity, especially during the northeast monsoon, further threaten meadow persistence along Malaysia's east coast. These patterns emphasize that *H. beccarii*'s survival depends not only on its physiological tolerance but also on minimizing human impacts, protecting seed bank health, and improving adaptive monitoring to observe short-term ecological changes.

Human activities have also contributed to the decline of *H. beccarii* in Peninsular Malaysia. In areas such as Chukai, Paka Lagoon, Paka River, Terengganu, and Pengkalan Nangka shoal, as well as Kampung Baru Nelayan, Kelantan, the species is now absent. The habitat is affected by large-scale disturbances, including land reclamation, dredging to deepen boat channels, and sand mining for construction. Dredging naturally removes bed material and seagrasses, causing increased sedimentation that smothers seagrasses over large areas and nearby regions. This sedimentation displaces *H. beccarii*, allowing more resilient species such as *H. pinifolia* to grow and dominate the area.

In disturbed or sediment-rich habitats, *H. pinifolia* often becomes the dominant species due to its higher adaptability and resilience. For example, Lamit and Tanaka (2019) reported that *H. pinifolia* thrived across sites with different sediment types and nutrient conditions, showing the highest biomass and leaf length in areas with increased silt and clay content related to ongoing coastal development. This adaptability is further supported by its exceptional tolerance to low-light conditions. Longstaff and Dennison (1999) demonstrated that *H. pinifolia* could survive extended periods of near darkness with minimal biomass loss, a trait not observed in other seagrass species such as *Heterozostera tasmanica* (Bulthuis, 1983) and *Posidonia sinuosa* (Gordon et al., 1994), which declined rapidly under similar stress. Additionally, the

TABLE 2 Habitat characteristics, physicochemical conditions, and substrate types of the Halophila beccarii ecosystem in Malaysia.

State/ location	Form and association	Depth range (m) ELWS	Visibility (m)	Water temp. (°CC)	Salinity (psu)	TSS (mg/L)	Ph	DO	Substrate
Johore									
1. Sungai Tebrau*	Unknown	-		-	-				Sandy mud
2. Jalan Skudai*	Halodule sp. and H. minor	-		-	-				-
3. Sungai Pendas	Pure meadow and occasionally with Halophila ovalis.	0.8-1.0	0.15-0.45	29-31	20-22	75-80	5.31-5.33	4.69-4.82	Sandy mud
4. Tanjung Surat, Kg. Nyior	Pure meadow and occasionally with Halophila ovalis.	1.0-1.5	0.15-0.45	30-31	25-28	101-162	7.58-7.62	4.71-4.95	Sandy mud
Terengganu									
5. Kemaman river	Pure meadow growing among the pneumatophores of Avicennia alba, Sonneratia caseolaris and under the sheltered of mangrove plants such as Bruguiera cylindrica, Kandelia candel, Rhizophora apiculata, Ceriops decandra and Nypa fruticans.	1.0-1.5	0.1-0.9	25.08-35.67	0-26.19 0-30.25	31.15-399.1	5.97-7.42	4.50-4.51	Sandy loam, loam
6. Chukai	Monospecific patches.	1.5-2.0	0.1-0.5	28.00-34.00	0-26.00	45-258	6.12-7.12	4.20-4.50	Sandy
7. Telaga Simpul	It grows among the pneumatophores of Sonneratia griffithii and occasionally with H. pinifolia.	1.0-1.5	0.38-0.57	30.00-32.00	29.00-31.00	100-258	6.21-7.32	4.06-5.07	Silty sand
8. Paka Lagoon	Monospecific patches, sometimes with <i>H. pinifolia</i> .	1.0-1.5	0.1-0.5	24.67-37.67	0-28.00 0-31.46	4-154.4	5.54-8.14	4.20-4.50	Sand, loamy sand
9. Paka river	Monospecific population among pneumatophores of Sonneratia caseolaris and Nypa fruticans clumps.	1.0-2.5	0.1-0.5	26.67-35.67	0-27.00	61-65	6.58-6.85	4.20-4.50	Sandy mud
10. Paka shoal	Damaged monospecific meadow by the construction of concrete Break Water. Construction of Break Water occupying the former <i>H. beccarii-H. pinifolia</i> meadow. Mangroves also inhabit this area.	2.7-3.0	0.1-0.2	30.00-35.00	13.00-32.00	198-225	5.91-6.6	4.19-4.96	Sandy mud
Kelantan									
11. Pengkalan Nangka lagoon	Monospecific meadow. Sometimes growing among seaside grasses of Fimbristylis dichotoma.	1.6-2.0	0.45-0.46	28.00-38.20	0-23.93 0-23.73	5.2-191.6	6.6-7.64	5.92-6.98	Sand

