Vegetative fragment production as a means of propagule dispersal for tropical seagrass meadows

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ABSTRACT

Background and aims: Long distance dispersal (LDD) contributes to the replenishment and recovery of tropical seagrass habitats exposed to disturbance, such as cyclones and infrastructure development. However, our current knowledge regarding the physical attributes of seagrass fragments that influence LDD predominantly stems from temperate species and regions. The goal of this paper is to measure seagrass fragment density and viability in two tropical species, assessing various factors influencing their distribution.

Methods: We measured the density and viability of floating seagrass fragments for two tropical seagrass species (*Zostera muelleri* and *Halodule uninervis*) in two coastal seagrass meadows in the central Great Barrier Reef World Heritage Area, Australia. We assessed the effect of wind speed, wind direction, seagrass growing/senescent season, seagrass meadow density, meadow location and dugong foraging intensity on fragment density. We also measured seagrass fragment structure and fragment viability; i.e., potential to establish into a new plant.

Key results: We found that seagrass meadow density, season, wind direction and wind speed influenced total fragment density, while season and wind speed influenced the density of viable fragments. Dugong foraging intensity did not influence fragment density. Our results indicate that wave action from winds combined with high seagrass meadow density increases seagrass fragment creation, and that more fragments are produced during the growing than the senescent season. Seagrass fragments classified as viable for *Z. muelleri* and *H. uninervis* had significantly more shoots and leaves than non-viable fragments. We collected 0.63 ($\pm$0.08 SE) floating viable fragments 100 m^{-2} in the growing season, and 0.13 ($\pm$0.03 SE) viable fragments 100 m^{-2} in the senescent season. Over a third (38%) of all fragments collected were viable.

Conclusion: There is likely to be a large number of viable seagrass fragments available for long distance dispersal. This study's outputs can inform dispersal and connectivity models that are used to direct seagrass ecosystem management and conservation strategies.

1. Introduction

Dispersal underpins the resilience of a species, its genetic diversity, and its ability to colonize new habitats or to recover from loss (Cowen et al., 2006; Van der Stocken et al., 2019). It allows for the spread of seeds or propagules, enabling plants to establish populations in favourable locations, escape competition, and adapt to changing environments, ultimately ensuring species' long-term persistence. Information on dispersal mechanisms is important for the design of effective management and conservation actions (Clobert et al., 2001; Van der Stocken et al., 2019).

To quantify dispersal potential, it is important to estimate the density of propagules and to understand the requirements for growth and survival if an organism is to successfully establish and persist (Bonte et al., 2012; Baguette et al., 2013). The capacity for propagules to disperse is influenced by wind, current, oceanic swells and tidal flows, and survival time (Kendrick et al., 2012; Baguette et al., 2013; Lai et al. 2018, 2020). Plants which primarily disperse abiotically, are limited to locations of suitable environmental conditions (e.g., sediment type, exposure, and depth) (McMahon et al., 2014; Sherman et al., 2018). Many factors must align before and after settlement for dispersal to be successful. Therefore, successful dispersal requires the production of large numbers of
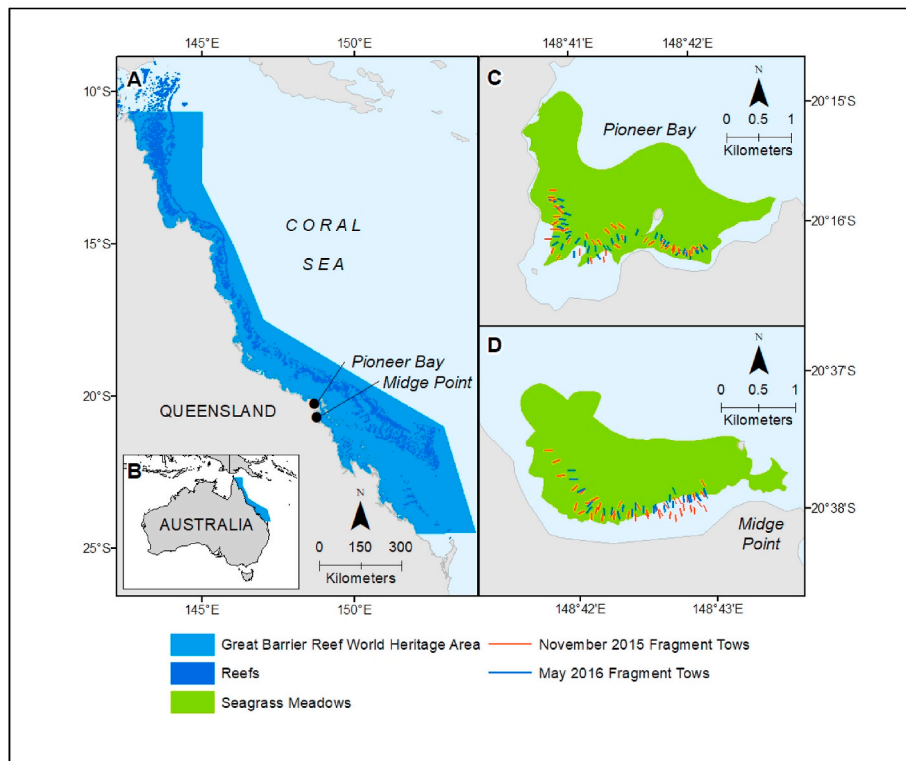
Fig. 1. Study site map, showing the location of the Great Barrier Reef World Heritage Area relative to **(A)** Queensland and **(B)** Australia, and fragment tow locations in **(C)** Pioneer Bay and **(D)** Midge Point seagrass meadows.

propagules or viable plant fragments to mitigate the low probability of settling at an appropriate location (Bonte et al., 2012; Baguette et al., 2013).

