



Seagrass seed bank spatial structure and function following a large-scale decline

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ABSTRACT: We examined the spatial structure (distribution, density) and function (viability) of the seagrass sediment seed bank, the storage of viable propagules (e.g. seeds, tubers, diaspores) in the sediment over time, in the northern Great Barrier Reef World Heritage Area in Cairns, Queensland, following a large-scale decline in seagrass area. A spatially explicit seagrass seed bank analysis was paired with a long-term annual assessment of seagrass distribution to assess seed bank spatial patterns and their relationship with the recovery and presence of seagrass, and water depth. Four years post-decline, the seed bank contained *Zostera muelleri*, *Halodule uninervis*, *Halophila ovalis* and *Cymodocea serrulata* seeds. Seed banks reflected adjacent meadow community composition; however, the density of seeds for all recorded species was significantly lower than analogous seagrass populations, indicating a reduction in the capacity for recovery from the seed bank. A spatial structure existed in both the total (viable + non-viable) and viable seed bank, and distance between seed clusters ranged from 50–550 m depending on species and seed type. Observed patterns in clustering may be explained by variation in water depth and the past distribution of seagrass in these meadows. These results demonstrate that the distribution of seagrass seeds within the seed bank, which directly influences the natural recovery of seagrass communities, is not uniform across species and may result in patchy recovery of the meadows. Therefore, the resilience provided by the seed bank in seagrass communities should not be viewed as a static level of insurance for the entire meadow, but rather as dynamic and species-specific, with variability over both space and time.

KEY WORDS: Viability · *Zostera muelleri* · *Halodule uninervis* · Resilience

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1. INTRODUCTION

Understanding biological and ecological drivers that interact to influence the natural resilience to and recovery from disturbances of plant communities is an emerging issue in ecology (Levin & Lubchenco 2008, Coles et al. 2015, Unsworth et al. 2015, Connolly et al. 2018). Functional seed banks, defined as the storage of viable propagules (e.g. seeds, tubers, diaspores) over time, are crucial for the re-establishment of both terrestrial and aquatic plant communities, increasing resilience to disturbance (Venable & Brown 1988, Fenner & Thompson 2005). In the marine environment, global loss of near-shore marine communities

including coral reefs (Pandolfi 2003, Pratchett et al. 2014), mangroves (Duke et al. 2007) and seagrass meadows (Orth et al. 2006, Waycott et al. 2009) over the last 50 yr has resulted in an accelerated loss of coastal ecosystem services (Costanza et al. 2014). Since 1990, seagrass populations were estimated to be declining at a global median rate of loss of 7% of the total global seagrass population per year (Waycott et al. 2009). However, within regions there is significant variation in meadow persistence, ranging from large-scale loss over short time periods (<1 mo) in response to acute disturbances to expansion in meadow area over long time scales (Emmerson & Yearsley 2004, Walker et al. 2006). One possible

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driver for differences in meadow persistence may be variations in the presence, persistence and structure of a sediment seed bank (Thompson 2000).

Seagrasses are the only submerged marine macrophytes capable of producing a persistent sediment seed bank (McMillan 1991, Zipperle et al. 2009). Seed banks provide resilience via the storage of propagules that can germinate and provide new individuals to help maintain a seagrass population or initiate recovery following large-scale declines (Jarvis & Moore 2010, Strazisar et al. 2016). Seed bank function is limited by seed supply, which is impacted by flowering, seed production, the density of viable seeds and the dispersal of seeds to suitable microhabitats conducive for germination and successful seedling establishment (Nathan & Muller-Landau 2000, Fenner & Thompson 2005). Seed viability, defined as an embryo that maintains the capability to germinate given the appropriate cues (Bewley et al. 2013), can be affected by biotic (i.e. seed source, pre/post-dispersal, predation) and abiotic factors (i.e. burial depth, oxygen, temperature, energy regime and sediment stability) in the surrounding environment (Darnell & Dunton 2015, Sherman et al. 2018).

For seagrasses, dispersal is a significant bottleneck limiting recruitment success (Kendrick et al. 2012, Grech et al. 2018). Seed dispersal mechanisms are species-specific (Kendrick et al. 2012), rely on both abiotic (e.g. currents, bulk sediment transport) and biotic (e.g. grazing by marine herbivores and birds) mechanisms (Les et al. 2003, Bell et al. 2008, Ruiz-Montoya et al. 2012, Tol et al. 2017) and can be restricted during the initial movement away from the source plant and after it is incorporated into the sediment seed bank (Chambers & MacMahon 1994). This can have significant impacts on large-scale seagrass meadow persistence through decreased genetic and species diversity (Hughes & Stachowicz 2004, Hughes & Stachowicz 2010, Massa et al. 2013) and a diminution in the supply of new propagules (e.g. seeds and vegetative fragments) between disparate populations (Harwell & Orth 2002, Ruiz-Montoya et al. 2015, Weatherall et al. 2016). Factors that impact the dispersal of seeds can either enhance or limit recruitment and seed germination, ultimately influencing the contribution of sexual reproduction to the resilience of existing populations.

Seed dispersal spatial patterns determine the potential rates of recruitment in plant populations (Nathan et al. 2008). Successful recruitment is further influenced by conditions seeds are exposed to once they are incorporated into the seed bank. For seagrass meadows, research on seed bank ecology has focused

on the role of abiotic conditions on seed germination (Orth et al. 2000), density and species composition of seed banks (Hootsmans et al. 1987, Strazisar et al. 2016), impacts of bioturbation (Johnson et al. 2018) and viability (Conacher et al. 1994a, Jarvis & Moore 2010, 2015). However, little is known about the spatial structure of seagrass seed banks. Variance of the spatial structure of seed distribution within the seed bank in other natural systems is known to influence abiotic and biotic processes and community structure across a range of scales, resulting in potential gradients and patchiness of resilience within vegetative communities (Wagner 2003). In order to link ecological drivers to changes in species resilience within plant communities, it is necessary to first understand the spatial structure of viable sediment seed banks within a system, and to define the critical spatial scales at which the structures are most functional (Nathan & Muller-Landau 2000, Wagner 2003).

