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Experimentally derived buoyancy duration of seagrass fragments for biophysical dispersal modelling in the Great Barrier Reef

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ABSTRACT

The re-establishment of seagrass meadows following dieback events depends on the availability of viable propagules, particularly vegetative fragments that facilitate recovery beyond the local meadow through long-distance dispersal. The dispersal of vegetative fragments by ocean currents, waves and wind can be predicted by biophysical models. Among the model parameters, the duration of fragment buoyancy is an important determinant of dispersal but remains poorly quantified for tropical seagrass species. Yet, few empirical studies have assessed fragment dispersal traits and only for a small number of seagrass taxa. This limitation is particularly pronounced in tropical ecosystems, including the Great Barrier Reef (GBR), Australia, where tropical species exhibit diverse life histories and form extensive mixed-species meadows. This study aims to improve the accuracy of biophysical dispersal models for tropical seagrass by generating robust, species-specific data. We quantified the buoyancy duration of fragments from three species—*Halophila ovalis*, *Halodule uninervis*, and *Zostera muelleri*—over 48 days, and assessed whether initial morphological traits influenced buoyancy, finding species type was the primary determinant rather than fragment size. We then incorporated these empirical estimates into a biophysical model to evaluate their effects on dispersal. Our results highlight major differences between species. *Z. muelleri* floated the longest (24.7 ± 3.0 days); *H. uninervis* sank the fastest; and *H. ovalis* was intermediate, generating broken fragments available for further dispersal. Integrating these experimental derived buoyancy values into a biophysical model reduced the mean predicted dispersal distances by 44% on average compared to previous models. These findings highlight interspecific dispersal behaviours and provide useable empirical data to refine future modelling studies. Such improvements are essential for predicting seagrass recovery, guiding restoration site selection, and informing management strategies that maintain connectivity and ecosystem resilience.

1. Introduction

Seagrasses form valuable ecosystems, providing numerous ecosystem services, including supporting biodiversity, providing habitat and nursery for marine life, improving water quality and sequestering carbon (Brodie et al., 2020; de los Santos et al., 2020; de los Santos et al., 2020). Seagrass meadows are impacted by a range of natural and anthropogenic disturbances, including storms, cyclones, and flooding, as well as coastal development, declining water quality, and climate change (Grech et al., 2012; Turschwell et al., 2021). Their natural recovery is influenced by clonal growth, seed banks, and the dispersal of either sexual (i.e. seeds, fruits) or asexual vegetative fragments (McMahon et al., 2014; Sherman et al., 2018). Dispersal is a critical process for recolonization after large-scale disturbances (e.g. cyclones and storms), connecting communities, and ensuring resilience to changing conditions (Kendrick et al., 2017; Lai et al., 2018).

The long-distance dispersal of tropical seagrass species over distances of tens to hundreds of kilometres is predominately facilitated by

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vegetative fragments (Hanuise et al., 2025; Thomson et al., 2014; Weatherall et al., 2016, 2025). These vegetative fragments consist of seagrass shoots with leaves and, in some cases, rhizome(s) and seeds (Sherman et al., 2018). Detachment occurs through wave action and currents, physical disturbance (e.g. storms) and grazing from megaherbivores (Balestri et al., 2011; Kendrick et al., 2017; Sherman et al., 2018). For some seagrass species, including *Z. muelleri*, a successful establishment following dispersal could be influenced more by the availability of viable vegetative fragments than by seeds (Stafford-Bell et al., 2015), with over a third of all floating vegetative fragments estimated to be viable (Tol et al., 2023; Weatherall et al., 2025). The persistence of vegetative fragments varies among species: some, including *Z. muelleri*, can remain viable for a few weeks, while others experience a quick degradation after a few days, including *H. ovalis* (Hall et al., 2006; Stafford-Bell et al., 2015). Despite their ecological importance, only a few studies have assessed vegetative fragment dispersal characteristics, as empirical observations are limited by scale and accessibility, leading to an important gap in knowledge of seagrass recovery and resilience in the tropics.

To address these knowledge gaps, researchers have turned to biophysical modelling to simulate dispersal processes (Evans et al., 2021; Grech et al., 2016; Jackson et al., 2021; Jahnke and Jonsson, 2022; Lai et al., 2024; Schlaefer et al., 2022). However, the accuracy of these models is dependent on assumptions of seagrass movement ecology due to the scarcity of empirical information, which can lead to model uncertainties (Wolanski, 2017). For tropical regions, only a few empirical studies assess key model parameters for seagrass vegetative fragment dispersal, such as the wind drag coefficient and buoyancy duration (Lai et al., 2020; Tol et al., 2024; Weatherall et al., 2016). These studies focus on seven different tropical species (*Halophila ovalis, Halophila spinulosa, Halophila decipiens, Thalassia hemprichii, Cymodocea rotundata, Halodule uninervis* and *Zostera muelleri*), with equivalent information for many seagrass taxa still unknown. Among the studies, only two provide data that were subsequently incorporated into biophysical dispersal models (Lai et al., 2024; Schlaefer et al., 2022), suggesting a gap between modelling and field studies.

The Great Barrier Reef (GBR) region of Queensland, Australia (Fig. 1) contains 23% of the world's seagrass species diversity and supports extensive, mixed species meadows characterised by high intraspecific trait variability (Brodie and Waterhouse, 2012; Collier et al., 2020;