Quantifying dispersal attributes is necessary to inform biophysical models of dispersal and connectivity (Kendrick et al., 2012; Grech et al., 2018). These models can then be used for more effective management and restoration programs by predicting recovery potential based on whether subpopulations within a metapopulation are highly connected or isolated (Källström et al., 2008; Grech et al. 2016, 2018; Jahnke et al., 2020). For seagrass, an ecological grouping of marine angiosperms, high levels of connectivity among meadows supports species replenishment and recovery after disturbance events, such as cyclones and large floods (Cowen et al., 2006; Grech et al., 2018). Quantifying the physical and biological factors (Erftemeijer et al., 2008; Källström et al., 2008; Grech et al., 2016) that enable propagule creation and dispersal is key to understanding how populations of seagrass function in an ecological network (Kendrick et al., 2012).

Seagrasses are marine angiosperms that can flower and fruit submerged in seawater (Hemminga and Duarte 2000; Larkum et al., 2006), but are also capable of growing clonally through asexual growth by rhizomes (Hemminga and Duarte 2000; Larkum et al., 2006). Seagrass seeds are generally negatively buoyant and settle close to the parent plant if no other dispersal vectors are involved (Orth et al., 2006b; Kendrick et al., 2012; McMahon et al., 2014). Dispersal of seagrass propagules and fragments can be aided by biotic processes (e.g., ingestion and excretion of seagrass seeds by marine herbivores; Charalambidou et al., 2003; Sumoski and Orth 2012; Wu et al., 2016; Tol et al., 2017) or abiotic vectors (e.g., waves and currents; Erftemeijer et al., 2008, Källström et al., 2008; Thomson et al., 2014, Smith et al., 2018). Long distance (>100s of metres) abiotic dispersal of seagrass can occur through the movement of viable propagules such as buoyant vegetative fragments (e.g. Thomson et al., 2014; Smith et al., 2018) or through seeds attached to rafting seagrass (e.g. Erftemeijer et al., 2008; Källström et al., 2008) via wind and tidal currents. Fragments of seagrass

can be uprooted by strong tidal and wave action and remain viable in the water column for prolonged periods (Harwell and Orth 2002; Hall et al., 2006; Berković et al., 2014; Lai et al., 2020). For these fragments to successfully settle, they must lose buoyancy and/or encounter the substrate in a location compatible with growth (i.e., appropriate light and sediment) (Kendrick et al., 2012; McMahon et al., 2014; Lai et al., 2018). The final step is establishment, which involves the anchoring of the fragment by root growth preventing further dislodgement (Kendrick et al., 2012; McMahon et al., 2014; Lai et al., 2018). All these steps need to be achieved for a fragment to be 'successfully dispersed' (McMahon et al., 2014; Lai et al., 2018).

Seagrasses grow along all continental coastlines except Antarctica (Hemminga and Duarte 2000; Green and Short 2003; Larkum et al., 2006). Seagrass habitats provide important ecosystem services, such as commercial fisheries habitat (Watson et al., 1993; Unsworth et al., 2010), stabilisation of sediments that prevent coastal erosion (Hemminga and Duarte 2000; Potouroglou et al., 2017), absorption of nutrients (Mellors et al., 2005), and keeping coral reefs healthy by filtering pathogens and particulates from the water column (Lamb et al., 2017). In some locations they can be a valuable mechanism for carbon sequestration (Kennedy et al., 2010; Macreadie et al., 2014). Despite their importance, seagrass meadows are not well protected in most of the world and have been declining globally due to multiple impacts (Waycott et al., 2009; Dunic et al., 2021; Turschwell et al., 2021). The human population is greatest in coastal regions (Creel 2003; Neumann et al., 2015), which exposes seagrass meadows to multiple stressors (Waycott et al., 2009; Grech et al., 2011). These stressors include but are not limited to increased nutrient loads from agricultural and urban run-off, coastal development, hydrological alterations, damaging fishing practices, and extreme weather events (Orth et al., 2006a; Waycott et al., 2009; Grech et al., 2011).

Tropical seagrasses are known to differ in their morphology (e.g., smaller, and shorter blades) and biology (e.g., fast growing) compared to temperate species, which can impact dispersal (Short et al., 2007).

Models have been used to estimate spatial scales of seagrass dispersal and the levels of connectivity; however, most variables used are specific to temperate species or are based on a range of assumptions (such as wind drift coefficient and survival/decay time) which could render them inaccurate for tropical species (Erftemeijer et al., 2008; Källström et al., 2008; Ruiz-Montoya et al. 2012, 2015; Grech et al. 2016, 2018). The limited information available on seagrass propagule dispersal is mostly concentrated on buoyancy and not on availability and potential viability of fragments (viability of fragments is measured by the presence of roots, rhizomes, leaves and a growing tip/apical meristem; Hall et al., 2006; Källström et al., 2008; Thomson et al., 2014; York et al., 2017), and quantitative information on these biological variables is incomplete (Kendrick et al., 2012; McMahon et al., 2014).