Seagrass communities in northeast Australia are among the most diverse in the world (Short et al. 2007) and are influenced by high levels of disturbance from both long-term weather patterns (e.g. wet/dry seasons) and extreme climatic events such as cyclones and flooding (Carruthers et al. 2002, Rasheed et al. 2014, McKenna et al. 2015). Between 2009 and 2012, multiple major flooding events, including the landfall of category 5 Tropical Cyclone Yasi in February 2011, resulted in a large-scale loss of seagrass meadows in Cairns Harbour, Queensland (Pollard & Greenway 2013, McKenna et al. 2015). While asexual colonization through horizontal rhizome growth can be the primary mechanism for recovery of tropical seagrass meadows from disturbance (Rasheed 1999, 2004, Kenworthy et al. 2002), following declines across large spatial scales (>1000 m) the mechanism for recovery may be species-specific, resulting in sexual reproduction playing a larger role in the reestablishment of seagrasses with high reproductive output and dispersal capacity (Olesen et al. 2004, Kendrick et al. 2012). In the context of repeated disturbance events, the presence of a functioning seed bank has been identified as a significant factor in the recovery of tropical seagrass meadows (Rasheed et al. 2014). Despite this recognition, there has been little attention on how seed banks operate to confer an ability to recover from loss, particularly for complex, tropical, multi-species meadows.

To quantify both the structural (spatial distribution, density) and functional (viability) metrics of seagrass seed banks in a multi-species seagrass meadow, we paired a spatially explicit seagrass sediment seed bank survey with multi-year (2009–2012) monitoring

data of seagrass aerial extent and biomass. The study addressed 4 main questions concerning the potential for a multi-species seagrass seed bank to provide a mechanism for recovery following a large-scale decline: (1) What is the species composition, density and viability of the seagrass seed bank? (2) Does the viable seed bank have spatial structure? (3) What are the potential abiotic (e.g. water depth) and biotic (e.g. previous seagrass cover) drivers of the spatial distribution of seeds in the seed bank? (4) What is the capacity for recovery of seagrass populations from the sediment seed bank?

2. MATERIALS AND METHODS

2.1. Study area

The study sites were located in Cairns Harbour in tropical north Queensland, Australia. The broader area includes Cairns Harbour and its associated estuary, Trinity Inlet. From the harbour, the study area extended seaward for 10 km, and contained 2140 ha of previously described seagrass habitat (Lee Long et al. 1993) (Fig. 1). Mean annual water temperature at the site ranges from 20.6 ± 0.1 to $30.6 \pm 0.1^\circ\text{C}$, tidal range is up to 3 m and rainfall varies seasonally with the majority of the mean annual rainfall (1987.4 mm)

occurring between December and March (Rasheed et al. 2019).

For this study, seagrass communities were divided into 2 meadows. Seagrasses on the western side of the harbour were grouped together and are referred to as the Esplanade Meadow (736 ha) while seagrasses on the eastern side were grouped together and named the Bessie Point Meadow (1206 ha) (Fig. 1). *Zostera muelleri*, *Halodule uninervis* and *Halophila ovalis* were recorded in both meadows and *Cymodocea serrulata* has been previously documented in both meadows (see Table 1).

2.2. Documenting the decline: seagrass mapping

Both the Esplanade and Bessie Point seagrass meadows have been subject to annual monitoring from 2001–2012, incorporating assessments of seagrass biomass, area and species composition (Campbell et al. 2002, Rasheed et al. 2013). Monitoring was conducted between October and December each year during the peak period for seagrass biomass in this region. Seagrass meadow boundaries were defined and mapped according to their dominant species mix. For the *H. uninervis*-dominated Bessie Point meadow, this incorporated all seagrasses present on the eastern side of Cairns Harbour (Fig. 1). On the western side of