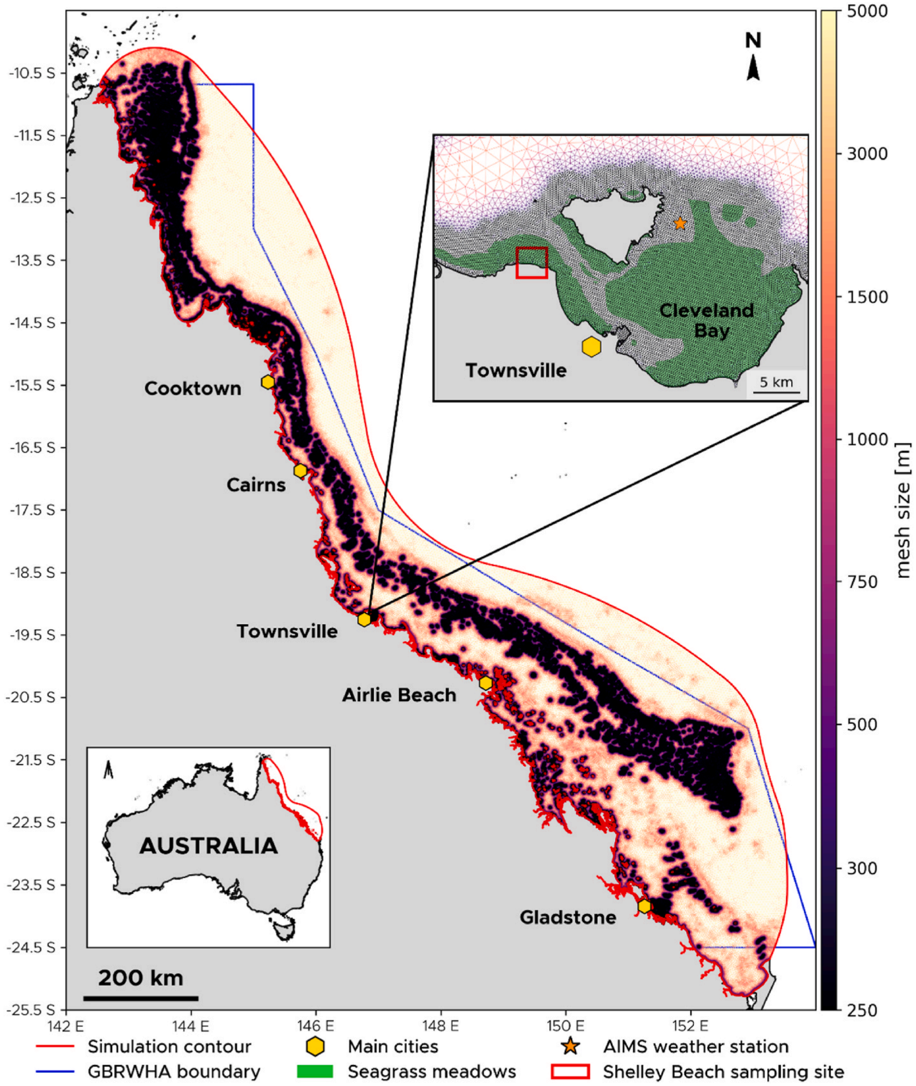

Fig. 1. The Great Barrier Reef region of Queensland, Australia. The simulation contour from Hanuise et al. (2025) is shown in red, and the boundaries of the Great Barrier Reef World Heritage Area (GBRWHA) In blue. The mesh used for the hydrodynamic simulation with its variations of resolution (from 250m to 5 km) is shown in the black to yellow colormap. Yellow hexagons show the main cities along the GBR coast. The inset map of the Townsville area displays the finer mesh resolution over seagrass meadows (represented in green), the sampling area (red square), and the location of the AIMS weather station (orange star). (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

Kilminster et al., 2015; Lin et al., 2024). Without species-specific data for this globally significant region, biophysical models risk over-simplifying dispersal dynamics and underestimating the complexity of seagrass connectivity in the GBR. For example, buoyancy duration has previously been identified as an important life-history trait in biophysical modelling as it directly influences dispersal distance (Schlaefer et al., 2022). Indeed, buoyancy duration constrains the maximum possible dispersal distance and directly influences vegetative fragment dispersal behaviour by determining its position in the water column. Fragments that remain buoyant and spend more time at the surface, experience greater exposure to wind, which can increase dispersal distances predicted by biophysical models (Huebert et al., 2011; Swearer et al., 2019). These dispersal processes subsequently influence estimates of connectivity, with important implications for the interpretation of metapopulation dynamics and spatial recovery potential.(Cowen et al., 2006; McMahon et al., 2014).

In this study, we focus on three common GBR seagrass species: *Halophila ovalis*, *Halodule uninervis* and *Zostera muelleri*. They are widespread along the coastal, estuarine and reef habitats of the GBR and are commonly reported as dominant in these habitats (Carter et al., 2021; Coles et al., 2015). These species differ in both growth strategies and dispersal abilities, as well as in their morphological traits (Lin et al., 2024). Among the three, *Z. muelleri* is an opportunistic species, with a moderate to high dispersal potential and long-lived leaves. *H. ovalis* is a colonizing species, with low to moderate dispersal ability and very small, short-lived leaves. *H. uninervis* occupies an intermediate position, sharing both colonizing and opportunistic traits, but has the poorest dispersal capacity of the three (Hanuise et al., 2025; Kilminster et al., 2015; Larkum et al., 2006; Lin et al., 2024). In addition, *H. uninervis and H. ovalis* are fast-growing species (La Nafie et al., 2013). Collectively, these three species represent contrasting functional traits and capture the life-history diversity of Great Barrier Reef seagrasses, providing a robust basis for evaluating dispersal potential across differing ecological strategies.

The goal of this study is to improve the accuracy of biophysical dispersal models for tropical seagrass by generating robust, species-specific life-history data on vegetative fragment buoyancy and viability. We assessed the buoyancy durations for vegetative fragments for three species (*H. ovalis, H. uninervis, Z. muelleri*), representing the interspecific variability in the GBR. We then implemented our estimates in a biophysical dispersal model to quantify how the new parameter estimates influence dispersal distance compared to current theoretical modelling assumptions. Considering these different species and their intra-species variability, allowed us to investigate movement ecology of fragment dispersal in the GBR by addressing the following questions: (1) What is the species-specific buoyancy duration of seagrass vegetative fragments (2) How do morphological traits (e.g. fragment size, rhizome length)?; affect the buoyancy of seagrass vegetative fragments?; and (3) How do the experimentally measured buoyancy durations influence the outcomes of seagrass biophysical dispersal models? Our outcomes improve the parameterisation of biophysical dispersal models and provide new insights into the movement ecology of tropical seagrasses. They also support more realistic predictions of seagrass dispersal, which are used to inform spatial planning, conservation, and management in tropical ecosystems.

2. Methods

2.1. Field collection

The collection of fresh seagrass vegetative fragments was conducted on the March 10, 2025 (a single sampling day) from Shelley Beach, Townsville, Queensland (Fig. 1). The vegetative fragments were collected from a single sampling site to ensure standardised environmental conditions and minimize site-related variability in fragment characteristics. The sampling meadow is located in a region that has been monitored as part of the Port of Townsville monitoring programme since 2007 (McKenna et al., 2024). In 2023, the meadow's condition was classified as ‘poor’ and then ‘very poor’ in 2024, due to a sharp biomass decline and contraction of meadow footprint, relative to baseline data (McKenna et al., 2024, 2025). In 2024-25 the Marine Monitoring Program also classified the broader Townsville region as ‘poor’ in both abundance and resilience for seagrass meadows (Leahy et al., 2026). Our sampling occurred at low tide, when most of the intertidal meadow was exposed to air. During sampling, *H. uninervis* was observed as the dominant species. *H. ovalis* was the second most dominant species, while *Z. muelleri* was present enough to allow sampling but rare relative to the other species. No other species were observed in the meadow.

We collected 45 fresh fragments of each species at random locations within the interior of the meadow (0.5 km^2). Using 45 fragments allowed us to allocate 15 fragments per tank, minimizing potential interactions among fragments within the same tank and ensuring that each fragment could be monitored individually throughout the experiment. Samples were collected with a shovel, by excavating intact plants, to ensure that all plant components (roots, rhizome and leaves) were removed from the sediment. Collected fragments were planted in sediment and placed in plastic bags filled with seawater to maintain health and prevent desiccation. This method also ensured that the fragments first began to float after being placed in the experimental tanks. Fragments remained in these bags for no more than 4 h during transit. The fragment sizes ranged from 5.5 to 13.5 cm for *H. ovalis* (9.01 ± 0.42 cm [SE]) with an average 8.0 ± 0.5 leaves per fragment; from 4.4 to 17.7 cm for *H. uninervis* (9.31 ± 0.47 cm [SE]) with an average 4.9 ± 0.3 shoots per fragment; and from 2.1 to 18.3 cm for *Z. muelleri* (7.61 ± 0.64 cm [SE]) with an average 5.5 ± 0.45 shoots per fragment.

