Centre for Tropical Water and Aquatic Ecosystem Research



Port Curtis Seagrass Seed Bank Density and Viability Studies - Year 2 Report

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Report No. 16/46

2016

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A report for the Ecosystem Research and Monitoring Program

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This report should be cited as:
Bryant, C.V., Carter, A.B., Jarvis, J.C., Reason, C.L. & Rasheed, M.A. (2016). Port Curtis Seagrass Seed Bank Density and Viability Studies - Year 2. Report produced for the Ecosystem Research and Monitoring Program Advisory Panel as part of Gladstone Ports Corporation's Ecosystem Research and Monitoring Program. Centre for Tropical Water & Aquatic Ecosystem Research (TropWATER) Publication 16/46, James Cook University, Cairns, 29pp.

This report has been produced for the Ecosystem Research and Monitoring Program Advisory Panel as part of Gladstone Ports Corporation's Ecosystem Research and Monitoring Program. The study was undertaken through a Consultancy Agreement (CA14000163) between Gladstone Ports Corporation and James Cook University

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Acknowledgements:
This project is funded by the Gladstone Ports Corporation's Ecosystem Research and Monitoring Program. We wish to thank the many staff at TropWATER that have assisted with data collection and monitoring work in the field and processing samples in the laboratory.

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KEY FINDINGS

This report details findings from the second year of a study examining the density of seagrass (*Zostera muelleri* subsp. *capricorni*) seeds and their viability in Port Curtis. The project builds on seagrass seed bank assessments that were originally conducted as part of the Western Basin Dredging and Disposal Project (WBDDP).

Results of the seed bank density and viability surveys undertaken, to date, have found that:

- Seeds were present at all sites during all quarterly sampling events, with total seed density relatively high compared with other locations in Queensland where seed banks have been assessed e.g. Moreton Bay, Cairns and Mourilyan Harbour.
- Seed bank density changed significantly at all sites over the duration of monitoring (2011 to 2016) but trends varied substantially between sites and years. Overall trends in seed bank density tended to mirror trends in peak seagrass density, particularly in the largest seagrass meadow at Pelican Banks.
- Viable seeds were found in the sediment seed bank at all sites immediately following the end of each growing season (February 2015 and 2016).
- We suspect that some meadows (Wiggins Island and Rodds Bay) may rely on nearby donor meadows for seed bank replenishment.
- The average proportion of viable seeds decreased at all sites over the senescent season (from February to May) in 2015, but remained stable (Pelican Banks North) increased (Rodds Bay) or decreased (Wiggins Island) in 2016.
- On average greater than 70% of all seeds were found at sediment depths >20mm, and for the majority of the sampling period greater than 40% were found at >50mm. This may limit seed bank function if burial depth inhibits germination and/or seedling success.
- Seasonal trends in total seed bank density were not consistent, with some sites unexpectedly containing significantly higher seed densities following the senescent period (May) compared with densities following replenishment (February), indicating secondary dispersal events or possibly delayed recruitment of seeds to some meadows.

Results of the first two years of this study have revealed significant new insights into seed banks in Port Curtis but have also highlighted the complexity of seed bank dynamics. The ongoing sampling planned in 2016 and 2017 will help to further resolve these dynamics but additional investigations would also enhance the understanding of seagrass resilience including studies on:

- The spatial structure of the seed bank across the broader meadow;
- Environmental cues for germination and rates of germination and seedling success; and
- Connectivity between seagrass meadows through seed dispersal within the Port Curtis region.

1 INTRODUCTION

Physical impacts to seagrasses resulting in loss can occur due to a range of environmental and anthropogenic events including storms and flooding (Preen et al. 1995; Poiner et al. 1989), grazing (Preen 1995), anchor and boat damage (La Manna et al. 2015; Kininmonth et al. 2014; Hallac et al. 2012), shipping accidents (Kenworthy et al. 1993) and dredging (Erftemeijer and Lewis 2006). The potential impacts on seagrasses caused by dredging include the physical removal and/or burial of vegetation and effects of increased turbidity and sedimentation (Erftemeijer and Lewis 2006).

The Western Basin Dredging and Disposal Project (WBDDP) was identified as potentially posing a high level of environmental risk to the marine habitats of the area, particularly to seagrass meadows. In 2009, Gladstone Ports Corporation Limited (GPC) commissioned a suite of research and monitoring including quarterly assessments of seagrass condition along permanent transects at key monitoring meadows throughout the harbour and in nearby Rodds Bay. These sites formed the key sensitive receptor locations for assessing seagrass condition before, during and after dredging related to the WBDDP. Monitoring has been conducted at least quarterly at permanent transect sites since November 2009. Various measures of the seagrass meadows are made during the regular quarterly assessments to determine changes in a) seagrass health; b) seagrass tissue nutrients; c) seagrass resilience; and d) seagrass productivity (Bryant et al. 2016).

1.1 Sediment seed banks and seagrass resilience

A key aspect in understanding the resilience of seagrass meadows to stressors is their capacity to recover from impact (Kenworthy et al. 2006). Seagrasses are clonal plants and meadows can recover from declines by vegetative means (asexual reproduction) through the extension of rhizomes, as well as by recruitment from propagules (seeds/sexual reproduction) (Rasheed 2004; 1999; Rollón et al. 1998). Seed banks are formed when flowering plants deposit seeds on or in the sediment (Fenner and Thompson 2005). The potential for seagrass meadows to recover from the sediment seed bank is dependent upon the species present, the availability of propagules (viable seeds) and a return to favorable growing conditions for germination.

A viable seed is defined as an embryo which maintains the physiological capability to germinate given the appropriate cues (Murdoch and Ellis 2000). Viability can be affected by many biotic (e.g. seed source, predation) and abiotic (e.g. burial depth, sediment type, temperature, salinity) factors in the surrounding environment (Murdoch and Ellis 2000; Baskin and Baskin 1998; Moore et al. 1993). Burial depth in particular can be limiting as cues for germination may be present at deeper depths (>5cm) which may initiate the germination process through the extension of the hypocotyl (Jarvis and Moore 2015; Churchill 1983). Seeds buried at deeper depths require a longer hypocotyl than shallower seeds, resulting in a greater period of time prior to the emergence of the seedling cotyledon from the sediment surface. As the cotyledon provides oxygen necessary for survival of the seedling, any delay in the emergence of the cotyledon may result in seedling mortality (Churchill 1983) and reductions in seed bank viability.

1.2 Existing information and knowledge gaps

This project builds on seagrass seed bank assessments that were originally conducted as part of the WBDDP. From 2009-2010 seed banks were assessed at permanent transect sites using standard Seagrass-Watch methodology (McKenzie et al. 2000). Sediment cores were sieved in the field using a 1mm mesh sieve and the contents inspected for *Halodule uninervis* and *Zostera muelleri* subsp. *capricorni* (herein referred to as *Z. muelleri*) seeds. These methods were not appropriate to capture seeds of many of the species, including the dominant *Z. muelleri*, and provided no information on what proportion of seeds remained viable and available for germination.

In March 2011, following large scale declines in seagrasses in the area, GPC commissioned a more in depth investigation into the status of seed banks in the harbour. Sediment cores were collected at permanent transect sites and transported frozen to the laboratory where they were thawed and run through a series of test sieves to separate various fractions of the sediment, then examined under a dissecting microscope. This method detected numerous *Z. muelleri* seeds in the 710 µm to 1mm fraction of the sample and seeds of the genus *Halophila* in smaller mesh fractions (McCormack et al. 2013). Since this time, sediment cores have been collected in the field during quarterly sampling events and stored frozen at the TropWATER laboratory for potential future detailed examination of seed banks.