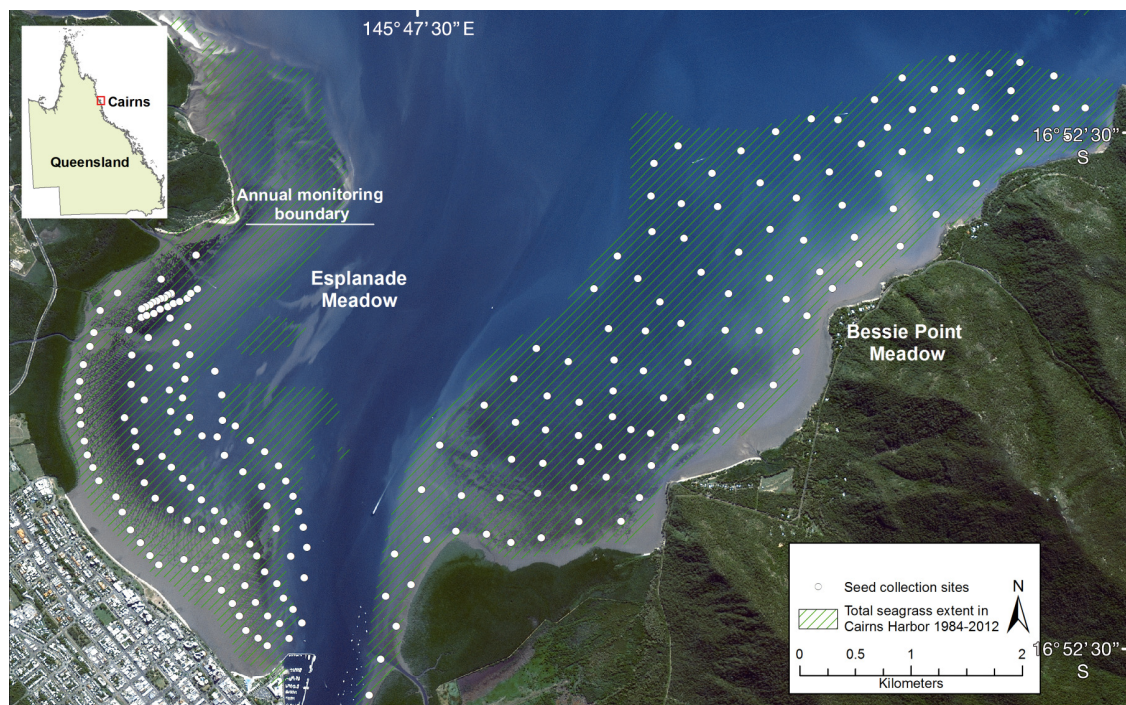


Fig. 1. Seagrass seed bank sampling locations based on seagrass extent in Cairns Harbour from 1984–2012

Cairns Harbour there is a large continuous meadow dominated by *Z. muelleri* that occurs on the intertidal bank (Esplanade meadow). The offshore edge of this meadow extends to the shallow sub-tidal slope of the bank, at which point conditions become unsuitable for *Z. muelleri*. The offshore edge of the Esplanade meadow is defined by the limit of *Z. muelleri* presence, and from time to time meadows of other seagrass species (e.g. *H. uninervis*, *H. ovalis*, *Halophila decipiens*, *Halophila spinulosa*, *C. serrulata*, *C. rotundata*) occur in adjacent deeper waters that were not part of this study (Rasheed et al. 2019). The boundary of the seagrass meadow was mapped from aerial surveys conducted at low tide when the intertidal sections of the seagrass meadows were exposed, or with free diving and underwater camera techniques for deeper sub-tidal areas (Rasheed et al. 2013). Waypoints were recorded around the edge of the meadow using a GPS and were digitized onto an ArcGIS 10.4® (ESRI) base map using a Geodetic Datum of Australia (GDA 94) projection. Each seagrass meadow was assigned a mapping reliability estimate based on the mapping methodology (underwater camera, free divers or aerial surveys) utilized for that meadow (McKenzie et al. 2001).

2.3. Seed bank structure: seed collection

Seed bank samples were collected in July 2013. In total, 120 samples were haphazardly collected in each meadow (240 total) at approximately 150–200 m intervals (Fig. 1). At each site, sediment samples were collected with a Van Veen sediment grab (area: 0.0625 m²), georeferenced and placed on ice until returned to the lab. All samples were stored at 8–10°C for no longer than 2 wk prior to processing. During processing, samples were wet-sieved (710 µm mesh) to remove all seagrass seeds (Scott et al. 1984, McFarland & Shafer 2011). Sieved samples were inspected for *H. uninervis*, *Z. muelleri*, *H. ovalis* and *C. serrulata* seeds using a dissecting microscope, and the number of seeds of each species was recorded. Seed density data were separated by species and reported as total number of seeds m⁻² (viable + non-viable).

2.4. Seed bank function: Seed viability

Once counted, all intact *H. uninervis* and *Z. muelleri* seeds were tested for viability using tetrazolium chloride (Lakon 1949, Conacher et al. 1994a). Seed embryos were removed from their seed coats

and soaked in a 0.5% tetrazolium chloride solution for 48 h before examination on a dissecting microscope at 10× magnification (Conacher et al. 1994a). Seeds with a pink to brown stained cotyledon and axial hypocotyl were considered viable. Viability data were separated by species and reported as the number of viable seeds m⁻² and as the percentage of viable seeds per sampling site. *H. ovalis* and *C. serrulata* were not analysed for viability due to insufficient numbers of seeds present to develop viability staining protocols.

2.5. Biotic drivers: presence/absence of seagrass and the sediment seed bank

The number of total and viable seeds by species was recorded for each georeferenced sampling site and entered into a GIS database. To quantify potential links between previous seagrass cover and current seed bank structure and function, aggregate layers of seagrass area from 1 (2012), 2 (2012–2011), 3 (2012–2010) or 4 yr prior to the survey (2012–2009) were mapped. Aggregate rather than individual maps of seagrass cover for each year were used as the year of production and deposition of individual seeds into the seed bank could not be determined. Seagrass cover from greater than 5 yr prior to the seed collection was not considered due to the expected loss of seagrass seed viability within 3 yr of entering the sediment seed bank (Zipperle et al. 2009, Dooley et al. 2013). The presence/absence of seagrass cover at all seed sampling sites by aggregate year was then calculated using the identity function in ArcGIS v.10.2 (ESRI 2012).

2.6. Abiotic drivers: water depth

Water depth was recorded for each georeferenced sampling site from the vessel depth sounder. Depth was converted to depth below mean sea level using validated real-time tidal data from Maritime Safety Queensland and formed part of the GIS database. A georeferenced depth contour shapefile was imported into the GIS database, and each georeferenced sampling site was overlaid. Depth files were derived from Australian Admiralty charts provided by the Australian Hydrographic Office.

2.7. Statistical analysis

All statistical analyses were conducted in the software environment R v.3.1.2 (R Core Team 2018). The

effect of seagrass meadow presence/absence on the seed bank was analysed separately by meadow. Relationships between meadow area, water depth and total and viable seed bank density were also analysed separately.

2.7.1. Seed bank spatial structure

The spatial structure of the total and viable seagrass seed bank in Cairns Harbour was determined with Moran's I test (Cressie 1993). To account for the non-normal distribution of the data, a permutation test for Moran's I statistic using the 'spdep' package (Bivand & Wong 2018) was calculated by first log transforming the data; 10 000 random permutations of seagrass seed density were then used for the defined spatial weighting scheme to finally establish the rank of the observed statistic in relation to the simulated values (Fortin & Dale 2005).