2.2. Experimental design

Experiments were conducted directly after field collection (i.e. starting date on the March 10, 2025) in the Marine and Aquaculture Research Facility Unit (MARFU) at James Cook University, Townsville. The design included nine 215 L tanks, at 63 cm diameter and 92 cm height (Fig. 2B). Tanks were maintained at 80 cm water depth with artificial saltwater supplied via a water circulation system (flow rate of 60 L/h per tank). The temperature and salinity in the tanks were maintained at 28.26 °C (SE ± 0.02; measured with Carel NTC030HP03 thermistor) and 35.22 PSU (SE ± 0.04; measured with Burkert Type 8228 conductivity sensor) and were monitored throughout the experiment. This temperature was representative of ambient sea surface temperature recorded at the Australian Institute of Marine Sciences (AIMS) weather station on Magnetic Island, adjacent to the field site of Shelley Beach (Fig. 1). The flow outlet was submerged to minimize turbulence and maintain a flat-water surface. The nine tanks were placed under natural light conditions, and under a transparent ceiling to protect them from rain. We recorded light through a Photosynthetic Active Radiation (PAR) logger placed at the bottom of one tank (Supplementary Materials – Fig. S1). The duration of the experiment was initially set to 60 days. This choice was made because previously published seagrass dispersal models in the region used a dispersal behaviour (i.e. lifespan, buoyancy duration, decay rate function) of 60 days or less (Grech et al., 2016; Hanuise et al., 2025; Schlaefer et al., 2022). Additionally, the survival time of seagrass propagules was previously estimated to a maximum of 56 days (Hall et al., 2006; Kendrick et al., 2012; Thomson et al., 2014). At its completion, our experiment ran for 43 days for *H. uninervis* and 48 days for *H. uninervis* and *Z. muelleri*, due to poor conditions of the remaining fragments at that stage.

To track the buoyancy of individual seagrass fragments over time, fragments from each species were initially individually labelled using a small paper tape attached to their rhizome (Fig. 2A and C). The fragments were equally distributed across the nine tanks, with each tank containing 15 fragments of the same species. This placement was to prevent interspecies influence, as different species display distinct

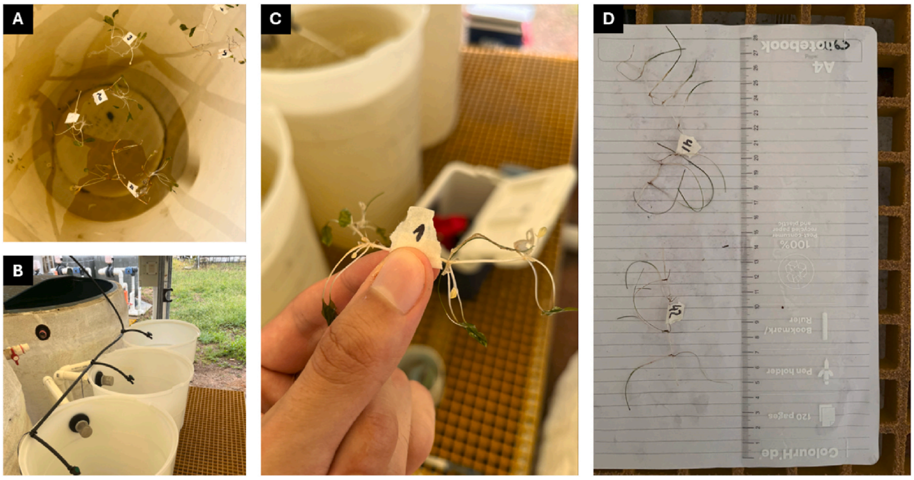

Fig. 2. Overview of the experimental setup and daily measurements. **A**: floating labelled fragments in the tank (*H. ovalis*). **B**: experimental tanks in the MARFU facility, Townsville, Queensland. **C**: labelling of seagrass fragments with paper tape (*H. ovalis*). **D**: example of pictures taken daily to record fragment health (*H. uninervis*).

dispersal behaviours (Weatherall et al., 2016). Based on previous studies, *H. ovalis* and *H. uninervis* were expected to remain buoyant for a shorter period than *Z. muelleri* (Weatherall et al., 2016). Mixing species could therefore have resulted in fragments of one species influencing the buoyancy behaviour of fragments from another species within the same tank.

To assess whether the labelling influenced buoyancy, control strips were placed in tanks and monitored. Labels floated for three days before sinking and were therefore considered unlikely to influence fragment buoyancy over the experiment's duration. However, some labels degraded during the experiment. To avoid losing track of fragments, all fragments were relabelled from day 25. This was particularly the case for *H. ovalis* fragments, for which 11 fragments lost their label. As it was not possible to keep track of those unlabelled fragments, they were removed from the analysis, leaving only 34 fragments useable for some of the statistical analysis for *H. ovalis*. Additionally, *H. ovalis* fragments broke at a greater rate compared to the other species, thereby generating “new” fragments in the tanks. The degraded part of the fragment detached from the original fragment, resulting in an increase in the number of fragments in the tank. We recorded this phenomenon and expressed the results at the individual scale (with the 34 labelled fragments), and as the total number of fragments in the tank (accounting for the newly created fragments and original labelled fragments).

2.3. Buoyancy and fragment growth measurements

Buoyancy and growth were checked daily at the same time (10:00 h), by measuring the depth below the water surface of individual fragments with a measuring tape and taking a picture of each fragment. These pictures were taken by a single observer, with an iPhone 13 equipped with a dual 12 MP camera system, to track the evolution in condition of each fragment; referred to here on as growth (i.e. new leaves, new shoots and their length – including rhizome length) and decay (i.e. loss of leaves and shoots) rates. To standardize the pictures, they were taken over a white sheet of paper with a scale for postprocessing purposes (Fig. 2D). Fragments were exposed to air daily when photographing (<5 min daily per fragment). This approach was necessary, as underwater photographs would have been technically challenging, prone to blurring, and difficult to standardize across days.

Buoyancy checks were performed daily. Fragments that were found at the bottom of the tank (therefore less than one day not floating) were removed from the experiment, and a last picture recorded. Buoyancy duration was calculated as the duration of days between the experimental start, to when the fragment was found at the bottom of its tank. Seagrass fragments mostly stuck together in the tanks, however they were released individually at the surface after the daily checks. This approach represents a limitation of the study, but it was necessary to allow individual tracking of each fragment while minimizing interactions with other fragments in the tank.