Based on the results of the initial assessments commissioned by GPC (McCormack et al. 2013), a subset of monitoring sites (Pelican Banks North (GH1), Wiggins Island (WW1) and Rodds Bay (RD1)) were selected to focus processing efforts (Map 1). These meadows provided a geographical spread relative to dredging associated with the WBDDP and have historically been dominated by *Z. muelleri,* the dominant species in the harbour. Quarterly assessments of seed bank density from 2011 to 2014 (Davies et al. 2015) were valuable in determining the presence or absence of seeds at most monitoring sites; and for a subset of these sites produced good information on changes in density over time. However, to determine the capacity of the seagrass sediment seed bank to provide resilience for existing meadows, critical knowledge gaps needed to be addressed. Specifically, information on total seed bank density, seed viability, burial depth of seeds and how these factors change over time needed to be identified. In recognition of these knowledge gaps, GPC commissioned TropWATER to conduct seagrass seed bank assessments as part of GPC's Ecosystem Research and Monitoring Program (ERMP).

1.3 Objectives and sampling approach

This study aims to address critical knowledge gaps related to the density and viability of *Z. muelleri* sediment seed banks in Port Curtis, by a) formally collating the existing information on Port Curtis seed banks; and b) integrating assessments of viability into the current program which monitors the recovery and resilience of seagrass meadows post dredging.

This new project has three major components:

1. Assessment of the back catalogue of stored seed bank core samples collected quarterly between March 2011 and May 2014 for total numbers of *Z. muelleri* seeds;
2. Continue quarterly assessments of total seed bank density for *Z. muelleri*;
3. Conduct biannual assessments of seed bank viability for *Z. muelleri.*

While we acknowledge that other species have ecological significance in the region, in order to minimise costs and ensure that information is produced within useful timeframes to inform future management of seagrass resources, we focused our studies on *Z. muelleri* seed banks at Pelican Banks, Rodds Bay and Wiggins Island (Map 1). *Z. muelleri* is the dominant species in the Port Curtis region and is present at the majority of meadows monitored for the WBDDP. The larger seeds of *Z. muelleri* (relative to *Halophila* spp.) are inherently easier to work with and seed core samples can be processed at a much faster rate when only a relatively small fraction (710µm to 1mm) of the sample needs to be examined.

Queensland seagrass communities are seasonal, with cycles defined according to the climate-induced pattern of growth and senescence during the year (Chartrand et al. 2012; McKenzie 1994). Two generalised seasons are distinguished; a) the growing season, which typifies seagrasses natural increase in biomass and distribution as ideal growth conditions provide a period of opportunistic expansion; and b) the senescent season, when seagrasses typically retract and rely on stores or seed banks to get through the wet season conditions, including flooding and poor water quality (Chartrand et al. 2012). In Port Curtis the growing season has been defined as the period from July to January, and the senescent season from February to June (Chartrand et al. 2016).

Z. muelleri have a specialised flowering shoot called a spathe. The spathe contain male and female flowers that once fertilised, swell to form seeds, and when mature release from the spathe, (Figure 1)(Waycott et al. 2004). Flowering and resulting seed production typically occurs in Port Curtis between August and February with peak production around November towards the end of the growing season (Bryant et al. 2016). Those seeds that are incorporated into the seed bank remain until they germinate or are functionally removed due to a loss of viability or through dispersal mechanisms.

Figure 1. *Z. muelleri* spathe and seeds (Waycott et al. 2004) .

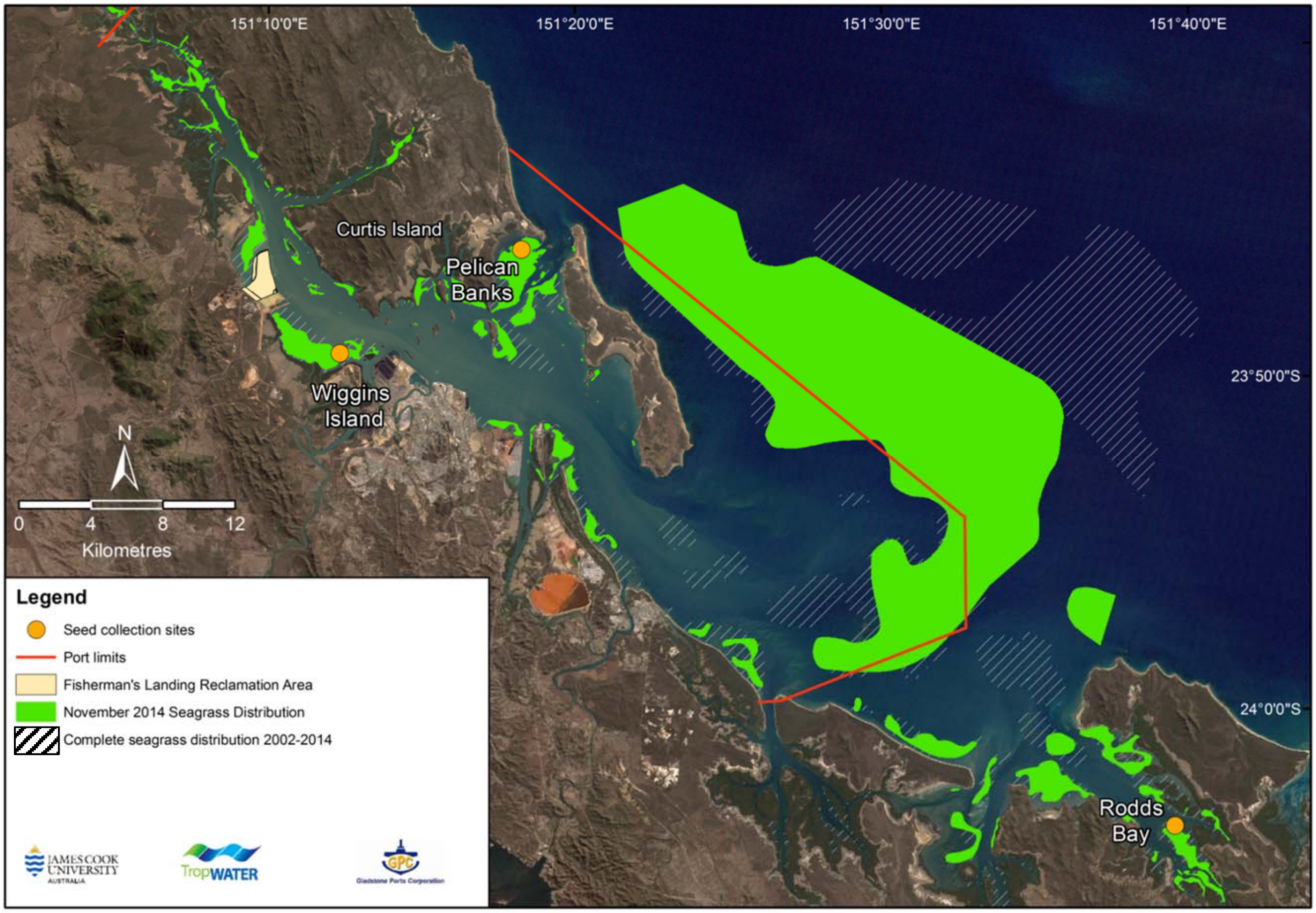
The objectives of this study were to:

1. Monitor changes in the density of *Z. muelleri* seed banks during the pre-dredging, dredging and post-dredging phases of the WBDDP.
2. Monitor changes in the proportion of viable *Z. muelleri* seeds in the seed bank before and after the growing season during the post-dredging phase of the WBDPP.

The sampling methods used followed those established for similar studies in the Port of Cairns (Jarvis et al. 2013). Seagrass seed bank density was assessed quarterly during regular seagrass condition monitoring around February, May, August and November each year. Viability assessments were conducted in February after peak seed release when viable seed densities are expected to be greatest; and in May prior to the onset of the growing season, to test densities of germinable seeds (McFarland and Shafer 2011). The objective was to quantify the ability of the seed bank to retain its function (i.e. viability) over the senescent period when seagrass biomass is lowest and therefore the meadows susceptible to disturbance.

