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Seagrass habitats of Singapore: Environmental drivers and key processes

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Abstract. Seagrasses are an important component of the marine ecosystems of Singapore. Using various assessment activities, we confirm 10 seagrass species within the waters of Singapore, with an additional two species under review for synonymy. Using long-term monitoring we examined the key attributes that affect the resilience of Singapore's seagrasses. We defined five broad categories of seagrass habitat in Singapore as estuary, coast, rocky fringing reef, sandy fringing reef, and patch reef. We identify the key features of the habitats and provide some insight into the drivers of change. In their natural state, seagrasses appear to follow a unimodal pattern of growth annually, which peaks in the late intermonsoon period prior to the onset of the southwest monsoon. Light availability appears to be the critical factor for seagrass growth in Singapore, and environmental factors, which modify the interactive effect of light availability and temperature are possibly the main drivers of change. Finally, we synthesised our understanding of seagrass ecosystems by classifying the attributes of the species present, meadow structure, and their possible drivers into a framework to assist ongoing monitoring and management decision-making. We also discuss the implications of seasonal growth in the Singapore context and identify research gaps that need to be urgently addressed. This understanding will help to better focus seagrass management and research in Singapore.

Key words. Seagrass, habitats, resilience, seasonality, growth, monitoring

INTRODUCTION

Seagrasses are marine flowering plants that grow in shallow, sheltered, nearshore waters. Seagrasses play a critical role in coastal ecosystem dynamics, such as food provision (Cullen-Unsworth et al., 2014), shelter and nursery grounds to many commercially important marine species (Waycott et al., 2011), coastal protection by stabilising sediments and sediment accretion (Madsen et al., 2001; Gacia et al., 2003), nutrient cycling (McGlathery et al., 2007), and the retention of carbon within their sediments contributes significantly to Blue Carbon sequestration (Fourqurean et al., 2012; Unsworth et al., 2012a). Seagrasses are also the primary food for sea turtles and dugongs, which are seagrass specialists (Marsh et al., 2011). The ecosystem services provided by seagrasses make them a high conservation priority (Cullen-Unsworth & Unsworth, 2013). Despite being economically valuable (Costanza et al., 1997; Costanza et al., 2014), the last five decades have seen widespread and substantial losses in global seagrass cover (Waycott et al., 2009) driven by anthropogenic activities such as land-use and coastal change (Yaakub et al., 2014) and declining water quality (Orth et al., 2006).

Seagrasses are an important component of the marine ecosystems of Singapore and meadows are distributed throughout the city state's shallow waters. To the north of Singapore Island, seagrass meadows tend to be mangrove associated, whereas meadows found among the southern islands are associated with reefs. Overall, the seagrass ecosystems of the Singapore are a complex mosaic of different habitat types comprised of multiple seagrass species (Yaakub et al., 2013) in which timing as well as mechanisms that capture their dynamism are relatively poorly understood (Yaakub et al., 2014).

The formation of healthy seagrass meadows requires adequate light, nutrients, carbon dioxide, suitable substrates for anchoring, along with tolerable salinity, temperature and pH (Hemminga & Duarte, 2000; Larkum et al., 2006). The form and composition of seagrass meadows are influenced by the seagrass species' life history characteristics and the habitat in which they grow. Habitats have a unique suite of environmental conditions that control the amount and variability of light, nutrients, freshwater input, and hydrodynamic conditions to which the seagrass is exposed (Kilminster et al., 2015).

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Table 1. Number of photographs examined within each division of Singapore via geo-tagged Flickr or title search.

Division	Geo-tagged Photographs	Title Search
Western Johor Strait	14	188
Eastern Johor Strait	576	788
Southern Mainland	1254	416
Southern Islands	2183	159
Western Islands	780	5233
TOTAL	4807	6784

To provide an understanding of the diversity and dynamics of seagrasses and their habitats in Singapore, we conducted various assessment and monitoring activities. We updated the list of species and their locations through extensive literature and herbarium surveys and participated in expeditions for the Comprehensive Marine Biodiversity Survey of Singapore (CMBS) (Tan et al., 2015). We also used long-term monitoring data to identify and define the seagrass habitats present, and to examine the relationship between seagrasses and climatic parameters to quantify seasonal changes in the seagrass abundance and community.

MATERIAL & METHODS

Site description. Singapore is an island state located at the southern tip of the Malaysian Peninsula, 137 km north of the equator. Owing to its geographical location and maritime exposure, Singapore is characterised by a hot and humid climate. The average temperature is 27°C, with relative humidity in the range of 80–90% (Meteorological Service Singapore, 2015). The average annual rainfall is 2,338.5 mm, and thunderstorms occur on 45% of all days (Meteorological Service Singapore, 2015). Singapore's climate is considered to be "Af" according to the Köppen-Geiger climate classification; i.e., all 12 months have average precipitation of at least 60 mm and is dominated by the doldrums low-pressure system all year round, so has no natural seasons (Peel et al., 2007). Although there are no clear-cut wet or dry seasons, there are two main monsoon seasons in Singapore: the northeast monsoon (December–March) and the southwest monsoon (June–September). The northeast monsoon is typified by northeasterly winds, which in the early part cause widespread continuous moderate to heavy rain (December–January), while in the later part result in relatively dry conditions (February–mid March) (Meteorological Services Division, 2009). December is usually the wettest month of the year in Singapore. The southwest monsoon season is characterised by southerly to southeasterly winds, with short duration showers common most days. Separating the two seasons are the inter-monsoon periods (April–May and October–November). The first inter-monsoon in the early part of year is generally drier than the second inter-monsoon in the later part of the year (Meteorological Services Division, 2009). It is usually hot and dry in the months of May–July and more frequent rain spells occur during November–January.

Seagrass diversity, distribution, and reproductive status. Observations and data were collected to update the seagrass baseline checklist (Yaakub et al., 2013) at a number of locations across Singapore. Between 20 May 2013 and 5 June 2013, 189 sites were assessed as part of the Southern Shores expedition for the Comprehensive Marine Biodiversity Survey of Singapore: an initiative of the National Parks Board (NParks) and the Tropical Marine Science Institute (TMSI). Intertidal and subtidal points (to depths >100 m) were assessed in the Singapore Strait and around the southern offshore islands as part of an initiative to document all of Singapore's marine life in its natural marine habitats. Points were sampled using a selection of methods, ranging from SCUBA to beam trawl, epibenthic sled, and rectangular dredge.

Additional information on seagrass species reported from Singapore was sourced from the Singapore Botanic Gardens Herbarium (SING), the Lee Kong Chian Natural History Museum Herbarium (SINU), literature (Sinclair, 1953; den Hartog, 1970; Loo et al., 1996; Noiraksar et al., 2012) and content analysis of photographs, using the freely accessible photo-sharing website Flickr (Richards & Friess, 2015). Flickr was accessed through the publicly available API, and a bounding box encompassing each of the key seagrass areas was searched for photographs using code in R 3.1.2 (R Core Team, 2014). The Flickr API returned geo-tagged photographs (Flickr, 2015), which were individually assessed after being overlayed on mapped seagrass meadows (Yaakub et al., 2014) using ArcGIS® (Environmental Systems Research Institute). However, as post-processing of photographs often removes geo-tagged metadata and not all photographs include geo-positioning, the search was widened to include the greater Singapore region and photograph title searches were conducted using a variety of keywords describing locations, seagrass common names and seagrass associated fauna. 11,591 photographs across five divisions of Singapore were examined for seagrass species and presence of reproductive structures/organs (i.e., flowers and fruits) (Table 1). Image metadata also provided the approximate date the photograph was taken.

Seagrass abundance and long-term monitoring. Long-term monitoring of seagrass meadows in Singapore commenced from February 2007 as part of the global Seagrass-Watch program (Yaakub et al., 2014). TeamSeaGrass, a non-

Table 2. Description of long-term seagrass monitoring locations and their conservation status in Singapore, 2007–2014. *established but not monitored. Area of seagrass from Yaakub et al., (2014).

Location	Monitoring Sites	Description	Conservation Status
Tanjong Chek Jawa (Pulau Ubin)	CJ1, CJ2	Shallow lagoon sheltered behind sand bar fringed by mangroves shoreward, on the eastern extent of Pulau Ubin. Area of seagrass = 6.5 ha.	Listed for use as Reserve Site in the URA Master Plan 2014
Cyrene Reef (Terumbu Pandan)	CR1, CR2	Submerged reef fringed by coral/rock with central sandy area. Located within main port area, adjacent to petrochemical plants (Jurong Island and Pulau Bukom) and Pasir Panjang container terminal. Area of seagrass = 17.5 ha.	Does not appear on the URA Master Plan 2014 or the Parks and Waterbodies Plan.
Pulau Semakau	PS1, PS2, PS3, PS4*	Sandy shore, with shallow lagoon fringed of sparse coral reef seaward and mudflats/ mangroves shoreward. Area of seagrass = 13.7 ha.	Listed for use as 'Open Space' in the URA Master Plan 2014 and "Marine Nature Areas", where" The government will keep these areas in their natural state for as long as possible." in Singapore Green Plan 2012.
Tanjung Rimau (Sentosa)	SE1	Narrow sandy rubbly flats boarded by rocky shore with pebbly stretches and natural cliffs with coastal forest.	Listed for use as 'Sports and Recreation' in the URA Master Plan 2008, and 'Park/Open Space' in Parks and Waterbodies Plan.
Labrador Nature Reserve	LP1, LP2*	Narrow rocky-rubbly flats interspersed with sand boarded by rocky shore with pebbly stretches and natural cliffs with coastal forest. Only remaining stretch of fringing reef along west and southwest coast of mainland and only remaining natural rocky shore on the southern coastline of mainland Singapore	10 ha of coastal secondary vegetation and the rocky shore of Labrador Park regazetted in 2002 as a nature reserve. Protected by the Parks and Trees Act 2005. Permanent limited access to Labrador beach to allow its recovery.
Tuas	TU1, TU2*	Intertidal mud/sand bank at Tanjong Merawang extending to Singapore's last natural western reef (Merawang Beacon). Shore is borded by seawall of cleared wetland developed for industrial use in the 1970s.	Does not appear on the URA Master Plan 2014 or the Parks and Waterbodies Plan

governmental organisation, established 13 sites across six locations (Table 2) from the northern shores to the southern islands, in association with NParks, to monitor the condition and status of Singapore's seagrass meadows (Yaakub et al., 2014). Monitoring occurs every 3–6 months, however, not all locations commenced in 2007, and data collection has not been at regular intervals across years and sites.