2.4. Statistical analysis

An objective of this study was to assess the influence of growth and decay on the buoyancy of the 122 fragments (34 *H. ovalis*; 43 *H. uninervis* and 45 *Z. muelleri*). For *H. uninervis*, two fragments had multiple rhizomes, with growing tips on both. We removed those fragments from the analysis, as rhizome length is a variable in our statistical model; to simplify the statistical model, we standardized fragments to one rhizome. We recorded morphological changes in fragments (as an indicator of condition) over time in two ways to account for the differences among species in plant growth morphology. For *H. uninervis* and *Z. muelleri* fragments, we measured shoot number, average shoot length and initial rhizome length. These measurements were facilitated using TagLab[1] (TagLab version 2025.9.23), an image segmentation tool oriented to marine data analysis (Pavoni et al., 2022). For *H. ovalis*, we calculated the number of leaves and initial rhizome length (using TagLab), as this species has a different morphology with individual petioles and leaf pairs growing straight from the rhizome. We assessed the mean and standard deviation of these fragment variables over time. We plotted fragment growth at different timesteps, every two days for *H. ovalis* and *H. uninervis* (fast-growing species) (La Nafie et al., 2013) and every five days for *Z. muelleri* (this species experienced a slower growth pattern during the experiment). To compare species growth, we computed a growth index:

$$\boldsymbol{Growth}_{index} = \frac{V_t - V_0}{V_0}, \tag{1}$$

where V_0 and V_t refer to mean shoot length initially (at time t_0) and at the time we are calculating the index (t) for *H. uninervis* and *Z. muelleri*, while theyrefer to the mean number of leaves initially (at time t_0) and at time t for *H. ovalis*. The growth index was used as an indicator of fragment change rather than a comprehensive measure of overall fragment condition.

To assess the impact of initial morphological traits on fragment

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[1] https://github.com/cnr-isti-vclab/TagLab.

buoyancy, we performed a PCA analysis (supp. materials Fig. S10–S12). For this PCA, we considered the following variables: initial shoot number, initial mean shoot length (cm), initial rhizome length (cm) and the ratio of initial rhizome length to shoot number. The PCA analysis was performed in Python (version 3.11.10), using the package ‘sklearn’.

As the PCA didn't show any trend, we ran a Cox proportional hazards regression model (Cox, 1972) to evaluate whether initial fragment traits can predict subsequent buoyancy duration. The Cox model was implemented in Python (version 3.11.10), using the package ‘lifelines’. This model allowed us to account for a censoring process (i.e. it considered that some fragments were still floating at the end of the experiment) and considered an increasing probability of sinking over time. The response variable of the model was the buoyancy duration (in days). For each fragment, we recorded whether the sinking event occurred or was censored. We performed two different models, one for *H. uninervis* and *Z. muelleri* fragments (eq. (2)) and one for *H. ovalis* fragments (eq. (3)), due to different metrics computed. *H. uninervis* and *Z. muelleri* were combined into a single model because their individual sample sizes were limited (43 and 45 respectively); pooling these two species increased statistical power and resulted in more robust and significant model outcomes. The Cox model expressed the hazard function (i.e. the instantaneous risk of sinking at time t) for fragment i with covariate vector X_i as:

$$h_{Zm+Hu}\,(t|\boldsymbol{X}_i) = h_0(\mathrm{t})\exp\left(\beta_1 S_i + \beta_2 SL_i + \beta_3 RL_i + \beta_4 \frac{RL_i}{S_i} + \beta_5 Sp_i\right), \qquad (2)$$

$$h_{Ho}(t|\boldsymbol{X}_i) = h_0(\mathrm{t})\exp\left(\beta_1 L_i + \beta_2 RL_i + \beta_3 \frac{RL_i}{L_i}\right), \qquad (3)$$

where $h_0(t)$ is the baseline hazard function common to all fragments, β_j are regression coefficients and the covariates are: S_i the initial number of shoots, SL_i the initial mean shoot length, RL_i the initial rhizome length, L_i the number of leaves and Sp_i the species identity. In this model, a positive coefficient ($\beta_j > 0$) indicates that an increase in the predictor variable will increase the hazard of sinking (i.e. a shorter buoyancy duration), while a negative coefficient ($\beta_j < 0$) suggests a protective effect (i.e. a longer buoyancy duration).

2.5. Biophysical dispersal model

We assessed the effect of our experimentally derived buoyancy estimates in a biophysical dispersal model using the multiscale coastal ocean model SLIM.[2] The SLIM model has already been applied and validated in the GBR at different scales and for different purposes, including coral larvae connectivity, hydrodynamics and the dispersal of seagrass propagules (Critchell et al., 2015; Hanuise et al., 2025; Lambrechts et al., 2008; Saint-Amand et al., 2023). We used the Lagrangian Particle Tracker (LPT) model and the outputs of Hanuise et al. (2025), who simulated hydrodynamics of the GBR (full validation and methodology in Hanuise et al. (2025)) and incorporated seagrass presence data from (Carter et al., 2021). Virtual particle release locations were identified as meadows within the GBR where the three species (i.e. *H. ovalis* (394 meadows), *H. uninervis* (538 meadows) and *Z. muelleri* (345 meadows)) were dominant based on the metadata in the seagrass polygon distribution layer from Carter et al. (2021). Forty-five virtual particles (i.e. the number of our experimental replicates – 34 for *H. ovalis*) representing seagrass fragments were released from every meadow at the start of the simulations and were run until all virtual particles settled (i.e. maximum 48 days). We didn't consider in the model that some fragments were still floating after the experiment ended. The buoyancy behaviours of the 45 modelled fragments were implemented on a one-to-one basis from the 45 (34 for *H. ovalis*) laboratory-observed fragments, reproducing their observed surface and water-column residence times prior to settlement (Fig. 3). When the virtual particles were at the surface, we considered the exact same windage, as established in Hanuise et al. (2025) – a random windage (i.e. fraction of the wind speed that contribute to the particle transport speed) for each virtual particle chosen within a species-specific range. Buoyancy durations from Hanuise et al. (2025) were derived from literature and expert opinion and expressed as probabilities through time (i.e. increasing probability to sink with time), with averaged buoyancy durations of 17.5 days for *H. ovalis* and of 40.9 days for both *H. uninervis* and *Z. muelleri* (but those averaged values were not fixed, and the buoyancy durations in this model were varying – see Hanuise et al. (2025) for detailed methodology).

The objective of this study was to compare an already implemented seagrass dispersal model based on theoretical biological behaviour (i.e. from available literature and expert opinion – Hanuise et al. (2025)) and the same model, but incorporating our experimentally-derived buoyancy estimates. We ran four simulations for each species (12 simulations total): two simulations during the wet season peak (one with buoyancy duration from Hanuise et al. (2025) and one with our empirical estimates – Fig. 3) and two during the dry season peak. We considered the month of January as it is the seasonal peak for the wet season and July for the dry season (Huang et al., 2024). The simulations started from the first day of both months and were stopped once all virtual particles settled (i.e. reached their end of life in the model). We extracted the trajectories of all simulations and calculated the dispersal distance by using the Euclidean distance between the release location and end of life location of each virtual propagule. We computed statistics for all simulations by calculating minimum, maximum, mean and median dispersal distances. We then compared these statistics to investigate the differences in dispersal distances between model outputs informed by literature and expert opinion (Hanuise et al., 2025) and those informed by experimental data derived in this study.