Jarvis et al. (2015) reported on the first year of the study including an assessment of the back catalogue of samples as well as results from quarterly (density) and biannual (viability) sampling in 2014/15. The current report updates these findings with results from quarterly (density) and biannual (viability) sampling in 2015/16.

Map 1: *Z. muelleri* seed collection sites in Port Curtis and Rodds Bay in 2015/16.



2 METHODS

2.1 Total seed bank density

Assessments of seed bank density were conducted in conjunction with regular measurements of seagrass condition at the permanent transect sites in February, May, August and November. At each sampling location, sediment cores (50mm in diameter and 100mm in depth) were collected adjacent to transects at 0m, 10m, 20m, 30m, 40m and 50m intervals (n = 6 per transect; 18 total). Cores were divided into three sections based on sediment depth (0-20mm, 20-50mm and 50-100mm). Samples were stored on ice for transport to the TropWATER laboratory in Cairns, and stored at -20°C until processing.

Cores collected in February and May were also used to assess seed viability (see below). These cores were stored on ice for transport to the TropWATER laboratory in Cairns, and then stored at 8-10°C until processing which occurred within 1 week of collection (Marion and Orth 2010).

All sediment samples were wet sieved with fresh water and the 710µm to 1mm fraction of the sediment was inspected for *Z. muelleri* seeds using a dissecting microscope (Figure 2). All seeds were identified, photographed and catalogued at the TropWATER seed bank library. The remaining fraction of the sediment was frozen and stored. Density data were reported as mean ± standard error for the total number of seeds m^{-2} per site and as a percentage of seeds in each depth category (see above) per site.

Figure 2. Processing of sediment seed bank samples.

2.2 Seed bank viability

Seed bank viability assessments were conducted in February and May of 2015 and 2016. All seed samples were tested for viability within one week of collection using tetrazolium chloride (Sawma and Mohler 2002; Conacher et al. 1994a; Lakon 1949). Seed embryos were removed from their seed coats and soaked in a 0.5% tetrazolium chloride solution for 48 hours before examination under a dissecting microscope at 10 x magnification (Conacher et al. 1994a). Seeds with a pink to brown stained cotyledon and axial hypocotyl were counted as viable (Conacher et al. 1994a; Harrison 1993; Taylor 1957) (Figure 3). Viability data were reported as mean ± standard error for the percentage of viable seeds at each sampling site and as the percentage of viable seeds in each depth category for each site.

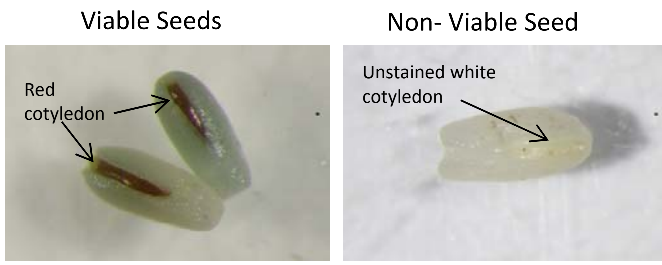


Figure 3. Examples of stained viable and non-viable *Z. muelleri* seeds using tetrazolium chloride.

2.3 Data analysis

Data analysis for each site (Rodds Bay, Pelican Banks, Wiggins Island) was conducted independently. Data exploration protocols prior to all analyses followed Zuur et al. (2010) and included checks for collinearity and zero inflation. Overdispersion was a problem in preliminary model runs due to the large number of zeros in each dataset; this was corrected with the use of zero inflated models in R version 3.3.1 (Abdelrhman 2003) using the *gamlss* package (Rigby and Stsinopoulos 2005). For each analysis a global model was compared against model subsets including the null hypothesis (See Appendices A to E). The best-fit model was considered the simplest model with the lowest Akaike's Information Criterion (AIC) that fell within two of the lowest AIC (Burnham and Anderson 2002), and where residual plots did not demonstrate any deviations from homoscedasticity or normality. Statistical significance of covariates in the best fit models were tested using likelihood-ratio-test-based backward selection with the "drop1" function in R.

Temporal Effects on Total Seed Bank Density

Total seed bank density (viable + non-viable seeds) was compared among all sampling dates (all sites sampled quarterly: Rodds Bay August 2011 to May 2016; Pelican Banks March 2011 to May 2016; Wiggins Island February 2011 to May 2016). The effect of sampling date on total seed bank density was modelled using a zero inflated Poisson regression model for count data. Five candidate models were compared for each site (global model: *seeds ~ sampling date*) using the AIC.

Seasonal Effects on Total Seed Bank Density

Seasonal changes in total seed bank density (viable + non-viable seeds per core) were quantified directly following the growing season (February), then towards the end of the senescent season (May), and among years. Data were analysed using zero inflated Poisson regression models. Five candidate models were compared for each site (global model: *seeds ~ season*year*) using the AIC. Analysis was limited to years where data were collected in February and May: Pelican Banks and Rodds Bay were analysed from 2012-2016 and Wiggins Island was analysed for 2012 and 2014-2016.

Sediment Depth and Temporal Effects on Total Seed Bank Density

The effect of sediment depth (0-20mm, 20-50mm, 50-100mm) was compared among all sampling dates (all sites sampled quarterly and sectioned for depth: Rodds Bay and Pelican Banks November 2013 – May 2016; Wiggins Island August 2014 – May 2016) on total seed bank density (viable + non-viable seeds per core) was analysed using zero inflated Poisson regression models. Five candidate models were compared for each site (global model: *seeds~depth*sampling date*) using the AIC. Sampling date was coded as an integer due to convergence errors when modelled as a factor in the depth analysis.

Temporal Effects on Seed Bank Viability

Seasonal changes in seed bank viability were quantified directly following the growing season (February), then towards the end of the senescent season (May), and among years (2015 and 2016). Data were analysed using zero/one inflated beta (ZOIB) regression models, which model response variables bound between or equal to 0 or 1, including percent and proportional data. Five candidate models were compared for Rodds Bay and Wiggins Island (global model: *proportion viable seeds~season*year*) using the AIC. Pelican Banks data could not be analysed due to the small sample size.

Temporal and Depth Effects on Seed Bank Viability

The effect of sediment depth (0-20mm, 20-50mm, 50-100mm), season (February and May) and year (2015 and 2016) on the proportion of viable seeds was analysed using zero/one inflated beta (ZOIB) regression models. Eleven candidate models were compared for Rodds Bay and Wiggins Island (global model: *proportion viable seeds~depth*season*year*) using the AIC. Pelican Banks data could not be analysed due to the small sample size.

3 RESULTS

3.1 Long term changes in total seed bank density

Seed bank density changed significantly over time at all sites (*seeds~sampling time*; likelihood ratio tests Pr(chi)<0.001; all sites). At Pelican Banks North, seed bank density ranged from 57 ± 39 seeds m^{-2} (February 2016) to 1160 ± 426 seeds m^{-2} (May 2014) (Figure 3). At Rodds Bay, seed bank density ranged from 113 ± 51 seeds m^{-2} (August 2013) to 1,613 ± 362 seeds m^{-2} (July 2011). At Wiggins Island seed bank density ranged from 114 ± 88 (November 2012) seeds m^{-2} to 1,019 ± 314 seeds m^{-2} (November 2014) (Figure 4). Seed bank data were not quantified at the Wiggins Island meadow in 2013 due to restrictions in site access.