In the Great Barrier Reef World Heritage Area (GBRWHA) in northeastern Australia (Fig. 1), seagrass meadows are foraging grounds for endangered green sea turtles (*Chelonia mydas*), and for one of the last remaining large populations of dugong (*Dugong dugon*) (Marsh et al., 2011; Jensen et al., 2016). Green sea turtles and dugongs may create seagrass fragments when foraging (Kendrick et al., 2012; McMahon et al., 2014); however their differing feeding styles can complicate our ability to estimate feeding efforts. Green sea turtles predominately crop leaves when consuming seagrass (Bjorndal 1980), making it difficult to identify turtle foraging impacts within a meadow. Dugongs commonly forage in an 'excavation' style, where they remove the entire shoot (leaves, rhizomes, and roots) and leave behind visible bare serpentine indentations in the meadow [Supplementary Fig. S1]. Unlike with green sea turtles, the dugong foraging style provides an easy measure of herbivore feeding within a meadow over a short time frame (Nakanishi 2005; Nakanishi et al., 2006; Tol et al., 2016). Dugongs are known to interact with seagrass meadows and can stimulate new growth through grazing (Preen 1995) or move seeds through their faeces (Tol et al., 2017), however their role in propagule (fragment) creation and dispersal has not been quantified.

The goal of our study was to quantify the number of fragments on the sea surface available for dispersal for two common tropical seagrass species in the GBRWHA (*Zostera muelleri* and *Halodule uninervis*), and to assess the attributes (structure, morphology, and viability) of seagrass fragments. We measured the number of total and viable fragments and describe the average fragment's characteristics. We quantify which factors (growing/senescent season, wind speed, wind direction, seagrass meadow density, and dugong foraging intensity) influence the formation and numbers of floating fragments. Our analysis provides critical inputs to dispersal and connectivity models that are used to inform seagrass ecosystem management and conservation.

2. Materials and Methods

2.1. Data collection

Positively buoyant seagrass fragments were collected from sheltered seagrass meadows at Pioneer Bay and at Midge Point in the central GBRWHA, Queensland Australia (Fig. 1). Both meadows have minimal boat/anchor traffic and a similar species composition [Supplementary Data Table S2].

Seagrass fragments were collected during the growing season (September to February) and senescent season (March to August, a period of slowed growth in the tropics) for tropical seagrass species in the southern hemisphere (Sherman et al., 2018). A total of 156 tows were conducted during the growing season (21–26th November 2015; Pioneer Bay n = 78 and Midge Point n = 78), and 130 tows were performed during the senescent season (4–8th May 2016; Pioneer Bay n = 78 and Midge Point n = 65). Seagrass fragments were collected from the water's surface by towing two partially buoyant nets (mesh size 0.5 cm), one on either side of the vessel, along a 100 m transect perpendicular to the coast, commencing within 30 minutes after high tide. Each net was attached to a 1 × 1 m frame; the top edge of the opening was positioned approximately 30 cm above and the bottom edge 70 cm below the water surface, to ensure all floating fragments in its path were captured.

We defined a fragment as any detached piece of seagrass where a rhizome and a leaf or leaves were present (Ewanchuk and Williams 1996; Hall et al., 2006). Fragment characteristics were recorded for each species, including presence of reproductive organelles and roots, number of shoots and leaves, length of leaves and rhizome (mm), and biomass (g dry weight). Viability of each fragment was assessed by the presence of a growing tip or apical meristem (Ewanchuk and Williams 1996). All fragments were dried in an oven at 60 °C up to 72 h to obtain a constant dry weight for biomass.

Seagrass meadow density and dugong foraging intensity were estimated from quadrats placed haphazardly within meadows exposed during low tides. Seagrass density was estimated at each sampling location and seasonal event using shoot counts for each species. Shoot counts were conducted in each meadow using ten 0.25 m^2 quadrats; four 0.01 m^2 quadrats were placed within each 0.25 m^2 quadrat, with the average shoot count for each species within the 0.01 m^2 quadrat extrapolated up to 1 m^2 values. Dugong foraging intensity was estimated for every sampling day by counting the presence of dugong feeding trails in 100 × 1 m^2 quadrats. Dugong foraging intensity was calculated for each high tide by subtracting the total number of quadrats with feeding trails at low tide for Time 0 (the low tide preceding high tide fragment tows) from the number of quadrats with feeding trails at Time 1 (the low tide following fragment tows). Wind data (wind speed km/h and wind direction) was obtained from the Australian Bureau of Meteorology Hamilton Island airport weather station (Station number 033106); located approximately 45 km from both meadows. Wind speed was averaged for the 12 h before towing began each sample day and assigned to the Beaufort Scale levels: 2 = 6–11 km/h, 3 = 12–19 km/h, 4 = 20–28 km/h, and 5 = 29–38 km/h. Wind direction was grouped into three categories: east, southeast, and south. North, northeast, and northwest winds were not present during our sample times, which is consistent with the climate of the sampling period.

