

Dispersal of seagrass propagules: interaction between hydrodynamics and substratum type

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ABSTRACT: Waves and currents influence not only the spatial distribution of seagrass meadows but also the transport, establishment and survivorship of seagrass propagules and hence the success of seagrass recruitment from sexual reproduction. We quantified the dispersal of propagules of 3 seagrass species (*Posidonia oceanica*, *Cymodocea nodosa* and *Zostera marina*) over substrata of different complexities (sand, coarse gravel and *P. oceanica* mattes of different shoot abundances) under unidirectional flow in a hydraulic flume. Threshold velocities indicate that *Z. marina* seeds start to move earlier over a flat sandy bottom (14 cm s^{-1}) than seeds of *P. oceanica* (20 cm s^{-1}) and *C. nodosa* (21 cm s^{-1}). Propagule trapping increased with bottom complexity, which was related to the flow reduction that each substratum generated and the boundary layer thickness. Trapping rates were higher in coarse gravel and in mattes with higher abundances of dead shoots, where flow was reduced more than 50%. Over sand, flow reduction was minimal and propagules were not trapped. Furthermore, notable differences between *P. oceanica* early life stages were observed, with seeds trapped first, followed by seedlings of increasing ages. This result may be related to the smaller frontal area (area exposed to water flow) and higher settling velocity of the younger life stages. Together, our results provide important insights into the drivers of seagrass recruitment, which are of interest for restoration purposes and numerical modelling.

KEY WORDS: Establishment · Seed transport · Recruitment · Drag coefficient · Morphology · Seedling · *Posidonia oceanica* · *Cymodocea nodosa* · *Zostera marina*

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INTRODUCTION

Seagrasses are a dominant feature of coastal environments and provide a suite of important ecosystem services, including coastal protection, carbon sequestration and nursery areas for many commercially and ecologically valuable marine species, among others (Hemminga & Duarte 2000). As a result of different human stressors, seagrasses have suffered important declines worldwide (Waycott et al. 2009). Sexual reproduction is an essential part of the life cycle of seagrasses, for its role in the consolidation of existing meadows and for the colonization of new ones, and thus may be an important process for seagrass recovery following disturbance (Preen et al. 1995, Olesen

et al. 2004). Furthermore, the products of sexual reproduction such as fruits, seeds and seedlings are critical not only for dispersal but also for providing genetic variation, which is crucial for adaptation (Kendrick et al. 2012, 2017). In fact, early life stages of other aquatic plants are decisive in limiting species distribution and abundance (Les et al. 2003). In addition to these ecological functions, early life stages can also be used as a source of transplanting material in seagrass restoration projects (Ganassin & Gibbs 2008, Renton et al. 2011, Orth et al. 2012), which is an important issue to consider given the dramatic rates of seagrass loss worldwide (Waycott et al. 2009).

Hydrodynamics (waves and currents) influence the spatial distribution of seagrass meadows (Koch 2001,

Frederiksen et al. 2004, Infantes et al. 2009), and are also crucial for seedling survival (Infantes et al. 2011a). Substratum type may also contribute to seagrass propagule trapping and establishment (Piazzi et al. 1999, Infantes et al. 2011b), and substratum roughness determines the height of the bottom boundary layer which influences the transport of seeds and seedlings (Koch et al. 2010, Alagna et al. 2015). Similarly, hydrodynamics are also an important factor in determining the success of seagrass restoration projects (Bos & van Katwijk 2007), and identification of adequate substratum type is critical for the survival and growth of transplanted seedlings in restoration activities (Balestri et al. 1998). Furthermore, bottom shear stress from the combined effect of waves and currents can mobilize unconsolidated sediment, producing erosion or accretion that can affect seagrasses negatively through uprooting and burial (Orth et al. 1994, Terrados 1997, Cabaço et al. 2008).