2.7.2. Zero-inflated Poisson and binomial spatial models

Total and viable seed density in each meadow was tested against the effect of standardized water depth (m) and the presence or absence of seagrass while also accounting for spatial correlation as necessary based on Moran's I test results. Following data exploration, the large number of zeros in the total seed bank data (Esplanade: 56%; Bessie Point: 77%) resulted in the selection of a zero-inflated Poisson (ZIP) generalized linear model to describe count data (Zuur et al. 2010, 2012). The ZIP regression model for seed density is given by:

$$\text{Seeds}_i \sim \text{ZIP}(\mu_i, \pi) \quad (1)$$

where μ_i (the count portion of the model) is the mean number of seeds (both positive counts and zeros) at location i and π is the probability of recording zeros only (Zuur et al. 2012). To relate the means of both these distributions of the model to a global linear mixed model, we used link functions defined as:

$$\log(\mu_i) = \beta_0 + \beta_1 \times \text{Depth}_i + \beta_2 \times \text{Cover}_{2009}_i + \beta_3 \times \text{Cover}_{2010}_i + \beta_3 \times \text{Cover}_{2011}_i + \beta_3 \times \text{Cover}_{2012}_i + \varepsilon_i \quad (2)$$

$$\text{logit}(\pi) = \gamma \quad (3)$$

where β_2 and γ are the regression parameters and ε_i is the spatial random effect at location i . From this calculation we determined the expected value and vari-

ance of the number of seeds at each location. Zero-inflated binomial (ZIB) models were calculated using the same equation but with the binomial distribution.

2.7.3. Bayesian inference using integrated nested Laplace approximations

Integrated nested Laplace approximations (INLAs), a computationally efficient alternative to Markov chain Monte Carlo (MCMC) methods, were used to calculate the distribution of the regression parameters (Rue et al. 2009, Beguin et al. 2012) using the INLA package. To reduce computational time, we specified the use of a Gaussian Markov random field (GMRF), and sampling locations were converted into areal triangulations using stochastic partial differential equations (SPDEs) (Rue & Held 2005, Lindgren et al. 2011). The spatial correlation structure of the residuals was then calculated using the Matérn correlation function (Cressie 1993, Lindgren et al. 2011). All models assumed a GMRF prior for the intercept, regression parameters and covariates with a mean of 0 and a sparse precision matrix.

After running the global model, all non-relevant covariates were removed and the model was re-run until only relevant covariates remained (Zuur et al. 2007). A covariate was considered to be non-relevant if the credible interval of the posterior distribution of the model output for that covariate included 0 (Zuur et al. 2012). For each model, residuals were also inspected for spatial correlation using variograms (Cressie 1993) in the 'gstat' and 'sp' packages (Pebesma 2004, Bivand et al. 2008). The best-fit model was considered to be the simplest model with the lowest deviance information criterion (DIC) (Zuur et al. 2012).

3. RESULTS

3.1. Seagrass mapping

Between 2001 and 2012, seagrass area in the Cairns Harbour meadows reached a maximum in 2007 of 418.9 ± 6.4 and 1062.5 ± 89.7 ha in the Esplanade and Bessie Point meadows respectively (Fig. 2). The dominant species of seagrass within each meadow varied between meadows, with *Zostera muelleri* dominating at the Esplanade meadow and *Halodule uninervis* at the Bessie Point meadow. There was a large-scale decline in seagrass area in 2010, whereby 75% of seagrass area was lost in the

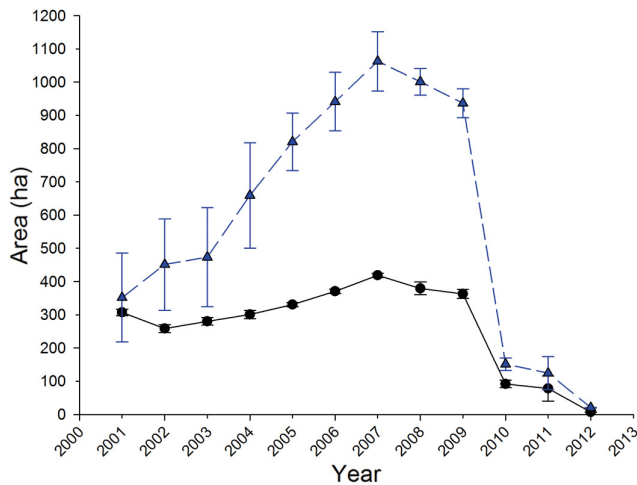


Fig. 2. Total area of Esplanade (blue line) and Bessie point (black line) seagrass meadows in Cairns Harbour and Trinity Inlet from 2001–2012 (error bars: area reliability estimate)

Esplanade meadow and 83 % was lost in Bessie Point. Seagrass area continued to decline until 2012, when the lowest areal extent was recorded since monitoring began in both the Esplanade (7.9 ± 0.4 ha) and Bessie Point (20.7 ± 0.5 ha) meadows. As a result, previously extensive *Z. muelleri* and *H. uninervis* seagrass meadows in Cairns Harbour were reduced to small remnant patches (Fig. 2).

3.2. Sediment seed bank density and viability

Seagrass seeds were found throughout Cairns Harbour, with greater combined total and viable seed densities found in the Esplanade compared to the Bessie Point meadow (Table 1, Fig. 3). All species documented in the annual monitoring surveys between 2009 and 2012 were present in the total seed bank. Interestingly, *Cymodocea serrulata* seeds were also found in the Esplanade meadow although established shoots had not been found in this meadow since 2009. The most abundant species in the seed bank mirrored the species with the greatest proportion of meadow biomass in both monitoring meadows (Esplanade: *Z. muelleri*; Bessie Point: *H. uninervis*). However, due to the large number of zeros in the seed bank data for the non-dominant species at both sites (*H. uninervis* seeds at the Esplanade, 89 % of samples = 0; *Z. muelleri* seeds at

Bessie Point, 92 % of samples = 0), all further seed analyses were restricted to the most abundant species in the seed bank. Overall, seed viability was <15 % for all seeds across both meadows (Table 1).