Within each location, 1–3 sites (50 × 50 m, permanently marked), were assessed by visually estimating seagrass percentage cover and species composition within 33 quadrats (50 × 50 cm) at each site. Sites represented the seagrass population within a meadow and the unit of measure (quadrat) was not anchored to the substrate between sampling events, so the probability of repeatedly sampling the same shoot or ramet was unlikely. Additional information collected from each quadrat included the presence of reproductive structures (e.g., flowers, fruits and seeds), herbivory (e.g., dugong excavating) and visual/tactile estimation of sediment grain size composition (0–2 cm below the sediment/water interface). Details of the Seagrass-Watch monitoring protocols are described in McKenzie et al. (2000, 2003).

Climate and environmental data. Climate data were accessed courtesy the Meteorological Service Singapore, National Environment Agency. As global solar radiation measures were unavailable for more than half the study period, daylight cloud cover (sunrise to sunset) was used as a surrogate for solar radiation. The average daily low level cloud cover (cloud ceiling <2000 m) was calculated from the hourly fraction of low level broken clouds (5/8–7/8 cloud coverage) and overcast (8/8 cloud coverage) sky conditions within daylight hours (sunrise to sunset). Tidal height predictions were calculated using WXTide32 (version 4.7) and the duration of daylight exposure (total hours between sunrise and sunset) was determined for each meadow (i.e., monitoring location) based on the meadows height relative to the chart datum: Chek Jawa <0.5 m, Pulau Semakau <0.3 m, Cyrene Reef < 0.25 m, and Sentosa <0.2 m.

For each monitoring event at each site, a mean value for all environmental factors for the previous 15, 30, and 90 days prior to seagrass monitoring was determined (Table 3). These three different durations represent biologically meaningful changes in seagrass growth and environmental

Table 3. Climate and environmental factors together with their averaging times used in regression analysis of seagrass meadow abundance (2007–2014).

Factor	Averaging Time used in Regression
total rainfall (mm)	previous 15, 30, and 90 days
daylight low cloud cover (8th^{-1} of sky)	previous 15, 30, and 90 days
average wind speed (m s^{-1})	previous 15, 30, and 90 days
maximum wind speed (m s^{-1})	previous 15, 30, and 90 days
average temperature (°C)	previous 15, 30, and 90 days
minimum temperature (°C)	previous 15, 30, and 90 days
maximum temperature (°C)	previous 15, 30, and 90 days
daylight tidal exposure (hours)	previous 15, 30, and 90 days

conditions (e.g., lunar) within these meadows. Seagrass leaf turnover rates for *Thalassia hemprichii* have been reported from Labrador Nature Reserve to be 16.8 ±1.5 to 26.6 ±2.9 days (October 2007 and October 2008, respectively) i.e., 2–4 weeks (Koh et al., 2008; McKenzie, 2009). The average time span between the formation of new shoots (plastochrone interval) for tropical Indo-West Pacific seagrasses vary from 10.2 days for *Halophila ovalis* to 107.1 days for *Enhalus acoroides* (Hemminga & Duarte, 2000; Rattanachot & Prathep, 2011).

Data analysis. Patterns in seagrass species assemblages and sediment-grain size composition were visualised using multivariate non-metric multidimensional scaling ordination (NMDS), based on Euclidean distances, and Bray–Curtis cluster analysis using PRIMER v. 6.1.5 (Clarke & Warwick, 2001). Seagrass species assemblages were determined by calculating the contribution of each species to the total quadrat cover for each sampling event and then averaging across all sampling events for each species. Grain-size composition of surficial marine sediment was differentiated according to the Udden-Wentworth grade scale (Udden, 1914; Wentworth, 1922) as this approach has previously been shown to provide an equivalent measure to sieve-derived datasets (Hamilton, 1999; McKenzie, 2007). Rock and gravel were further separated as terrigenous or biogenous (e.g., calcareous) in origin.

Analysis of seagrass abundance was conducted using the long-term dataset at the site level, and we averaged the above ground percent cover data for each location. To examine within-year patterns in seagrass abundance (i.e., seasonality), we selected the years 2008–2009, as they included the most consistent datasets across the sites (monitored every three months). Sampling frequency decreased from 2010 and abundance data from 2007 were excluded to factor out the impact of extreme weather events in December 2006 and January 2007 (the heaviest rains in 100 years resulting in two major flood events (Malaysian Meteorological Department, 2006, 2007; Loh et al., 2009)). Only four seagrass meadows or localities were included (Chek Jawa, Cyrene Reef, Pulau Semakau and Sentosa) (Table 2, Fig. 1) and three of the locations represented the largest continuous seagrass meadows in Singapore (Yaakub et al., 2013). The same four locations were used to examine relationships between seagrass percent cover and abiotic (climatic and environmental) factors (Table 3).Within and between year differences in each abiotic variable were also examined, using the seasonal averages within each year. Analysis of variance (ANOVA) and regression analyses were performed using SPSS Statistics v. 22.0 (SPSS Inc, Chicago, IL) after checking for normality and homogeneity of variance. In the event when either of these assumptions was violated, data were arc-sine transformed.

Relationships between seagrass abundance (percent cover) and abiotic factors were tested using backward stepwise removal multiple regression in SPSS Statistics v. 22.0 (SPSS Inc, Chicago, IL). Only abiotic factors measured at 30 days were submitted into the models, as regressions were not significant between seagrass abundance and abiotic factors averaged over the previous 15 or 90 days.

RESULTS

Seagrass species. Ten seagrass species, with an additional two species under review for synonymy, were confirmed from across 41 localities in Singapore; supporting the baseline of Yaakub et al. (2013) (Table 4). The earliest record of a seagrass from Singapore was *Enhalus acoroides* from Changi in 1889 (SING), and the most recent addition to the species list was *Halophila decipiens* off Pulau Semakau, approximately 120 years later in 2007 (SING 2008-273).

The greatest number of species (excluding those under review) in Singapore was reported from Cyrene Reef (Table 4 and Fig. 1). The most widely distributed species was *Halophila ovalis*, followed by *Enhalus acoroides* and *Thalassia hemprichii*. With the exception of the species under review for synonymy, the rarest species in Singapore were *Halophila beccarii* and *Halophila decipiens*. *Halophila beccarii* is one of seven seagrass species globally listed as Vulnerable (Short et al., 2011) and although it has a relatively large range in the Tropical Indo-Pacific (Green & Short, 2003), it is patchily distributed with a low area of occupancy, only inhabiting the high intertidal zone. *Halophila beccarrii* was first reported in Singapore from the then Kranji Nature Reserve (August 1961) and with global populations declining,