3. Results

3.1. Buoyancy duration

The three seagrass species exhibited distinct buoyancy patterns over the experimental period (Fig. 3). On average, *Z. muelleri* fragments remained buoyant for 24.7 ± 3.0 days, while *H. uninervis* and *H. ovalis* had shorter durations (Table 1). *H. ovalis* fragments remained mostly at the surface (65% of the 34 tracked fragments floated at the surface before losing buoyancy), whereas *Z. muelleri* and *H. uninervis* experienced more transitions through the water column, spending on average 5.5 ± 0.8 and 3.8± 0.5 days in the water column respectively (Fig. 3 and Table 1). Despite spending less time in the water column, the 35% of fragments that experienced a water column floatation period were associated with the highest probability to lose buoyancy straight after this time through the water column; *H. uninervis* and *Z. muelleri* being more resilient to moving up and down the water column. Buoyancy patterns in the early phase of the experiment were highly variable (see supp. materials – Fig. S2–S4), with some fragments sinking and refloating within minutes. *Z. muelleri* fragments were particularly variable at the beginning of the experiment, as 13 fragments lost buoyancy in three days. By the final week, buoyancy had stabilised across all species, with no day-to-day buoyancy variation of the remaining fragments in the tanks (Fig. 3).

3.2. Fragment morphological growth and decay through time

All fragments exhibited different behaviours through the experiment's duration, with large interspecific differences observed (Fig. 4). While *H. uninervis* fragments displayed a slow steady decline of growth (and leaf length) during the experiment, *Z. muelleri* and *H. ovalis* fragments were able to grow before a decline in growth after day 25

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[2] https://www.slim-ocean.be/.

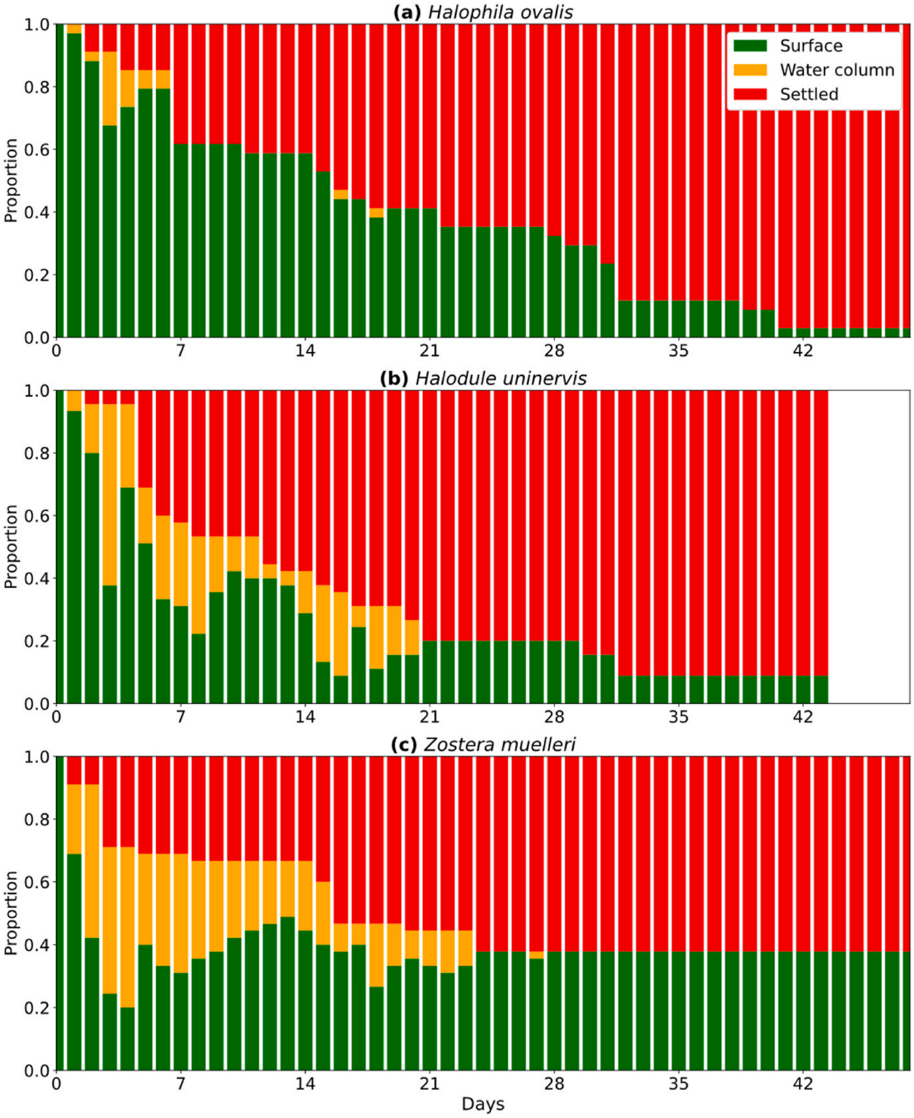

Fig. 3. Buoyancy duration and position in the water column (at the water surface, in the water column and settled at the bottom of the tank) of the seagrass vegetative fragments through time for the three species (n = 34 for *H. ovalis* and n = 45 for *H. uninervis* and *Z. muelleri*). Vertical axis is expressed in proportion of fragments.

(Fig. 4A). Indeed, 26 *Z. muelleri* fragments (57%) had an increase in their mean shoot length during the experiment duration (48 days), despite an overall decrease in shoot number (17 fragments lost at least one shoot – see supp. Materials Fig. S5). Fourteen *H. ovalis* fragments (31%) doubled their number of leaves, with 5 reaching this doubling number before the mean peak at day 22. *H. uninervis* fragments observed a decline in both shoot length and shoot number over time (Supp. materials – Fig. S6). Most of these fragments (72%, 31 fragments) kept the same number of shoots during their entire survival time, with some losing shoots in the process (8 of 43), while very few grew new shoots (4).

H. ovalis fragments were observed to break and generate new fresh individuals (Fig. 4B and supp. Materials Fig. S7). From day 16, new fragments appeared due to the degradation of existing labelled fragments. This phenomenon happened when a section of the rhizome was too degraded, leading to breakage of the original fragment and sinking to the bottom of the tank, with the remainder at the surface without a label. These new fragments included the labelled fragments that lost their label (i.e. due to strip degradation, n = 11) as well as fragments generated by breaking. They reached a maximum number of 23 new fragments on day 30 (Fig. 4B).

3.3. *Morphological factors influencing buoyancy duration*

The principal component analyses did not reveal a clear clustering of fragments according to buoyancy duration for any species (Supplementary Materials – Fig. S10–S12). The first two axes explained a substantial proportion of the variance (76–97%), indicating that the lack of separation was not due to low explanatory power. Principal components were primarily driven by initial morphological traits (rhizome length, shoot or leaf number, and their ratios), while buoyancy duration showed no consistent association with either axis. Overall, the PCA results suggest that buoyancy duration is weakly related to fragment morphology alone and likely influenced by additional physiological or structural factors not included in the PCA.