Beyond hydrodynamics, the physical properties of seagrass propagules, such as morphology, density, settling velocity and drag coefficient, are highly determinant of their dispersal potential (Infantes et al. 2011a, Ruiz-Montoya et al. 2012, 2015). Once dispersed, seedling establishment, survival and development depend on the environmental characteristics of the settlement area, such as depth, substratum type, hydrodynamic conditions or erosion events (Piazzi et al. 1999, Orth et al. 2006a, Infantes et al. 2011a, Alagna et al. 2013). In fact, the period between seed germination and seedling establishment is one of the most vulnerable phases for plant development, when plants experience the highest mortality rates (Orth et al. 2006a, Alagna et al. 2013). Thus, elucidating the interactions between hydrodynamics and substratum type affecting the dispersal of seagrass propagules is necessary to understand natural colonization processes and, in particular, secondary dispersal (sensu Chambers & MacMahon 1994) of seagrass species that have floating propagule stages. In order to identify safe recruitment microhabitats and the establishment potential of seagrass seedlings in different substrata, it is essential to consider these processes from a fluid dynamics perspective.

Here we investigated how hydrodynamics and substratum types affect the transport and establishment of propagules of different seagrass species. We focussed on 3 temperate species with different morphological and physical traits that likely affect their interaction with hydrodynamics and substratum: *Posidonia oceanica* (endemic to the Mediterranean

Sea), *Cymodocea nodosa* (representative of the Mediterranean Sea and the Atlantic coast of North Africa) and *Zostera marina* (widespread in northern latitudes; Green & Short 2003). *P. oceanica* produces floating fruits, which are transported by surface currents until they dehisce and the seeds are released, whereas *Z. marina* produces reproductive shoots which contain seeds that mostly dehisce within the meadow, although some are transported inside the reproductive shoots by surface currents until they dehisce. In contrast, the fruits of *C. nodosa*, which are negatively buoyant, develop buried at the shoot base and are released within the meadow, although they may be exported during sediment erosion events, such as storms. As the seeds of the 3 species are negatively buoyant and fall to the bottom, their dispersal at the bottom will depend on hydrodynamic processes occurring within the bottom boundary layer (Orth et al. 1994, 2006a). Hereafter, their secondary dispersal depends on the physical characteristics of the propagules and on the interaction between hydrodynamic conditions and substratum type (Infantes et al. 2011a,b, Ruiz-Montoya et al. 2012, 2015, Alagna et al. 2015). In this study, we specifically aimed to (1) estimate transport velocities of floating propagules of *P. oceanica* and *Z. marina* at different current velocities, (2) determine the minimum flow velocities at which seeds and seedlings of the 3 species start moving over the substratum (threshold velocities) and (3) estimate the capacity of different substrata to retain propagules ('trapping') and how this process is influenced by the propagules' physical characteristics.

MATERIALS AND METHODS

Seed collection and physical properties

Seeds of *Posidonia oceanica* (Fig. 1a) were obtained from fruits collected on the shore during June 2015 in Mallorca (Balearic Islands, Western Mediterranean Sea). Fruits were opened and their seeds removed and placed in 20 l aquaria with seawater (salinity 37), at a temperature of 20°C and illuminated by white fluorescent lamps that provided $76 \pm 2 \mu\text{mol m}^{-2} \text{s}^{-1}$ of photosynthetically active radiation in a 14:10 h light:dark photoperiod. Seeds successfully germinate under these conditions and first leaves and roots are produced within 2 wk (Terrados et al. 2013). In addition, fruits collected in June were also conserved unopened in seawater under the same conditions.