3.3. Total and viable seed bank spatial distribution

Moran's *I* test of the spatial distribution indicated significant clustering of both total (Moran's *I* = 0.017, $p = 0.020$) and viable *Z. muelleri* seeds (Moran's *I* = 0.023, $p = 0.003$) in the Esplanade meadow seed bank (Fig. 3A). Within the Bessie Point meadow the total seed bank was also significantly clustered for total *H. uninervis* seeds (Moran's *I* = 0.002, $p = 0.007$; Fig. 3B); however, there were too few viable seeds collected to analyse the spatial structure in the distribution of viable seeds.

3.4. Seed bank spatial structure in relation to seagrass cover and depth

When taking spatial autocorrelation into account, the *Z. muelleri* seed bank at the Esplanade meadow had the highest total seed densities in areas that were last colonised by seagrass 4 yr before sampling (Table 2, Fig. 4); however, there was no effect of water depth (Table 2). Viable *Z. muelleri* seed density was low across the entire meadow, and was not related to depth or previous seagrass cover (Table 3). *H. uninervis* total seed density at the Bessie Point meadow was also greater in areas where seagrass was observed 4 yr prior to sampling and in shallow

Table 1. Mean (\pm SE) density of the sediment seagrass seed bank in Cairns Harbour in July 2013. Dashes (–) indicate no data was collected due to insufficient numbers of seeds present to develop viability staining protocols

Species	Total seeds m^{-2}	Viable seeds m^{-2}	% Viable	Total seeds mean water depth (m)	Viable seeds mean water depth (m)
Esplanade Meadow					
Combined	34 \pm 5	7 \pm 1	14 \pm 3	1.44 \pm 0.05	1.45 \pm 0.08
<i>Halodule uninervis</i>	8 \pm 2	2 \pm 1	5 \pm 1	1.56 \pm 0.05	1.56 \pm 0.07
<i>Zostera muelleri</i>	24 \pm 4	5 \pm 1	9 \pm 2	1.39 \pm 0.06	1.40 \pm 0.11
<i>Halophila ovalis</i>	1 \pm 0	–	–	–	–
<i>Cymodocea serrulata</i>	1 \pm 0	–	–	–	–
Bessie Point Meadow					
Combined	18 \pm 4	3 \pm 1	4 \pm 1	1.26 \pm 0.08	1.22 \pm 0.08
<i>Halodule uninervis</i>	13 \pm 3	2 \pm 1	2 \pm 1	1.31 \pm 0.09	1.24 \pm 0.09
<i>Zostera muelleri</i>	3 \pm 1	0 \pm 1	0 \pm 1	1.10 \pm 0.12	1.01 \pm 0.10
<i>Halophila ovalis</i>	2 \pm 1	–	–	–	–
<i>Cymodocea serrulata</i>	0 \pm 0	–	–	–	–

