BIODIVERSITY RESEARCH

Spatial patterns of seagrass dispersal and settlement

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ABSTRACT

Aim The movement of propagules among plant populations affects their ability to replenish and recover after a disturbance. Quantitative data on recovery strategies, including the effectiveness of population connectivity, are often lacking at broad spatial and temporal scales. We use numerical modelling to predict seagrass propagule dispersal and settlement to provide an approach for circumstances where direct, or even indirect, measures of population dynamics are difficult to establish.

Location Great Barrier Reef, Australia.

Methods We used the finite-element *Second-generation Louvain-la-Neuve Ice-ocean Model* (SLIM) to resolve the hydrodynamics of the central Great Barrier Reef and to simulate the dispersal of seagrass. We predicted dispersal and settlement patterns by releasing 10.6 million passive particles representing seagrass propagules at known sites of seagrass presence. We considered two fractions when modelling seagrass dispersal: floating and suspended propagules. Both fractions were modelled using 34 simulations run for a maximum of 8 weeks during the peak seagrass reproductive period, capturing variability in winds, tides and currents.

Results The 'virtual' seagrass propagules moved on average between 30 and 60 km, but distances of over 900 km also occurred. Most particle movement was to the north-west. The season (month) of release and source locations of the particles correlated with their dispersal distance, particularly for particles released offshore, with the complex coastal topography impeding movements close to the coast. The replenishment and recovery potential of the northern-most meadows was influenced by southern meadows. Protected north-facing bays were less likely to receive particles.

Main conclusions Our approach advances the conservation and management of marine biodiversity by predicting a key component of ecosystem resilience at a spatial scale that informs marine planning. We show a complex interaction among time, wind, water movement and topography that can guide a management response to improving replenishment and recovery after disturbance events.

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INTRODUCTION

Safeguarding biodiversity and the delivery of marine ecosystem services requires the maintenance of ecological processes that underpin their functioning and resilience (Roberts *et al.*, 2003; Magris *et al.*, 2014). The multiple factors that

contribute to resilience and their interactions are complex (Kilminster *et al.*, 2015; Unsworth *et al.*, 2015). An important component of marine ecosystem resilience is the capacity to recover from loss or degradation. Recovery is supported by the dispersal of larvae, adults or propagules via the convective forces of ocean waves and currents (Bereuman

et al., 2012; Bode *et al.*, 2012). The rate of exchange or connectivity among populations affects the replenishment and recovery of populations after major disturbances (e.g. storms) and population dynamics (Treml *et al.*, 2008). However, our understanding of dispersal and connectivity via ocean waves and currents is poor for many ecosystems, especially seagrasses (McMahon *et al.*, 2014).

Seagrasses comprise a group of angiosperms that have successfully dispersed and colonized throughout the world's coastal seabeds. Seagrass meadows can be found on all continents except Antarctica, and from the high intertidal zone down to 61 m deep (Coles *et al.*, 2009). The 15 species that are found in the Great Barrier Reef World Heritage Area (GBR) in north-eastern Australia (Fig. 1) are a vital part of the reef ecosystem and provide food for numerous fish, crustacean, sea turtles and dugong (Unsworth *et al.*, 2014). Seagrasses are widespread in these waters (Coles *et al.*, 2009; Grech & Coles, 2010); however, recent tropical cyclones and floods have had severe impacts on the viability of some meadows and resulted in losses occurring at scales of hundreds of kilometres (Rasheed *et al.*, 2014; Coles *et al.*, 2015; McKenna *et al.*, 2015). The effect of climatic disturbances on seagrasses in the GBR is exacerbated by the impacts of coastal development and poor water quality (Coles *et al.*, 2015). Predicting the effect of disturbances and potential recovery trajectories requires information on factors influencing resilience of seagrass meadows, including replenishment and recolonization modes (Kendrik *et al.*, 2012).

Propagule dispersal has been well studied in terrestrial plants, although the predictability of successful dispersal mechanisms is less well understood, particularly over longer distances and when animal mediated (Nathan & Muller-Landau, 2000; Nathan *et al.*, 2008). Propagules can be seeds, fruit or viable plant fragments. Dispersal mechanisms include movement with wind, waterborne, through ingestion by or attachment onto birds and land animals, and through various transport methods during the movement of soil. Seed pollination can be mediated by insects or wind transport. Wholly marine seagrass species can grow and colonize vegetatively by rhizome extension over short distances (100 s of metres), but must use other mechanisms for dispersal over broad spatial scales. Most seagrass fruits are short-lived, and have negatively buoyant seeds with primary movement likely to be no more than several kilometres (Kendrik *et al.*, 2012; Berković *et al.*, 2014). Seagrass seeds can also be transported in the gut and faeces of fish, water fowl, sea turtles and
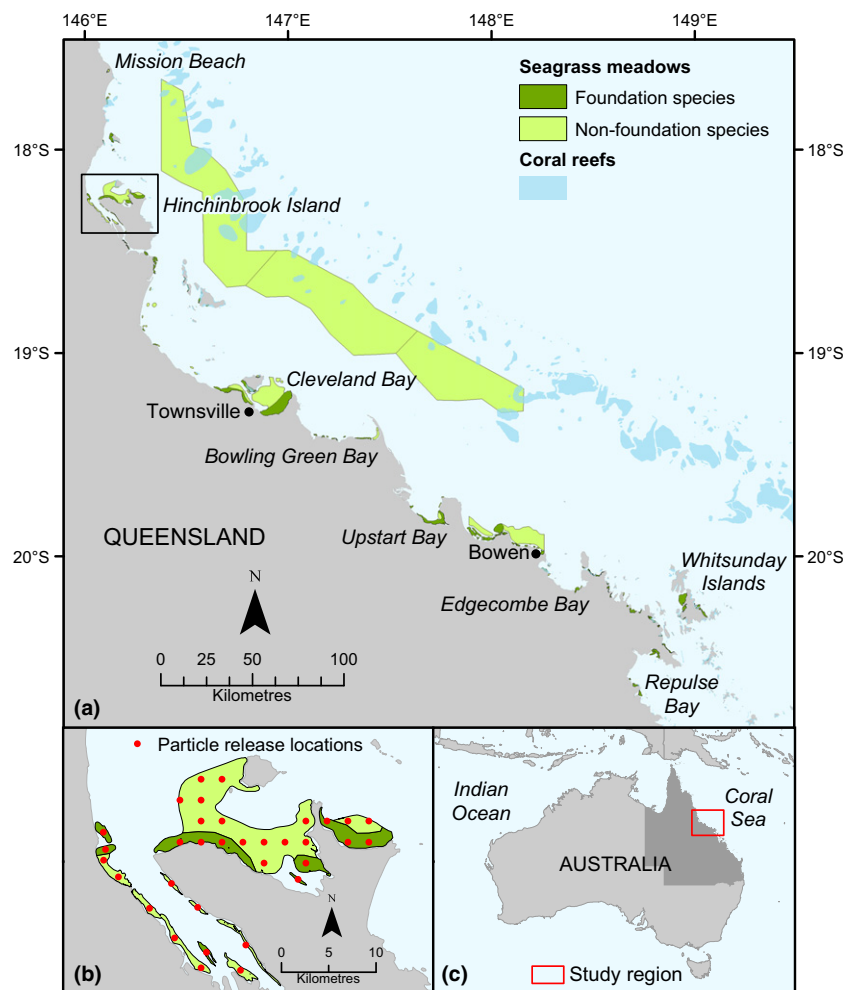