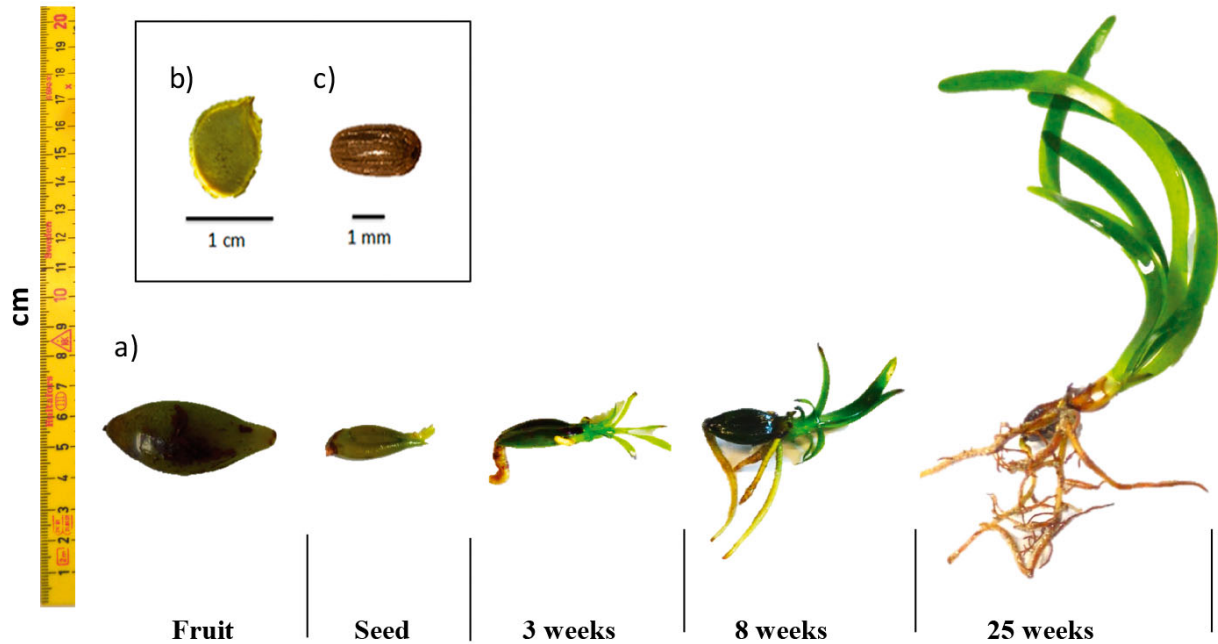


Fig. 1. *Posidonia oceanica* early life stages: (a) fruit and seed (0 wk old), and seedlings at 3, 8 and 25 wk of age. Also shown are seeds of (b) *Cymodocea nodosa* and (c) *Zostera marina*

Seeds of *Cymodocea nodosa* (Fig. 1b), which are typically buried in the sediment, were collected during February 2015 in Mallorca from shallow meadows by scuba diving. They were placed in darkness inside 20 l aquaria under the same conditions as described above. All seeds were transported to the Lovén Centre for Marine Science, Kristineberg Station, Sweden, and were kept in seawater aquaria under the same conditions as described above.

Seeds of *Zostera marina* (Fig. 1c) were collected by harvesting reproductive shoots at 1–3 m depth in the Gullmars fjord, Gåsö, Sweden, in July 2015. These reproductive shoots were stored in outdoor tanks at Kristineberg until the seeds were released (Infantes & Moksnes 2018). *Z. marina* seeds were stored at salinity 34 and temperature of 5°C to prevent germination (Infantes et al. 2016).

Physical characteristics of fruits, reproductive shoots, seeds and seedlings were measured and compared, since they influence propagule transport and trapping (Koch et al. 2010, Infantes et al. 2011a, Ruiz-Montoya et al. 2012). Propagule length, width and height were measured using an electronic precision calliper (mm), and the volume (ml) was determined by fluid displacement in a 12 ml graduated cylinder. Propagule mass was measured as wet weight (g). The density of each fruit, reproductive shoot, seed or seedling was calculated from mass and volume measurements. The number of spathes was meas-

ured for *Z. marina* reproductive shoots. The number and length of leaves, width of the second youngest leaf and root number and length were measured for all *P. oceanica* seedlings.

Settling velocities (w_s) of seagrass propagules ($n = 10$) were estimated as the time needed to sink to the bottom in a vertically placed glass tube (70 cm long and 20 cm diameter) filled with seawater. Each measurement was repeated 3 times for each individual propagule, and the mean value was calculated. Propagule drag coefficient (C_d) was calculated following Dean & Dalrymple (2004) as:

$$C_d = 2 \left(\frac{\rho_s - \rho}{\rho} \right) \frac{g V_s}{w_s^2 A_F} \quad (1)$$

where ρ_s is the density of the propagule, ρ is the density of seawater, g is the acceleration of gravity, V_s is the volume of the propagule, and A_F is the estimated propagule frontal area exposed to the flow.