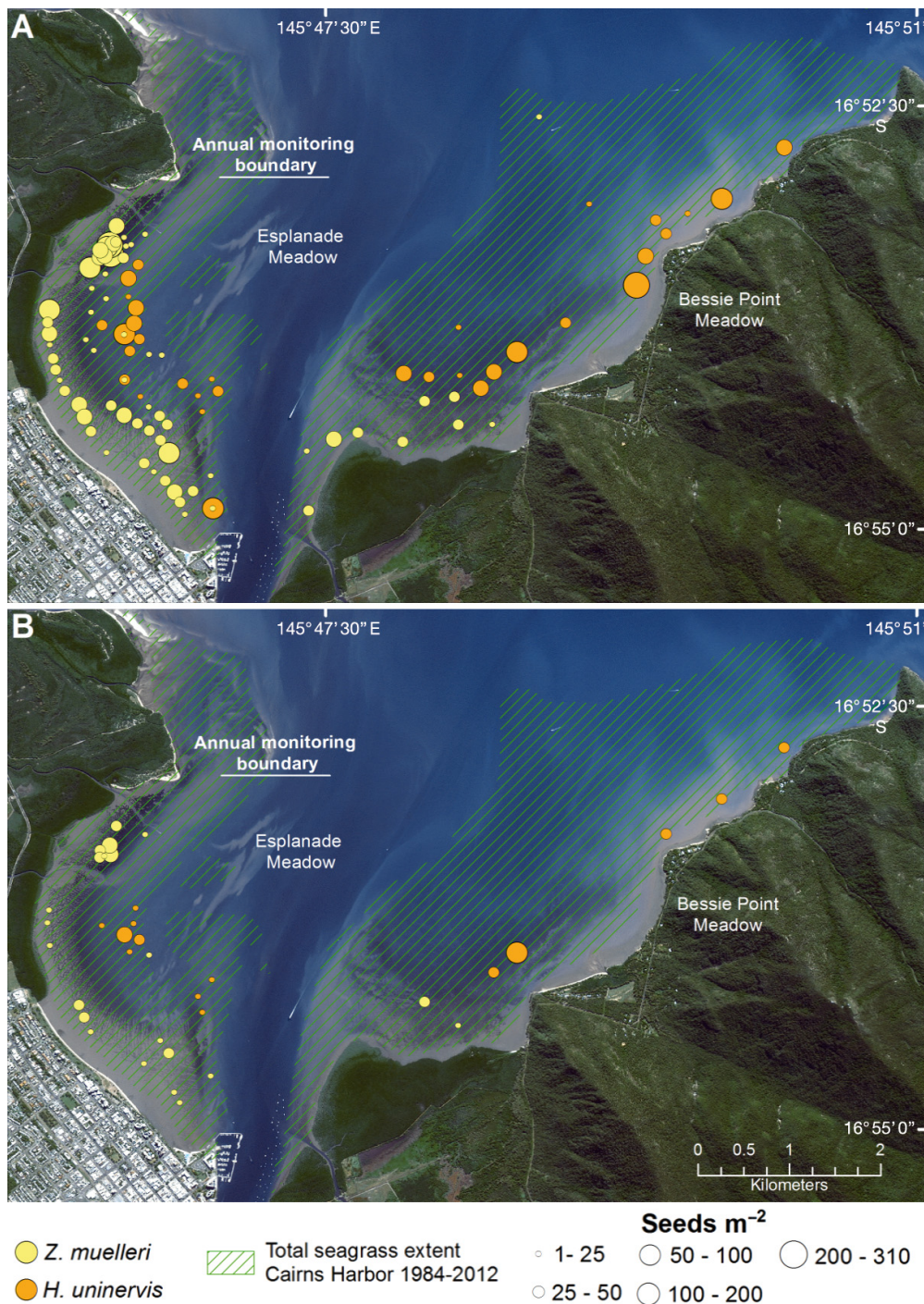


Fig. 3. Map of (A) total and (B) viable sediment seed bank density in July 2013 for *Zostera muelleri* and *Halodule uninervis* seeds in Cairns Harbor

compared to deeper water depths (Table 2, Fig. 5). Due to the low number of samples containing viable *H. uninervis* seeds, no clear patterns were evident in their spatial distribution.

The strength of the spatial correlation between seed bank samples and historical seagrass presence

was significant over distances of 100–150 m for the total *Z. muelleri* seed bank at the Esplanade and over 500–550 m for the total *H. uninervis* seed bank at Bessie Point. For viable seeds, the strength of the spatial correlation was reduced after 50–100 m for *Z. muelleri* seeds in the Esplanade meadow. *H. unin-*

Table 2. Summary statistics for selected models of total (viable + non-viable) seed density. Posterior mean, posterior standard deviation (SD) and posterior 95% credible interval for the fixed effects are shown; *relevant variables (see Section 2.7.3 for a definition of relevance)

Variable	Mean	SD	2.5%	97.5%
Esplanade Meadow (<i>Zostera muelleri</i>)				
Intercept	1.40	0.92	-0.24	3.39
Depth	0.17	0.43	-0.67	1.00
1 yr prior cover	-9.26	10.06	-32.95	5.21
2 yr prior cover	-0.08	0.40	-0.87	0.72
3 yr prior cover	0.02	0.35	-0.68	0.71
4 yr prior cover*	2.02	0.75	0.37	3.30
Bessie Point Meadow (<i>Halodule uninervis</i>)				
Intercept	7.54	1.19	5.36	10.11
Depth*	-2.26	0.68	-3.74	-1.10
1 yr prior cover	0.01	0.84	-1.76	1.60
2 yr prior cover	9.14	7.19	-1.44	25.96
3 yr prior cover	-9.38	7.18	-26.20	1.16
4 yr prior cover*	-1.02	0.49	-2.06	-0.10

ervis seed viability was not analysed due to their low abundances in the collected samples.

4. DISCUSSION

Seed banks provide a mechanism for maintenance and recovery in vegetative communities. However, the functionality of the seed bank can be affected by biotic and abiotic factors, which vary over space and time. This study demonstrated that seagrass meadows in Cairns Harbour, Queensland, retained a seed bank with a species-specific spatial structure for a minimum of 4 yr following a large-scale decline. In addition, seeds were 'clustered' at distances between 50 and 550 m, and the presence or absence of seagrass cover and water depth were found to be potential drivers of the observed grouping of seagrass seeds. The density of viable seeds also varied over space and between species, signifying that the

recovery function provided by the seed bank is unevenly distributed throughout these meadows. In addition, low numbers of seeds for all recorded species indicate that in systems where seed supply is limited, the functionality of the seed bank may decrease significantly over relatively short time scales (<5 yr). Therefore, the resilience provided by the seed bank in seagrass communities should not be viewed as a static level of insurance for the entire meadow, but rather as dynamic and species-specific, with variability over both space and time.

Within aquatic habitats, the species composition of the seed bank is closely related to the diversity of the surrounding vegetation cover (Terrados 1993, Bonis et al. 1995, Steinhardt & Selig 2007). In this study, the density and distribution of both *Zostera muelleri* and *Halodule uninervis* seeds was directly related to seagrass cover prior to a large-scale decline recorded in 2010, but not in the subsequent post-decline years. This may have been related to a lack of propagule production in the years following 2009 when seagrass area decreased up to 83%. While dispersal of seeds from outside meadows into the impacted sites could have provided new propagules for the