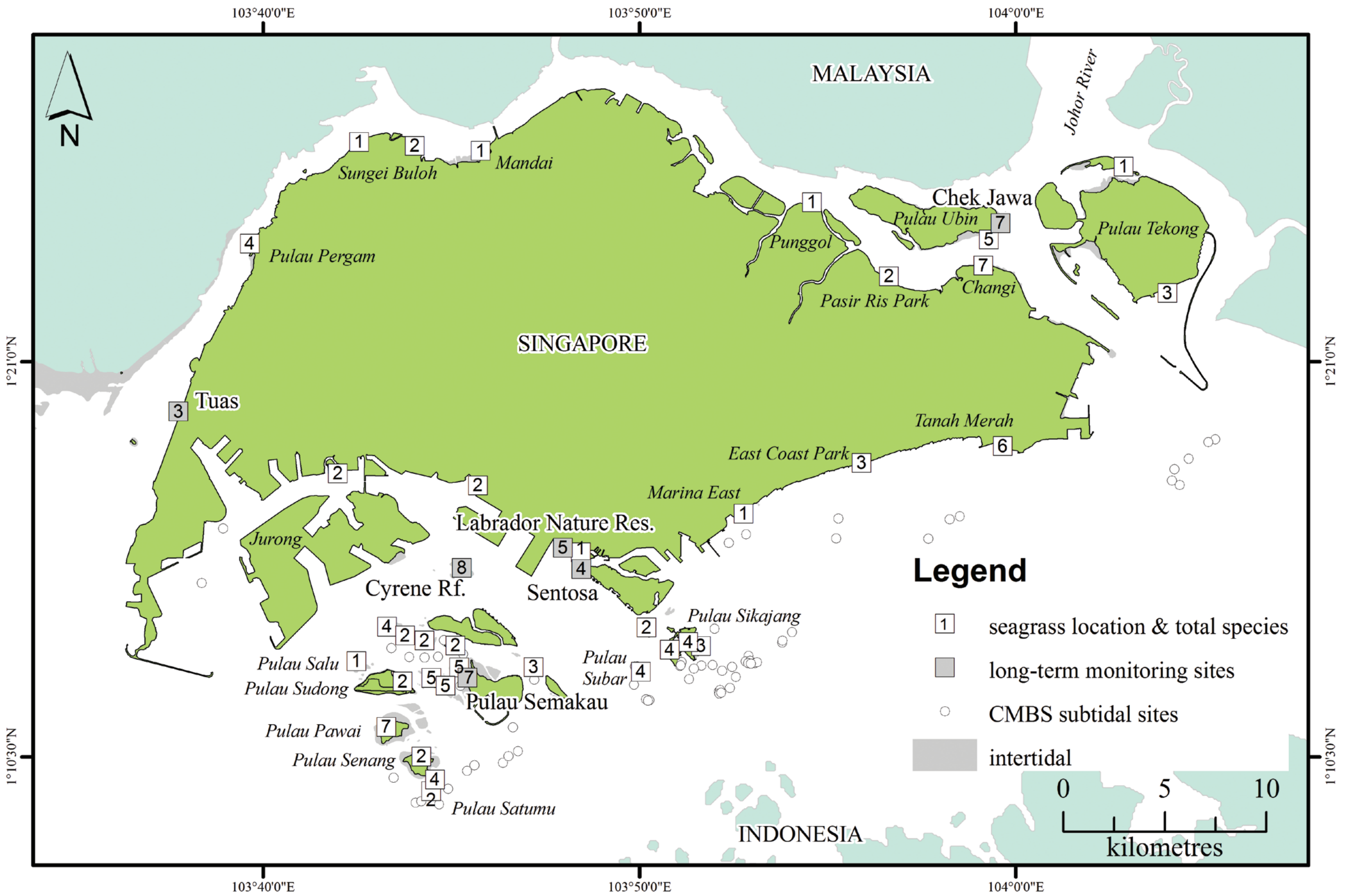

Fig. 1. Map showing locations where seagrass (including total number of species) has been reported from around Singapore. Positions of long-term monitoring sites and subtidal sites examined as part of the Comprehensive Marine Biodiversity Surveys (CMBS) are shown.

Table 4. List of seagrass species reported from Singapore, including historic and current records. Species include: CR, *Cymodocea rotundata*; CS, *Cymodocea serrulata*; HP*, *Halodule pinifolia*; HU, *Halodule uninervis*; SI, *Syringodium isoetifolium*; EA, *Enhalus acoroides*; HB, *Halophila beccarii*; HD, *Halophila decipiens*; HM*, *Halophila minor*; HO, *Halophila ovalis*; HS, *Halophila spinulosa*; TH, *Thalassia hemprichii*. NB: HP* and HM* are synonymous with HU and HO, respectively. Data sources: 1, (Yaakub et al., 2013); 2, herbaria only; 3, denotes species observed during field observations (2010–2014); 4, Loo et al., (1996); 5, Singapore herbarium; 6, Sinclair, (1953); 7, den Hartog, (1970); 8, Noiraksar et al., (2012); 9, www.flickr.com; 10, Chng & Chou, 2014.

Locations	Habitat	CR	CS	HP*	HU	SI	EA	HB	HD	HM*	HO	HS	TH
Western Johor Strait													
Tuas	estuary						1,9				1	4	
Lim Chu Kang Mangroves	estuary							1					
Sungei Buloh + Kranji	estuary						1	1					
Mandai	estuary							1					
Pulau Pergam	estuary						1		1	1	1	1	
Eastern Johor Strait													
Punggol	estuary								9				
Pasir Ris Park (incl. Loyang)	estuary								9		1,9		
Changi (incl. Telok Paku)	estuary	5		5	1,4	2	1		1,9		1	1	
Pulau Ubin (incl. Chek Jawa)	estuary	1		1	1		1	1			1	1	1
Pulau Sekudu	estuary		9				1		9		1	1	
Pulau Tekong	estuary						1			4	1,4	4,7	
Beting Bronok	estuary										1		

Table 4. continued

Locations	Habitat	CR	CS	HP*	HU	SI	EA	HB	HD	HM*	HO	HS	TH
Southern Mainland													
Jurong East (RSYC)	estuary							7			7		
Labrador Nature Reserve	fringing reef	4		5			1,4				1,4		1
Belayer Creek	estuary										1		
East Coast Park	coast				1		1				1		
Marina East	coast				10								
Tanah Merah	coast	1				2	1				1		9
Southern Offshore Islands													
Pulau Belakang Mati (Sentosa Is.)	fringing reef				1		1				1		
Pulau Samulun (Jurong)	fringing reef		5										6
Pulau Tekukor	fringing reef										1,3		1,3
Pulau Subar Laut (Big Sister)	fringing reef	4					3				3,4		
Pulau Sakijang Pelepah (Lazarus Is.)	coast						4				1,3,4		1
Pulau Sakijang Bendera (St. John's Is.)	fringing reef				3		3			8	1,3,8		8
Pulau Tembakul (Kusu Is.)	fringing reef						1				1		
Pulau Hantu	fringing reef						1,4				1,4		
Pulau Semakau	fringing reef		1		1	1	1,4		1,9		1,4		1
Pulau Jong	fringing reef										1,4		1
Pulau Sudong	fringing reef						1				1		
Pulau Salu	fringing reef										3		
Pulau Pawai	fringing reef	1	1	5	1	1	1				1		1
Pulau Senang	fringing reef			5							7		
Pulau Biola	fringing reef				1		1				1		1
Pulau Satumu (Raffles Lighthouse)	fringing reef										1		
Southern Offshore Reefs													
Terumbu Pandan (Cyrene Reef)	patch	1	1		1	1	1,4		1		1		1
Terumbu Pempang Darat	patch									2	2		
Terumbu Pempang Laut	patch					1	1				1		1
Terumbu Pempang Tengah	patch										2		2
Beting Bemban Besar	patch	4	1			1	1, 4				1		1
Terumbu Raya	patch	4	3				1,3,4				1, 3		3
Terumbu Semakau	patch		1				1				1		

its occurrence in Singapore has conservation significance, as its habitat is threatened by near-shore human activities such as reclamation (Yaakub et al., 2014).

Seagrasses in Singapore only grow in intertidal and shallow subtidal waters, with no seagrasses reported in waters deeper than 9 m. No seagrass was observed from the SCUBA diver assessments to 19.6 m or collected from benthic trawls/dredges to 150 m during the CNBS in May or June 2013 (Fig. 1). Historical records reported *Halophila spinulosa* from 9 m at Pulau Tekong in 1929 (den Hartog, 1970), however, the only recent reports of a subtidal seagrass was *Halophila decipiens* in 5–8 m off Pulau Semakau's southwest reef slope in 2007 and 2008 (Yaakub, 2008; Yaakub et al., 2013).

Seagrass meadows. All the seagrass meadows at the locations examined were classified as enduring, as they have all been present for durations greater than five years (Kilminster et al., 2015). Using the seagrass species and sediment compositions across all sampling events, monitoring sites were classified into four similarity clusters which corresponded to four different habitats: estuary, sandy fringing reef, rocky fringing reef, and patch reef (Fig. 2). In accordance to the similarity clusters, the main monitoring locations each represented a

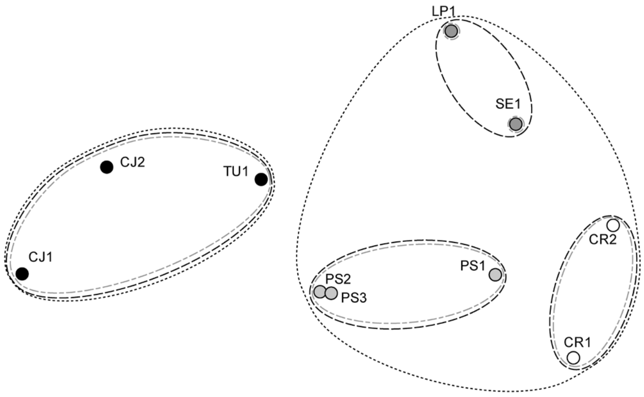

Fig. 2. Two-dimensional NMDS scaling (Kruskal stress = 0.07) configuration with superimposed Bray–Curtis similarity clusters (oval shapes) at the 80% (grey dashed lines), 75% (black dashed lines) and 70% (black dotted lines) level for comparisons between seagrass species and sediment assemblages in Singapore in the predominant coastal habitats: patch reef (white circle), sandy fringing reef (light grey circle), rocky fringing reef (dark grey circle) and estuary (black circle).