Statistical analysis indicated that fragments of *H. uninervis* and *Z. muelleri* with longer rhizomes and shoots showed a non-significant trend toward longer buoyancy ($p \approx 0.06$ and $p \approx 0.12$), suggesting these factors may influence dispersal potential (full results in Supplementary Materials – Fig. S8–S9). In contrast, the species covariate was significant, showing that *Z. muelleri* fragments floated much longer than *H. uninervis* fragments ($p < 0.005$). For *H. ovalis*, the Cox model (n = 34) was not significant due to the small number of replicates and only one

Table 1
Observations of buoyancy behaviours derived from the experiment for seagrass fragments of the three tropical species.

/	*Halophila ovalis*	*Halodule uninervis*	*Zostera muelleri*
Average floating time (i.e. surface + water column) [days] ± SE	20.20 ± 1.87	15.22 ± 1.85	24.67 ± 3.01
Median floating time (i.e. surface + water column) [days]	20.00	12.00	16.00
Average time in the water column [days] ± SE	0.53 ± 0.16	3.78 ± 0.53	5.53 ± 0.79
Median time in the water column [days]	0.00	3.00	4.00
Average surface time [days] ± SE	19.67 ± 1.92	11.4 ± 1.70	19.13 ± 2.94
Median surface time [days]	20.00	6.00	6.00
Maximum consecutive days in the water column [days]	5	9	18
Probability to drop at the bottom after a water column buoyancy period [%] (i.e. number of water column buoyancy periods followed by a drop at the bottom divided by total number of water column buoyancy periods)	50.00	23.60	28.60
Number of fragments still buoyant at the end of the experiment	1 (48 days)	4 (43 days)	17 (48 days)

censored observation (i.e., one fragment still floating at the end); all variables had $p > 0.30$. The proportional hazards assumption was verified for all Cox models.

3.4. Biophysical dispersal model outputs

The empirical buoyancy estimates generated in this study resulted in lower modelled dispersal distances when compared to previous seagrass dispersal biophysical models (Fig. 5 and Table 2). These differences in dispersal distance occurred for the two seasons in Queensland, with a larger difference during the dry season (which is windier) compared to the wet season for all three species. *Halodule uninervis* had the largest difference, with an average reduction of 14.32 km in the wet season and 38.97 km in the dry season. On average for all species, the simulations based on previous parameter values (from Hanuise et al. (2025)) predicted a 44% higher dispersal distance over the 12 simulations, compared to simulations generated with our experimentally derived parameters values. Interestingly, the maximum dispersal distance is always higher with experimental estimates, with one exception for *H. uninervis* in July 2016 (Table 2; Fig. 5b).

4. Discussion

To address the lack of empirical life-history data on seagrass fragment buoyancy for tropical species of the GBR, we quantified buoyancy duration and fragment condition for three common species and incorporated these buoyancy estimates into a biophysical dispersal model. We found marked differences in buoyancy potential among the three species, and that there is capacity for vegetative fragments to grow while drifting. When integrated into a biophysical dispersal model, our empirical data suggest previous models may overestimate dispersal distances by approximately 44% on average. These findings underscore the critical role of experimental life-history data in improving the accuracy of dispersal models and advancing our understanding of large-scale dispersal dynamics across the GBR and elsewhere.

We found that *Z. muelleri* had the longest buoyancy potential, floating on average 24.7 days (Table 1). In addition to its longer buoyancy, 17 *Z. muelleri* fragments remained positively buoyant in the tanks at the end of the experiment. Other buoyancy studies found average floatation durations of 21 days (Port Curtis, Queensland - (Weatherall et al., 2016)) and up to five weeks positively buoyant (Stafford-Bell et al., 2015), with the latter study conducted in Victoria, Australia in temperate conditions. Despite differences in locations and collection methods across the studies (collecting floating fragments in the sea and fragment wrack on the beach, respectively), these results suggest a long-buoyancy potential for *Z. muelleri* fragments. Additionally, 13 *Z. muelleri* fragments sank straight to the bottom of the tank during the

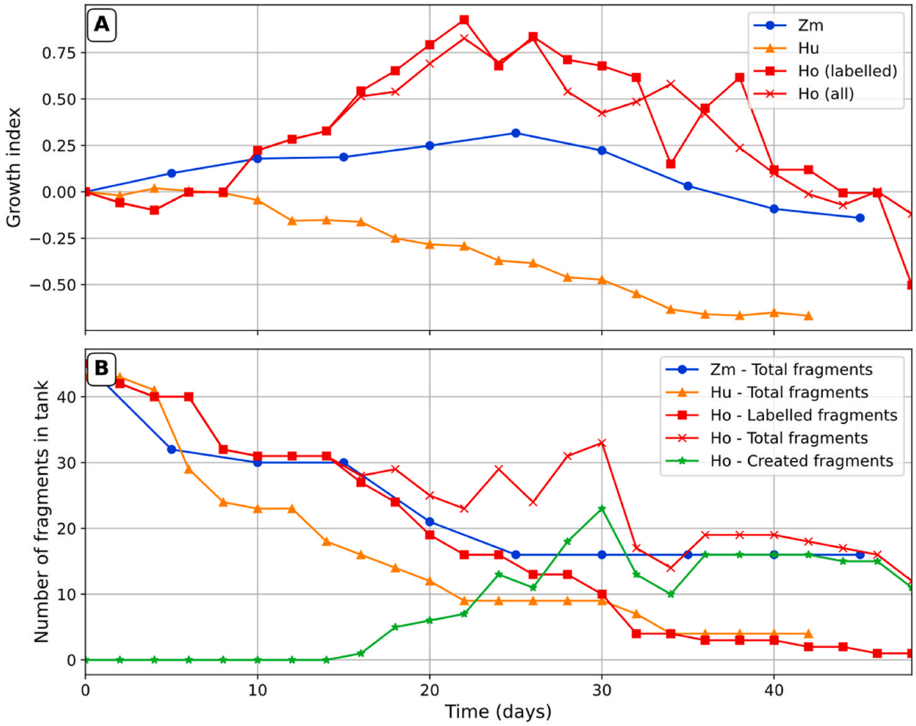

Fig. 4. Fragment growth and decay over time for all species (Zm: *Zostera muelleri*; Hu: *Halodule uninervis*; Ho: *Halophila ovalis*). **A**: Growth index of mean shoot length (Zm and Hu) and of mean number of leaves (Ho). **B**: Number of floating fragments during the experiment (separating labelled and created fragments for Ho).