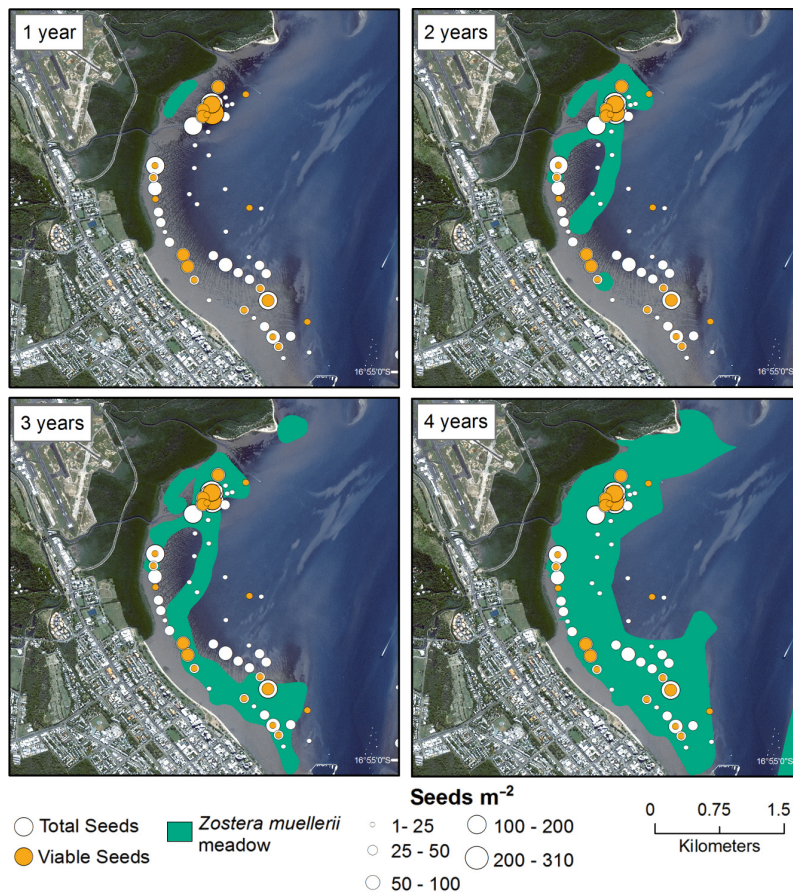


Fig. 4. Distribution of the Esplanade *Zostera muelleri* total and viable seed bank compared to *Z. muelleri* meadow distribution for previous 4 yr prior to the 2013 sampling (1 year = 2012; 2 years = 2011; 3 years = 2010; 4 years = 2009)

Table 3. Fixed effects summary statistics for selected models of the density of viable *Zostera muelleri* seeds at the Esplanade meadow and *Halodule uninervis* seeds in the Bessie Point meadow. Posterior mean, posterior standard deviation (SD) and posterior 95% credible interval for the fixed effects are shown; * relevant variables (see Section 2.7.3 for a definition of relevance)

Variable	Mean	SD	2.5 %	97.5 %
Esplanade Meadow (<i>Zostera muelleri</i>)				
Intercept	0.00	1.68	-3.40	3.23
Depth	-0.90	0.90	-2.75	0.82
1 yr prior cover	-7.38	11.41	-34.27	8.98
2 yr prior cover	1.18	1.03	-0.74	3.33
3 yr prior cover	-1.06	0.87	-2.86	0.58
4 yr prior cover*	2.71	1.40	0.20	5.71
Bessie Point Meadow (<i>Halodule uninervis</i>)				
Intercept	10.47	3.17	5.07	17.50
Depth	-5.26	2.12	-10.01	-1.71
1 yr prior cover	-3.84	2.89	-9.65	1.70
2 yr prior cover*	15.73	7.72	4.22	33.74
3 yr prior cover	-9.01	7.39	-26.32	1.88
4 yr prior cover	-2.05	1.67	-5.25	1.30

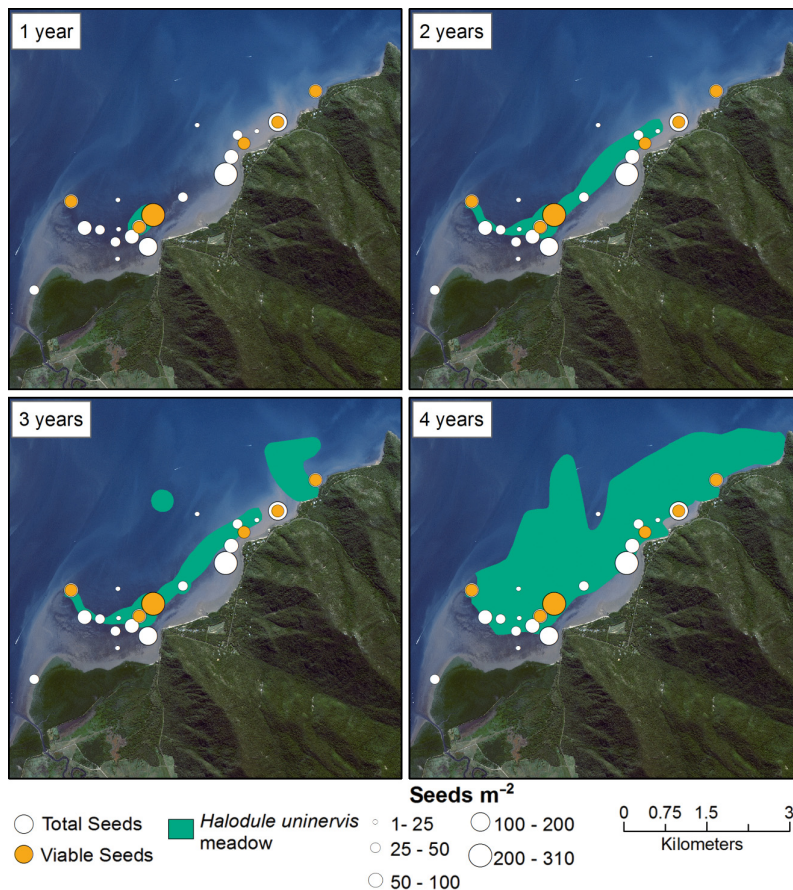


Fig. 5. Distribution of the Bessie Point *Halodule uninervis* total and viable sediment seed bank compared to *H. uninervis* meadow distribution for previous 4 yr prior to the 2013 sampling (1 year = 2012; 2 years = 2011; 3 years = 2010; 4 years = 2009)

seed bank (Kendrick et al. 2012, Grech et al. 2016, 2018), given that the 2010 decline was regional rather than local (McKenna et al. 2015) and that the relative abundance of seeds in the seed bank mirrored the species with the greatest proportion of meadow biomass in sites, the impact of dispersed propagules from outside the meadows was likely to be limited.