TABLE 2 Continued

State/ location	Form and association	Depth range (m) ELWS	Visibility (m)	Water temp. (°CC)	Salinity (psu)	TSS (mg/L)	Ph	DO	Substrate
Kelantan									
12. Pengkalan Nangka shoal	Monospecific meadow. It also grows among the pneumatophores of Sonneratia caseolaris and coexists with seaside grass, Fimbristylis dichotoma.	1.5-2.5	0.45-0.50	28.00-38.20	0-23.83	36.4-51.4	6.47-7.48	4.20-4.82	Sandy mud
13. Kg. Baru Nelayan	Monospecific meadow with seaside grasses <i>Cyperus distans</i> , <i>Cyperus</i> sp. and aquatic plant <i>Cryptocoryne ciliata</i> .	1.0-2.5	0.45-0.50	28.00-36.00	0-23.00	12-50	6.52-7.25	4.18-5.11	Sandy mud
14. Pantai Baru lagoon	Monospecific meadow among the pneumatophores of young Sonneratia caseolaris and Nypa fruticans clumps.	1.0-2.5	0.45-0.50	30.00-32.00	0-24.00	15-51.4	6.47-7.58	4.51-5.15	Sandy mud
Penang									
15. Korea island	Monospecific meadow and sometimes with <i>H. ovalis</i>	1.5-3.5	0.5-0.7	30.00-32.00	25.00-32.00	150-215	6.42-7.58	4.01-4.21	Calcareous mud
16. Seberang Prai	Monospecific meadow in front of Avicennia alba stands	1.0-2.0	0.5-0.7	30.00-32.00	15.00-25.00	100-200	6.4-7.5	4.10-4.20	Sandy mud
Sarawak									
17. Punang Sari-Lawas River estuary	Monospecific bed	1.0-1.5	0.30-0.50	30-32	20-25	50-80	7.71-7.82	4.70-5.30	Sandy mud

Note (*) - den Hartog (1970), ELWS, ebb low water spring. Salinity is at low and high tides.

TABLE 3 Vegetative measurement of *H. beccarii* from various locations.

Location	Petiole length (mm)	Leaf length (mm)	Leaf width (mm)
Sungai Pendas	12.52 ± 2.38^{a} (7.27-17.18)	8.58 ± 1.20^{a} $(5.75-11.31)$	2.55 ± 0.29^{a} $(1.98-3.14)$
Tanjung Surat	8.03 ± 2.7^{e} $(3.87-12.24)$	5.00 ± 1.01 ^d (3.01-6.39)	0.94 ± 0.3^{e} $(0.44-1.42)$
Sungai Kemaman	1.87 ± 0.42^{b} (1.11-2.5)		
Telaga Simpul	$8.55 \pm 1.36^{\circ}$ (6.12-11.36)	6.61 ± 0.63 ^{bc} (5.68-7.59)	$1.45 \pm 0.18^{\circ}$ $(1.19 + 1.88)$
Sungai Paka Lagoon	11.68 ± 2.68^{ab} (5.81-15.3)	7.29 ± 2.38 ^b (3.5-11.67)	$1.48 \pm 0.35^{\circ}$ (0.92-2.09)
Paka shoal		1.26 ± 0.28^{d} $(0.69-1.82)$	
Pengkalan Nangka Lagoon	$9.70 \pm 2.74^{\text{cd}}$ (4.56-13.95)	6.40 ± 1.71° (3.54-9.24)	$1.58 \pm 0.47^{\circ}$ (0.91-2.23)
Pengkalan Nangka shoal	10.27 ± 1.99^{c} (6.77-15.31)	5.38 ± 0.68^{d} (3.95-6.77)	1.23 ± 0.21^{d} (0.76-1.63)
Korea Island	9.11 ± 2.38 ^{cde} (3.36-13.1)	5.00 ± 0.67^{d} (3.64-6.33)	0.81 ± 0.21^{e} (0.2-1.17)
Punang Sari Lawas	10.52 ± 262^{bc} (6.11-14.62)	6.52 ± 2.57 ^{bc} (3.27-13.17)	1.58 ± 0.48^{c} $(0.93-2.53)$