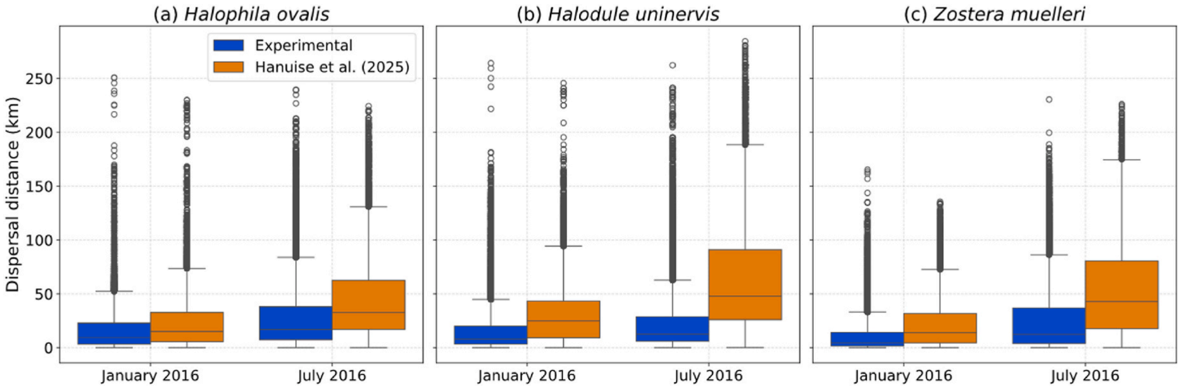

Fig. 5. Boxplot of dispersal distances simulated in the Langrangian Particle Tracker model (LPT) for January and July 2016 for each species (*H. ovalis*; *H. uninervis* and *Z. muelleri*). Blue boxplots represent the distances simulated with our experimental estimates in the LPT while the orange boxplots are the distances simulated using Hanuise et al. (2025) theoretical buoyancy assumptions. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

Table 2
Median, mean and range of dispersal distance (kilometres) of all "virtual" seagrass fragment for each species (Ho: *Halophila ovalis*; Hu: *Halodule uninervis*; Zm: *Zostera muelleri*) and each scenario (dry/wet season and previous model/experimental buoyancy estimates) of the biophysical model.

/		Hanuise et al. (2025)				Experimental			
Season	Species	Median	Mean	Min	Max	Median	Mean	Min	Max
Jan 2016	*Ho*	16.04	23.73	0.03	230.09	10.45	17.87	0.02	250.87
	Hu	25.00	30.42	0.08	245.70	8.38	16.10	0.03	264.18
	Zm	15.71	23.36	0.13	135.51	5.39	12.15	0.03	165.27
July 2016	*Ho*	32.71	43.26	0.15	224.27	17.15	29.16	0.06	239.62
	Hu	47.96	61.53	0.12	284.43	12.63	22.56	0.02	262.28
	Zm	42.84	53.02	0.14	226.23	13.00	26.52	0.01	230.52

first three days of the experiment. This might reflect a combination of different factors, such as fragment damage during collection, individual-specific morphological characteristics, and the environmental conditions at the collection site for this particular species.

H. uninervis and *H. ovalis* fragments were found to have shorter buoyancy durations in our experiments, with averages of 15.2 and 20.2 days respectively (Table 1). In Singapore, Lai et al. (2020) found that *H. ovalis* fragments became negatively buoyant after a 28-day period. The climate ofn Singapore is tropical with abundant rainfall events, high uniform temperatures and high humidity levels all year round (Li et al., 2016). This is different from our study location in the central GBR (Townsville), where temperatures vary seasonally and where high levels of humidity are observed only during the wet season. Another study in the southern GBR (Gladstone) estimated buoyancy durations of 3.0 and 4.5 days, respectively for *H. uninervis* and *H. ovalis* (Weatherall et al., 2016). Once again, large variations are found in fragment buoyancy potential, suggesting differences in local environmental conditions and methodologies. Weatherall et al. (2016) collected already detached fragments from intertidal meadows and conducted experiments in an indoor mesocosm under controlled conditions. Their results and ours are both ecologically relevant but likely correspond to different fragment origins, with shorter floatation durations reflecting passively detached fragments and longer durations representing the upper bound of buoyancy potential associated with physical disturbance. Townsville and Gladstone are both situated within the tropical to subtropical transition zone of the central and southern GBR, where comparable climatic and oceanographic conditions, such as seasonal rainfall, tidal regimes, and cyclone exposure, may also play a role in shaping fragment dispersal.

H. ovalis generated more floating fragments than those initially present in the experimental tanks (Fig. 4B). This constant increasing of fragments for *H. ovalis* has the potential to increase their dispersal success compared to the other species, although the viability and buoyancy duration of the newly formed fragments were not assessed here. These results are not surprising, given the growth pattern for this species (i.e. new leaves growing every 2-3 days (Kaewsrikhaw et al., 2016) and experiencing a star-shaped rhizome expansion). Neither Weatherall et al. (2016) nor Lai et al. (2020) reported this fragmentation process. As a colonising species, *H. ovalis* has a good buoyancy and dispersal potential, which has significant ecological implications, as this species will be able to establish in a new area and stabilise sediments, potentially creating good conditions for opportunistic species to establish (Kilminster et al., 2015).

Most of the fragments experienced growth during the first half of the experiment, except for *H. uninervis* (Fig. 4). This finding was supported by previous studies that show seagrass fragments can continue to grow while floating in the water column when a viable growing tip is present (Thomson et al., 2014; Tol et al., 2023). The reduced growth observed in *H. uninervis* may reflect specific local environmental conditions of the sampling meadow. In contrast, the continued growth observed for *H. ovalis* and *Z. muelleri* demonstrates that fragments of these species can remain physiologically active during dispersal. This behaviour is consistent with, and provides mechanistic support for their classification as colonising and opportunistic species (Kilminster et al., 2015). These results indicate that some seagrass fragments can disperse while actively growing, thereby extending their dispersal potential and enhancing the likelihood of successful establishment after settlement.

The seagrass fragments spent most of their floating time at the water surface (Fig. 3), despite high variability in the first days of the experiment (see supp. materials – Fig. S2–S4). This differs to previous studies that have observed vegetative fragments maintaining a neutral buoyancy in flume tank experiments (i.e. in the water column), suggesting some overestimations of the wind drag coefficients used in biophysical dispersal models (Tol et al., 2024). Lai et al. (2020) also performed flume tank experiments and found some lower wind drag coefficients than those used in biophysical models, but didn't include the buoyancy state of the fragments. Experiments in flume tanks used freshly collected fragments rather than older fragments, which may have been floating for days. In our study, we observed a lot of variability in buoyancy during the first days of our experiments before a stabilization at the surface of the tanks. This indicates that conducting flume tank experiments with older fragments may result in different behaviours. Integrating buoyancy measurements with flume tank experiments could provide a more comprehensive understanding of the dispersal potential of seagrass vegetative fragments. Such an approach would offer valuable insights into how windage influences fragments under varying floating durations and health conditions.