Figure 1 (a) Distribution of foundation and non-foundation seagrass meadows in the central Great Barrier Reef; (b) particle release locations off north Hinchinbrook Island; and (c) the location of the central Great Barrier Reef study site relative to Australia.

dugongs (McMahon, 2005; Sumoski & Orth, 2012; Tulipani & Lipcius, 2014); viable seeds have been found in the faeces of dugong (James Cook University, unpublished data). However, for tropical and subtropical seagrass species, by far the most likely mechanism for transport over broad spatial scales is by waterborne transport of viable propagules (i.e. vegetative fragments, fruits and plant fragments with attached fruits and seeds) (Berković *et al.*, 2014). Buoyancy and survival times (although not necessarily leading to successful establishment) for seagrass propagules may be as long as 85 days in temperate species (Thomson *et al.*, 2014), but vary for subtropical species with 0.5 days for *H. decipiens*, 4.5 days for *H. ovalis* and 21 days for *Z. muelleri* (Weatherall *et al.*, 2016). The maximum dispersal distances recorded in the literature are generally less than 100 km, except during extreme weather events when dispersal has been recorded over distances of up to 400 km (Lacap *et al.*, 2002).

There is a considerable body of literature on survival of propagules in the water column, as well as on their buoyancy and potential distance moved (Ruiz-Montoya *et al.* 2012; McMahon *et al.*, 2014). However, there is little comprehensive analysis using hydrodynamics to predict seagrass dispersal over broad scales (Ruiz-Montoya *et al.* 2012, e.g. Erftemeijer *et al.*, 2008; Källström *et al.*, 2008; Ruiz-Montoya *et al.*, 2015), and no studies relevant to tropical species. This leaves a gap in our ability to provide management agencies with evidence-based science on the capacity for the replenishment and recovery of tropical seagrass meadows from natural and anthropogenic disturbances.

The focus of this study was to address this gap using as an example the spatial dispersal of seagrass propagules in the central GBR, an area encompassing the major regional city and port of Townsville, as well as Hinchinbrook Island, Cleveland Bay, Bowling Green Bay and the Whitsunday Islands (Fig. 1). It is one of a few regions in the world with a long history of seagrass research and mapping (Coles *et al.*, 2007; McKenzie *et al.*, 2010; Petus *et al.*, 2014) as seagrasses in the area are exposed to urban and port developments, poor water quality from terrestrial run-off and tropical storms (Grech *et al.*, 2011; Rasheed *et al.*, 2014; Coles *et al.*, 2015). Effective management is therefore required to protect and enhance seagrass resilience and its subsequent long-term survival.

We used a numerical modelling approach to resolve the hydrodynamics of the central GBR and to simulate the dispersal of floating and suspended 'virtual' seagrass propagules. The hydrodynamic model used was the finite-element *Second-generation Louvain-la-Neuve Ice-ocean Model* (SLIM), a model ideally suited to studying areas of complex topography and flow patterns at very high spatial resolution (Lambrechts *et al.*, 2008). We predicted the dispersal and settlement patterns of seagrass by simulating the release of millions of passive 'virtual' propagules (seagrass propagules are represented as particles in the model) at known sites of seagrass presence. The simulations were timed to capture variability in winds, currents and tides during the peak seagrass reproductive period. The simulation outputs were used

to identify factors which facilitate abiotic seagrass dispersal and settlement, and to assess, spatially, the likelihood of replenishment and post-disturbance recovery of seagrass meadows in the central GBR.

METHODS

Study region

The central GBR coast between 17.5°S and 20.7°S (~730 km) is characterized by a series of small estuaries and north-facing bays (Fig. 1a). The region includes the city and port of Townsville, and a developing port at Abbot Point near the town of Bowen. The largest island in the GBR, Hinchinbrook, is in the north, and the complex of islands that make up the tourist destination of the Whitsunday Islands is in the south. The climate is influenced by monsoonal wind and rainfall patterns. Strong south-easterly winds dominate during the dry season (April–October). Weaker variable winds are more common during the wet (monsoon) season (November–March).

Water circulation on the GBR continental shelf is driven by tides, wind and water exchanges with the neighbouring Coral Sea (Wolanski *et al.*, 2013). Tides in the GBR range from 2.5 to 9 m (Hopley *et al.*, 2007) and tidal currents play an important role in cross-shelf mixing, although their amplitude can vary considerably with latitude (Andrews & Bode, 1988). The westward-flowing South Equatorial Current impinges on the GBR continental shelf from the Coral Sea, bifurcates into northward and southward components and drives the southward-flowing Coral Sea Lagoonal Current through the central and southern parts of the GBR, and the East Australian Current at the shelf break and seaward of it (Church & Boland, 1983; Church, 1987; Wolanski *et al.*, 2013). During periods of sustained south-easterly trade winds however, these act to drive a northward longshore current through the central and southern regions of the GBR which opposes the Coral Sea Lagoonal Current, and can result in a reversal of the net direction of flow through the shelf, towards the north (Andrews & Furnas, 1986). At finer scales, flow patterns are influenced by the high complexity of the reef topography (Wolanski & Spagnol, 2000; Hamann *et al.*, 2011; Thomas *et al.*, 2014).