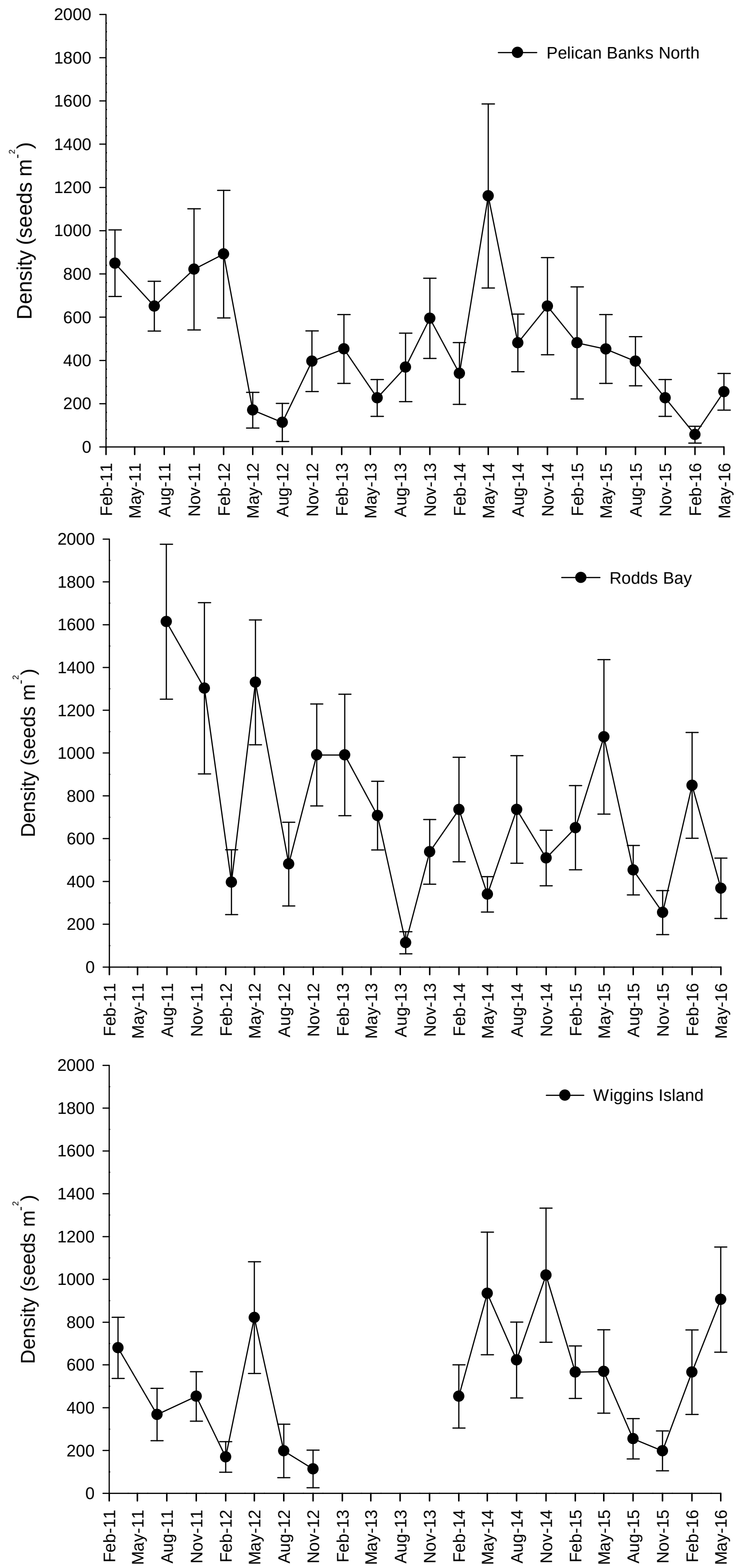


Figure 4. Average seed bank density (± SE) at Pelican Banks, Rodds Bay and Wiggins Island from February 2011 until May 2016. Data were not collected at Wiggins Island in 2013.

At Pelican Banks North, trends in sediment seed bank density in February (following expected peaks in seed release) generally followed trends in peak seagrass percent cover and peak spathe production (in November) the previous year with the exception of 2013/2014 (Figure 5).

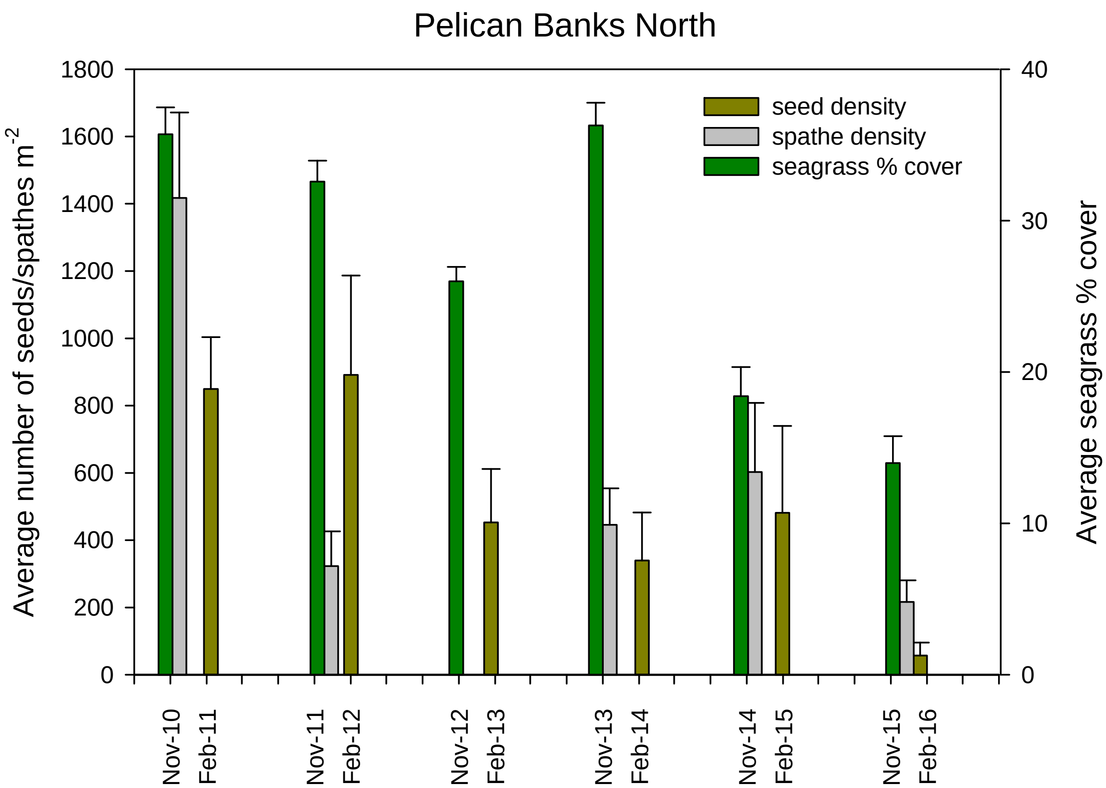


Figure 5. Seagrass percent cover and spathe density at the annual peak in the seagrass growing season (November) and sediment seed bank density in February following expected periods of peak seed production at Pelican Banks North 2010 to 2016. Data are reported as mean ± SE.

3.2 Seasonal changes in total seed bank density

Seed bank density varied significantly among seasons and years at Pelican Banks and Rodds Bay (*seeds~season*year*; likelihood ratio tests Pr(chi)<0.001; both sites). In some years, seed bank densities were greater following the senescent season (May) than after the growing season (February), while in other years the seasonal patterns were reversed (Figure 6). Regardless of year, seed bank density at Wiggins Island was consistently greater in May than February (*seeds~season*; likelihood ratio test Pr(chi)<0.001).