In this study we found that biophysical models, using assumptions on dispersal behaviour from literature and expert opinion, predicted, on average, a 44% higher dispersal distance compared to the same model using our experimentally calibrated buoyancy behaviour for the same species (Fig. 5). This discrepancy demonstrates that previously used GBR-scale dispersal models may overestimate connectivity and dispersal when fragment buoyancy duration is not empirically constrained. Higher dispersal distances on average were observed with the model from Hanuise et al. (2025), but the virtual propagules within our experimental values travelled further at their maximum distance (Table 2). This could be explained by the fact that the theoretical model included more time spent in the water column by the virtual propagules, while experimental fragments spent most of their time at the surface, therefore subject to more windage effect in the simulations. Another explanation is stochastic variation, given our study incorporated a relatively small number of particles (i.e. 45 per meadow – 34 for *H. ovalis*). This divergence between mean and maximum dispersal distances suggests that rare long-distance dispersal events may still occur. Such events, although infrequent, can contribute to genetic connectivity, which might not be as unlikely as the mean dispersal distances suggest.

The outputs of the particle-tracker model used in this study has several limitations, including a dispersal duration capped at 48 days, corresponding to the duration of the experimental observations. While this constraint was chosen to align the model with empirical estimates, it may lead to an underestimation of dispersal distances. This is particularly relevant for *Z. muelleri,* which exhibit long buoyancy durations, and for *H. ovalis*, given the fragmentation phenomenon observed in the tanks (i.e. initial fragments could generate secondary fragments capable of floating for additional periods). Our results highlight the importance of parameterizing dispersal models using empirically derived traits, as model outcomes can be highly sensitive to these inputs. Future research should aim to implement longer empirical behaviour in future seagrass dispersal models, particularly for *H. ovalis,* as this species is likely to have a greater dispersal capability through repeated fragmentation.

This study is limited by the spatial scale of fragment collection (Fig. 1). The sampling occurred in March 2025, shortly after a major flood event in Townsville (29th January to 3rd February), which likely influenced local seagrass meadows. Its condition was classified as poor in 2023 (McKenna et al., 2024), and the fragments used in this study may reflect site-specific conditions. Their physiological condition may not be representative of fragments produced under better environmental conditions, potentially influencing observed growth, buoyancy and degradation patterns. Given the known intraspecific variability across the GBR (Lin et al., 2024), driven by high environmental heterogeneity (Andrews et al., 2023), our results represent species under a shared set of localised stressors. While the three species are widespread and ecologically important throughout the GBR, regional differences may lead to variation in buoyancy, growth, and fragmentation dynamics. Nevertheless, our results fall within the broad range reported in previous studies, with variation likely reflecting differences in methodology, collection timing, and site-specific environmental conditions (Lai et al., 2020; Weatherall et al., 2016).

We tracked fragment buoyancy and integrity at an individual scale, and our methodology included everyday exposure to air and separation of fragments attached together. As fragments were mostly stuck together in the tank, the daily separation could have influenced both degradation and the duration of buoyancy. In particular, non-buoyant fragments could have remained at the surface due to the influence of buoyant fragments, potentially increasing apparent buoyancy duration. Conversely, repeated handling and separation may have accelerated degradation, thereby reducing buoyancy duration relative to undisturbed conditions. Although this manipulation disrupts natural clumping behaviour, its effects are likely bidirectional and partially offsetting. As such, while this represents an experimental artifact, it is unlikely to have systematically biased buoyancy duration estimates in a single direction. Our fragments were repeatedly exposed to air during daily data collection, presenting a potential experimental limitation. There is no direct documentation on air exposure affecting floating capacity, although observations of seagrass wrack dynamics indicate that fragments can be stranded on beaches or intertidal zones during tidal cycles and subsequently resuspended and transported again when re-flooded (Oldham et al., 2014; Stafford-Bell et al., 2015; Sutera et al., 2024). Such studies suggest that brief exposure to air does not necessarily compromise fragment viability or the potential for re-floating. In our experiment, fragments were returned to the water surface within a short period following air exposure (<5 min, i.e. less than what could affect fragments in the natural environment between tides).

This study delivers new empirical buoyancy data to enhance the parameterisation of seagrass biophysical dispersal models. Previous biophysical models of fragment dispersal used a wide range of buoyancy durations, from gathering all species and propagules to a unique behaviour (Grech et al., 2016; Schlaefer et al., 2022) to setting multiple dispersal durations to capture all scenarios due to the scarcity of empirical data (Evans et al., 2021). For tropical species, two biophysical models included more species-specific buoyancy durations (Hanuise et al., 2025; Lai et al., 2024). Lai et al. (2024) used a decay rate function based on an experimental approach, while Hanuise et al. (2025) relied on published data and expert knowledge. Here, we compared our experimental estimates with a robust biophysical model integrating species-specific traits, and we observed large differences in predicted dispersal distances. This discrepancy underscores the gap between modelling assumptions and empirical measurements of dispersal behaviour. By generating species-specific buoyancy data, our study contributes new, accessible information to refine the assumptions underpinning seagrass dispersal models.

Integrating empirical and species-specific data into dispersal models is crucial for advancing both ecological understanding and evidence-based management. Our results show that *Zostera muelleri* fragments exhibit a long buoyancy duration, favouring long-distance dispersal. At the GBR scale, this suggests that even though the species is relatively scarce, it can maintain connectivity and facilitate recovery from distant sources. In contrast, *H. uninervis* has a limited buoyancy potential, limiting its dispersal range. These differences highlight the need for species-specific management strategies. For example, restoration or protection efforts for species with short buoyancy durations may need to prioritise spatially closer source meadows, whereas species with longer buoyancy durations can benefit from maintenance of broader scale connectivity. By providing new data directly applicable to dispersal models, our study improves modelling assumptions and strengthens predictions. In a management context, these improved predictions can be used to identify restoration sites likely to receive sufficient propagule supply, determine areas where local donor meadows are essential, as opposed to those supported by regional connectivity, and prioritise protection of key source meadows that contribute to recovery. More broadly, these findings highlight the importance of coupling experimental movement ecology with dispersal modelling to enhance predictions of coastal ecosystem dynamics. Integrating experimentally derived data into biophysical models moves beyond theoretical assumptions, providing a mechanistic understanding of how seascape structure, climatic variability and species traits interact to shape connectivity and potential recovery. This integrative approach offers an adaptable framework for predicting connectivity dynamics in other habitat-forming marine plants, with similar dispersal processes. Such frameworks are essential for guiding adaptive restoration and informing management strategies that sustain biodiversity and ecosystem services across tropical and temperate coasts.

CRediT authorship contribution statement

Douchan Hanuise: Writing – review & editing, Writing – original draft, Software, Project administration, Methodology, Data curation, Conceptualization. **Chieh Lin:** Methodology, Data curation, Conceptualization. **Samantha Tol:** Validation, Supervision, Conceptualization. **Severine Choukroun:** Supervision, Conceptualization. **Michael A. Rasheed:** Validation, Supervision, Conceptualization. **Thomas Dobbelaere:** Writing – review & editing, Supervision. **Paul H. York:** Writing – review & editing, Supervision, Conceptualization. **Timothy M. Smith:** Writing – review & editing, Validation, Supervision, Conceptualization. **Robert G. Coles:** Writing – review & editing, Validation. **Emmanuel Hanert:** Writing – review & editing, Supervision. **Alana Grech:** Writing – review & editing, Validation, Supervision, Conceptualization.

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.

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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.2026.107937.

Data availability

Data will be made available on request.

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