Seed frontal area (A_F) for *Z. marina* and *P. oceanica* was determined assuming an elliptical shape with semi axes a and b , (i.e. $A_{F \text{ SEED}} = \pi \times a \times b$). In contrast, the frontal area of each *C. nodosa* seed was estimated by multiplying its maximum length by its width since the seed shape resembles a flat disc (Fig. 1b). The frontal area of *P. oceanica* seedlings was determined by adding the foliar surface (estimated as a rectangular shape) to the area of the seed (approximated to an ellipsoid) and the area of roots

(obtained by multiplying the root diameter by the total root length), i.e. $A_{F\text{ SEEDLING}} = A_{F\text{ SEED}} + \left(\sum_{i=1}^n l_i \cdot w_i \right) + (d_r \cdot l_{rT})$, where l and w are the length and width of each leaf, n is the number of leaves, d_r is the root diameter, and l_{rT} the total root length. Seawater density used for the calculations was taken as a constant 1025 kg m^{-3} (equivalent to the value at 20°C).

In order to evaluate the effect of the substratum type on the boundary layer, we estimated the boundary layer thickness assuming the flow turbulence as:

$$\delta = \frac{0.37x}{\text{Re}^5} \quad (2)$$

where Re is the Reynolds number and x is the distance downstream from the start of the boundary layer.

Flume description and flow-substrate characterization

A unidirectional (current) flume located at Kristineberg Station was used to (1) identify the threshold velocities of the propagules to initiate movement and to be retained by the substrata, and (2) to simulate the horizontal transport of propagules, including dispersal and trapping. A flume was used to identify threshold velocities and propagule trapping since it allows modifying 1 variable (substratum) while leaving others constant (e.g. flow). Current velocities from 5 to 30 cm s^{-1} , typical for the locations where the propagules were collected (Anthony & Svane 1994, Balbín et al. 2012), were applied in the flume. The flume was 4 m long, 0.5 m wide and 0.5 m deep (Fig. 2). The test section was 2 m long, and the water level was maintained at 0.15 m . Flow velocities were generated by a motor-run propeller at the far end of the flume controlled by an adjustable speed drive

(Dayton Electronic, model 6K119). The measurements were conducted during 2 periods, July and October 2015, in order to examine the properties of different plant developmental stages.

Flow velocities were measured with an acoustic Doppler velocimeter (ADV, Nortek, Vectrino) at a sampling rate of 25 Hz . Vertical velocity profiles were measured over different substrata at 6 positions ($0.5, 1, 2, 3, 5$ and 7 cm above the bottom) before and after the test section. Percentage of flow reduction due to substratum type was calculated from the flow before and after the test section at a current velocity of 20 cm s^{-1} in order to ensure that all propagules had initiated their movement (see 'Results').

Transport of fruits and reproductive shoots

Transport velocities of floating propagules, i.e. *P. oceanica* fruits and *Z. marina* reproductive shoots, were measured in the unidirectional flume. The surface flow velocity was measured at $1\text{--}2 \text{ cm}$ below the water surface with the ADV positioned upwards. Floating propagules of each species ($n = 10$) were placed independently on the water surface, and their velocity was assessed by recording the time needed to travel along 1 m at different flow velocities (from 5 to 30 cm s^{-1}).

Threshold velocities for transport and trapping measurements

Threshold velocity, defined as the flow velocity at which a propagule initiates and maintains a continuous movement along the whole test section, was measured for each of the 3 seed species and for 4 different developmental stages of *P. oceanica* propagules

