

## The role of hydrodynamics on seed dispersal in seagrasses

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### Abstract

Two widely distributed seagrasses in Western Australia with contrasting dispersal strategies were studied in terms of their physical characteristics and morphology to understand how physical processes (wind, waves, and currents) drive dispersal. *Posidonia australis* releases floating fruit that contain a single negatively buoyant seed that lacks dormancy. *Halophila ovalis* produces fruit and dormant seeds that sit on the sediment surface. The floating stage of *P. australis* was assessed in situ by tracking the movement of the fruit directly on the ocean surface, together with drifter devices to differentiate between the transport induced by surface currents and wind. The dehiscence time of *P. australis* fruit was evaluated in seawater tanks, and the associated viability of the seeds was assessed by growth after dehiscence. The settling velocities of *P. australis* seeds and *H. ovalis* fruit and seeds were quantified in settling tubes with image-processing techniques to track the fall trajectories. The re-suspension thresholds of the seeds were calculated based on the critical bed shear stresses required to transport the seeds in a unidirectional flow flume. *P. australis* can travel long distances at the air–sea interface ( $\sim 55$  km), due to wind alone, during its floating stage. The settling velocities of *P. australis* and *H. ovalis* seeds ( $w_s = 10.6 \pm 0.4$  cm s<sup>-1</sup> and  $4.7 \pm 0.1$  cm s<sup>-1</sup>, respectively) and their re-suspension thresholds ( $\tau = 107 \pm 4$  mPa and  $66 \pm 1$  mPa, respectively) suggest that secondary movement is restricted, but likely to be produced by stronger wave-induced shear stress events.

The rate of global seagrass loss has accelerated during the past several decades due to a range of human activities in the coastal zone (Waycott et al. 2009). It is therefore critical to understand the processes controlling temporal and spatial dynamics of existing seagrass populations, including their growth, stability, and resilience. Sexual reproduction is an essential part of the life cycle of seagrasses, not only for colonization as previously thought, but also for consolidation of existing meadows as identified by high genetic diversity found in old meadows (Jover et al. 2003; Kendrick et al. 2012). Yet surprisingly, we still know very little about how the physical mechanisms of seed dispersal influence the distribution and structure of seagrass meadows. Despite the importance of sexual reproduction to seagrass population dynamics, most seagrass studies on reproductive effort have focused on clonal growth rather than sexual input (Orth et al. 1994). Research focused on sexual reproduction has led us to understand the biology of seed dispersal but not the demographic consequences.

Seagrasses have evolved several times in the past from different terrestrial ancestral lineages (Les et al. 1997). Thus, despite sharing a common ecological niche, there are many differences between seagrass species. Some seagrasses are short-lived, with fast growth and a high production of seeds (termed R strategists; Duarte et al. 2006). Other species are slow-growing and longer lived; these species use more specialized reproductive strategies, but with a lower production of seeds (termed K strategists). This diversity is easily identifiable by the differences in seagrass fruits and seeds, which support a range of different dispersal strategies (Fig. 1). Ultimately, the dispersal potential that

is achieved by seagrasses depends on poorly understood interactions between physical drivers (e.g., currents and wind) and the specific characteristic of seagrass fruit and seeds (including their physical properties).

There have been some attempts to estimate dispersal for a number of seagrass species. Harwell and Orth (2002) predicted transport of  $\sim 100$  km for floating rhipidia (detached shoots bearing the seeds) of *Zostera marina* in Chesapeake Bay, United States of America, by estimating the distance between newly recruited sites and possible bed donors. They discussed the importance of hydrodynamic conditions to dispersal (i.e., tides and winds), but did not directly attempt to predict the transport pathways of seeds in response to the hydrodynamics. Conversely, Orth et al. (1994) found that there was little movement ( $\sim 5$  m) of negatively buoyant *Zostera marina* seeds on the seafloor following release from shoots. However, the relationship of this movement to the local hydrodynamic conditions (e.g., the bed shear stresses that were present) was not studied; hence, their conclusions may only be applicable to that particular study site.

Lacap et al. (2002) investigated the dispersal potential of two tropical seagrass species (*Thalassia hemprichii* and *Enhalus acoroides*) in the Philippines, and their results suggested dispersal distances of  $\sim 20$  km and  $\sim 40$  km for those species, respectively. These distances were estimated based on in situ tracking of the seeds and fruits during field experiments, combined with measurements of how long the seeds and fruits typically float. While these results emphasized the important role that flotation plays in facilitating long distance dispersal, the study did not delineate which hydrodynamic transport mechanisms were ultimately responsible for the observed transport. Understanding the mechanisms is critical to predicting dispersal