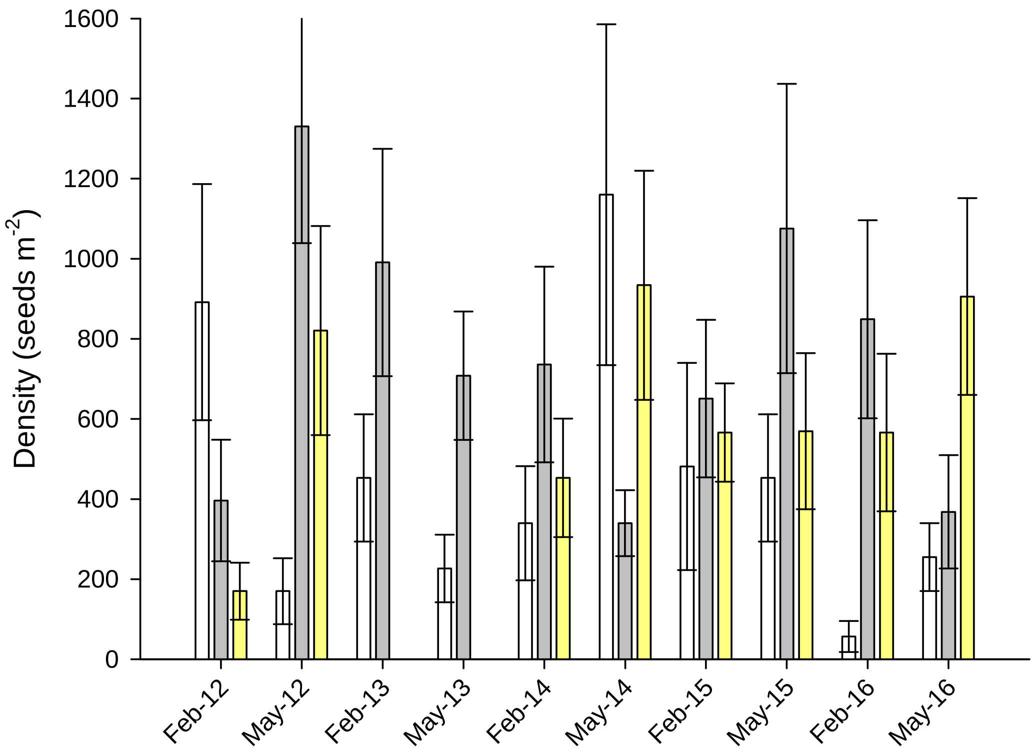


Figure 6. Total seed bank density (mean ± SE) at Pelican Banks (white bars), Rodds Bay (grey bars) and Wiggins Island (yellow bars) following periods of maximum seed production (February) and before the start of the growing season (May). Data were not collected at Wiggins Island in 2013.

3.3 Seed bank density and sediment depth

Across all sites an average of >70% of seeds were found at sediment depths deeper than 20mm (Figure 6). Depth had a significant effect on seed density at Rodds Bay and Wiggins Island, where seed density increased with increasing depth (*seeds~depth*; likelihood ratio tests Pr(chi)<0.001; both sites). Seed density varied with depth and month sampled at Pelican Banks (*seeds~depth*month*; likelihood ratio test Pr(chi)<0.001) (Figure 7).

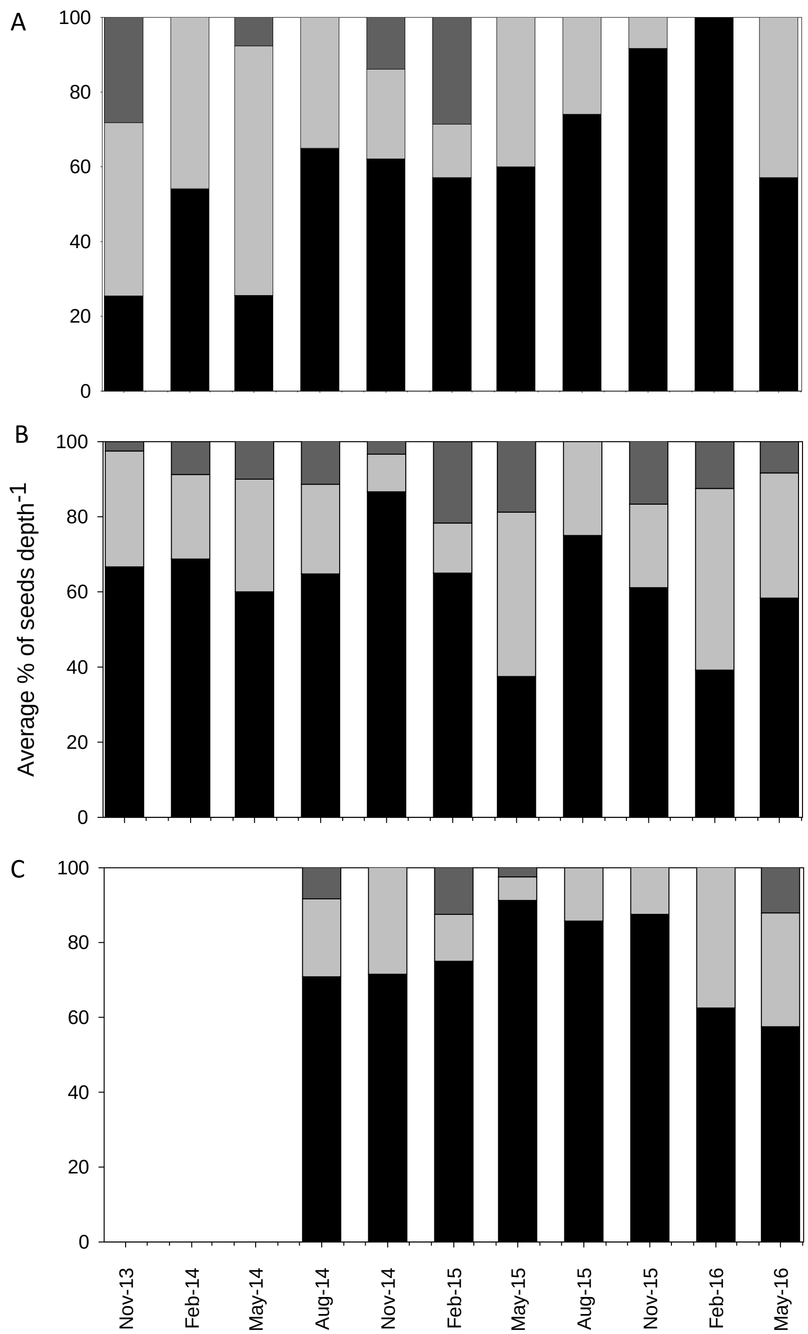


Figure 7. Mean percentage of total (non-viable + viable) *Z. muelleri* seeds at 0-20mm (dark grey), 20-50mm (light grey) and 50-100mm (black) depths for (A) Pelicans Bank, (B) Rodds Bay and (C) Wiggins Island.

3.4 Seed bank viability

At Rodds Bay, the proportion of viable seeds was greater in February (end of growing season) than in May (end of senescent season) in 2015, while seed viability was greater in May in 2016 (Figure 8, Table 1). At Wiggins Island, the proportion of viable seeds declined between February and May in both years, and seed viability was significantly greater in 2015 than 2016 (Figure 8, Table 1). Wiggins Island was characterised as having the lowest proportion (mean = 17 %) of viable seeds among sites. The low number of seeds found at Pelican Banks in 2016 did not allow for statistical analysis of seed viability; however the seeds collected in both February and May samples were all viable (Figure 8).