Value is given as mean \pm standard deviation and range in parentheses. (n=30). Means with different letters (a > b > c > d>e) differ significantly at p < 0.05 (Duncan's Multiple Range Test, DMRT).

ovember	November to January: Absence of a				
December	living plant. There was a dormant period of three months prior to seed	3 mm			
January	germination.				
February	February : Recolonization of the meadow.				
March	March to April: Progressive	A B C 10 mm			
April	development of germinating seed to seedlings.	10 r			
April	April to September: Juvenile plants continue to propagate vegetatively, forming adult plants.				
May		AND THE WAY			
June		The state of the s			
July		D 10 mm			
August					
September		E . JII			
October	October to November: Absence of	5 mm 5 mm 5 mm			
November	living plants.				
December	December to January:				
January	Recolonization of the meadow by germinating seeds and seedlings.	FGHH			

FIGURE 6

The growth cycle of annual plants from Pengkalan Nangka Lagoon, Kelantan, and Paka Shoal, Terengganu. (A) Recolonization of the meadow by germinating seed in February. Progressive development of (B) germinating seed to (C, D) seedlings with an array of rhizome network systems from March to April. (E) Juvenile plants continue to propagate vegetatively, forming adult plants that produce (F) male flower, (G) female flower, (H) fruit and (I) seeds from April to September.

life cycle of *H. pinifolia*, characterized by quick colonization through seed banks, provides an extra advantage in post-disturbance environments. As Unsworth et al. (2015) observed, these early successional species can stabilize sediments and promote recovery, often outcompeting more sensitive taxa like *H. beccarii*.

This vulnerability differs from more resilient taxa like *E. acoroides* and follows similar patterns observed in other small seagrass species, *Halodule pinifolia* and *H. ovalis*, which are also vulnerable to sedimentation and habitat alteration (Short et al., 2011; Yaakub et al., 2014). The ecological impacts are significant, as *H. beccarii* meadows serve as habitat for juvenile fish, invertebrate nurseries, and support coastal food webs (Waycott et al., 2009). Moreover, their ability to sequester carbon is reduced under low-light and turbid conditions (Premarathne et al., 2021; Mishra et al., 2021). Recovery at these disturbed sites appears slow and likely depends on seed banks, a pattern also observed in Bangladesh (Rakib et al., 2022).

On the west coast of Peninsular Malaysia, the absence of *H. beccarii* from previously recorded sites, such as Sungai Tebrau and Jalan Skudai, Johor (den Hartog, 1970), suggests possible extirpation. Recent reappearances in 2021 in Sungai Pendas, Johor, suggest that populations may persist in less-disturbed habitats. These findings highlight the importance of adaptive and site-specific monitoring strategies, particularly for cryptic or small-bodied seagrass species that are easily overlooked during conventional surveys. Using rotational monitoring combined with more frequent or community-based assessments could enhance detection and provide early warning signs of biodiversity changes. Although this study benefited from long-term revisit data, it also highlights the need for consistent, frequent monitoring to capture local dynamics and support effective conservation efforts.

Data availability statement

The original contributions presented in the study are included in the article/supplementary material. Further inquiries can be directed to the corresponding author.

Author contributions

MZ: Data curation, Resources, Visualization, Conceptualization, Formal analysis, Project administration, Validation, Software, Writing – review & editing, Methodology, Supervision, Investigation, Writing – original draft, Funding acquisition. NS: Writing – review & editing, Methodology, Formal analysis, Visualization. JB: Conceptualization, Visualization, Investigation,

Supervision, Methodology, Funding acquisition, Validation, Software, Project administration, Formal analysis, Resources, Data curation, Writing – review & editing, Writing – original draft.

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