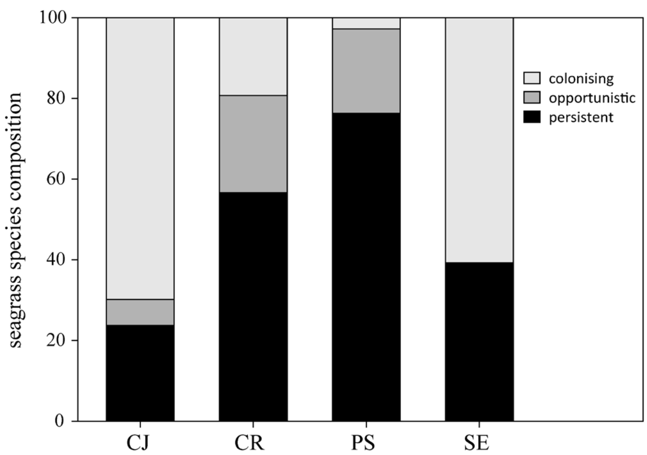

Fig. 3. Composition of seagrass species groups to total % cover of seagrass at each long-term monitoring site (seagrass habitat type) in Singapore. CJ= Chek Jawa (estuary), CR=Cyrene Reef (patch reef), PS= Pulau Semakau (sandy fringing reef), SE= Sentosa (rocky fringing reef). Species groups includes: Opportunistic = *Halodule uninervis* (HU) + *Syringodium isoetifolium* (SI); persistent= *Cymodocea rotundata* (CR) + *Cymodocea serrulata* (CS) + *Enhalus acoroides* (EA) + *Thalassia hemprichii* (TH); and colonising = *Halophila ovalis* (HO)+ *Halophila spinulosa* (HS).

different habitat, i.e., Chek Jawa (Pulau Ubin) = estuary; Pulau Semakau = sandy fringing reef; Sentosa = rocky fringing reef; and Cyrene Reef = patch reef.

An examination of the species present at each of the locations (Fig. 3) revealed aspects of the meadows based on attributes of seagrass life histories. For example, the estuarine meadows at Chek Jawa are composed predominantly of colonising species (low physiological resistance to disturbances but recovering rapidly) which would suggest a dynamic environment, whereas the sandy fringing reef meadow at Pulau Semakau was dominated by more persistent species (high physiological resistance but slow to recover from disturbances), suggesting a more stable environment (Kilminster et al., 2015). The diversity of species at the patch reef meadow (Cyrene Reef)

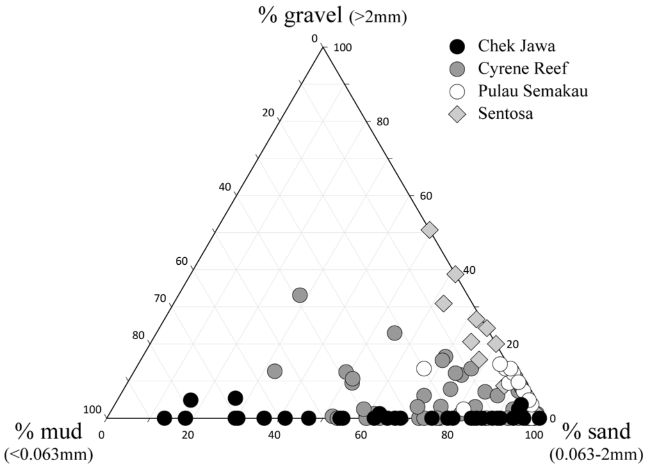

Fig. 4. Ternary plot of average sediment-grain size each sampling event at long-term seagrass monitoring sites/habitats in Singapore, 2007-2014.

suggests a level of spatial and temporal dynamism, with not only persistent and colonising species, but a significant composition of opportunistic species (moderate physiological resistance but ability to rapidly recover from seed or new recruits) (Kilminster et al., 2015).

The composition of sediments differed between each of the habitat types, with a higher proportion of mud in the estuarine meadow (Chek Jawa), and coarser sediments (sand and gravel) dominating the sandy and rocky fringing reefs, respectively (Fig. 4).

Seagrass abundance and phenology. Over the 2008 and 2009 monitoring periods, there was a significant effect of season on percentage cover of seagrass at the estuarine habitat, Chek Jawa ($F_{3,13} = 3.623$, $p = 0.045$). Post-hoc analysis showed that percentage cover of seagrass in the southwest monsoon (June–September) and the later months of the first inter-monsoon (April–May) were the same and significantly higher than the northeast monsoon (December–early March) and second inter-monsoon (October–November) (Fig. 5). For all other locations, season had no effect (Cyrene Reef, $F_{3,10} = 0.372$, $p = 0.775$; Pulau Semakau, $F_{3,12} = 1.002$, $p = 0.425$; Sentosa, $F_{3,4} = 1.827$, $p = 0.282$) (Fig. 5). Although not significant, the change in seagrass percentage cover suggests a unimodal seasonal pattern at the sandy and rocky fringing reef habitats. However, no pattern in seagrass percentage cover was apparent at the patch reef habitat (Cyrene Reef) over the same 2008–2009 period.

Other seagrass parameters in addition to abundance also show seasonal patterns, such as flowering and asexual shoot production (Duarte et al., 2006). With the exception of *Halophila beccarii* and *Halophila decipiens*, all seagrass species in Singapore are dioecious (Bujang et al., 2006). Overall, there were 94 separate observations or reports (separate days and locations) of seagrass flowers (male or female) or seed-set (mature fertilised plant ovules, i.e., fruit with seed) from four seagrass species, between January 2000 and October 2014. The most frequently observed species with sexual structures was *Enhalus acoroides*, which flowered

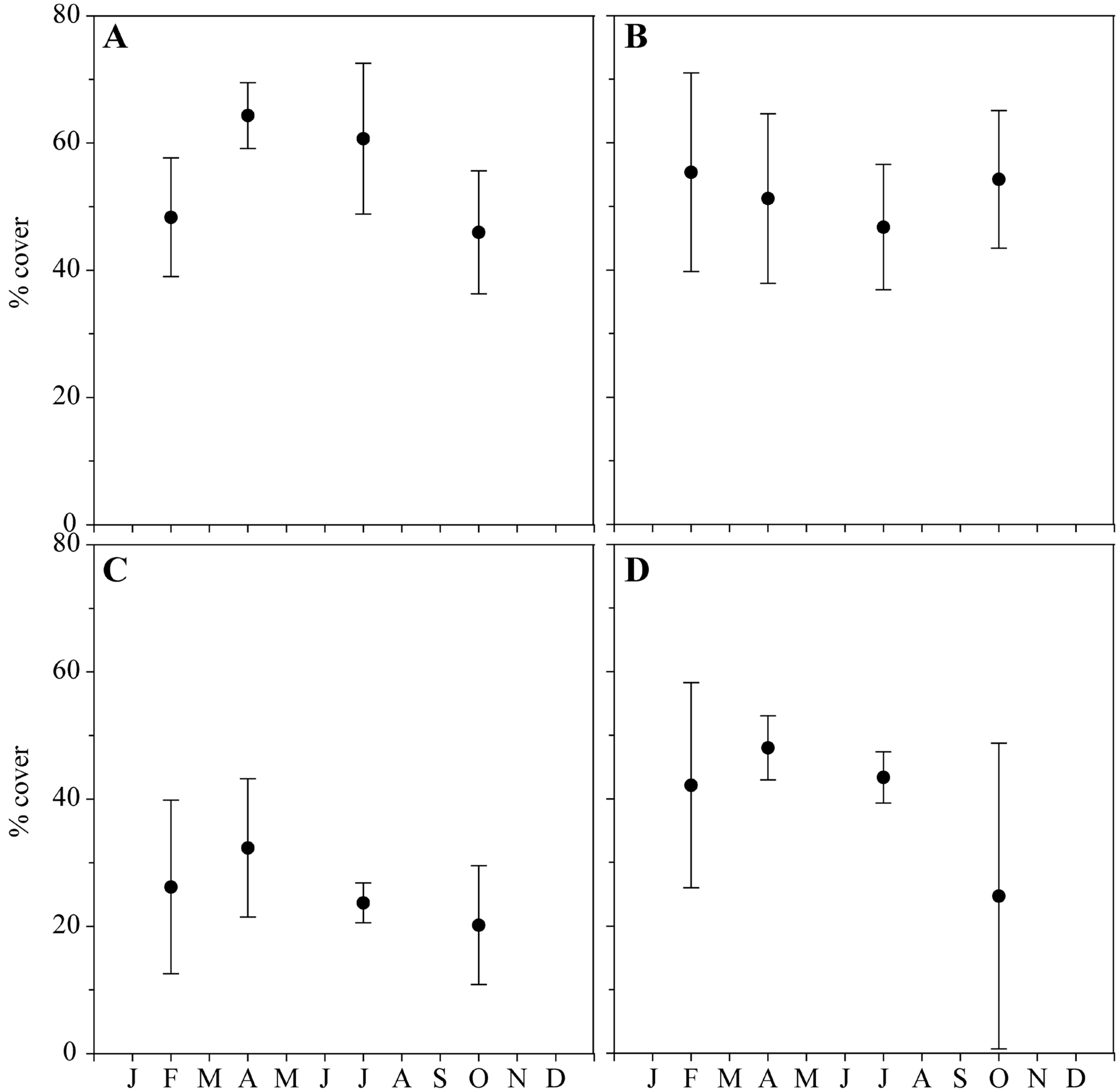

Fig. 5. Average total percentage cover of seagrass each season for years 2008–2009 pooled (±95% confidence intervals displayed) for each representative seagrass habitats (sites pooled). A, Chek Jawa (estuary); B, Cyrene Reef (patch reef); C, Pulau Semakau (sandy fringing reef); D, Sentosa (rocky fringing reef).

throughout the year, with peaks in January to February and May to early June (Table 4). The number of observations of sexual structures in *Halophila* species was fewer than *Enhalus* or *Thalassia*, possibly a consequence of the size and inconspicuous appearance of *Halophila* flowers/fruits, and should be interpreted with caution. Also, overall observations of flowers and seed-set were opportunistic and ad hoc, advocating a more detailed study of sexual reproductive effort in *Halophila, Halodule and Syringodium* species in future. Nevertheless, from the available data, January to late March appeared the peak flowering and seed-set period for Singapore's seagrass, with a possible second, albeit smaller, period in November.