Seagrass distribution

We investigated the dispersal of the most common seagrass genera in the central GBR: *Halophila*, *Halodule*, *Cymodocea* and *Zostera* (Lee Long *et al.*, 1993; Carruthers *et al.*, 2002; Coles *et al.*, 2003). A spatial [geographic information system (GIS)] layer of intertidal and shallow subtidal seagrass distribution was obtained from McKenzie *et al.* (2014a) (Figs 1a and 2). The layer incorporates the composite outputs of seagrass surveys conducted between November 1984 and June 2010 (McKenzie *et al.*, 2010). The total area of intertidal and shallow subtidal seagrass

in the study region was 848.3 km^2, and the number of meadows 121. The size of individual meadows ranged from 0.4 to 155.0 km^2 (mean = 7.0 km^2; see Table S1 in Supporting Information).

Each intertidal and shallow subtidal meadow was allocated into one of two generalized species classes to facilitate analysis of dispersal and settlement among meadows dominated by species of similar life history traits (Figs 1a and 2) (see Kilminster et al., 2015 for full discussion): the structurally robust opportunistic and persistent tropical seagrass species (genera Halodule, Cymodocea and Zostera) ($n = 83$), hereafter referred to as foundation species; and the structurally small ephemeral and transient species of the genus Halophila ($n = 41$), hereafter referred to as non-foundation species. We also allocated meadows into 28 discrete habitat units (Fig. 2) based on their species class and similarities in biogeographical properties (i.e. located in the same bay, estuary or island system) to facilitate statistical analysis (Table S1).

A spatial layer of deep-water (>15 m depth) seagrass (genus Halophila; non-foundation species) was obtained from Coles et al. (2009). We assumed that Halophila was present at locations where the layer predicted $a > 25\%$ likelihood of seagrass presence. The total area of deep-water seagrass with $a > 25\%$ likelihood of seagrass presence in the study area was 5792.5 km^2. We divided the deep-water layer into three meadows and discrete habitat units (Fig. 2) of approximately equal latitudinal distance to facilitate statistical analysis (Table S1).

Oceanographical model

The dispersal of 'virtual' seagrass propagules (i.e. fruit, seeds or fruit attached to plant material or viable fragments) was modelled using the finite-element, unstructured-grid ocean model SLIM (Legrand et al., 2006; Lambrechts et al., 2008) in Gmsh (Geuzaine & Remacle, 2009). SLIM is well suited to modelling complex oceanography because of its variable resolution; the model has a fine-scale spatial resolution near the coast, reefs and islands (minimum 200 m), and coarser resolution in homogenous areas (maximum 5 km). SLIM has previously been calibrated and used to simulate the hydrodynamics and sediment transport in the GBR (Lambrechts et al., 2008; Andutta et al., 2012), as well as dispersal of coral larvae (Thomas et al., 2014, 2015) and turtle hatchlings (Hamann et al., 2011).

Data on daily wind speed and direction (9 am and 3 pm) and tides for the time period 1 August 2012–31 January 2013 were obtained from the Australian Bureau of Meteorology, NOAA NCDC Climate Forecast System Reanalysis (Saha et al., 2014) and the TOPEX satellite altimetry (Egbert & Erofeeva, 2002). Depth-integrated shallow-water equations were used to compute the water elevation η and the current 2-D velocity vector $\boldsymbol{u}$:

$$\frac{\partial \eta}{\partial t} + \boldsymbol{\nabla}\cdot(H\boldsymbol{u}) = 0 \qquad (1)$$

$$\frac{\partial \boldsymbol{u}}{\partial t} + (\boldsymbol{u}\cdot\boldsymbol{\nabla})\boldsymbol{u} = -f\boldsymbol{e}_z \times \boldsymbol{u} - g\boldsymbol{\nabla}\eta - C_D|\boldsymbol{u}|\boldsymbol{u} + \frac{\tau}{\rho H}$$
$$+ \frac{1}{H}\boldsymbol{\nabla}\cdot[H\nu(\boldsymbol{\nabla}\boldsymbol{u})] \qquad (2)$$
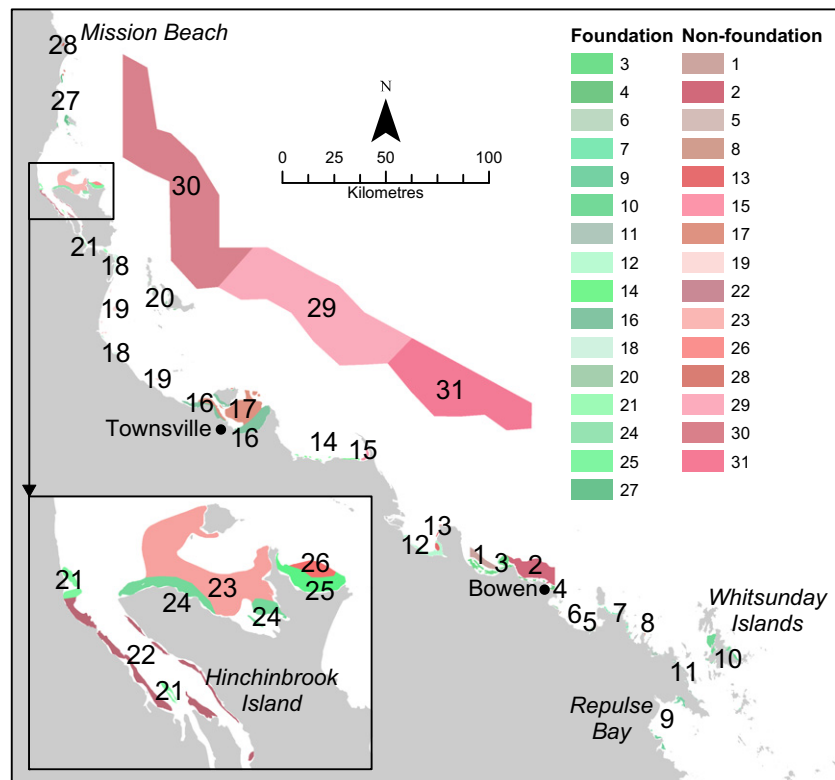