2.2. Statistical analysis

Differences in shoot count, leaf count, leaf length, rhizome length and biomass between viable and non-viable fragments for each species (*Z. muelleri* and *H. uninervis*) were analysed using a Mann-Whitney *U* Test, as the data did not conform to a normal distribution. To ensure a robust statistical analysis, fragments were pooled across sites.

Statistical analyses for seagrass fragment density were conducted for *Z. muelleri* and *H. uninervis* combined due to their morphological similarities (both being strap blade species) (Coles et al., 2002; Waycott et al., 2004). A set of global models were used to quantify the effects of season (S), meadow location (ML), meadow density (MD), dugong foraging intensity (DFI), wind speed (WS) and wind direction (WD) on counts of total seagrass fragments ($F_t = S + ML + MD + DFI + WS + WD$) and viable seagrass fragments ($F_v = S + ML + MD + DFI + WS + WD$). Subsets of each global model were ranked using the dredge function in the 'MuMIn' package (Barton 2019). The best-fit model was considered that with the lowest Akaike Information Criterion corrected for small sample sizes (AICc) (Burnham and Anderson 2002; Glatting et al., 2007). The best fit model for total fragments was $F_t = S + MD + WS + WD$, while the best fit model for viable fragments was $F_v = S + WS$. We used generalized linear models (GLM) with a negative binomal distribution using the 'MASS' package (Venables and Ripley 2002). A negative binomal distribution was selected to correct for overdispersion of count data (Lindén and Mäntyniemi 2011). Residuals were inspected visually for patterns by plotting the fitted versus response variables. Tukey post hoc for pairwise comparisons were computed using the 'emmeans' package (Lenth 2020).

A small number of *Halophila ovalis* fragments were collected during this experiment, however the sample size was too small for statistical analysis.

Table 1
Number of seagrass fragments (total and viable) collected from Pioneer Bay and Midge Point in November 2015 (growing season) and May 2016 (senescent season).

	Total Fragments			Viable Fragments		
	Z. muelleri	H. uninervis	H. ovalis	Z. muelleri	H. uninervis	H. ovalis
Pioneer Bay						
November 2015	115	6	3	33	3	1
May 2016	12	24	2	6	5	1
Midge Point						
November 2015	101	12	0	56	6	0
May 2016	1	33	1	0	6	0

All data prior to analysis was examined for outliers and normality, and predictor variables assessed for collinearity using variance inflation factors (Zuur et al., 2010). All statistical analyses were conducted in the statistical software environment R (R version 4.1.0; R Core Team 2020).

3. Results

A total of 264 fragments were collected in the growing season (*Z. muelleri* = 91%; *H. uninervis* = 8%; *H. ovalis* = 1%) and 46 fragments in the senescent season (*Z. muelleri* = 18.5%; *H. uninervis* = 80%; *H. ovalis* = 1.5%). Just over one third of all fragments collected were classified as viable (38%; Table 1). Nearly all fragments collected at both locations and seasons had roots present (96%). Five fragments had fruits/seeds attached, all of which were collected in the growing season; one *H. uninervis* fragment with a seed attached (from Pioneer Bay), one *H. ovalis* fragment with a fruit attached (from Pioneer Bay) and three *Z. muelleri* fragments with spathes attached (two from Pioneer Bay and one from Midge Point) (Fig. 2).

Viable *Z. muelleri* fragments had more shoots and leaves, and longer rhizomes, but shorter leaves than non-viable fragments (Shoot count: W = 4679.5, p = <0.0001; Leaf count: W = 4555.5, p = <0.0001; Rhizome length: W = 6023, p = <0.0001; Leaf length W: = 12,462, p = 0.0257; Fig. 3) [Supplementary Data Table S3]. An average viable *Z. muelleri* fragment had 2.5 ± 0.1 shoots, 7.1 ± 0.4 leaves, an average leaf length of 28 ± 1 mm, a rhizome length of 26 ± 2 mm, and weighed 0.026 ± 0.001 g. Viable *H. uninervis* fragments had more shoots and leaves than non-viable fragments, but no difference in leaf and rhizome lengths (Shoot count: W = 255, p = 0.0006; Leaf count: W = 190.5, p = <0.0001; Fig. 3) [Supplementary Data Table S4]. An average *H. uninervis* viable fragment had 2.1 ± 0.2 shoots, 4.5 ± 0.6 leaves, an average leaf length of 20 ± 1 mm, a rhizome length of 19 ± 2 mm, and weighed 0.005 ± 0.001 g. There was no difference in biomass for both *Z. muelleri* and *H. uninervis* viable and non-viable fragments (Fig. 3) [Supplementary Data Table S4]. Only 18% of all fragments had greater than two shoots, with the maximum number being six shoots for *Z. muelleri*, five shoots for *H. uninervis* and four shoots for *H. ovalis*.