Relationships between seagrass abundance and environment. Over the long-term monitoring period (2006–2014), rainfall seasonality was pronounced; increasing in October, peaking during the early part of the northeast monsoon (November and December) and drier conditions during the southwest monsoon (June and July) (Fig. 6A). Rainfall during the northeast monsoon (784.0 ±115.3mm) was significantly higher (ANOVA F= 5.27, $p<0.001$) than in the southwest monsoon or inter-monsoons.

Air temperatures ranged between 21 and 35.5°C and were variable among years. The months of the warmest air temperatures were during the first inter-monsoon (ANOVA F=16.4, $p<0.001$), reaching their maximum in May, while the

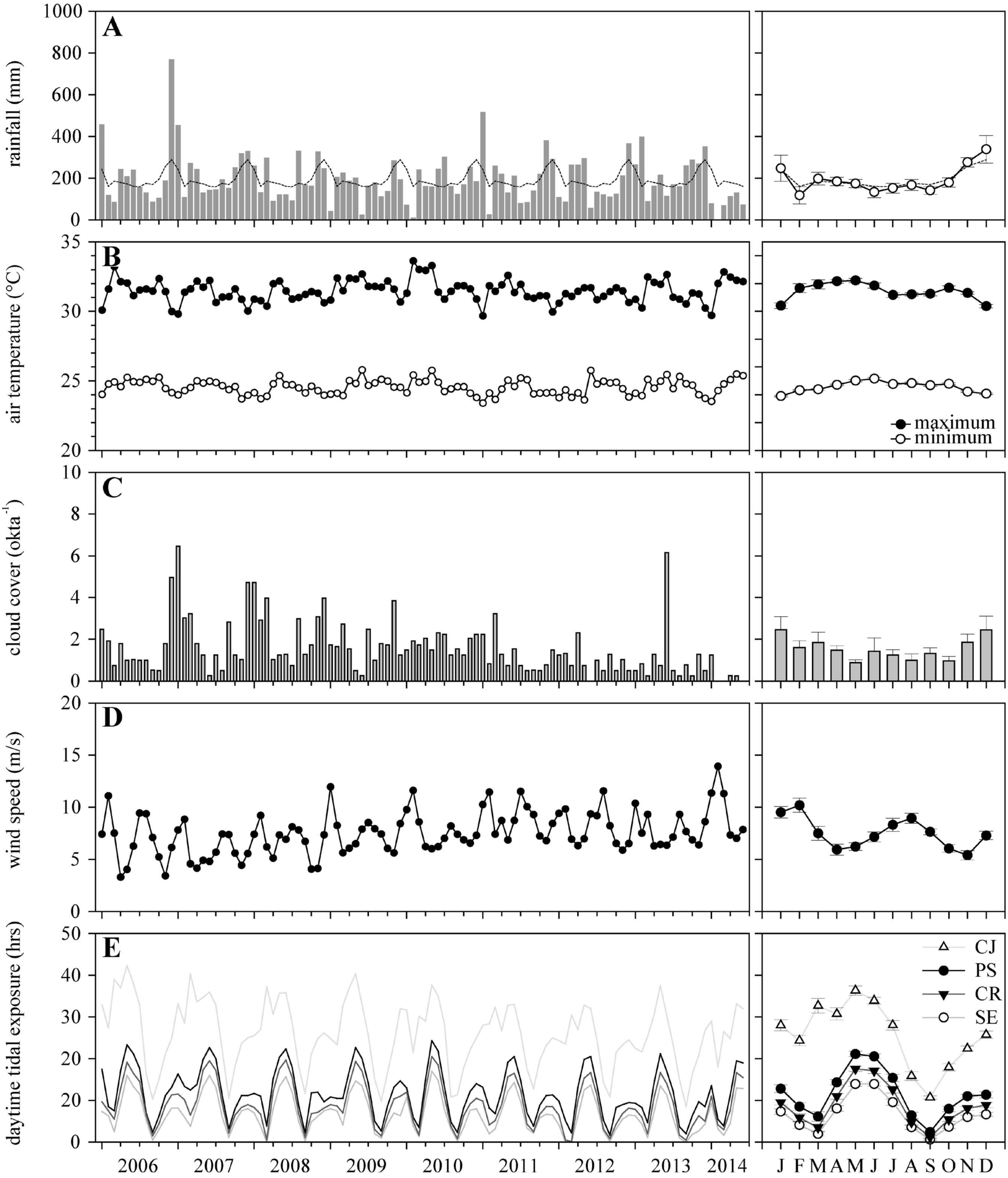

Fig. 6. Environmental parameters during each month 2006–2014 and average across all years at Changi, Singapore. A, total monthly rainfall; B, mean daily maximum air temperature; C, cloud cover; D, mean wind speed; E, total daytime hours that each monitored seagrass meadow was exposed during low tide (CJ = Chek Jawa, PS = Pulau Semakau, CR = Cyrene Reef, SE = Sentosa).

Table 5. Regression analysis (final models following stepwise removal analysis) of seagrass abundance (% cover) relative to available climate and environmental data (average of 30 days prior to abundance measure) at each location in Singapore (2007-2014). Seagrass abundance represented as total (all species pooled), opportunistic (*Halodule uninervis* + *Syringodium isoetifolium*), persistent (*Cymodocea rotundata* + *Cymodocea serrulata* + *Enhalus acoroides* + *Thalassia hemprichii*) and colonising (*Halophila ovalis* + *Halophila spinulosa*). Climate and environmental data: total rainfall (mm); min temperature = average daily minimum air temperature (°C); tidal exposure = total daytime hours seagrass meadow exposed during low tide (hrs); cloud cover = average daily total cover of low level cloud ($okta^{-1}$); wind speed = mean daily wind speed ($m\ s^{-1}$). ANOVA statistics (significance level of 0.05) and R^2 value for each regression model shown, including individual regression coefficients of the specific abundance predictors (environmental variables). n.s. = not significant, $p \geq 0.05$.

Location	Abundance (% Cover)	ANOVA			Model R^2	Predictor Regression Coefficient				
		p	F	DoF		Total Rainfall	Min. Temperature	Tidal Exposure	Cloud Cover	Wind Speed
Chek Jawa	total	0.019	4.3	2,49	15.5	–1.87	–10.4			
	opportunistic	n.s.								
	persistent	n.s.								
	colonising	0.014	4.67	2,47	16.6		–6.23	0.642		
Cyrene Reef	total	n.s.								
	opportunistic	n.s.								
	persistent	<0.001	30.49	1,42	42.1				762.9	
	colonising	n.s.								
Pulau Semakau	total	<0.001	5.86	4,70	25.1	–1.54	–6.5		373.3	–2.7
	opportunistic	0.01	6.88	1,73	8.6					–0.248
	persistent	<0.001	5.56	5,69	28.7	–1.41	–7.047	0.406	315.2	–2.1
	colonising	n.s.								
Sentosa	total	0.03	5.4	3,7	69.8		–10.72	1.516		–5.2
	opportunistic	n.s.								
	persistent	0.04	4.55	2,8	53		–12.75		–282.1	
	colonising	0.035	6.16	1,9	40.7					–3.3

Table 6. Overview of phenological data (flowering, fruiting, and seed set) for four seagrass species across Singapore, between 2007 and 2014. No observations of flowers or seed set were made for species of *Cymodocea*, *Halodule*, or *Syringodium*.

	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
Enhalus acoroides	peak flower and seed set	peak flower and seed set	flowers and seed set observed	flowers observed	peak flower and seed set	peak flower and seed set	flowers observed	flowers observed	flowers observed	flowers observed	flowers and seed set observed	flowers observed
Halophila decipiens								peak flower and seed set				
Halophila ovalis				flowers observed							peak flower and seed set	
Thalassia hemprichii		flowers and seed set observed	peak flower and seed set	flowers observed						flowers observed		

flowers observed (female and/or male) | flowers and seed set observed | peak flower and seed set

coolest months were during the wet phase of the northeast monsoon (December and January) (Fig. 6B). The annual pattern in temperature shows dual peaks, coinciding with each of the inter-monsoon periods. Although highly variable, low level cloud cover was generally higher during the northeast monsoon season (not significantly, ANOVA F= 2.44, p=0.08) (Fig. 6C). Surface wind speeds in and around Singapore were generally low, with the exception of the northeast and northwest monsoon periods when long-term (145 yr) average wind speeds between 2–3 $m\ s^{-1}$ occur (Fig. 6D). Surface winds are generally light and variable in April and May. Significantly higher wind speeds occur during the northeast monsoon, peaking in February (ANOVA F=13.1, p<0.001).