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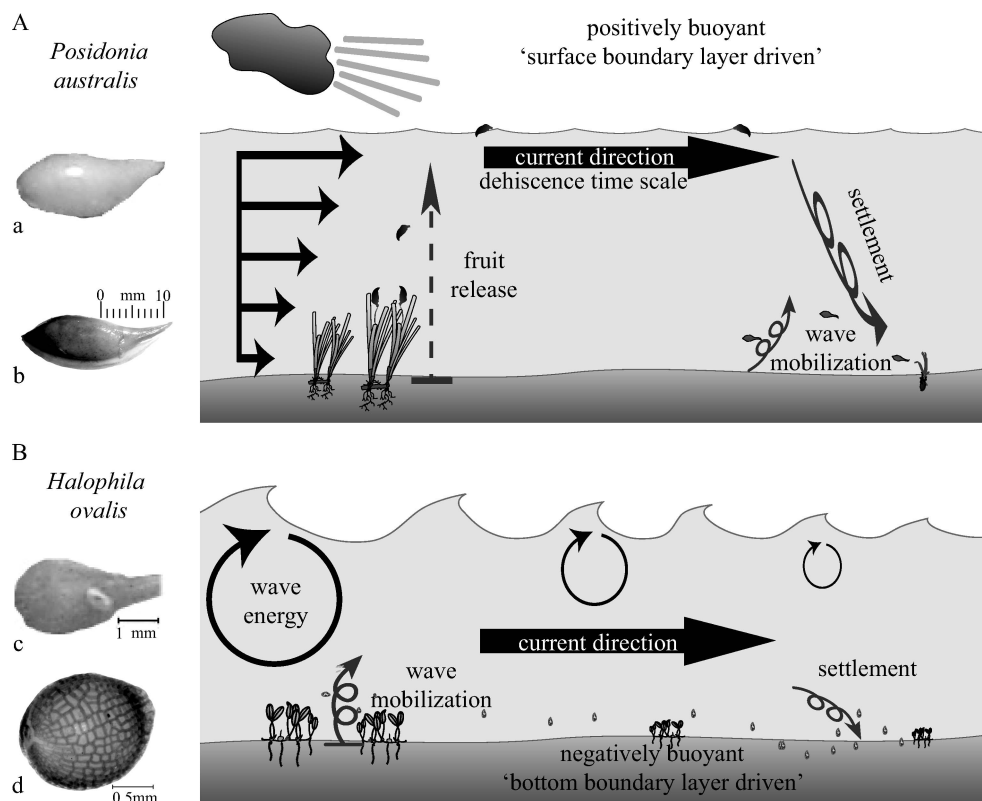


Fig. 1. Different dispersal strategies of (A) *Posidonia australis*: (a) fruit and (b) seed photos with a diagram that summarizes transport processes during its positively buoyant stage, with transport driven by processes in the surface-ocean boundary layer; (B) *Halophila ovalis*: (c) fruit and (d) seed photos with a diagram showing the negatively buoyant seeds released on the sediment, with transport driven by waves and bottom currents along with sediment.

for these species under different hydrodynamic conditions. In the Mexican Caribbean, Van Dijk et al. (2009) predicted a much greater dispersal potential for *Thalassia testudinum* of around 350 km. In this study, the estimated dispersal distances were supported by independent results that showed genetic connectivity among populations over distances comparable with those scales. Despite the importance of hydrodynamics to fruit and seed dispersal identified in these previous studies, studies have generally been site-specific, which reduces our ability to estimate dispersal under a range of hydrodynamic conditions.

The relationship between the physical characteristics of seeds and their movement under different hydrodynamic conditions was studied by Koch et al. (2010) for three aquatic, mesohaline angiosperms (*Ruppia* sp., *Potamogeton* sp., and *Stuckenia* sp.), all of which have negatively buoyant seeds. They noted that dispersal was very limited for seeds released over vegetated areas. However, transport over unvegetated areas occurred when the currents reached a threshold of  $\sim 4\text{--}6\text{ cm s}^{-1}$ . They concluded that secondary dispersal of settled seeds would likely occur after seeds are released in summer, when mobilized during more energetic autumn or early winter conditions.

Recently there have been some attempts to explicitly quantify seagrass seed dispersal distances and pathways using particle tracking incorporated into numerical ocean circulation models. Along the Swedish coast, Källström

et al. (2008) used a numerical model to predict the transport of *Zostera marina* floating rhipidia. Transport distances up to  $\sim 150\text{ km}$  were predicted during their study period, based on the local time-varying wind conditions and in situ measurements that showed that the shoots were transported on the ocean surface at roughly 4% of the wind velocity. While emphasizing the importance of wind stresses to seagrass seed dispersal, there is still the need to differentiate between potential wind transport mechanisms (i.e., how much of the transport is due to wind-forced surface currents vs. direct wind forces acting on the exposed surfaces of the floating shoots [that is, above the air-sea interface; termed 'windage' effects]). Erftemeijer et al. (2008) simulated dispersal of floating *Zostera marina* shoots in the Wadden Sea, Netherlands, using a three-dimensional hydrodynamic numerical model. The shoots were advected by a combination of surface currents from the model plus an additional direct windage contribution. The contribution of windage was not directly measured, but was taken as 3% of the wind speed, a value used for oil-spill modeling (the same value also assumed by Harwell and Orth 2002).

Seed dispersal studies have mainly focused on *Zostera* spp. and *Thalassia* spp. Therefore, there is a need to broaden our knowledge of dispersal in a greater range of seagrass taxa to assess the generalizability of the outcomes of studies on these genera. Southwestern Australia has one

of the most diverse and largest temperate seagrass meadows in the world, and it offers the opportunity to study dispersal over semi-continuous meadows for 2000 km of coastline. Seagrass diversity results in landscapes that are visually dominated by larger species such as *Posidonia* and *Amphibolis*, mixed with beds or meadow-understory of smaller, less dominant genera such as *Halophila* and *Zostera* (Kirkman and Kuo 1990; Kendrick et al. 2000). *Posidonia australis* is a slow-growing K strategist that invests in multi-year vegetative growth, which results in extensive meadows that dominate shallow, subtidal, temperate landscapes (Kendrick et al. 2008). It produces positively buoyant fruit that contain a single negatively buoyant seed that displays no seed dormancy (Fig. 1). *Halophila ovalis* is an R strategist (Kirkman and Kuo 1990) that has less investment in multi-year vegetative (clonal) persistence. *H. ovalis* produces negatively buoyant fruit that develop at or below the sediment surface, which contain several small seeds (~ seven) that can remain dormant in sediments for periods ranging from 1 month to 2 yr (Mcmillan 1991; Kuo and Kirkman 1992).