There was a significant and positive relationship between the number of total fragments and seagrass meadow density (Shoot count: LRχ^2_1 = 5.47, p = 0.02; Fig. 4a) [Supplementary Data Table S5], and there were more total fragments during the growing season (Season: LRχ^2_1 = 19.76, p = <0.001; Fig. 4b), when winds were a moderate breeze (Beaufort Wind Scale 4) (Wind speed: LRχ^2_3 = 17.38, p = 0.0006; Tukey post hoc, p < 0.05; Fig. 4c), and during south-easterly winds (Wind direction: LRχ^2_2 = 9.25, p = 0.001; Fig. 4d).

There were significantly more viable fragments during the growing season (0.63 ± 0.08 fragments 100 m^{-2}) than the senescent season (0.13 ± 0.03 fragments 100 m^{-2}) (Season: LRχ^2_1 = 42.16, p = <0.001; Fig. 5a) [Supplementary Data Table S6]. Moderate winds (Beaufort 4 = 20–28 km/h) produced significantly more total fragments than lower winds (Wind speed: LRχ^2_2 = 6.71, p = 0.03; Tukey post hoc, p < 0.05; Fig. 5b) [Supplementary Data Tables S5 and S6]. Dugong foraging intensity and meadow location had no effect on the number of total fragments or viable fragments.

4. Discussion

Our study quantified seagrass fragment numbers in two tropical coastal seagrass meadows. Over one third of fragments floating freely in the water were viable. If these fragments settle in a location with suitable environmental conditions, they have the potential to establish as a new plant and contribute to seagrass meadow growth and connectivity (Hall et al., 2006). At our study locations in the GBRWHA of Queensland, Australia, total fragment density was influenced by seagrass meadow density, season, wind speed and wind direction. Viable fragment density was influenced by season and wind speed. Surprisingly, foraging by the large herbivorous dugong did not affect seagrass fragment density.

Less than 2% of all fragments collected in our study had a fruit/spathe attached, indicating that abiotic dispersal is mainly of non-reproductive shoots. Viable fragments for *Z. muelleri* and *H. uninervis* had more shoots and shorter leaves than non-viable fragments. A greater number of shoots and shorter leaves on viable fragments is expected, as new young shoots would have a mean shorter leaf length compared to older shoots. Previous research has found that fragments can continue to grow in the water column when a growing tip or apical meristem is present (Hemminga and Duarte 2000; Larkum et al., 2006; Thomson et al., 2014). Our findings of more shoots with shorter leaves on viable fragments suggest that our viable fragments are continuing to grow when in the water column. Conversely, when a fragment is incapable of rhizome extension from a growing tip, they could re-direct growth into leaves (Hemminga and Duarte 2000; Larkum et al., 2006). This might explain why our *Z. muelleri* viable fragments had longer rhizomes, and why non-viable fragments had longer leaves. Our results complement other studies that found viable floating fragments continue to grow in the water column, increasing their ability to establish into a new plant if they settle in a suitable environment (Kendrick et al., 2012; McMahon et al. 2014, 2018).

We found that the total number of seagrass fragments was dependent on seagrass meadow density, season, wind speed and wind direction, while the number of viable seagrass fragments was dependent on season and wind speed only. As seagrass meadow density and meadow area
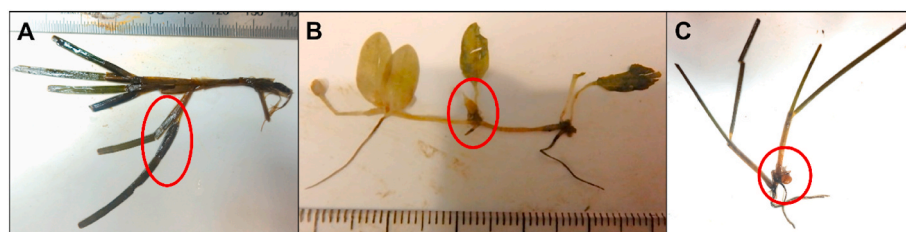