Seagrasses at all monitoring locations were at or near exposure during daylight hours for at least 59.5 hours each month of the year. Although hereafter referred to as exposure, in reality, most seagrass at the monitoring locations persisted within shallow pools or depressions which retained some water even during the lowest of spring tides (Personal Observation). Daytime exposure followed a strong 'seasonal type' pattern, with an annual peak reached regularly in May–June and minima in September (Fig. 6E). The annual mean total daytime tidal exposure varied from 79.5 hrs to 306.6 hrs from the deepest to shallowest locations across all years.

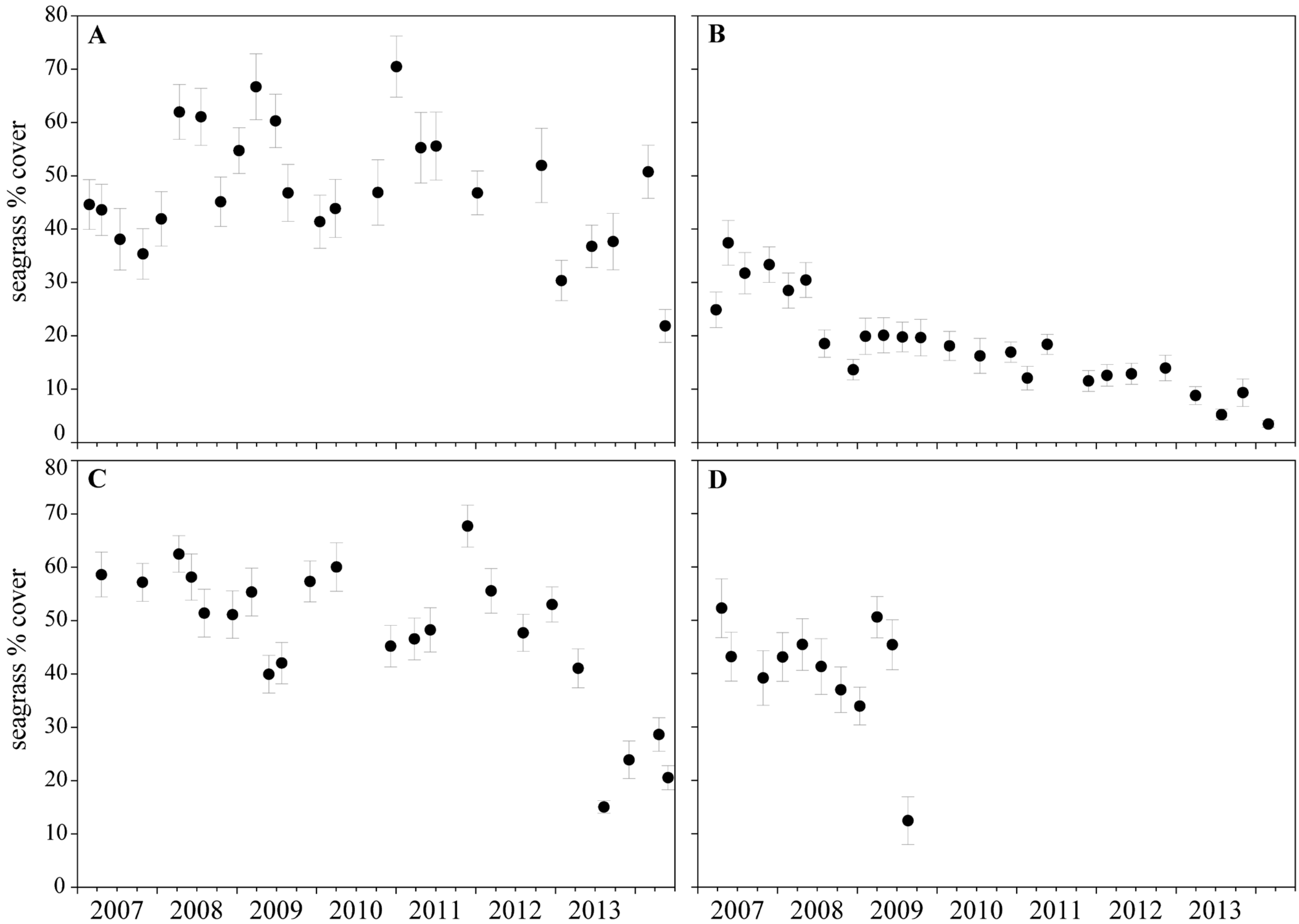

Fig. 7. Average total percentage cover of seagrass (±standard error) for each long-term monitoring location (sites pooled) in Singapore, 2007–2014. A, Chek Jawa (estuary); B, Pulau Semakau (sandy fringing reef); C, Cyrene Reef (patch reef); D, Sentosa (rocky fringing reef).

During the seven-year period of observations, seagrass cover varied greatly between years and locations (Fig. 7). The stepwise regression analysis revealed some significant relationships between variations in environmental variables and seagrass abundance (Table 5). At the estuary habitat (Chek Jawa), it appears that 15.5% of the variance in total seagrass percentage cover (all species pooled) may be explained (negatively) by total rainfall and minimum temperature. As the habitat was dominated by colonising species, a similar relationship (16.6%) was significant for the abundance of the colonising species with minimum temperature and tidal exposure. It appears that seagrass abundance is negatively influenced by rainfall and minimum temperature, but positively influenced by daytime tidal exposure.

Seagrass cover at the patch reef habitat (Cyrene Reef) appeared to have only been influenced (positively) by low level cloud cover, which also explained approximately 40% of the variance in the cover of persistent seagrass species. At the sandy fringing reef habitat (Pulau Semakau), the cover of the total seagrass and the persistent species were influenced by low level cloud cover and to a lesser extent by minimum air temperature, wind speed, total rainfall, and daytime tidal exposure. At the rocky fringing reef, however, total seagrass cover was mainly influenced (negatively) by minimum air temperature and wind speed, but a positive influence by daytime tidal exposure. Low levels of cloud cover had a strong negative influence of the cover of the persistent seagrass species at rocky fringing reef habitats (Sentosa).

The weak correlations of seagrass abundances with environmental factors indicate that the growth function in tropical seagrass meadows is possibly complex. In Singapore's seagrass habitats, seagrass abundance appears to be primarily driven by environmental factors that influence light availability and sea water temperature. Available light is possibly an interactive balance between incoming solar radiation (e.g., cloud cover), water depth (daytime tidal exposure), and water quality (e.g., resuspension (wind speed) and flood plumes (rainfall)).

DISCUSSION

Singapore's enduring seagrass meadows are diverse, comprised of 10 seagrass species with an additional two species under review for synonymy. The taxonomic authenticity of *Halodule pinifolia* and *Halophila minor* remain under review. Waycott et al. (2004) suggested that *Halodule pinifolia* and *Halodule uninervis* were conspecific, recognising that the plasticity of the leaf blade size can be attributed to local conditions. However, recent rbcL gene sequencing has suggested that the species may be separate

(Wagey & Calumpong, 2013). Similarly, *Halophila minor*, originally reported as *Halophila ovata* (Kuo, 2000), is considered synonymous with *Halophila ovalis* (Waycott et al., 2004), as it is difficult to distinguish the species visually in the field and phylogenetic studies indicate either no or some potential divergence (Waycott et al., 2002; Uchimura et al., 2008; Xu et al., 2010).

While Singapore's seagrass biodiversity is comparable to that of the bordering countries of Indonesia and Malaysia, Singapore lacks *Thalassodendron ciliatum*. *Thalassodendron ciliatum* has a wide but disjunct distribution throughout the Indo-Pacific region, and has been reported from Bintan Island (Indonesia), located 80 km south east of Singapore (Kuriandewa & Supriyadi, 2006). The absence of *Thalassodendron ciliatum* in Singapore may be a consequence of few comprehensive resource inventories of the most southern reefs or lack of recruitment of viable propagules. *Thalassodendron ciliatum* produces floating, viviparous seedlings which can disperse large distances (Kendrick et al., 2012), although the strong east west flow velocities (up to 3 m s^{-1}, Chen et al., 2005) in the Singapore Strait possibly presents a northward dispersal barrier to recruits.

A key feature of seagrasses in Singapore is their restriction to intertidal and shallow subtidal waters, which indicates limited light availability. Chronic levels of sedimentation since the 1970s has reduced underwater visibility from 10 m recorded in the early 1960s to a contemporary average of 2 m (Erftemeijer et al., 2012). With <0.6% surface Photosynthetically Active Radiation (PAR) reaching 8.9 m in the southern islands (Todd et al., 2004), the high light requirement of seagrass restricts them to much shallower waters in Singapore (Ralph et al., 2007). Therefore, it is during the periods around and during tidal exposure that may provide critical windows of sufficient light for positive net photosynthesis (Brouns, 1985; Pollard & Greenway, 1993). However, during periods of low tide, intertidal seagrasses can be physiologically damaged by elevated temperatures (Campbell et al., 2006), desiccation, and extreme irradiance (Unsworth et al., 2012b).