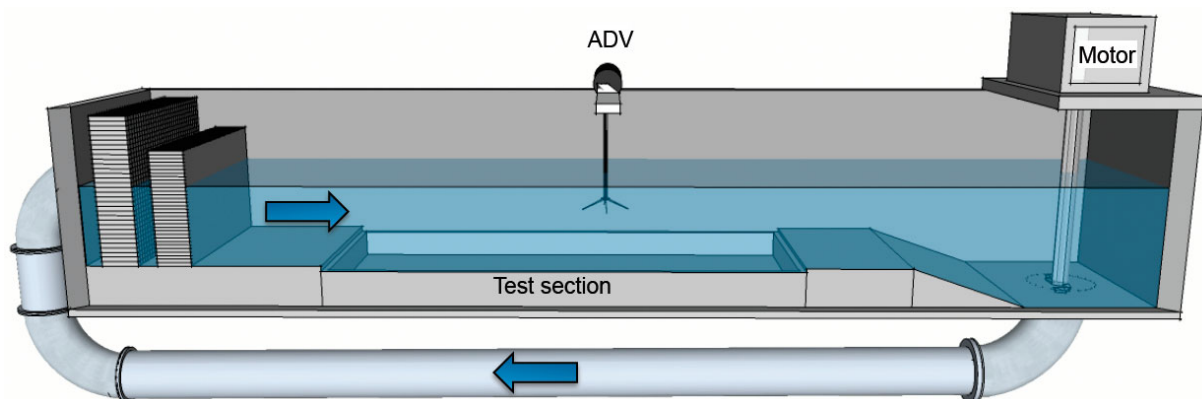


Fig. 2. The hydraulic flume used in the laboratory to simulate hydrodynamic conditions. ADV: acoustic Doppler velocimeter

(i.e. seeds and 3, 8 and 25 wk old seedlings). Propagules were separately placed over a flat sand bed prepared in the flume. The water flow was increased at 1 cm s^{-1} intervals until they started to move. The velocity of the propagule was estimated by measuring the time needed to cross 1 m distance once it had initiated the movement at different flow velocities. Trials were repeated 10 times (using different propagules each time) for each propagule type, and the mean threshold velocity values were calculated.

Trapping was defined as the substratum capability to retain *P. oceanica* seeds and seedlings, and it was calculated by measuring the distance travelled by the propagules over a specific substratum type under different flow velocities. Three common substratum types were evaluated: sand (0.25–0.50 mm in diameter), coarse–very coarse gravel (in the range of $5 \times 3 \times 2 \text{ cm}$) and *P. oceanica* matte (i.e. a network of rhizomes from dead plants). We constructed a model of matte by burying in the sand different numbers of orthotropic (i.e. vertical growth) fragments of *P. oceanica* rhizomes collected from beach-cast plants after a storm. Six different matte types were built combining 3 dead shoot abundances of 75, 150 and 300 shoots m^{-2} (75, 150 and 300 shoots placed in the flume test section, respectively) and 2 heights above sand (1 and 4 cm) by haphazardly distributing the shoots along the box. These shoot abundances represent the range of shoot density values found in highly degraded meadows, but can also be contextualized in terms of depth variations, since shoot density typically decreases with increasing depth (Pergent et al. 1995).

In order to recreate the propagule transport over the substratum types at several flow velocities, the flume had a 2 m long test section containing the substrate analysed (Fig. 2). Seeds and seedlings were placed over a 10 cm thick, flat sand bed of 1 m longitude that preceded the box with the specific substratum. This enabled the propagules to develop an initial movement and continue over the 100 cm of the corresponding substrata. We measured the distance travelled and the velocity of the propagules from the beginning of the test section (containing a specific substrate) until the propagule was trapped or until it passed over the entire test section without being trapped.

Trapping results are presented depending on the difference between the length of the test section and the distance travelled by the propagules. If the distance travelled was equal to the total length of the test section, then trapping was considered 0, while trapping was maximum (i.e. 100) if the propagule

was retained at the beginning of the test section. Substrata were ranked according to their complexity, from the lowest complexity (i.e. sand), along the different matte substrata of increasing rhizome abundance and height, to the highest (i.e. coarse gravel). The complexity of matte was calculated as the number of rhizomes $\text{m}^{-2} \times$ rhizome height (cm). For coarse gravel, complexity was calculated as the number of gravel pieces $\text{m}^{-2} \times$ gravel height. Complexity assigned to sand was 0. Therefore, substratum complexity increased from sand (0) to matte with rhizomes of 1 cm height ($75 \times 1 = 75$, $150 \times 1 = 150$, $300 \times 1 = 300$), 4 cm high ($75 \times 4 = 300$, $150 \times 4 = 600$, $300 \times 4 = 1200$) and coarse gravel (1500).