Figure 2 Discrete habitat units of foundation and non-foundation seagrass meadows in the central Great Barrier Reef. A total of 124 seagrass meadows were grouped into 31 discrete habitat units based on similarities in their seagrass genera and biogeographical properties (i.e. located in the same bay, estuary or island system).

where H is the water column depth, f is the Coriolis factor, e_z is a unit vector pointing vertically upwards, g is the gravitational acceleration, C_D is the bottom stress coefficient, τ is the surface wind stress, ρ is the water density and ν is the horizontal eddy viscosity. The model parameters and external forcing were taken from Thomas *et al.* (2014).

The dispersal of passive 'virtual' propagules (i.e. particles were unable to direct their own motion) was simulated using a Lagrangian particle tracker, similar to Spagnol *et al.* (2002). This model uses a random-walk formulation of the 2-D advection–diffusion equation:

$$x_{n+1} = x_n + v_n \Delta t + \frac{R_n}{\sqrt{r}}\sqrt{2K\Delta t} \qquad (3)$$

$$v_n = \left(u + C_w u_w + \frac{K}{H}\nabla H + \nabla K \right)\Big|_{x_n} \qquad (4)$$

where x_n and x_{n+1} are the particle positions at iterations n and $n + 1$, Δt is the time interval between iterations, R_n is a horizontal vector of zero-mean random numbers of variance r, u is the depth-averaged horizontal water velocity computed from Equation (2), u_w is the wind velocity at a height of 10 m over the sea surface, C_w is the wind drag coefficient and K is the horizontal diffusivity coefficient.

Simulation parameters

The time period of simulations covered the Southern Hemisphere spring reproductive period (Table 1), which follows the peak of the flowering period and time of highest seagrass abundance (beginning of August through to the end of November; Waycott *et al.*, 2004; Kuo *et al.*, 1991, 1993; Kuo & Kirkman, 1992). The start dates of individual simulations were chosen to capture variability in tides (spring, neap and first- and last-quarter tides) across the reproductive period (Table 1).

The total number of particles (representing 'virtual' seagrass propagules) released per simulation was optimized for the model domain ($n = {\sim}154{,}000$). An equal number of particles were released per release location. Release locations were spread evenly across intertidal and shallow subtidal meadow at intervals of ${\sim}2$ km ($n = 266$; Fig. 1b). Meadows of size <4 km^2 had one release location placed at its geometric centre. Release locations were spread evenly across each deep-water meadow at intervals of ${\sim}10$ km ($n = 53$). The number of particles released per unit area was smaller in deep-water meadows than in intertidal and shallow subtidal meadows because deep-water seagrasses generally have lower biomass and abundance relative to coastal seagrass (Coles *et al.*, 2007, 2009; Rasheed *et al.*, 2014). Particles were released at an equal rate over the first 24 hours of the simulations to capture daily variation in tidal conditions.

We assumed that the size and shape of seagrass propagules (fruit, seeds or fruit attached to plant material or viable fragments) were the same. We attempted to capture variability in the buoyancy of 'virtual' propagules by simulating the dispersal of propagules floating at the surface and suspended

Table 1 Date and tide parameters of seagrass dispersal simulations. Two simulations were started at each date to simulate particles that were floating and suspended in the water column

Simulation	Start date	Tide
1	1 August	Spring
2	5 August	–
3	9 August	Neap
4	13 August	–
5	17 August	Spring
6	20 August	–
7	23 August	Neap
8	26 August	–
9	29 August	Spring
10	3 September	–
11	8 September	Neap
12	11 September	–
13	15 September	Spring
14	18 September	–
15	21 September	Neap
16	23 September	–
17	26 September	Spring
18	1 October	–
19	7 October	Neap
20	10 October	–
21	14 October	Spring
22	17 October	–
23	21 October	Neap
24	24 October	–
25	27 October	Spring
26	2 November	–
27	6 November	Neap
28	10 November	–
29	14 November	Spring
30	17 November	–
31	20 November	Neap
32	22 November	–
33	25 November	Spring
34	28 November	–

below the surface, and using a first-order decay function to simulate the gradual settlement of propagules, as described below.

We considered two different fractions when modelling seagrass dispersal using our 'virtual' propagules: (1) floating propagules; and (2) suspended propagules. In Equation (4), the term depending on the wind velocity represents the wind contribution to the particle advecting velocity. The value of the wind drag coefficient C_w is usually determined empirically as it depends on the particle mass, shape, buoyancy and the wind angle of attack. We used a sensitivity analysis to determine the wind drag coefficient by running eight simulations with $C_w = 0.5, 1, 1.5, 2, 2.5, 3, 3.5$ and 4% and measured the distance between release and settling location. Increasing the wind drag coefficient resulted in particles moving further from their release location in a linear function. We used the outputs of the sensitivity analysis to

determine a conservative wind drag coefficient of 2% (i.e. a velocity equal to 2% of the wind speed was added to the velocity of the particles) when 'virtual' propagules were assumed to float at the surface. Erftemeijer et al. (2008) and Harwell & Orth (2002) use a wind drag coefficient of 3% to predict the dispersal of the structurally more robust Northern Hemisphere Zostera marina (eelgrass) fragments with reproductive shoots that contain seeds. However, the fragments and seeds of eelgrass are much larger then tropical seagrass propagules. A wind drag coefficient of 0% was used when particles were suspended below the surface.