As with total seed density, the average proportion of viable seeds was greatest at depths of >50mm, except at Rodds Bay where there was an equal split between the average proportion of viable seeds at depths of <50mm and >50mm (Figure 9). When the seed viability data were stratified among depths and the ZOIB models re-run on the expanded data set, the same significant seasonal and annual effects were present at Wiggins Island, while neither depth, season or year were significant for Rodds Bay (Table 2). These results should, however, be interpreted with caution due to the high number of zeros at each site: 94% Rodds Bay and 82% at Wiggins Island, which may skew results. Again, the low number of seeds found at Pelican Banks in 2016 did not allow for statistical analysis of seed viability.

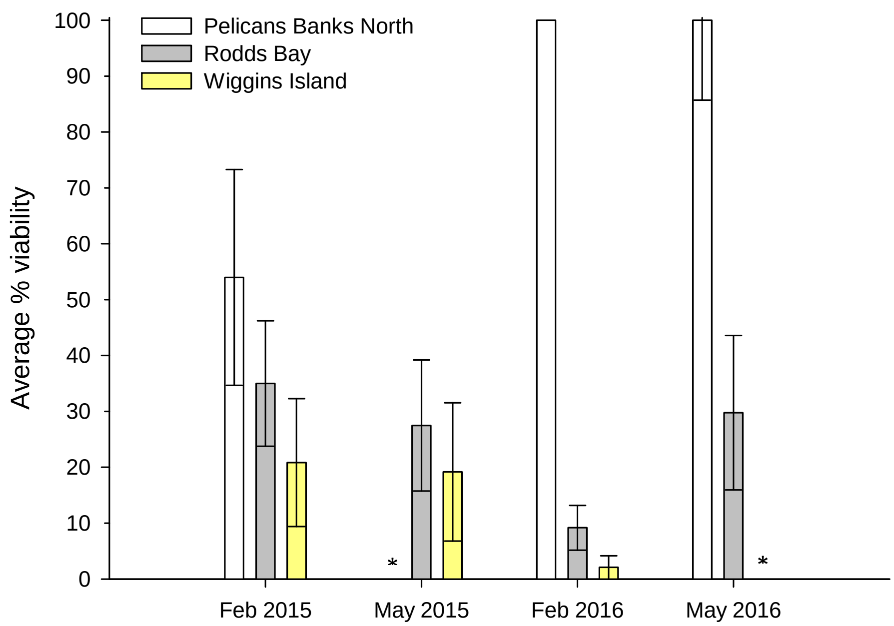


Figure 8. Mean (± SE) percentage of viable seeds in the seed bank at Pelican Banks, Rodds Bay and Wiggins Island following periods of maximum seed production (February) and before the start of the growing season (May). * represents zero viable seeds collected.

Table 1. Zero/One Inflated beta (ZOIB) regression model analysing the effects of season (February/May) and year on proportion of viable seeds. All significant values ($p < 0.05$) are denoted with an *.

Coef.	Est.	SE	t value	p value
RD1				
Zero Inflation Model				
Intercept	-1.050	0.216	-4.853	<0.001*
Beta Model				
Intercept	0.000	0.232	0.000	1.000
Season	-1.109	-0.374	-2.963	0.006*
Year	-1.137	-0.376	-3.028	0.005*
Season:Yr	1.688	-0.569	2.969	0.006*
WW2				
Zero Inflation Model				
Intercept	-2.151	0.389	-5.532	<0.001*
Beta Model				
Intercept	0.000	-0.209	0.000	1.000
Season	-1.034	-0.267	-3.866	<0.001*
Year	-1.56	-0.344	-4.536	<0.001*

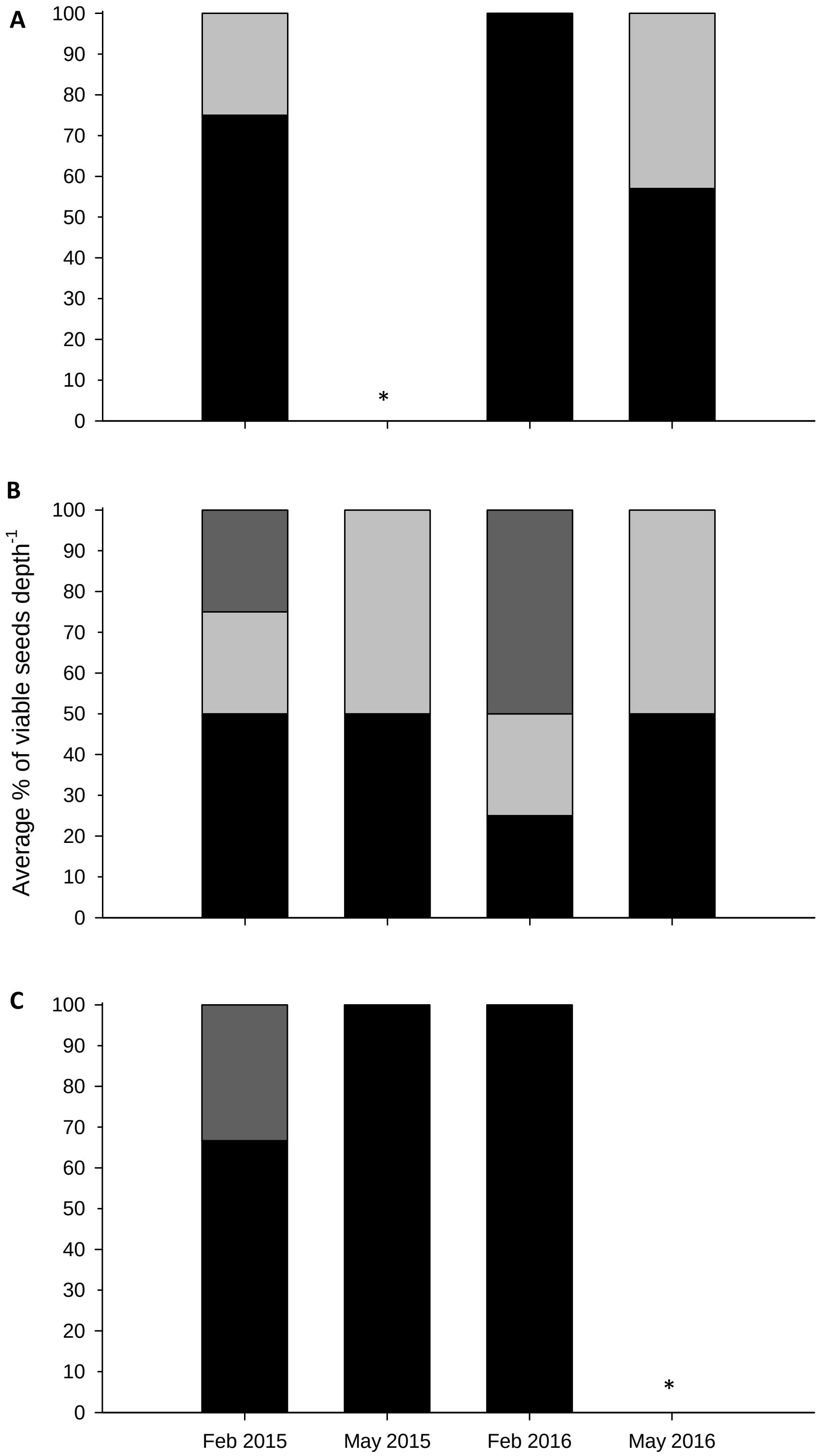


Figure 9. Mean proportion of viable *Z. muelleri* seeds at 0-20mm (dark grey), 20-50mm (light grey) and 50-100mm (black) depths for (A) Pelican Banks North, (B) Rodds Bay and (C) Wiggins Island. * represents no viable seeds collected.

Table 2. Zero/One Inflated beta (ZOIB) regression model analysing the effects of depth, season (Feb/May) and year on proportion of viable seeds. Significant values ($p < 0.05$) are denoted with an *.