Another key feature of Singapore's seagrass meadows is the difference in the size of the sediment grains, which provides an indication of the major forces shaping the habitats. For example, habitats with a higher proportion of coarser sediments (sand and gravel) suggest high-energy environments (waves and fast moving currents) while sediments are usually finer in low-energy environments (Fonseca, 1996). The origin of the sediment type also determines the habitat type, with calcareous sediments of biological origin dominating reef habitats and siliceous sediments derived from the erosion of terrigenous rocks and soil dominating the estuarine and rocky reef habitats. The physical and chemical nature of the sediments, in turn, influences the seagrass species. For example, in mud-dominated estuarine sediments, seagrasses must tolerate higher organic content and sulfides (Erftemeijer & Middelburg, 1993). Alternatively, carbonate sediments on reefs can be limiting to seagrass growth as phosphorous tends to bind to the carbonate particles (Fourqurean et al., 1992), and seagrasses growing on carbonate sediments can also be very prone to sulfide toxicity (Hemminga, 1998).

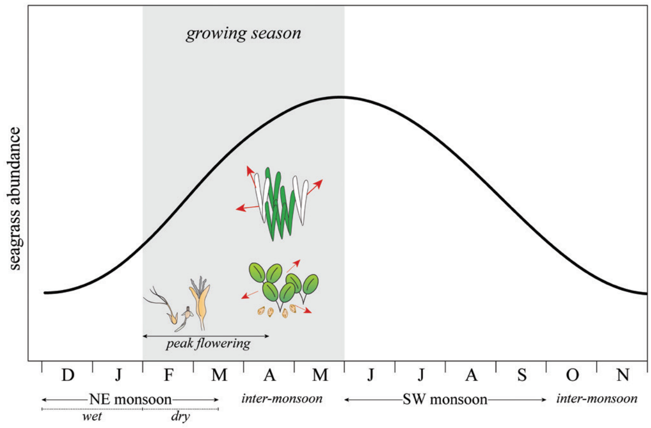

Fig. 8. Proposed annual seasonal pattern of seagrass abundance in Singapore. Climatic season, annual seagrass growth and peak flowering phases displayed.

Seagrasses in Singapore vary not only spatial, but temporally; both within and between years. Seasonal variation in the above-ground abundance of tropical seagrasses has been reported as being unimodal (Brouns & Heijs, 1986; Erftemeijer & Herman, 1994; McKenzie, 1994; Mellors et al., 2008), bimodal (Estacion & Fortes, 1988; Mellors et al., 1993; Rollón, 1998) or absent/non-significant (Johnstone, 1979; Brouns, 1985; Brouns, 1987; Erftemeijer & Herman, 1994). This is often dependent on seagrass species and may be related to the size and capacity of plants to store and allocate resources among ramets. Smaller seagrass species with their lower capacity for storage tend to vary more seasonally, whereas large seagrass species with their larger internal resources stored in the belowground parts tend to grow more independently of environmental conditions (Marba et al., 1996). This may explain why the seasonal pattern in the abundance of Singapore's estuary habitat meadows, dominated by small-sized colonising species, was significant, whereas, the seasonal variation in habitats dominated by the larger persistent species was either not significant or absent.

The lack of a clear seasonal pattern in some seagrass habitats is not unexpected, as abundance in tropical seagrass meadows is often highly variable and unpredictable because seasonal variations in water temperature and light availability are relatively small compared to other environmental drivers, such as rainfall (Erftemeijer & Herman, 1994; McKenzie, 1994; Uku & Bjork, 2005). As photosynthetic rates increase with temperature, it would be expected that the warmer equatorial waters would result in higher rates of seagrass growth (Perez & Romero, 1992; Collier et al., 2011), however, at higher temperatures, photorespiration, photosynthetic impairment and respiration rates also increase, leading to declines in net productivity (Campbell et al 2006; Collier et al., 2011). Higher light levels are required to meet metabolic demands when temperatures are higher (Perez & Romero, 1992; Collier et al., 2011), however, low light will trigger seagrass decline at higher (e.g., equatorial) temperatures (Bulthuis, 1983; Alcoverro et al., 2001).

A key driver of light availability for seagrass growth in tropical regions is the seasonal discharge of turbid waters from rivers draining adjacent catchments; a consequence of the seasonal rainfall. Several rivers drain into the nearshore waters surrounding Singapore, the largest of these is the Johor River, flowing into the Johor Estuary. The Johor River would be expected to have the greater influence on coastal ecosystems in the region, with a long-term average daily discharge of 70 $m^3 s^{-1}$ in December and approximately 30 $m^3 s^{-1}$ from February to October (van Maren et al., 2014). Most of the influence, however, is localised to the Johor estuary, as approximately half of the suspended load entering the estuary from the Johor River deposits in the estuary itself (van Maren et al., 2014). Although a large proportion of the fine sediments from the Johor River is flushed into the Singapore Strait, dilution by marine currents reduces the concentrations so that they have only marginal influence as they are transported westward to the southern islands (van Maren et al., 2014).

The availability of light for seagrass is not only influenced by the incoming solar radiation, and attenuation within the water column (phytoplankton, inorganic particles, water absorptic properties), it is also influenced at the leaf surface (e.g., epiphytes) (Dennison et al., 1993). In the nutrient rich waters of Singapore, epiphyte cover on the surface of seagrass leaves is high (20–40% on average) and extremely variable (McKenzie & Yoshida, 2013). As epiphytes respond faster to reduced light than seagrass due to the absence of storage organs, reduced incoming solar radiation (from increased cloud) may initially impact epiphytes, providing some respite from the low light conditions for the seagrass. To help elucidate the relationship between seagrass, temperature and light availability, will require additional in situ monitoring including seagrass epiphytes and the deployment of PAR and temperature loggers at and within the seagrass canopy. The interactive effect of light and temperature also plays an important role in seagrass sexual reproduction. Seagrass inflorescences and fruit dehiscence appears primarily influenced by the rate at which water temperature rises following a senescent period, with increasing photoperiod playing a limited role (Durako & Moffier, 1985). The timing of flowering, fruiting and seed set of seagrasses in Singapore were similar to those of comparable locations such as in southern Sulawesi, Indonesia (Verheij & Erftemeijer, 1993).

Biological interactions, such as grazing, can also influence seagrass habitats. For example, macrograzers cause meadows to fragment by removing considerable amounts of plant material (Fourqurean et al., 2010; Marsh et al., 2011), or stimulate growth and productivity by grazing/cropping (Preen, 1995; Christianen et al., 2012). Very little information exists on seagrass grazing by fish or sea turtles in Singapore. However, evidence of grazing (excavating) by the globally vulnerable dugong (*Dugong dugon*), is often observed in estuary meadows (e.g., Chek Jawa and Changi), sandy fringing reef meadows (e.g., Pulau Semakau) and meadows on patch reefs (e.g., Cyrene Reef and Terumbu Pempang Laut) habitats (Tan et al., 2012; pers. obs.). Coastal surveys indicate dugongs are rare in Singapore's waters (Marsh et al., 2002), although the prevalence of excavating trails in our recent assessments suggests a small resident population.

A conceptual framework. Classifying the attributes of the species present, meadow structure, and their possible drivers, provides the framework to inform effective monitoring, research, and management of seagrass ecosystems in Singapore. These primary attributes are also critical in providing an understanding of the resilience of Singapore's seagrasses. Ecological resilience includes resistance to disturbance (resistance) and capacity to recover (recovery) and determines the capacity of a system to maintain function in the face of disturbance (Folke et al., 2004; Bernhardt & Leslie, 2013; Unsworth et al., 2015). These characteristics are important for Singapore's seagrass meadows which are faced with multiple cumulative stressors (Yaakub et al., 2014), and it is therefore helpful to consider monitoring in the context of resistance and recovery attributes. Critical information is needed on the characteristics that facilitate resistance, such as abundance, species composition, genetic diversity, and storage reserves. As recovery is facilitated by reproductive output, seed banks, and species composition, critical information is also needed on these elements.

Knowledge of natural temporal patterns in seagrass ecosystems, and their possible drivers, is a prerequisite to inform monitoring and management activities. We propose that the natural growth cycle for seagrass in Singapore is a unimodal seasonal pattern; the likely result of an interactive combination of climatic factors (total irradiance, photoperiod, temperature) (Fig. 7). During the wet phase of the northeast monsoon (December–January), seagrass abundance in Singapore appears to be at or near its annual minima, a consequence of the less conducive conditions for seagrass growth. It is during this period that rainfall, cloud, and winds would be at or near their annual peaks, which would result in lower available light for photosynthesis and greater osmotic stress. In the latter part of the northeast monsoon, seagrass abundance begins to increase with the improved light availability (decreasing rainfall and associated cloud), and the rapidly increasing temperatures. These conditions are also optimal for seagrass sexual reproduction, and flowering peaks. With the onset of the inter-monsoon, seagrass abundance continues to increase at a relatively rapid rate, assisted by increasing temperatures and PAR (shallower water during daylight, less wind, and less rain). This is the main growing phase and seagrass reaches its annual maxima near the end of the season (April–June). At the onset of the southwest monsoon (June), climbing temperatures, extreme daytime exposure, and increasing winds possibly create a less favorable environment for growth (temperature stress, desiccation, and increased turbidity) and seagrass abundance begins a slow decline. This senescent phase continues into the second inter-monsoon where PAR is reduced by higher daytime tides. With the onset of the northeast monsoon, seagrass growth reaches its annual minima when temperatures and PAR are low (more cloud, increasing rainfall, increasing wind). Terrestrial runoff further exacerbates the seagrass decline, due to low salinities and high turbidities at a time when PAR would be at its lowest. The seagrass abundance remains at a minimum until late January when growth increases, possibly assisted by the elevated nutrients from coastal runoff. This natural seasonal pattern appears to occur across most seagrass habitats in Singapore, however, on occasions, it may be less apparent due to large within-year variability.