Two sets of simulations were conducted at each start date with either 2% or 0% wind drag coefficient to assess differences in the dispersal of floating and suspended particles, and the role of wind in particle transport ($n = 68$). The ratio of floating and suspended propagule fractions in the central GBR at any given time is unknown. We assumed that the outputs of the two sets of simulations represent equally plausible realities based on our present knowledge.

Each of the 68 simulations was run for a maximum likely survival time of propagules in the tropics (8 weeks/56 days; Harwell & Orth, 2002; Lacap et al., 2002; Hall et al., 2006; Källström et al., 2008; Kendrick et al., 2012; Thomson et al., 2014). A first-order decay function was used to simulate the gradual settlement of particles after their release following a previously published approach (Erftemeijer et al., 2008; Fig. S1):

$$C(t) = C_0 \cdot e^{-kt} \tag{5}$$

where the decay rate $k = 0.075$ day^{-1} (Erftemeijer et al., 2008) and $C(t)$ is the particle concentration at time t.

Statistical analysis and replenishment index

Dispersal distance was calculated as the Euclidean distance between the release location and the settling location in ArcGIS® 10.3. The dispersal distance was aggregated at each release location for the 34 simulations of floating propagules and the 34 simulations of suspended propagules, and the 95th percentile calculated. We used a linear mixed-effect model (package 'nlme') in R (R Core Team, 2013) and release location as a random factor to test for significant effects of predictor variables on the dispersal distance of particles at each release location: month of release (August, September, October or November); tide on start date of simulation (neap, spring or first- and last-quarter tide); depth (intertidal/subtidal or deep); species (foundation or non-foundation species); and Euclidean distance (metres) between mainland coast and release location. The continuous variables of dispersal distance and distance to coast were log-transformed to achieve normal distribution and heterogeneity of variances. Model selection was conducted using the function 'dredge' in R package 'MuMIn'. The model with lowest AICc value was considered as 'best fit'. Competing models were ignored because delta AIC values were >3 and virtually all weight was given to the first model.

The study region was converted to a raster grid of 1 km² resolution. We calculated the number of settled particles and the number of discrete habitat units that were sources of the settled particles at each 1-km² grid cell. We assumed that the capacity of a meadow to recover from a disturbance depends both on the number of particles that settle on that meadow and on the number of different sources from which these particles originate. We used discrete habitat units rather than meadows as an indicator of the number of source locations due to the large variability in size and number of individual meadows in the region (Table S1). A potential replenishment index was mapped for both foundation and non-foundation species classes by multiplying the logarithm of the number of settled particles by the number of source discrete habitat units at each grid cell. We used the logarithm of the number of particles for visualization purposes.

RESULTS

Our simulations predicted a mean dispersal distance of floating 'virtual' seagrass propagules (particles) of 60.0 km, and suspended particles of 33.8 km. The maximum dispersal distance of particles was 950 km (simulation of floating particles, release 1 August, discrete habitat unit 31) and a minimum distance of 0 km (simulations of suspended particles, 29 August, 7 October, 17 October, 25 November, discrete habitat units 22 and 19). Animations of seagrass dispersal simulations at multiple locations and release dates are provided in Appendix S1.

Boxplots (Fig. 3) summarize the range of possible dispersal distances of particles for each discrete habitat unit (Fig. 2) generated by the 34 simulations of floating particles and 34 simulations of suspended particles. Simulations of floating particles were affected by wind and had higher dispersal distances (i.e. particles moved further) than simulations that were not affected by wind (i.e. suspended particles). The deep-water non-foundation meadows (discrete habitat units 29, 30 and 31) had the highest range and median dispersal distances for both floating and suspended particles. Particles released from deep-water meadows and coastal regions of high exposure to wind activity (e.g. discrete habitat units 7, 8, 28, 4, 2; Fig. 2) travelled further than meadows in protected bays because they were exposed to strong offshore currents or were not trapped by tidal movements in complex coastal topographical features (Fig. 3).

We used the orientation of settlement locations relative to release locations to develop wind roses of the proportion of floating and suspended particles dispersed at various directions and distances (Fig. 4). Most (77%) floating particles were dispersed towards the north-west quadrant because the seagrass reproductive period is dominated by south-easterly trade winds. Most suspended particles were also dispersed towards the north-west quadrant due to wind-induced water currents; however, 32% of particles were dispersed towards the south-east quadrant due to strong water current movement in that direction in September.
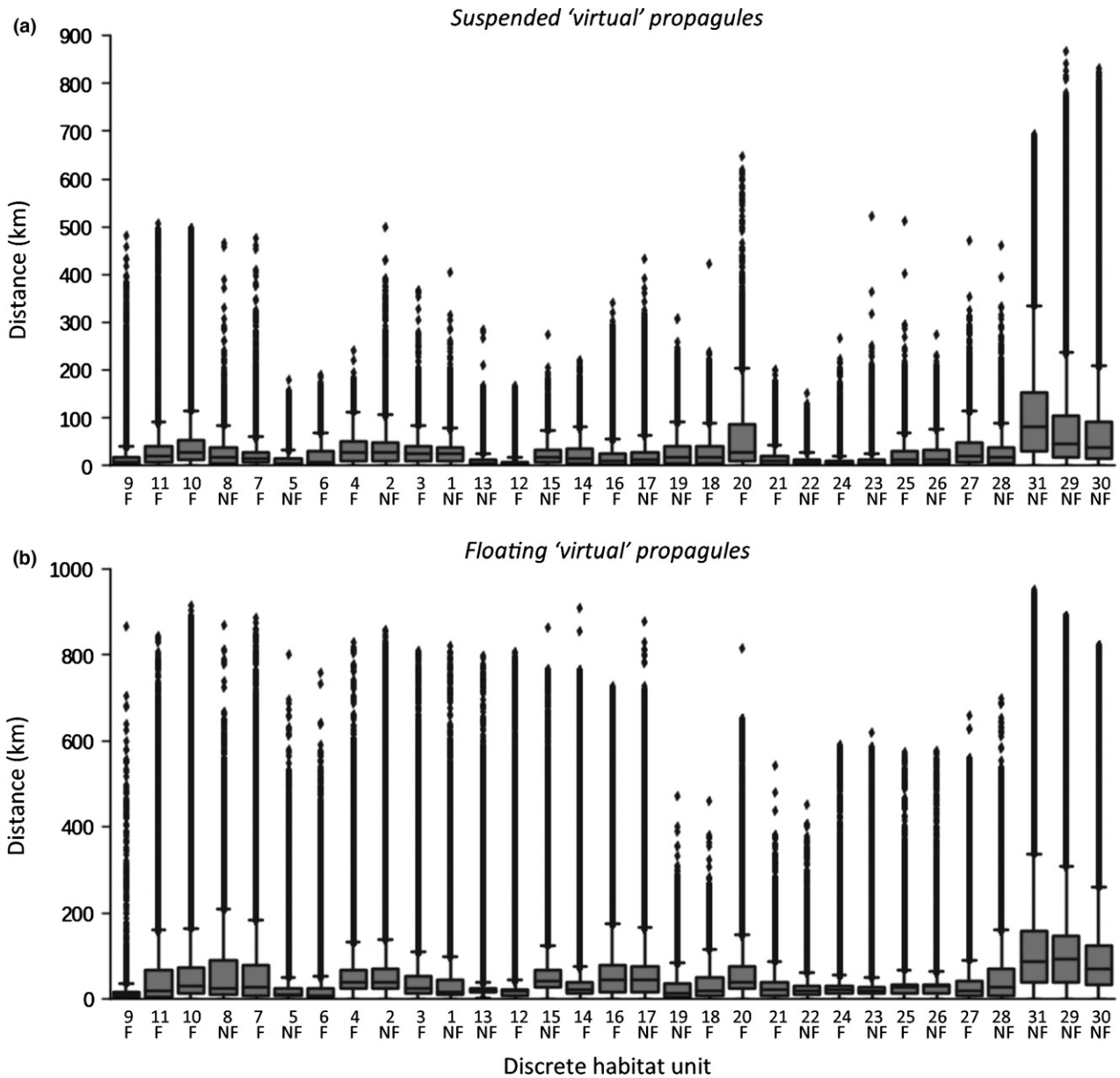
(a)