The main objective of this study was to quantitatively compare the dispersal processes in *Posidonia australis* and *Halophila ovalis*, with a focus on understanding (1) the properties important for transport; (2) how their movements are controlled by physical forces acting directly on the propagules; and (3) the ecological implications that seed dispersal has for these contrasting species. To achieve this, the morphology of the fruits and seeds and their density and settling velocities were compared. For primary or long-distance dispersal of *P. australis*, the surface dispersal was studied in situ to assess movement by surface currents and wind. Also, because *P. australis* displays no seed dormancy, the viability of seeds was assessed using seeds that naturally dehisced at different times from floating fruit in seawater tanks. To understand the potential role of secondary dispersal on *P. australis* and overall transport in *H. ovalis*, re-suspension thresholds were also quantified based on the critical shear stresses required to consistently move the seeds in a hydrodynamic flume. All of this information is essential to understand and ultimately predict seed dispersal for these seagrass species.

## Methods

**Sample collection**—Mature fruits of *Posidonia australis* and *Halophila ovalis* were collected during the early austral summer (Nov 2009–Jan 2010) from five different sites in the coastal region of Perth, Western Australia (Fig. 2). The samples were either collected via scuba-diving or snorkeling, depending on depth and accessibility, with care taken to ensure only mature fruits were collected. For *P. australis*, the stems bearing the fruit were gently shaken and only those freely released were collected, thereby simulating a release that would occur after a small natural disturbance. As they grow, *H. ovalis* fruit transform from an ellipsoid to a spherical shape when the fruit containing the seeds reach a mature size (Kuo and Kirkman 1992); thus, only spherical fruit were examined in this study.

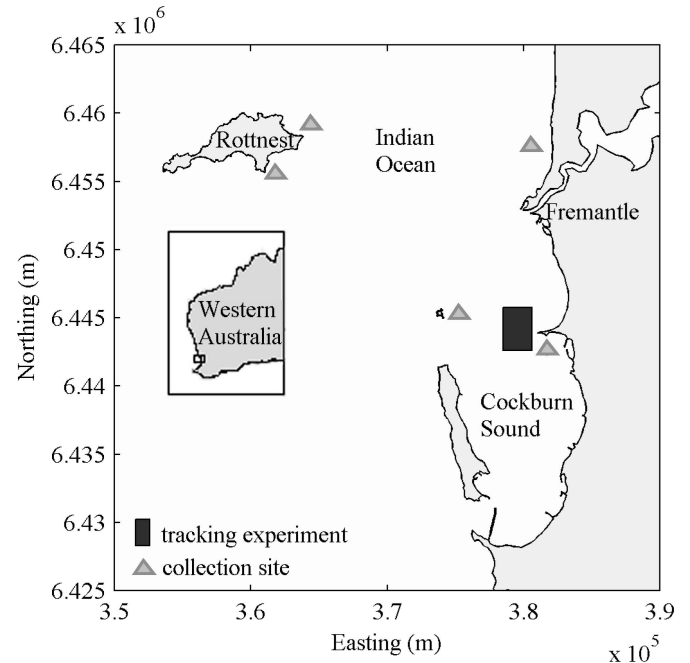


Fig. 2. Study area, seagrass sampling sites, and location of the tracking experiments.

**Fruit and seed measurements**—*P. australis* fruit were collected in November 2010. The dimensions of the fruit were measured immediately following collection and were subsequently held in seawater containers located on shore to allow the seeds to naturally dehisce (see below). The mass of each fruit and seed was measured to the nearest 1 mg, and the dimensions (length, width, and height) were measured using a vernier caliper to the nearest 0.02 mm. The volumes ( $V_s$ ) of *P. australis* fruit and seeds were determined by fluid displacement to the nearest 0.1 mL in a 12-mL graduated cylinder (note that vegetable oil was used to allow the weakly positively buoyant fruit in water to be fully submerged). The density of each fruit or seed (denoted  $\rho_s$ ) was then estimated from the mass and volume measurements. The fluid displacement by one seed was small, so batches of five seeds were measured together and the mean was recorded.

*H. ovalis* fruit and seeds are approximately spherical (see Fig. 1); due to their small size, only their diameters were measured. The mass of the *H. ovalis* seeds were measured in the laboratory to the nearest 0.01 mg. The volume was estimated from the measured diameter assuming a perfect sphere (this volume was then used to estimate the density  $\rho_s$ ).

**Settling velocity**—The settling velocities ( $w_s$ ) of the negatively buoyant fruit of *H. ovalis* and the seeds of both *P. australis* and *H. ovalis* were measured using a settling tube (transparent vertical cylinder) filled with seawater. The fruit and seeds were manually released at the top of the settling tube and their fall trajectory was recorded using a Sony high-definition video camera (HDR-CX12; 1920 × 1080 pixels) recording at 25 frames s<sup>-1</sup>, with the camera rotated sideways to maximize the number of pixels along



the vertical fall axis. Due to differences in the size of the particles, two different settling tubes were used: for *P. australis* a 19-cm-diameter  $\times$  120-cm-long tube was used, whereas for *H. ovalis* a 3.5-cm-diameter  $\times$  32-cm-long tube was used. The camera was positioned a fixed distance away from the tube to fit the full length of the tube in the camera field of view. The camera pixel coordinates were converted to real-world coordinates by imaging a grid ( $2 \times 2$ -cm cells) over the full length of the tube, and transforming the coordinate system using a two-dimensional linear interpolation in Matlab (Mathworks). Video sequences of the particle fall trajectories were analyzed with Matlab to manually capture the particle coordinates every 0.5 s (and thus derive the fall velocity as a function of time). The terminal settling velocity ( $w_s$ ) of each fruit or seed was then obtained from a linear least-squares fit of the linear (constant fall) portion of the fall record, which occurred after a brief initial acceleration period. The resulting uncertainty in each settling velocity record was estimated to be  $\sim 0.1 \text{ cm s}^{-1}$  for both species (or roughly 2% of the velocity of the slower falling *H. ovalis* seeds [see below]).