The final critical attribute is classifying Singapore's seagrasses into separate habitats, based on the suite of environmental conditions that control the conditions to which the seagrasses are exposed. We define five broad seagrass habitat types and their key features in Singapore.

Estuarine: Estuary habitats occur primarily along the northern shores of Singapore. Seagrasses grow along the high intertidal mangrove fringe of the Johor Strait or in shallow lagoons of northern islands (e.g., Pulau Ubin) adjacent to the mouth of the Johor River. Sediments are predominately mud with a high organic content. Seagrass species diversity is high, but colonising species of *Halophila* dominate these habitats, suggesting that these are highly dynamic environments with variable river flow and ocean openings resulting in fluctuations in salinity, temperature, light, and nutrients, and often high sediment deposition. Estuarine habitats are also highly threatened, as the sheltered shores are prone to the pressures of coastal development and calm waters provide safe anchorages for vessels and aquaculture cages. Singapore's estuarine shores also provide habitat for *Halophila beccarii*, one of the world's most threatened seagrass species, and provide important food for the dugong, as evidenced by the extent and frequency of excavating trails observed.

Rocky fringing reef: Rocky fringing reefs are the rarest seagrass habitats and occur along the southwestern shores of mainland Singapore where wave action can be moderate to high (e.g., the western end of Sentosa Island and the shore of Labrador Nature Reserve) (Table 4, Fig. 1). Intertidal seagrass meadows in these habitats are patchily distributed as a consequence of available substrate. The seaward edge / crest of rocks or coral reef (e.g., Labrador Nature Reserve) regulates disturbances from waves and affords shelter to the shoreward boulder fields or platforms where unconsolidated sediments accumulate. These sheltered microhabitats of sediments, where water pools during low tide, provide the foundation for seagrass to grow. On these shores, seagrass grow in sediments dominated by coarse grains (e.g., sand and gravel). To survive, seagrass in these environments must tolerate wave action and the associated movement of sediments, as well as exposure to air, availability of nutrients, and the ability to grow in coarse-grained sands and gravels of shallow depth (Terrados et al., 1998; Coles et al., 2005; Waycott et al., 2007). Pooling of water at low tide affords some protection from desiccation of the plants during low spring tides. Coarser-grained sediments (a mixture of terrigenous and biogenic) by their nature are nutrient-poor and in these locations are often unstable and their depth can be very shallow, restricting seagrass growth and distribution. Only a few species of seagrass can tolerate such environments, including *Thalassia hemprichii* and *Halophila ovalis*. Rocky fringing reefs are among the rarest of Singapore's seagrass habitats, with only small remnants remaining. For example, the Labrador Nature Reserve (protected by the Parks and Trees Act 2005) contains the only remaining natural rocky shore and stretch of fringing reef along the west and southwest coast of mainland Singapore.

Sandy fringing reef: Sandy fringing reefs dominate the seagrass habitats of Singapore and are scattered throughout the southern islands (Table 4 and Fig. 1). They occur around islands where wave action is slight to moderate, providing intertidal areas with stable sediments that support diverse and dense seagrass meadows. There can be considerable differences in seagrasses inhabiting fringing reefs due to variation in exposure to air, availability of nutrients, wave action and the associated movement of sediments (Terrados et al., 1998; Coles et al., 2005; Waycott et al., 2007). Pooling of water at low tide at the landward side of fringing reefs allows the seagrasses there to attain greater leaf heights (e.g., *Enhalus acoroides*), and prevents desiccation of the plants. In contrast, intertidal areas expose seagrasses to damage, particularly when low tides occur during daytime in summer. Variation in environmental conditions across fringing reefs often results in a progression of seagrass communities from colonising to persistent, with a mixture of opportunistic species. Calm clear waters and a range of stable sandy substrates in lagoons behind reefs enable a diverse range of seagrass species to establish dense meadows in both subtidal and intertidal areas. *Halodule uninervis* often grows well in such locations. In some places, it is patchy and intermixed with other seagrass species (e.g., *Halophila* spp.). Another dominant species of seagrass in these locations is *Syringodium isoetifolium*, which often occurs in shallow lagoons and is usually the first species to re-establish after a disturbance (den Hartog, 1977).

Patch reef: Patch reefs are submerged reefs encircled by a coral or rock crest with a central sandy area and they are quite common in the southern islands of Singapore. *Thalassia hemprichii* is common on patch reefs because it is able to tolerate shallow sediments, high temperatures, and moderate currents. In some very rare situations, *Halodule univervis* can form scattered patches mixed with *Halophila ovalis*. Conversely, *Cymodocea* spp., *Halodule univervis*, and *Thalassia hemprichii* form dense beds on lagoonal patch reefs. These environments have suitable conditions for the growth of seagrasses because there is generally limited disturbance from wave action, protection from currents by the reef crest, and coarse carbonate sediments. Seagrasses in these habitats showed high variability, and no seasonal pattern in annual abundance was apparent. The weak correlations with abiotic factors further indicated that either the growth function is more complex or there may be some other external factor (e.g., anthropogenic) which may be masking a natural pattern.

Coastal: The most poorly represented seagrass habitat in Singapore are coastal sandy shores. These coastal habitats are the result of modified shorelines (i.e., constructed wetlands) where foreign-sourced sand lagoons are constructed behind the shelter of rock groynes and breakwaters for recreational activities (e.g., swimming lagoon at Pulau Seringat, now part of the extended Lazarus Island (Pulau Sakijang Pelepah; Raju et al., 2012)) and industrial developments (e.g., Tanah Merah Ferry Terminal). Although these constructed habitats are only recent (since the 1970s), they have been successfully colonised by at least half of Singapore's seagrass species. Seagrass only persists in locations which are sheltered from wave action as sediments are predominately mobile sands. Seagrasses in these environments are dominated by colonising and opportunistic species (e.g., *Halophila ovalis* and *Halodule uninervis* at East Coast Park), however, if shelter is greater, then persistent species are able to dominate (e.g., *Cymodocea rotundata, Enhalus acoroides*, and *Thalassia hemprichii* in the constructed lagoon, adjacent to the Tanah Merah Ferry Terminal). Currently there are no long-term monitoring sites established in coastal habitats and this should be a priority focus in the future.

Conclusions. Singapore is a unique mesocosm with a variety of seagrass species and habitats within a relatively small area in close proximity to significant anthropogenic threats (Yaakub et al., 2014). For seagrasses to persist in such an environment, they will need to be resilient, and effective management will require informed research and monitoring activities.

We have provided a framework to assist ongoing monitoring and management decision-making. The classification and models developed provide an understanding of the differences in habitats. This will help to better focus seagrass management and research in Singapore. The current long-term seagrass monitoring program is providing critical information and its continuation should be a high priority. The lack of seagrass monitoring in coastal habitats is a gap in the current program and should be a priority for future research activities. An improvement of our understanding of seagrass resilience will require research examining genetic connectivity between seagrass populations (movement of propagules and vegetative fragments) and the examination of sexual reproductive effort and seed banks. Long-term reproductive studies are needed to understand the capacity of these meadows to recover from disturbance events.

Effective management of nearshore resources will necessitate consideration of conservation needs within the constraints of a rapidly developing economy. We acknowledge that not all nearshore areas can be protected, but recognise that remnant and key or critical habitats (including maintaining connectivity) should be protected using either traditional instruments or novel approaches.

Traditional instruments may be necessary for some high value or rare habitats (e.g., rocky fringing reef), being guided by the operational principles of comprehensiveness, adequacy, and representativeness (Fernandes et al., 2009). Singapore has already moved toward this approach with the declaration of the Sisters' Islands Marine Park in July 2014. Under the management of NParks, Singapore's statutory board for the management of nature parks (under the Parks and Trees Act 2006, statutes.agc.gov.sg), the park covers approximately 40 hectares and includes Big Sister Island (Subar Laut), Little Sister Island (Subar Darat) and the western shores of Pulau Tekukor and St. John's Island (Pulau Sakijang Bendera). The area was previously zoned as a marine nature area within the Parks and Waterbodies Plan of the Urban Redevelopment Authority (URA), and protects a variety of habitats (including coral reefs, sandy shores, and seagrass meadows) for outreach, educational, conservation, and research activities related to marine biodiversity.

Where traditional instruments (such as Marine Projected Areas) may not always be possible, more novel approaches may need to be considered where losses can be to some extent offset by mechanisms such as constructed wetlands or biodiversity arks. Although an unintended side effect of reclamation, current indications are that these may be successful in some instances, e.g., Tanah Merah. Such enhancement activities will build resilience in seagrass ecosystems.

As Singapore celebrates its 50th year as a nation, its management of natural marine resources is at a crossroad. In the new millennium, there is an increased awareness and recognition of the importance of biodiversity and the environment to human wellbeing as a coupled social–ecological system (Cullen-Unsworth et al., 2014). Minimising or mitigating stressors through effective management is critical. To underpin effective management, however, will require developing a clear Government policy which sets out clear goals and strategies to manage ecosystem impacts and build resilient nearshore communities and ecosystems to enable them to adapt to a variable and changing climate.

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