Fig. 2. Seagrass fragments collected floating on the water's surface in November 2015 at study site; **A)** *Zostera muelleri* fragment with spathes attached, **B)** *Halophila ovalis* fragments with an immature fruit attached, and **C)** a *Halodule uninervis* fragment with a seed attached.
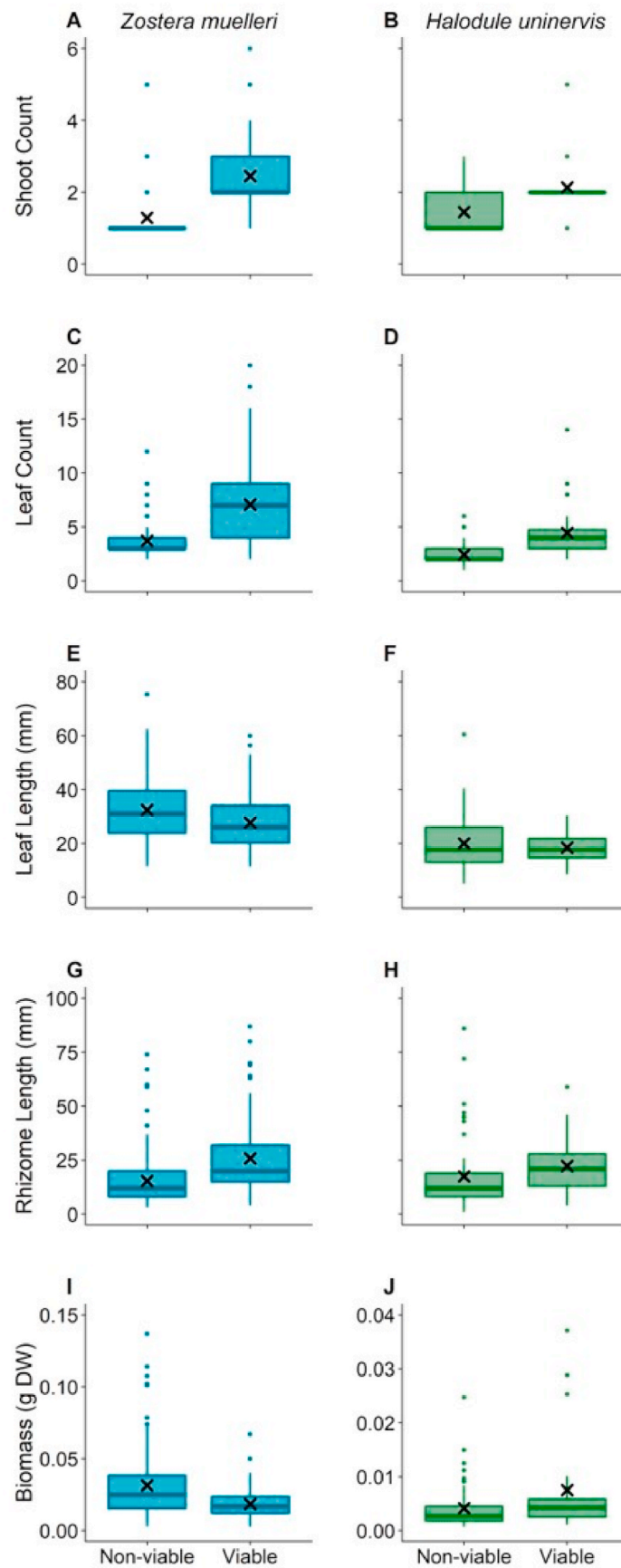
Fig. 3. Boxplots of floating seagrass fragment characteristics for *Zostera muelleri* (n = 93 viable and n = 136 non-viable) and *Halodule uninervis* (n = 22 viable and n = 53 non-viable); **X** depicts the mean value.
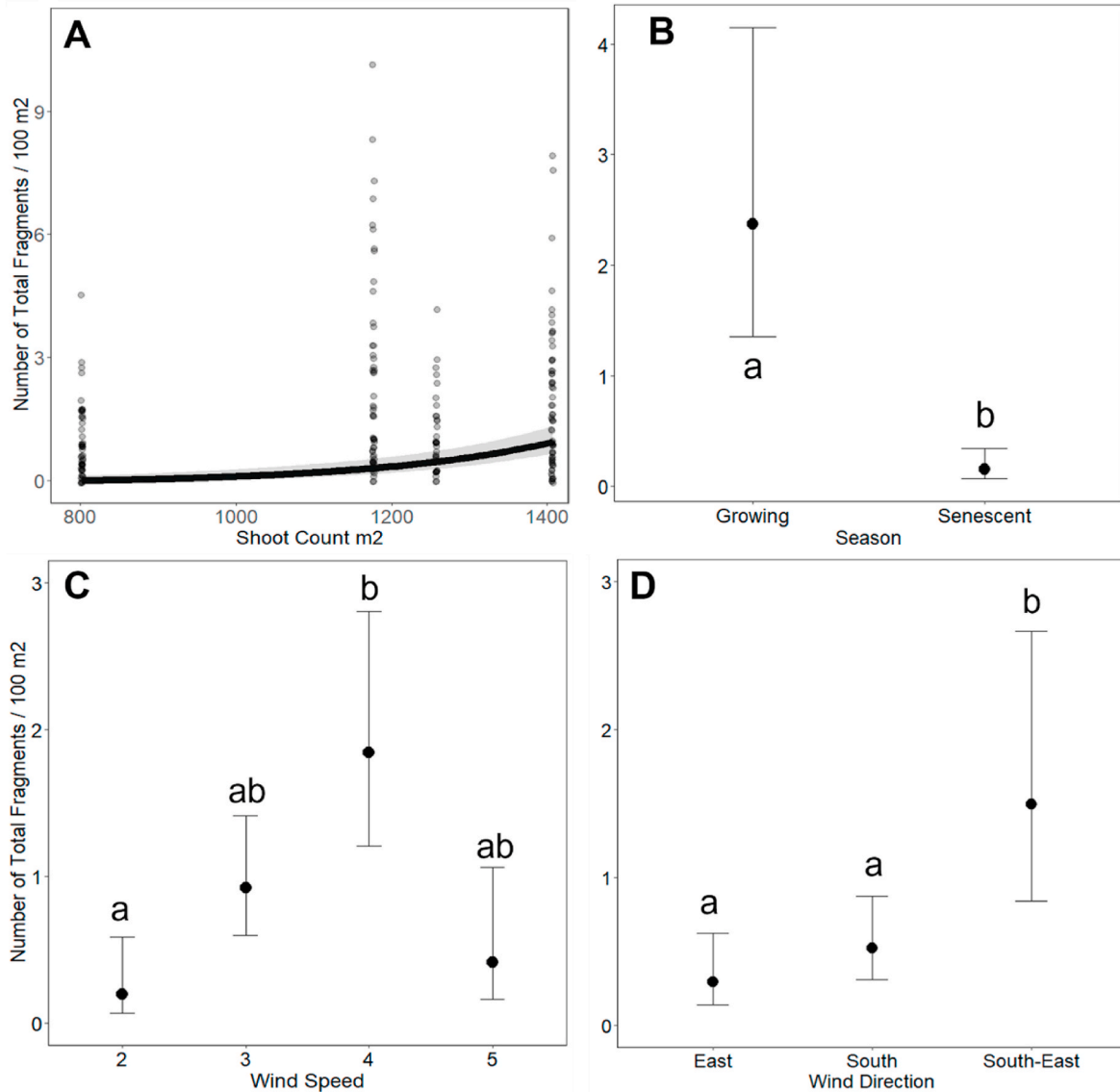
Fig. 4. Number of total seagrass fragments by **A)** shoot count 100 m^{-2} (95% CI); **B)** season; **C)** wind speed (Beaufort Scale: 2 = 6–11 km/h, 3 = 12–19 km/h, 4 = 20–28 km/h, and 5 = 29–38 km/h); and **D)** wind direction. Different letters above the bars indicate statistically significant differences (Tukey post hoc, p < 0.05).