Coef.	**Est.**	**SE**	**t value**	**p value**
RD1				
Zero Inflation Model				
Intercept	-0.960	0.262	-3.662	<0.001*
Beta Model				
Intercept	-0.417	0.170	-2.448	0.016*
WW2				
Zero Inflation Model				
Intercept	-2.711	0.375	-7.229	<0.001*
Beta Model				
Intercept	5.285×10^{-16}	0.125	0.000	1.000
Season	-0.899	0.158	-5.690	<0.001*
Year	-1.379	0.199	-6.926	<0.001*

4 DISCUSSION

Quarterly assessments of *Z. muelleri* sediment seed banks in Port Curtis have shown that seed bank densities are relatively high compared with similar populations in subtropical Queensland (Conacher et al. 1994b). We found seeds at all sites during each quarterly sampling event (around February, May, August and November) but temporal trends in seed bank density differed between sites and did not always follow expected seasonal patterns.

The precise timing of seed release in Port Curtis is not well understood and is likely controlled by a suite of environmental factors, such as water temperature, depth, and day length (Conacher et al. 1994b). Quarterly monitoring (around February, May, August and November) at Pelican Banks North since 2009 has shown peaks in spathe density in November each year with lower densities also present in August during some years (Bryant et al. 2016). Flowering is therefore thought to last up to four months over the seagrass growing season (from August to November) but it is possible that flowering extends beyond this period. Given the absence of spathes in February samples, maximum seed release and replenishment of the sediment seed bank is expected to occur towards the end of the growing season (November to January) following peaks in spathe density. At Rodds Bay and Wiggins Island, *Z. muelleri* spathes have not been detected growing locally during routine monitoring since November 2009 (Bryant et al. 2016). Seagrass cover at both sites is significantly lower than at Pelican Banks North and low densities of spathes and/or shorter flowering events may lead to a lack of detection during routine quarterly sampling. Alternatively, these meadows may rely on the dispersal of sexual propagules from nearby donor meadows.

Based on similar studies (Conacher et al. 1994b) and local spathe density data (Bryant et al. 2016), we expected to find higher seed densities in the summer (February) sediment samples immediately following periods of maximum seed production. At Pelican Banks North, seed densities followed these expected trends for some years but seasonal trends for other years and at other sites were less clear. We also expected that seed density would remain stable or decline over the seagrass senescent period (from February to May) due to mortality, predation or the 'secondary dispersal' through biotic or abiotic mechanisms (Kendrick et al. 2012; Orth et al. 2006). However, seasonal analysis often revealed significant increases in seed density over this senescent period, particularly at Wiggins Island where seed densities were consistently higher in May than in February (all years except 2015), but also at Rodds Bay (2012 and 2015) and Pelican Banks (2014 and 2016). If the Wiggins Island and/or Rodds Bay meadows rely in part on the dispersal of sexual propagules from nearby donor meadows, the discrepancy in seasonal seed density results may reflect the time taken for incorporation of donor propagules into the seed bank.

Connectivity between seagrass meadows via dispersal of propagules, including seeds, is essential for maintaining resilience of meadows to large scale disturbance (Kendrick et al. 2012). *Zostera* spp. seeds tend to be negatively buoyant with restricted dispersal distances of only a few meters (Orth et al. 1994) however several mechanisms for the wider dispersal of sexual propagules are described in the literature. Vegetative fragments dislodged by natural processes such as wave action, storm events and grazing herbivores or anthropogenic disturbances such as dredging and anchor or propeller scarring have the ability to carry seeds and reproductive structures distances of 100s of kilometers (Stafford-Bell et al. 2015; McMahon et al. 2014). The spathes containing fruits of *Z. mulleri* remain buoyant for some time once broken off from the parent plant and are commonly seen as rafts of material that offer a mechanism for longer distance dispersal (Stafford-Bell et al. 2015; Källström et al. 2008). Vegetative fragments of *Z. muelleri* in Port Curtis have recently been shown to remain buoyant for an average of three weeks (Weatherall et al. 2016) and similar studies have shown prolonged buoyancy up to five weeks (Stafford-Bell et al. 2015) providing ample time for dispersal to nearby meadows.

Seeds can also be dispersed via the consumption of plant reproductive material by marine herbivores. Tol et al. (In Review) recently documented the consumption and excretion of significant numbers of viable *Z.*

muelleri seeds by dugong and turtle in tropical Queensland and estimated dispersal distances of more than 600km. In Port Curtis, dugong foraging is well documented at all of our seed bank study sites and elsewhere throughout the harbour (Davies et al. 2016; Rasheed et al. 2016) and may play a significant role in the dispersal of seeds between meadows. Further investigations into connectivity between seagrass meadows via biotic and abiotic dispersal mechanisms would enhance our understanding of the resilience of these meadows provided by the sediment seed bank.

Another form of secondary dispersal that may explain unexpected seasonal trends in seed bank density is the movement of seeds within the seed bank after the initial period of incorporation (Kendrick et al. 2012; Orth et al. 2006). Bioturbation by animals living in the sediment (Townsend and Fonesca 1998) as well as wind and storm activity (Hammerstrom et al. 2006) can move seeds both horizontally and vertically within the sediment and may explain increases in seed bank densities outside of periods of maximum seed production. In highly disturbed seagrass meadows, a period of seed dormancy is an obvious advantage, enabling the regeneration of seagrasses even where all plant material has been lost. Storm related secondary dispersal has been shown to expose *Halophila decipiens* seeds formerly buried in the seed bank inducing germination (Hammerstrom et al. 2006). While it is possible these processes may occur in Port Curtis they are currently poorly understood.

Burial depth of seagrass seeds can have a limiting effect on the resilience provided by the seed bank (Jarvis and Moore 2015). Seeds that are buried too deep are effectively removed from the viable seed bank as they are not capable of germinating and successfully producing seedlings once buried beyond a species-specific depth threshold (Jarvis and Moore 2015; Granger et al. 2000). While the effects of burial depth on the viability and germination of *Z. muelleri* are unknown, germination of the similar species *Z. marina* is limited when seeds are buried deeper than 50mm (Jarvis and Moore 2015). In Port Curtis, more than 40% of seeds were found at depths deeper than 50mm during most sampling events. At Pelican Banks North, there was an increasing trend in the proportion of seeds found deeper than 50mm over the majority of the 2015/2016 sampling year. These findings coincide with field observations (in February and May 2016) of changes at the site including an increase in areas of bare sandy sediment and the burial of seagrasses at the site. The resilience to disturbance and capacity for a seagrass meadow to recover following an impact will be directly influenced by factors affecting germination and seedling success (Jarvis and Moore 2015). Bottlenecks in germination of viable seeds due to the depth at which seeds are found may limit the resilience provided by the sediment seed bank for Port Curtis seagrass meadows.

Viability assessments undertaken biannually (February and May) in 2016 found a relatively high proportion of seeds remained viable at both Pelican Banks North and Rodds Bay to initiate recovery over the coming growing season (compared with 2015); however low numbers of seeds detected at Pelican Banks North means that these results should be treated with caution. The increase in the average proportion of viable seeds detected at Rodds Bay (from February to May) was somewhat surprising but provides further evidence of secondary dispersal or that sexual propagules are being supplied from an outside source or through the movement of viable seeds from greater depths. Large dense *Z. muelleri* meadows are found at the entrance to Rodds Bay (Rasheed et al. 2016; Bryant et al. 2014) that may provide seeds via dispersal. The low proportion of viable seeds at Wiggins Island in 2016 means that the meadow is heavily reliant on the remaining adult population and the recruitment of viable fragments or seeds from donor meadows to recover over the coming growing season.

It is not currently known how long the remaining viable seeds will persist in the seed banks in Port Curtis. Decreases in viability have been attributed to germination, predation and mortality (Sumoski and Orth 2012; Fishman and Orth 1996). Further investigation into the change in seed viability over time (persistence) by directly following a cohort of seeds of a known age would help quantify the level of resilience provided by Port Curtis seagrass seed banks.