Drag coefficients  $C_d$  for the fruit and seeds were computed from their density, dimensions, and settling velocity according to (e.g., Dean and Dalrymple 2004)

$$C_d = 2 \left( \frac{\rho_s - \rho_{\text{H}_2\text{O}}}{\rho_{\text{H}_2\text{O}}} \right) \frac{g V_s}{w_s^2 A_p} \quad (1)$$

where  $\rho_{\text{H}_2\text{O}}$  is the density of seawater,  $g$  is the gravitational acceleration,  $V_s$  is the volume of the fruit or seed, and  $A_p$  is the estimated exposed frontal area by the fruit or seed as it falls. *P. australis* seeds fall sideways (i.e., long-axis horizontal); hence, the frontal area,  $A_p$ , was determined based on assuming an ellipsoid shape and a sphere for *H. ovalis*. The density  $\rho_{\text{H}_2\text{O}}$  was computed from the seawater equation of state (Gill 1982) based on the measured salinity (35.2) of the source waters of the adjacent Perth coastal waters and the temperature recorded in situ in the settling tube during each experiment, averaging  $20^\circ\text{C}$  ( $\pm 2^\circ\text{C}$  SD). Note that the effect of these small temperature fluctuations varied  $\rho_{\text{H}_2\text{O}}$  by  $< 0.1\%$ ; hence, the seawater density for the calculations was taken as a constant  $1024.9 \text{ kg m}^{-3}$  (equivalent to the value at  $20^\circ\text{C}$ ).

**Resuspension**—The hydrodynamic force required to mobilize the seeds once they settle on the seafloor was quantified by measuring the critical shear stress ( $\tau_{cr}$ ) required for re-suspension. This was specifically defined as the stress required to drive consistent movement of the seeds in the flow direction. For these experiments, a unidirectional flow flume of  $3 \times 0.4 \times 0.4 \text{ m}$  (length  $\times$  width  $\times$  height) was filled to a depth of 0.25 m. The seeds were deposited over a 2-cm-thick, flat, sediment bed that consisted of fine sand (median diameter  $\sim 0.4 \text{ mm}$ ). Six seeds at a time were deposited 1.5 m away from the back of the flume and  $\sim 6 \text{ cm}$  apart from one another. The flow velocity was increased at around  $0.2\text{--}1.0 \text{ cm s}^{-1}$  intervals every 2 min, and during each flow increase, the motion of seeds was monitored.

The water-column flow was continuously measured with a Nortek Vectrino acoustic Doppler velocimeter (ADV) sampling at 25 Hz. As the flow was gradually increased in the flume, the free stream current velocity (taken as the velocity measured 20 cm above the sediment interface) was monitored. When a seed was observed to consistently move in the direction of the flow, the measured mean velocity (2-min averaged) was recorded as the critical free stream flow-speed ( $U_{cr}$ ) that mobilized the seed. Following the seed re-suspension experiments, additional experiments were conducted to measure detailed velocity profiles with the ADV at each of the flow speeds previously used. This involved profiling the ADV measurements over the water column, with the sampling heights roughly logarithmically distributed with  $\sim 0.5\text{-cm}$  spacing near the bottom to  $5\text{-cm}$  spacing near the surface ( $\sim 14$  total measurements). Once the profile was measured, the instantaneous horizontal (stream-wise;  $u$ ) and vertical ( $w$ ) velocity time series at each height (5-min duration) were used to compute the turbulent Reynolds stresses  $u' w'$  (Nielsen 1992), where  $u'$  and  $w'$  are the respective turbulent velocity fluctuations with their mean values removed. The magnitude of the Reynolds stresses (roughly constant) within the bottom boundary was used to estimate the critical shear stress ( $\tau_{cr}$ ) associated with that flow as

$$\tau_{cr} = -\rho_{\text{H}_2\text{O}} \overline{u' w'} \quad (2)$$

Therefore, a value of the critical shear stress required to move each seed placed in the flume was assigned.

**In situ *Posidonia* fruit tracking**—During two field experiments, roughly a thousand *P. australis* fruit were collected for a fruit-tracking study. These experiments were conducted off Woodman Point, within Cockburn Sound just south of Fremantle (Fig. 2), on 29 November 2010 and on 08 December 2010. The aim was to understand and describe how these fruit were transported in response to a combination of ocean currents and the direct influence of wind (i.e., windage). To improve visibility of the fruit, prior to their release they were coated with a thin layer of fluorescent paint. The fruit were then released in a single patch and were manually tracked by Global Positioning System (GPS) from a small boat. To avoid interference of the patch trajectory by the boat (i.e., by the boat wakes), GPS coordinates were consistently collected  $\sim 5 \text{ m}$  away from the patch center on its eastern side (parallel to the wind direction).

During the study, high-frequency wind data (available every minute) were obtained from the Bureau of Meteorology weather station located at nearby Rottnest Island (Fig. 2). The local water-column velocities during each study were also measured at various depths, using different instruments. A Nortek Vector ADV recorded the velocities near the middle of the  $\sim 3\text{-m}$ -deep water column, sampling at 2 Hz. For each experiment, the surface currents were also measured using a pair of cruciform drifters, based on a design similar to Austin and Atkinson (2004). These cruciform drifters were 60 cm in height, with 45-cm cross-plates on four sides; hence, they recorded velocities in the top 60 cm of the water column internally with a logging

Table 1. Physical properties of fruits and seeds of *Posidonia australis* and *Halophila ovalis*.