Suspended 'virtual' propagules

(b)

Floating 'virtual' propagules

Discrete habitat unit

Figure 3 Boxplot of the minimum, first-quartile, median, third-quartile and maximum Euclidean (straight line) distance (kilometres) between the release location and the settling location of particles across 34 simulations at each discrete habitat unit (Fig. 2). Data in the top graph did not include a wind advection coefficient and simulated seagrass propagules suspended in the water column; data in the bottom graph included a 2% wind advection coefficient to simulate the dispersal of floating seagrass propagules.

Particles released from the southern limit of our modelling domain (i.e. discrete habitat unit 9; Fig. 2) did not move towards the north-west and were either trapped in Repulse Bay or were moved south-eastwards by water currents. Particles released from the adjacent Whitsunday Islands moved towards the north-west and settled in deep offshore waters and some coastal locations. Due to the shape and direction of the coast south of Repulse Bay (Fig. 1c), it is likely that the southern limit of seagrass connectivity in the central GBR is the Whitsunday Islands.

The linear mixed-effect models of floating and suspended particles at the 95th percentile (Table S2) showed significant seasonal effects (month), and species (foundation and non-foundation) and location (distance to coast) effects. The south-east trade winds, a feature of the region during the mid-year winter, decrease towards the beginning of the monsoon in summer, influencing propagule movement through direct wind effects and indirectly through movement of water. Particles from meadow locations away from the coast in deeper water travelled further than those from coastal locations (Fig. 3) as they entered ocean currents and winds
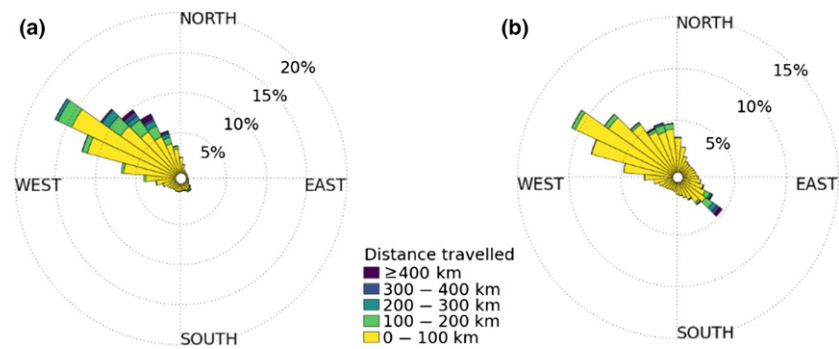
Figure 4 Wind roses of the proportion (%) of particles dispersed at various directions and distances from their origin of simulations that were (a) floating and (b) suspended in the water column.

unimpeded by the configuration of coastal topography. Deeper meadows are also populated by non-foundation species and not the foundation species, leading to significant interaction terms.

The potential replenishment indexes of both foundation and non-foundation species indicate a site's relative potential for re-establishment and recovery of seagrass via natural biotic processes (Fig. 5). High levels of replenishment potential were observed along most of the coast. Coastal areas of low replenishment potential included the southern edge of protected bays (e.g. Cleveland Bay, Bowling Green Bay, Upstart Bay), and Edgecombe Bay, Repulse Bay and the Whitsunday Islands. The shape of Edgecombe Bay shelters most of the bay from south-easterly winds, preventing seagrass propagules from neighbouring southern meadows from entering the site. The Whitsunday Islands are exposed to strong south-easterly winds, and seagrass propagules are quickly transported away from their release locations. The region between Townsville and Hinchinbrook Island also had a low level of replenishment potential for foundation species, but a higher level of replenishment potential for non-foundation species because of settlement of propagules from deep-water seagrass meadows.