The structure of the sediment seed bank can vary significantly due to species-specific traits such as flower and seed morphology (Guo et al. 2000), life history strategies (Harper 1977) and dispersal patterns (Nathan & Muller-Landau 2000, Kendrick et al. 2012). While all species observed in the meadows described here are perennial and flower yearly (Rasheed et al. 2013), seed shape and strategies for dispersal differ between the 2 dominant species. *Z. muelleri* discharges oval seeds produced in groups on spathes in flowering shoots from the canopy (Conacher et al. 1994b) whereas *H. uninervis* releases spherical seeds at or below the sediment surface (Kendrick et al. 2012). Based on the floral morphology and the location of *H. uninervis* seed release, it is assumed that few seeds are exported out of the meadow, limiting primary dispersal (Inglis 1999, Darnell et al. 2015). In comparison, dispersal of *Z. muelleri* flowering shoots and biotic movements of seeds by grazers may result in dispersal distances ranging between <1 m and >100 km (Grech et al. 2016, 2018, Tol et al. 2017). Both species also differ in patterns of secondary dispersal. Because of their spherical shape, *H. uninervis* seeds are susceptible to secondary dispersal by large-scale water movement and foraging of large marine herbivores (Inglis 2000, Darnell et al. 2015, Tol et al. 2017). For *Z. muelleri*, secondary dispersal may be reduced due to an elongated oval seed shape and sediment microtopography restricting movement (Orth et al. 1994). Variations in dispersal patterns due to species-specific traits may explain differences in the spatial scales at which seed clustering was observed in the seed bank in our study, despite the fact that both species were found in the same meadow at the same time. Although beyond the scope of this

research, additional biotic drivers of seed bank function (e.g. changes in the faunal community associated with large-scale declines of seagrass) should also be considered, as these interactions could have significant impacts on seed bank structure and function (Blackburn & Orth 2013).

Differences in species-specific seed bank structure could have been exacerbated by changes in abiotic conditions over time and between meadows. Temporally, the loss of seagrass across Cairns Harbour in 2010 may have resulted in an increase in water movement over previously vegetated areas at both sites due to a loss of canopy structure, resulting in increased shear stress along the sediment surface (Koch 2001). Increased water movement can enhance sediment resuspension (Fonseca & Bell 1998), possibly exceeding the critical erosion threshold required to move seeds. The seed bank may also have been susceptible to mass sediment movement and bed load transport associated with large-scale storms (Bell et al. 2008), such as Cyclone Yasi which impacted the Cairns region in 2011 (McKenna et al. 2015). Between sites, interactions among local physical and biological drivers may have diverged between the Esplanade and Bessie Point sites due to differences in sediment features, bottom topography, and wind exposure (Campbell et al. 2002). More specifically, water depth impacted the spatial structure of the seed bank only at Bessie Point (the subtidal site) and not in the Esplanade meadow (which is intertidal). While the direct mechanism between water depth and the seed bank spatial structure is unknown, links between physical factors (e.g. waves and currents) that are affected by depth and metrics that may impact seed bank dynamics such as habitat suitability (Koch 2001), reproductive effort (Phillips et al. 1983) and interspecific competition for resources (Robbins & Bell 2000) are well established. Additional research into physical drivers of seagrass seed bank structure is required to fully understand the link between water depth and the clustered pattern observed here.

Regardless of the seed bank spatial structure, without an influx from outside sources or until remnant populations in Cairns Harbour repopulate the seed bank, the density of viable seeds will continue to decline due to processes such as mortality and predation (Fenner & Thompson 2005), burial (Blackburn & Orth 2013) or germination (Jarvis & Moore 2010). As a result, total maximum seed densities in Cairns Harbour in 2013—which are already substantially lower than similar *Z. muelleri* (177 ± 23 seeds m^{-2}) and *H. uninervis* (3333–8333 seeds m^{-2}) meadows

documented in this region (McMillan 1981, Conacher et al. 1994b, Inglis 2000)—may continue to decrease. Four years following the decline, the function of the seagrass seed bank in Cairns Harbour was severely limited as <15% of all seeds recorded were viable. At these reduced levels, the seed bank within Cairns Harbour may not provide resilience to future disturbances and struggle to initiate sustained recovery from previous declines, resulting in highly vulnerable seagrass populations at this site. There is likely to be only a short window remaining for the existing viable seeds to germinate before they too are lost.

Given the lack of recovery of seagrass meadows at both sites during the years immediately following the loss reported in 2010, it is probable that the seed bank was non-functional in Cairns Harbour. However, the results reported here indicate a viable, albeit reduced, seed bank 4 yr following the decline. Due to the low densities of viable seeds it is unknown if the seed bank is still ecologically functional, or able to provide the materials necessary to generate recovery. Given the spatial distribution of the seed bank, any recovery produced from the remaining seeds in Cairns Harbour may be characterized by discrete patches of seagrass separated by 10s to 100s of m. Meadow establishment and expansion driven by many small patches that are separated by distances similar to those reported here may be further limited by a lack of abundance-related positive feedback mechanisms (Maxwell et al. 2017). Currently, the direct relationship between seed bank density, seedling growth and survival and meadow establishment is unknown. Therefore, it is unclear if characterizing the functionality of the seed bank by the presence of viable seeds alone provides enough information to determine if a seed bank can stimulate a recovery. A more thorough definition of a functioning seed bank that includes both a species-specific spatial component and a minimum density of viable seeds is necessary to better understand the level of recovery potential provided.

The results of this study highlight the complex interactions between species, time, site and depth that may affect the ability of seagrass meadows to recover from seeds. Current models that only account for viable seed density may be overestimating the potential for recovery from the sediment seed bank by not also considering these interactions. We conclude that resilience provided by the seed bank in seagrass communities should not be viewed as a static level of protection distributed equally across the entire meadow, but rather as dynamic and species-

specific, with variability over both space and time. Understanding these spatial and species-specific dynamics is an important consideration for the management of seagrass meadows, especially for decisions on interventions such as active restoration programs in the tropics, where information is generally lacking (Tan et al. 2020).

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