	<i>Posidonia</i> seeds			<i>Halophila</i> seeds			<i>Posidonia</i> fruit			<i>Halophila</i> fruit		
	Mean	SE(±)	n	Mean	SE(±)	n	Mean	SE(±)	n	Mean	SE(±)	n
Longitudinal length (mm)	21.2	0.34	151	—	—	—	24.5	0.33	70	—	—	—
Transversal length (mm)	5.8	0.13	146	—	—	—	10.0	0.11	70	—	—	—
Diameter (mm)	—	—	—	1.29	0.03	108	—	—	—	3.0	0.15	97
Mass (mg)	232	9.01	151	1.5	0.06	108	810	18.83	70	30	3.17	70
Area (mm <sup>2</sup> )	401	14.00	146	5.5	0.23	108	778	16.23	70	31	2.23	97
Volume (cm <sup>3</sup> <sub><i>Posidonia</i></sub> , mm <sup>3</sup> <sub><i>Halophila</i></sub> )	0.22	0.01	123	1.31	0.08	108	1.03	0.10	50	19	1.95	97
Density (g cm <sup>-3</sup> )	1.10	0.03	123	1.36	0.05	108	0.86	0.02	50	1.82	0.08	70
Settling velocity (cm s <sup>-1</sup> )	10.6	0.38	86	4.7	0.14	97	—	—	—	5.4	0.26	28
Drag coefficient	1.5	0.43	50	0.8	0.06	73	—	—	—	2.1	0.12	67
Critical stress (mPa)	107	3.58	154	66	1.26	124	—	—	—	—	—	—
Length hypocotyl (mm)	13.5	0.17	151	—	—	—	—	—	—	—	—	—
Length epicotyl (mm)	7.7	0.22	151	—	—	—	—	—	—	—	—	—

GPS. Finally, to measure the combined wind-driven surface transport (i.e., due to both the surface currents and potentially enhanced windage effects), five small ( $4.4 \times 2.6$  cm) GPS loggers (PhotoMate 887 by TranSystem) were deployed in small dry bags ( $15 \times 8.5$  cm) recording their position every second. These dry bags were partially filled with some air so that they were raised slightly above the air-sea interface, similar to the *P. australis* fruit. To quantify this windage effect, we computed the excess transport, taken as the difference between the cruciform drifter velocity and fruit (or surface drifter) velocity, and related this to the instantaneous wind speed.

***Posidonia* dehiscence time and viability experiments**—*P. australis* ripe fruit were collected daily from 20 November to 01 December 2010. These fruit were placed into an insulated container filled with seawater and then transported to the nearby Watermans Marine Research Station on the coast of Perth. There the fruit were placed into tanks (500 liters) supplied with a continuous flow of seawater sourced from the adjacent Perth lagoon to simulate natural temperature conditions. Once floating within the tanks, the fruit and seeds were counted, initially within 3 h after collection, and were subsequently counted every 24 h. Seed viability was assessed by the detection of leaf growth after seed germination. To achieve this, 10 of the dehiscent seeds from each dehiscence time were randomly selected and planted in sediment according to Statton et al. (in press). The seeds were considered viable if leaf growth was present within 2 weeks of when they were planted. For *H. ovalis*, seed viability was not measured, because the germination time that would terminate the dispersal phase has already been studied in detail by Kuo and Kirkman (1992).

## Results

***Fruit and seed properties, settlement, and re-suspension***—*Posidonia australis* contain a single seed per fruit, with both the fruit and seed having an ellipsoid shape (Fig. 1). The fruit (hereinafter expressed as mean  $\pm$  SE) had a lower density  $\rho_s = 0.86 \pm 0.02$  g cm<sup>-3</sup> than seawater ( $\sim 1.025$  g cm<sup>-3</sup>) and hence were positively buoyant, whereas each seed was weakly negatively buoyant  $\rho_s = 1.10 \pm$

$0.03$  g cm<sup>-3</sup>. The settling velocity ( $w_s$ ) for these seeds averaged  $10.6 \pm 0.4$  cm s<sup>-1</sup>. A critical shear stress of  $\tau_{cr} = 107 \pm 4$  mPa was required to mobilize the seeds over the sandy bed of the flume.

For *Halophila ovalis*, the densities for both the fruit and seeds were  $\rho_s = 1.82 \pm 0.08$  g cm<sup>-3</sup> and  $1.36 \pm 0.05$  g cm<sup>-3</sup>, respectively; hence, both were negatively buoyant. The fruit settled at  $w_s = 5.4 \pm 0.2$  cm s<sup>-1</sup>, while the seeds settled at a comparable velocity of  $w_s = 4.7 \pm 0.1$  cm s<sup>-1</sup>. The flume experiments predicted that a lower critical shear stress of  $\tau_{cr} = 66 \pm 1$  mPa was required to mobilize the *H. ovalis* seeds. Detailed dimensions, mass, area, volume, and the drag coefficient statistics computed via Eq. 1 are included in Table 1.

***Floating-fruit tracking: Role of currents vs. windage***—The first tracking experiment was conducted during a period of calmer winds, and within this experiment, the conditions can be further split into two stages: (1) an initial period, when the wind was blowing at  $\sim 30$  km h<sup>-1</sup> toward the southwest, with the fruit and surface (PhotoMate) drifters moving at roughly the same speed, but with the cruciform drifters lagging behind (Fig. 3); and (2) a subsequent period, when the wind velocity dropped to  $\sim 20$  km h<sup>-1</sup> at around 10:40 h and slightly changed direction toward the south, at which time the fruit, cruciform, and surface drifters all moved at a more comparable speed.