increases, there are more plants available for the creation of fragments. Meadow density and area also influenced the dominant fragment species type. More *Z. muelleri* fragments were present in the water during the growing season when this species has the highest meadow density. In the senescent season, when *H. uninervis* is dominant in the meadows, its fragments were more common in the water. There were nearly five times more viable fragments floating on the water's surface during the seagrass growing season compared to the senescent season. Many seagrass species (including *H. uninervis* and *Z. muelleri*) grow during the warmer months and are dormant during the cooler months (Marba et al., 1996; Waycott et al., 2004; Chartrand et al., 2016; Sherman et al., 2018). Increased growth during the growing season would produce greater volumes of growing tips compared to the senescent season, increasing the chance of growing tips being present on a fragment.

Physical disturbance by waves, an effect of wind speed and direction, may create seagrass fragments either due to sediment erosion or through rhizome breakage (Kendrick et al., 2012; McMahon et al., 2014). Our study found significantly more fragments in the water during times of moderate wind speed (20–28 km/h) and when the wind direction was ideal for moving fragments away from the meadow into the ocean (i.e., south-easterlies). Low winds produce low energy waves with little

impact on the seabed (Donelan et al., 2012), with few fragments likely to be produced. At low wind speeds fragment drift speeds will be similar to tidal flows (Ryan et al., 2018), and fragments may not be dispersed into coastal waters. At the other end of the scale, high winds can cause wave crests to break, inducing turbulence which can reduce fragment movement (Simeone et al., 2013). Wind direction also has the potential to wash fragments on to the adjacent shore as wrack before they leave the source meadow. Exposure to wind (fetch) has been identified as one of the most important factors in predicting the presence of seagrass meadows in the GBRWHA (Carruthers et al., 2002; Grech and Coles 2010). This is also evident in extreme weather events, such as storms, cyclones, and hurricanes, where high sediment turnover leads to the erosion of seagrass meadows (Carruthers et al., 2002; Orth et al., 2006a; Pollard and Greenway 2013; McKenna et al., 2015). Our study supports this through a new line of evidence, as high wind and waves (and high levels of energy in the system) would make it less likely for propagules in the form of fragments to be available for dispersal and replenishment.

We expected that active foraging by dugongs would increase the density of seagrass fragments (Kendrick et al., 2012; McMahon et al., 2014; York et al., 2017), as direct grazing and bioturbation by herbivores is theorised to create fragments/propagules (Figuerola and Green
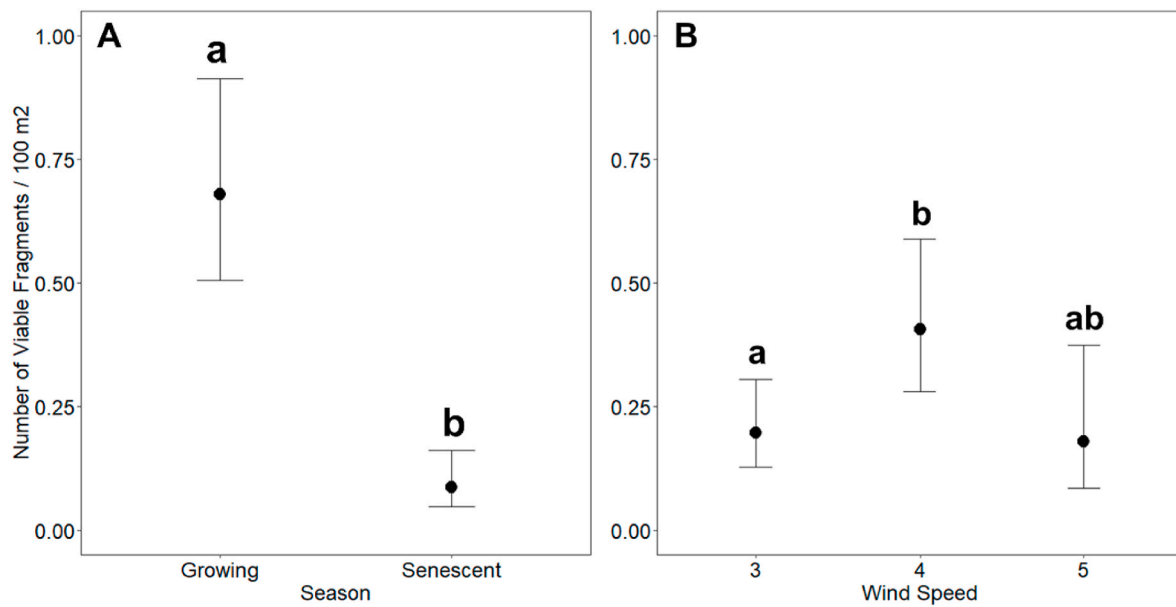
Fig. 5. Average number of viable seagrass fragments 100 m^{-2} by **A)** season, and **B)** wind speed (Beaufort Scale: 3 = 12–19 km/h, 4 = 20–28 km/h and 5 = 29–38 km/h. Different letters above the bars indicate statistically significant differences (Tukey post hoc, p < 0.05).