DISCUSSION

We used hydrodynamic modelling and parameters informed by the literature to investigate the potential dispersal and settlement patterns of simulated particles representing seagrass propagules in the central GBR. This approach enabled the assessment of factors that influence an important component of resilience: the potential for re-establishment of seagrass meadows after loss or damage (Unsworth et al., 2015). From a global perspective, the knowledge gaps identified in this process are first in the assumptions that viable propagules do actually settle and establish as plants in a new location and that the physical characteristics of propagule fragments of different species interact with wind and water movements in the same way; and second in our poor overall understanding of the movement behaviour of propagules (including loss rates and buoyancy times) in the real world of open ocean transport. The size and density of seeds, fruits and vegetative fragments can vary over orders of magnitude (mms to

10 cms; Oldham et al., 2014) and more information is needed to appropriately incorporate this variation in hydrodynamic models. Our results based on the example of the central GBR represent a theoretical approach to modelling seagrass dispersal based on the best available knowledge to provide an insight into how these complex systems work at a scale that is useful for management. Our results also enable testing of hypotheses to evaluate the specifics of dispersal ranges by testing this model in situ.

The results of the simulations indicated that most seagrass propagules on average do not travel far from their source location, especially when suspended in the water column. The average distance travelled by particles within the 8-week time period was between 30 and 60 km (Fig. 3). Particles from deep-water meadows travelled further than those closer to the coast (Fig. 3). 77% of particles had a northerly component to movement if floating and slightly less when suspended (Fig. 4). Time of release influenced the distance travelled with longer distances observed earlier in the reproductive period due to the greater strength of south-easterly trade winds in August and September compared with later in the year.

Coastal topography influenced the trajectory of particles in the model. Model release locations in offshore meadows allowed particles to move unimpeded and travel further than coastal meadows. Topography also influenced the number of discrete habitat units that could contribute to a recipient meadow (a likely key component of a meadow's recovery capacity) with greater potential for replenishment in northern locations and shadows of low replenishment, particularly in the lower portion of north-facing bays (Fig. 5).

The maximum dispersal distance of 'virtual' propagules was 950 km, approximately half the length of the GBR coast line. While this travelled distance may represent a rare event, propagule dispersal over long distances may be critical for adaptability at these scales. Propagules that travel only short distances or remain within the boundary of an existing meadow will have a better chance of remaining in locations likely to be conducive to seagrass growth. However, in the tropics and subtropics, dispersal strategies of marine angiosperms must also operate at scales that explain existing distributions (thousands of kilometres) (Coles et al., 2009; McKenzie et al., 2010; Waycott et al., 2014). Many tropical meadows

(a) Foundation species (combined)

(b) Non-foundation species (combined)

(c) Foundation species (suspended)

(d) Non-foundation species (suspended)

(e) Foundation species (floating)
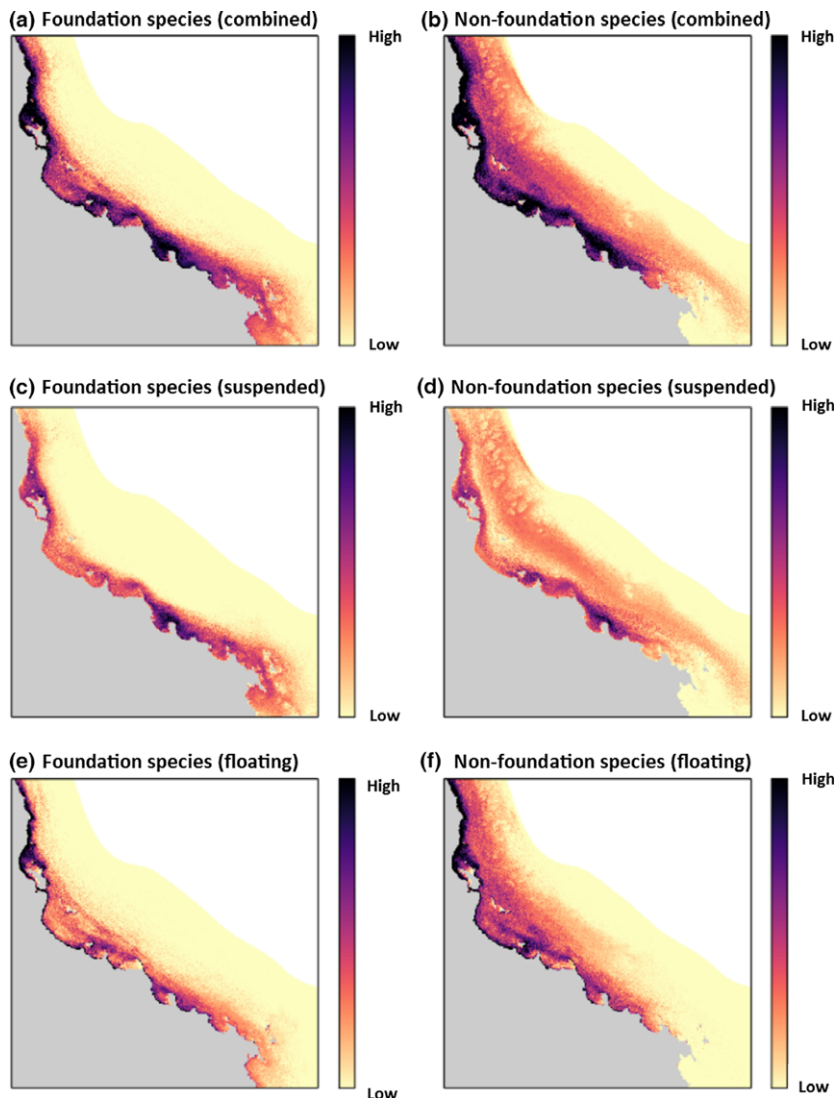
(f) Non-foundation species (floating)

Figure 5 Potential replenishment index for foundation and non-foundation species when particles float (e and f, respectively), are suspended (c and d) in the water column, and both floating and suspended (combined; a and b). Particle supply was mapped by multiplying the logarithm of the number of settled 'virtual' propagules by the number of source discrete habitat units at each grid cell.

have persistent viable seed banks, but effective methods must be available for longer distance dispersal and replenishment (even if these mechanisms are rare), simply because of the high number of propagules released from meadows over many years. Our modelling demonstrates that most dispersal is limited to short distances, especially when propagules are suspended in the water column, and replenishment is certain to occur within the 30- to 60-km range. Longer distance dispersal is possible, but likely to be uncommon and have a proportionally reduced role in meadow recovery after loss.