The second experiment was conducted during a period of strong winds of 35–40 km h<sup>-1</sup> directed toward the northeast. Here, the surface (PhotoMate) drifters moved ( $31 \pm 0.5$  cm s<sup>-1</sup>) together with the fruit. However, the cruciform drifter again moved much more slowly ( $19 \pm 0.7$  cm s<sup>-1</sup>). The recorded data show a similar trajectory, but with only around half the distance traveled during the study period. Furthermore, the fruit, surface drifters, and cruciform drifter all showed faster transport compared with the current speed measured at 1.5-m depth with the ADV (thus, roughly sampling at the middle of the 3-m water column) under strong wind-driven conditions (second experiment). The results indicate that the surface-water motion (measuring in the top 60 cm of the water column by the cruciform drifter) was much faster than the depth-averaged flow, and the fruit and surface (PhotoMate)

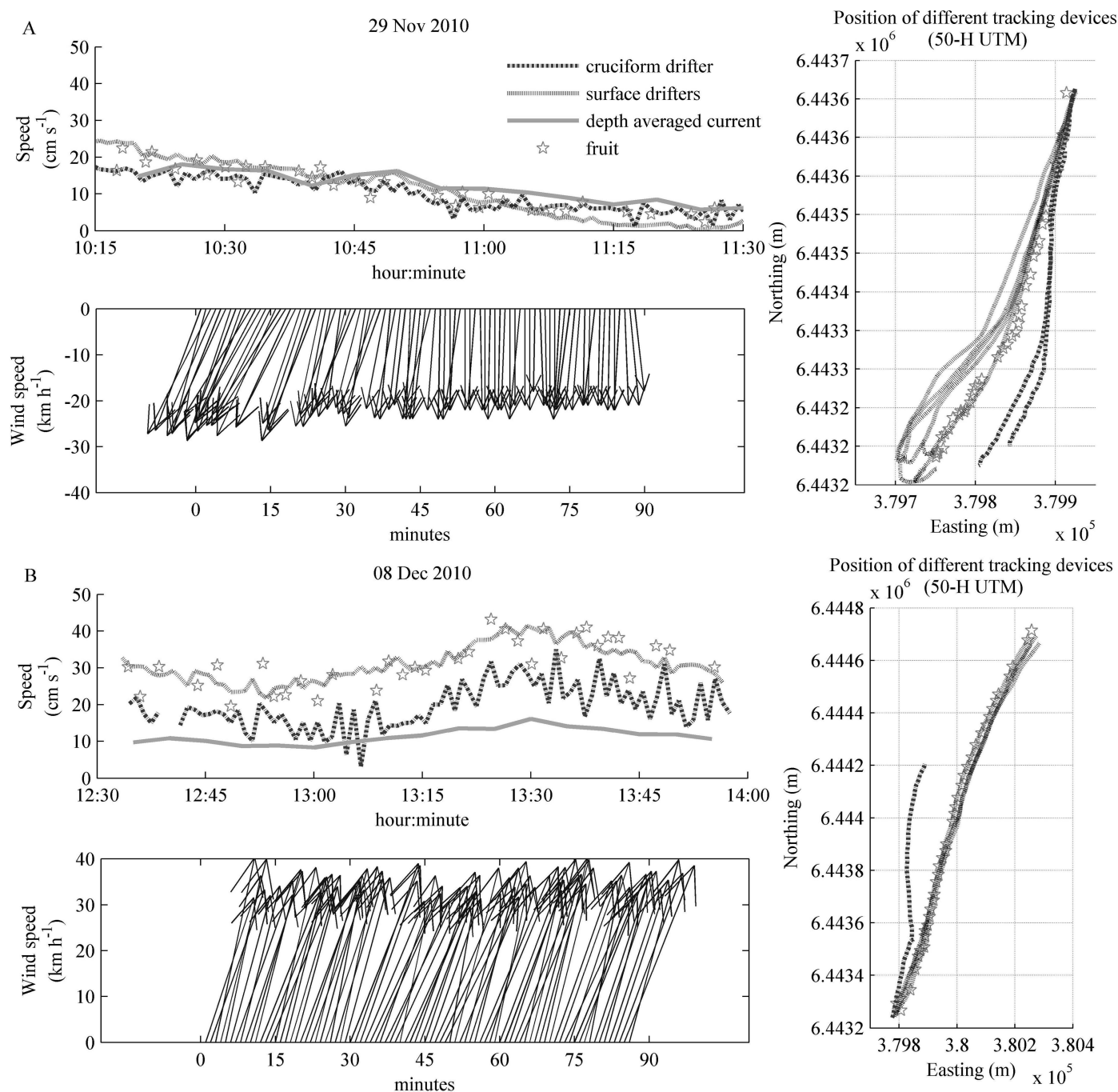


Fig. 3. Velocity comparison between measurements from in situ (50-H UTM) seagrass fruit tracking, drifter devices, and ADV measurements that show results from the two study periods: (A) 29 November 2010 (transition from strong to weaker wind conditions), and (B) on 08 December 2010 (period of strong sustained winds).

drifters themselves moved much faster than the surface-water motion during periods of strong winds. We attribute the latter effect to surface windage that results from wind forces acting directly on the exposed surface of the fruit (i.e., the part of the fruit located above the air-sea interface). The windage results suggest that an additional 1–2% of the wind velocity was transferred to the actual fruit, thereby substantially enhancing the surface transport (Fig. 4).