2002; Bakker et al., 2016). Dugongs consume up to 40 kg wet weight of seagrass daily (Aragones 1996; Marsh et al., 2011), and consume the whole plant when undertaking excavation foraging (Nakanishi 2005; Marsh et al., 2011; Tol et al., 2016). These factors suggest a high level of bioturbation within active foraging meadows. Our results do not support this theory at our study sites. However, dugongs, including at our study sites, produce large volumes of seagrass wrack (leaves and shoots not attached to a rhizome) which did not meet our requirements to be classified as a fragment. Current population estimates for dugongs within the central GBRWHA (Whitsundays to Hinchinbrook Island, ~350 km of coastline) is approximately 2000 (Sobtzick et al., 2017). The central GBRWHA dugong population density is relatively smaller than other local populations in northern (Torres Strait: approximately 15,700 individuals (Sobtzick et al., 2014)) and southern Queensland (Hervey Bay: approximately 2055 individuals (Sobtzick et al., 2017)). At our study sites, the amount of dugong foraging is likely to be relatively low and this might explain why we found little effect on fragment density. Areas with denser dugong populations may still provide a source of fragment creation and increase seagrass fragment frequency and dispersal potential.

Although fragment density initially appears low in our study, with <1 fragment 100 m^{-2}, when scaled up to a meadow size the number of available fragments for dispersal is considerable. The seagrass meadow at Pioneer Bay is 4.63 km^2 in size, and the meadow at Midge Point is 3.19 km^2 (Carter et al., 2016). When scaled up to the area of the meadow, there would be between 25,465 and 32,873 viable fragments in Pioneer Bay, and 17,545–22,649 viable fragments in Midge Point per day during the growing season, and 4,630–7,408 viable fragments in Pioneer Bay and 3,190–5,104 viable fragments in Midge Point per day during the senescent season. The probability of successful dispersal by individual vegetative fragments is low (Ewanchuk and Williams 1996; Smith et al., 2018) due to deterioration over time (Weatherall et al., 2016), consumption by various herbivores (Valentine and Duffy 2006), and settlement in locations incompatible with growth (Grech et al., 2016). However, the large number of viable fragments available for settlement discovered in our study indicates this mode of dispersal could play an important role in meadow connectivity. Viable fragments collected in this study have the potential to disperse short or long distances, dependent on how long they remain buoyant and viable. For dispersal to be successful, these fragments need to drop out of the water

column and settle in a location compatible with growth and establish into a rooted plant. The difficulty of observing this in the real world of the open coast leaves a gap in our knowledge. It is assumed that with sufficient numbers successful settlement would occur (McMahon et al., 2014; Grech et al., 2016; Kendrick et al., 2017; Smith et al., 2018).

Dispersal and connectivity are fundamental processes that shape the distribution, structure, and resilience of marine ecosystems. The forces of ocean waves and currents are efficient vectors for long distance dispersal and facilitate the replenishment and recovery of seagrass populations after disturbance (Nathan 2008). Biophysical models predict dispersal and connectivity by combining oceanographic simulations with biological information on species life histories. Previous studies using data from biophysical models have been limited in predicting the potential connectivity of seagrass meadows because biological information is lacking, such as the number of fragments in the system (e.g. Grech et al., 2018; Schlaefer et al., 2022). Here we have quantified the availability of viable seagrass fragments for dispersal. Many seagrass dispersal and connectivity models do not use particle release numbers based on calibrated data, as it is not available for most seagrass locations. Providing this data for at least the GBRWHA will enable future biophysical models to be more informed, particularly when outputs are used in metapopulation analyses. The processes we developed here could be applied to other areas to estimate on the number of available floating seagrass propagules generated and inform estimations of connectivity and advance our predictive capacity and understanding of replenishment, recruitment, and recovery in seagrass ecosystems.

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Author statement

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Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

All data is publicly available on Research Data JCU.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.marenvres.2023.106160.

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