The destructive tropical storms and sediment loads from land run-off from 2007 to 2011 (McKenzie *et al.*, 2012; Rasheed *et al.*, 2014; McKenna *et al.*, 2015) were the catalyst to ask questions regarding propagule dispersal, modes of re-establishment and seagrass recovery in the central GBR. Previous losses of seagrass on the east coast of Queensland have generally recovered naturally in a 3- to 5-year time frame (Preen *et al.*, 1995; Campbell & McKenzie, 2004), but depending on the habitat and location, can take longer (York *et al.*, 2014; McKenzie *et al.*, 2015), even more than a decade

(Birch & Birch, 1984). There is little guidance on potential recovery trajectories at the scale of hundreds of kilometres. The results of our study show it would be reasonable to generalize for management in the central GBR that provided there was a healthy meadow nearby and to the south, then re-establishment and/or recovery of a damaged meadow by natural propagule supply would be possible. However, not all meadows have a replenishment potential as great as others (Fig. 5) due to the influences of topography, location and time of year, and individual meadows could be recruitment limited if and when local supplies of propagules are exhausted through disturbance.

Coastal development and watershed impacts from farming and urban and industrial land use have largely been confined to the southern half of the GBR (Grech *et al.*, 2011). The results of our study reduce the comfort provided to management by the assumption that the lack of development in the northern GBR provides a buffer to losses in the south. Impacts on meadows from run-off and coastal development in the southern half of the GBR may reduce propagule

supply northward, and therefore reduce the replenishment of northern meadows after loss or damage from climatic disturbances. At the scale of the central GBR, southern meadows and meadows in north-facing bays are less likely to be replenished after disturbance events. The lesson from these results more globally is that losses of seagrass meadows may have unexpected consequences for the resilience of meadows many kilometres away. Management actions that protect factors influencing resilience other than dispersal (e.g. genetic diversity, species diversity, energy reserves and seed banks) should target sites with low or potentially low replenishment capacity to improve their post-disturbance recovery trajectories. Management actions that protect factors influencing resilience are likely also to lead to enhanced dispersal. Maintaining and enhancing resilient seagrass systems require keeping food webs intact (i.e. balancing herbivore grazing pressure), conserving functionally important species and ensuring connectivity with adjacent supporting ecosystems (e.g. mangroves; Unsworth *et al.*, 2015).

We have used a 'big picture' approach to model the likely interactions among seagrass meadows. This approach has provided valuable insights into how seagrass ecosystems may respond to impacts such as widespread loss after a major storm. These insights can be used to evaluate and improve environmental decision-making and marine planning. However, it is important to consider an exercise such as this as a starting point from which to test biological realities and for directing further research in the field to test the parameters that modelling has identified as critical to our understanding.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Video S1. Discrete habitat unit 3, Foundation species, Suspended, released 1 August.

Video S2. Discrete habitat unit 3, Foundation species, Floating, released 1 August.

Video S3. Discrete habitat unit 16, Foundation species, Suspended, released 1 August.

Video S4. Discrete habitat unit 16, Foundation species, Floating, released 1 August.

Video S5. Discrete habitat unit 24, Non-foundation species, Suspended, released 1 August.

Video S6. Discrete habitat unit 24, Non-foundation species, Floating, released 1 August.

Video S7. Discrete habitat unit 29, Non-foundation species, Suspended, released 1 August.

Video S8. Discrete habitat unit 29, Non-foundation species, Floating, released 1 August.

Video S9. Discrete habitat unit 3, Foundation species, Suspended, released 3 September.

Video S10. Discrete habitat unit 3, Foundation species, Floating, released 3 September.

Video S11. Discrete habitat unit 16, Foundation species, Suspended, released 3 September.

Video S12. Discrete habitat unit 16, Foundation species, Floating, released 3 September.

Video S13. Discrete habitat unit 24, Non-foundation species, Suspended, released 3 September.

Video S14. Discrete habitat unit 24, Non-foundation species, Floating, released 3 September.

Video S15. Discrete habitat unit 29, Non-foundation species, Suspended, released 3 September.

Video S16. Discrete habitat unit 29, Non-foundation species, Floating, released 3 September.

Video S17. Discrete habitat unit 3, Foundation species, Suspended, released 1 October.

Video S18. Discrete habitat unit 3, Foundation species, Floating, released 1 October.

Video S19. Discrete habitat unit 16, Foundation species, Suspended, released 1 October.

Video S20. Discrete habitat unit 16, Foundation species, Floating, released 1 October.

Video S21. Discrete habitat unit 24, Non-foundation species, Suspended, released 1 October.

Video S22. Discrete habitat unit 24, Non-foundation species, Floating, released 1 October.

Video S23. Discrete habitat unit 29, Non-foundation species, Suspended, released 1 October.

Video S24. Discrete habitat unit 29, Non-foundation species, Floating, released 1 October.

Video S25. Discrete habitat unit 3, Foundation species, Suspended, released 2 November.

Video S26. Discrete habitat unit 3, Foundation species, Floating, released 2 November.

Video S27. Discrete habitat unit 16, Foundation species, Suspended, released 2 November.

Video S28. Discrete habitat unit 16, Foundation species, Floating, released 2 November.

Video S29. Discrete habitat unit 24, Non-foundation species, Suspended, released 2 November.

Video S30. Discrete habitat unit 24, Non-foundation species, Floating, released 2 November.

Video S31. Discrete habitat unit 29, Non-foundation species, Suspended, released 2 November.

Video S32. Discrete habitat unit 29, Non-foundation species, Floating, released 2 November.

Table S1. Attributes of 124 seagrass meadows.

Table S2. Results of the linear mixed-effect model.

Figure S1. Graph of the first-order decay function.

Appendix S1. Detail on the animations of the dispersal of particles representing 'virtual' seagrass propagules.

BIOSKETCH

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