**Dehiscence and viability**—Dispersal distances for *P. australis* can depend on both their transport rate and the time it takes for the fruit to release the seed (dehiscence). Our results indicate that around 40% of 1196 fruits dehiscenced within the first 3 h; with 13% and 15% of total seeds releasing within 24 h and 48 h after collection, respectively. By the fourth day, 75% had released. The remaining 25% were released over the fifth and sixth days (Fig. 5). Every planted *P. australis* seed grew new leaves

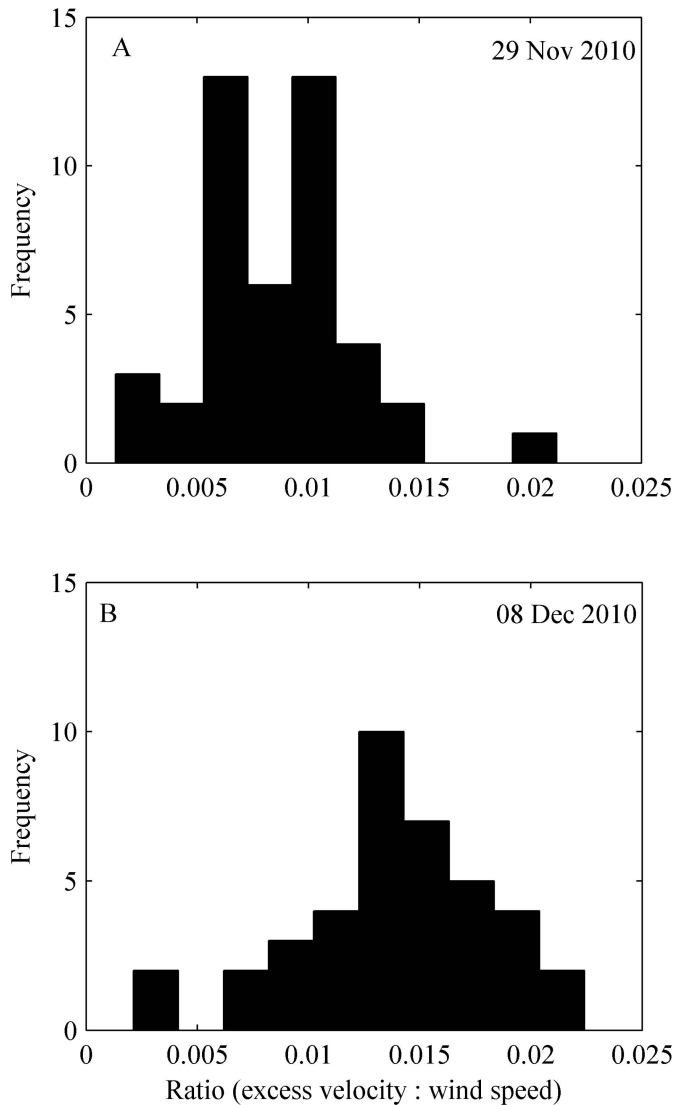


Fig. 4. Ratio of the excess velocity, calculated as the difference between the in situ fruit transport velocity and surface currents measured by the surface drifter, relative to the wind speed.

within 2 weeks of being planted, which indicated that the viability of the seeds was independent of the dehiscence time for each fruit.

## Discussion

The seagrasses *Posidonia australis* and *Halophila ovalis* display different seed characteristics and mechanisms of seed dispersal. This is not surprising in some ways, given that seagrasses are an angiosperm group that represents multiple evolutionary events of reinvasion of the sea (Les et al. 1997). *Posidonia australis* (Posidoniaceae) is a slow-growing species adapted to seasonal reproduction, including seed production and dispersal. Along the southwest coast of Australia, their seeds are dispersed during the austral summer months when strong northward winds (averaging  $\sim 30 \text{ km h}^{-1}$ ) blow parallel to the shore. The prevailing winds exert a direct force on the fruit (windage),

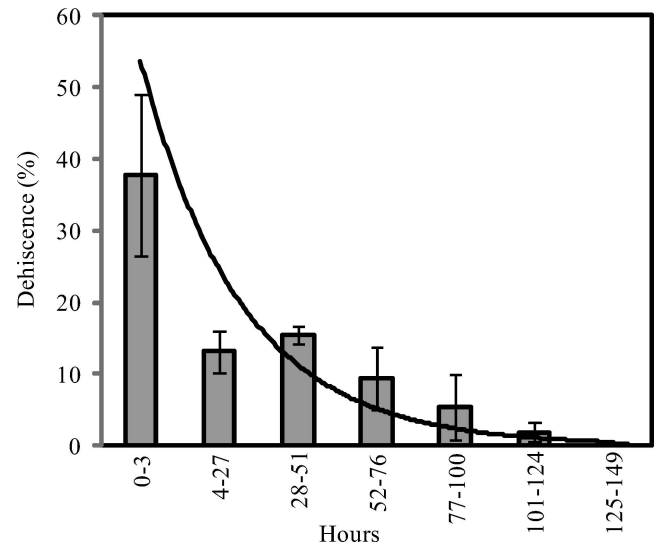


Fig. 5. Percentage of dehiscence ( $n = 4$ ) of *Posidonia australis* fruit according to time after release. Exponential fit as  $y = 117.28e^{-0.781x}$  ( $r^2 = 0.82$ ).

as well as transport them northward via wind-driven surface currents. Also, the relatively calm wave conditions during summer (significant wave heights typically  $\sim 1 \text{ m}$ ; Lemm et al. 1999) may increase the chance for successful seed settlement and recruitment after they are dehiscenced from the floating fruit. This investment in dispersal by floating fruit of *P. australis* facilitates long-distance dispersal, which, combined with vegetative reproduction, results in both colonization of new locations and consolidation and expansion of recruits into meadows through vegetative clonal growth. *H. ovalis* is a small, fast-growing, short-lived species. On average, it produces seven smaller seeds per fruit (Kuo and Kirkman 1992). The seeds are negatively buoyant and do not travel far from where they are released unless subjected to very energetic events (Bell et al. 2008). These seeds display dormancy and germinate when conditions are favorable. Storms that could redistribute seeds occur in the southwest of Australia during winter, bringing swell waves with typical significant wave heights of  $\sim 2\text{--}3 \text{ m}$  (Lemm et al. 1999). These storms may enhance the probability for dormant *H. ovalis* seeds and small seedlings of both *P. australis* and *H. ovalis* to be secondarily dispersed.