The high variance recorded in both the total numbers of seeds and seed viability in this study may be typical for many seed banks. Previous studies have found seed banks to be naturally patchy and as such taking many smaller samples is recommended to reduce variation (McFarland and Shafer 2011). In our study, we were limited by the number of samples we could process in the timeframe dictated by the viability sampling methodology (samples collected and processed completely within one week of sampling). Additional samples taken at each site would be expected to reduce variation in the data, however this would come at a substantial logistical cost and expense to ensure viability processing could occur. Establishing the spatial structure of the seed bank across the meadow rather than focusing work at the smaller permanent transect sites may further assist in reducing variability in results, but this was outside the current scope of the study.

5 CONCLUSION & RECOMMENDATIONS

Results of the first two years of this study highlight the complexity of seed bank dynamics in Port Curtis and demonstrate that quantifying resilience provided by sediment seed banks requires moving beyond enumerating densities of seeds to include temporal measurements of seed bank viability. The results to date provide evidence for the presence of a viable sediment seed bank, however this is only the second year of the study and results (particularly for seed viability) should not be considered representative of all years. Sampling over the 2016/2017 will further enhance our understanding of the dynamics of seed banks in Port Curtis and the level of resilience provided to meadows in the region. However, results to date show that viable seeds in the sediment have been maintained during the first two years of the study even at meadows where very little adult seagrass has been found in recent years. This is likely to be critical for the ongoing resilience and capacity for recovery of these seagrass meadows.

Based on the results of the first two years of this study we recommend:

1. Continuing both the seed bank density and viability assessments in order to continue to resolve and quantify the resilience provided by seed banks and to monitor any changes over time.
2. Increasing the number of cores taken at each site to reduce variability in seed bank density and viability data (noting that this would require additional resources and funding due to the requirements for rapid processing of seed viability after collection).
3. Increasing the viability assessments to quarterly to gain a clearer understanding of the patterns of viability decline through the year.

Several additional studies would also greatly enhance our understanding of the resilience provided by *Z. muelleri* sediment seed banks in Port Curtis should additional resources be available. These include:

1. Broader (meadow wide) assessments of the seed bank to establish spatial seed bank structures.
2. Manipulative field studies examining the persistence of *Z. muelleri* seed banks, i.e. changes in viability over time (see Jarvis & Moore 2015).
3. Studies examining the environmental cues for germination and rates of germination and seedling success.
4. Examinations of seed dispersal mechanisms within Port Curtis to assess likely sink and source meadows.

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6 APPENDICES

A) Zero Inflated Poisson distribution models for the effect of sampling date, month and year on total seed density. The best fit model selected for each site is in **bold**.

Site	Candidate models	df	AIC
Wiggins Island	**M3 = seeds ~date**	**17**	**810.9626**
	M6 = month + year	9	815.1149
	M5 = seeds ~month	5	822.1884
	M4 = seeds ~year	6	829.7977
	M1 = seeds ~ 1	2	835.4964
Rodds Bay	**M3 = seeds ~date**	**21**	**1186.178**
	M6 = seeds ~month + year	10	1215.18
	M4 = seeds ~year	7	1219.106
	M1 = seeds ~ 1	2	1249.472
	M5 = seeds ~month	5	1255.419
Pelican Banks North	**M3 = seeds ~date**	**22**	**987.035**
	M4 = seeds ~year	7	992.0939
	M6 = seeds ~month + year	10	992.171
	M1 = seeds ~ 1	2	1004.623
	M5 = seeds ~month	5	1007.01

B) Zero Inflated Poisson distribution models for the effect of season and year on total seed density. The best fit model selected for each site is in **bold**.

Site	Candidate models	df	AIC
Wiggins	**M3 = seeds ~season**	**3**	**444.8981**
	M5 = seeds ~season*year	9	446.9807
	M4 = seeds ~ season + year	6	448.5634
	M1 = seeds ~ 1	2	455.7197
	M2 = seeds ~year	5	458.6982
Rodds	**M5 = seeds ~season*year**	**11**	**616.595**
	M2 = seeds ~year	6	631.5938
	M1 = seeds ~ 1	2	632.1245
	M4 = seeds ~ season + year	7	633.5265
	M3 = seeds ~ season	3	634.1183
Pelicans	**M5 = seeds ~season*year**	**11**	**452.5731**
	M2 = seeds ~year	6	461.9639
	M4 = seeds ~ season + year	7	463.7872
	M1 = seeds ~ 1	2	478.6915
	M3 = seeds ~ season	3	480.451

C) Zero Inflated Poisson distribution models for the effect of depth and sampling date on total seed density. The best fit model selected for each site is in **bold**.

Site	Candidate models	df	AIC
Wiggins Island	**M2 = seeds ~depth**	**4**	**440.6683**
	M4 = seeds ~depth + date)	5	442.3454
	M5 = seeds ~depth * date	7	442.9182
	M1 = seeds ~ 1	2	546.8661
	M3 = seeds ~ date	3	548.8656
Rodds Bay	**M2 = seeds ~depth**	**4**	**684.0321**
	M4 = seeds ~depth + date	5	685.3178
	M5 = seeds ~depth * date	7	688.0349
	M1 = seeds ~ 1	2	758.8385
	M3 = seeds ~ date	3	760.6384
Pelican Banks North	**M5 = seeds ~depth * date**	**7**	**563.3461**
	M4 = seeds ~depth + date	5	573.6905
	M2 = seeds ~depth	4	579.1468
	M3 = seeds ~ date	3	624.879
	M1 = seeds ~ 1	2	627.9335

D) Zero/One Inflated Beta distribution models for the effect of season and year on proportion of viable seeds. The best fit model selected for each site is in **bold**.

Site	Candidate models	df	AIC
Wiggins Island	**M4 = viable ~ season + year**	**6**	**45.27049**
	M5 = viable ~ season*year	7	47.27049
	M1 = viable ~ 1	4	49.06782
	M3 = viable ~ year	5	49.42322
	M2 = viable ~ season	5	50.90837
Rodds Bay	**M5 = viable ~ season*year**	**7**	**60.08347**
	M1 = viable ~ 1	4	63.6160
	M3 = viable ~ year	5	64.51460
	M2 = viable ~ season	5	64.68058
	M4 = viable ~ season + year	6	65.11945

E) Zero/One Inflated Beta distribution models for the effect of depth, season and year on proportion of viable seeds. The best fit model selected for each site is in **bold**.

Site	Candidate models	df	AIC
Wiggins Island	**M6 = viable ~ season + year**	**6**	**57.44447**
	M10 = viable ~ season*year	7	59.44447
	M1 = viable ~ 1	4	64.17607
	M4 = viable ~ year	5	64.21248
	M3 = viable ~ season	5	66.01744
	M2 = viable ~ depth	5	66.17607
	M7 = viable ~ depth + year	6	66.21248
	M5 = viable ~ season + depth	6	68.01744
	M9 = viable ~ year*depth	7	68.21248
	M11 = viable ~ season*depth*year	12	69.44447
	M8 = viable ~ season*depth	7	70.01744
Rodds Bay	**M1 = viable ~ 1**	**4**	**132.9921**
	M3 = viable ~ season	5	133.5647
	M2 = viable ~ depth	5	134.7968
	M4 = viable ~ year	5	134.9919
	M5 = viable ~ season + depth	6	135.3973
	M10 = viable ~ season*year	7	135.4659
	M6 = viable ~ season + year	6	135.5484
	M7 = viable ~ depth + year	6	136.7863
	M8 = viable ~ season*depth	7	137.0278
	M9 = viable ~ year*depth	7	138.2361
	M11 = viable ~ season*depth*year	11	140.8433