The physical properties of the *P. australis* fruit and seeds measured in this study indicate that the production of positively buoyant fruit is an effective adaptation for dispersal over longer distances (Kendrick et al. 2012). Previous estimates of the transport of floating seagrass seeds for *Zostera marina* (Erftemeijer et al. 2008) and *Thalassia testudinum* (Van Dijk et al. 2009) assumed that winds contributed some percentage of their speed (3% and 10%, respectively) to the transport of seeds. However, there is still the need to distinguish between the various mechanisms by which winds may transport seeds at the air-sea interface (i.e., directly by drag forces, or indirectly by wind-driven surface currents). Our measurements showed that *P. australis* fruit move significantly faster than



the wind-driven surface currents, due to direct wind forces on the emergent portion of the floating fruit (i.e., an enhancement of the transport by an additional 1–2% of the local wind speed). In southwest Australia, winds historically average  $\sim 23 \text{ km h}^{-1}$  when *Posidonia* fruit are released (Nov to Dec), which suggests that they can be moved by wind at an average rate of  $0.23 \text{ km h}^{-1}$  to  $0.46 \text{ km h}^{-1}$ . This suggests that the effect of windage alone (even in the absence of any surface currents) can transport a fruit distances of 55 km or more during a single reproductive event, based on a typical 5-d floating period for the fruit. Moreover, the results emphasize the importance of distinguishing between windage effects and wind-driven surface-water motion, particularly in the development of future numerical models to predict dispersal by fruits. With surface currents influenced (and frequently dominated) by other processes (e.g., tides and shelf boundary currents), the dominant surface-water motion will generally not align with the wind direction, resulting in more complex dispersal pathways.

Once the *Posidonia* fruit dehisces, a single large seed designed for fast sinking ( $10.6 \pm 0.4 \text{ cm s}^{-1}$ ) results in rapid settlement. However, Orth (1999) described much faster settlement rates ( $17.0 \pm 2.3 \text{ cm s}^{-1}$ ) for the related species *P. sinuosa*. This difference might be due to differences in size, because *P. sinuosa* is slightly narrower ( $\sim 2 \text{ mm}$ ) and shorter ( $\sim 5 \text{ mm}$ ) compared with *P. australis*, hence reducing its surface area and creating less drag. Secondary dispersal for *P. australis* appears to be restricted to only small distances, more likely as a result of wave-induced bed stresses generated by surface waves (see discussion below) that would generally be much higher than current-induced stresses.

*Halophila* seeds are very different from those of *Posidonia*, because they lack buoyant transport mechanisms. They tend to remain on the seafloor close to their release site. Both the fruit and seeds of *H. ovalis* settle at similar velocities ( $\sim 5 \text{ cm s}^{-1}$ ) when suspended in the water column. On the other hand, the critical shear stress found to mobilize the seeds of this species ( $\tau_{cr} \approx 70 \text{ mPa}$ ) in unvegetated areas was roughly two times smaller than that of *P. australis*. Such a critical threshold may still not be generated by typical near-bottom currents in the Perth coastal lagoon region during summer, which Zaker et al. (2007) reported to average on the order of  $4 \text{ cm s}^{-1}$  (equivalent to a bed shear stress of only  $\sim 3 \text{ mPa}$ ). However, due to their unsteady oscillatory nature, surface waves are much more efficient at exchanging momentum with the seafloor, which leads to much greater bottom-shear stresses for the same velocity (i.e., bed friction coefficients for currents over sandy beds are on the order of  $10^{-3}$  vs.  $10^{-2}$  to  $10^{-1}$  for waves; Lowe et al. 2007). Thus, even under small summer-wave conditions off Perth (1-m wave height, 8-s period), the near-bottom wave orbital velocities in 10 m of water would be  $\sim 40 \text{ cm s}^{-1}$ , which would lead to shear stresses of 600–6000 mPa, far exceeding this critical threshold. With *Halophila* seeds having the capability to remain dormant for up to 2 yr (McMillan 1991), they can be readily mobilized under even moderate wave events.

When we compare the distribution of vegetative stands of these two species with dispersal potential in the studied area, we note that the *Posidonia* species, including *P. australis*, are the dominant seagrass over many square kilometers (Kendrick et al. 2000, 2008; Holmes et al. 2007), whereas beds of *H. ovalis* are restricted in their distribution. The combined ability of *Posidonia* to disperse, settle, and recruit over longer distances using floating fruit, as well as its extensive clonal growth and persistence, appears to have contributed to the dominance of this genus in the study area. Interestingly, in a landscape comparison of measured vs. modeled clonal growth, Kendrick et al. (1999) proposed that recruitment events from seeds were necessary to account for the rates of colonization of *Posidonia* in this temperate region. *H. ovalis*, on the other hand, has persisted, but in isolated small populations, in highly disturbed environments, or as understory in meadows of the larger *Posidonia*. Dispersal for *H. ovalis* has resulted in maintenance and colonization of specific habitats within the shallow subtidal regions of southwestern Australia.

Our studies of seed dispersal infer potential recruitment distances for these species of seagrass. It is clear that distances of  $\geq 55 \text{ km}$  are possible for *P. australis* seeds, but how many of these dispersed seeds produce adult reproductive plants remains unknown. Still, our increased understanding of dispersal potential opens great opportunities for determining the importance of recruitment and demographic connectivity in seagrasses. The parameters calculated can also be the foundation for future process-based numerical hydrodynamic models of seagrass seed transport, which will allow seagrass dispersal pathways to be much more accurately predicted for different areas with a range of hydrodynamic conditions. This study can also be a tool for planning seagrass restoration, given that transplantation efforts can be enhanced by natural recruitment, by effectively choosing key populations that can provide new recruits to adjacent populations based on the seed characteristics and their local environment.

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