Data analysis

One-way analysis of variance (ANOVA) was used to compare physical characteristics and threshold velocities among seeds of the different species and among *P. oceanica* early life stages. An analysis of covariance (ANCOVA) was used to compare the slopes of the 2 regression lines obtained from the data on floating propagule velocity (dependent variable) of the 2 species analysed (categorical factor) in relation to the surface flow velocities (continuous covariable). Two different regressions were conducted to evaluate the relation between *Z. marina* morphological characteristics (length and number of shoots) and their velocity. A factorial ANOVA was used to evaluate the effects on trapping of *P. oceanica* propagules regarding 2 factors: substratum type (with 8 levels: sand, 6 different *P. oceanica* matte treatments and coarse gravel) and life stage (with 4 levels: seeds, and seedlings of 3, 8 or 25 wk of age). For a better comparison between the treatments, this analysis was conducted using the results obtained with a flow velocity of 20 cm s^{-1} , since at this velocity all of the propagules moved. To examine differences between levels of each factor and between factors, a post hoc Tukey test was conducted. Data were analysed after ensuring normality and homogeneity of variances using Kolmogorov-Smirnov and Cochran's tests.

RESULTS

A linear relationship between floating-propagule velocity and the surface flow velocity was found for *Posidonia oceanica* fruits and *Zostera marina* reproductive shoots, which was different between the 2 species (Fig. 3; ANCOVA: $F_{1,7} = 7.6054$, $p < 0.05$). At

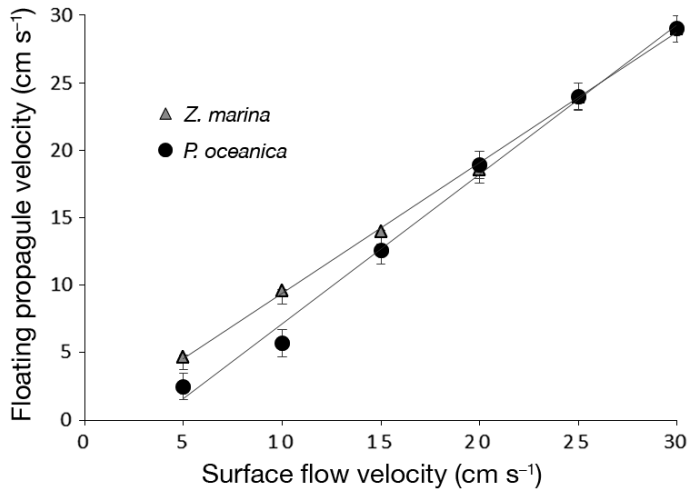


Fig. 3. Velocity of *Zostera marina* reproductive shoots ($y = 0.92x + 0.24$, $R^2 = 0.99$) and *Posidonia oceanica* fruits ($y = 1.12x - 4.11$, $R^2 = 0.98$), transported by different flow velocities

low flow velocities (5 and 10 cm s^{-1}) *P. oceanica* fruits, whose density is lower than water (Table 1), emerge and move at half the flow velocity of the water (2.5 and 5.7 cm s^{-1} , respectively). In contrast, at higher flow velocities (15 and 20 cm s^{-1}) the fruit velocity resembles the flow velocities of the water (12.6 and 18.9 cm s^{-1} , respectively). In contrast, *Z. marina* reproductive shoots move almost at the same velocity as the water flow throughout the range of measured velocities (Fig. 3). The length of *Z. marina* reproductive shoots varied from 20 to 135 cm, and the number of spathes between 4 and 35 shoot $^{-1}$, and their mean weight, volume and density were 7.4 ± 1.4 g, 9.9 ± 1.4 cm^3 and 0.74 ± 0.05 g cm^{-3} . We did not find a significant relationship between the length of *Z. marina* reproductive shoots and their velocity ($R^2 = 0.33$), nor between the number of shoots and their velocity ($R^2 = 0.43$).

Seed size differed amongst seagrass species, with *P. oceanica* exhibiting the largest frontal area, density, settling velocity and volume, while *Cymodocea nodosa* had higher frontal area, weight and volume than *Z. marina* (Table 1, Tukey tests). Density and settling velocity of *Z. marina* seeds were higher than those of *C. nodosa*, and drag coefficient of *Z. marina* was highest, followed by *P. oceanica* and *C. nodosa* (Table 1, Tukey tests). Regarding *P. oceanica* early life stages, as propagules grew, their frontal area, weight, volume and drag coefficient increased while their settling velocities decreased (Table 2, Tukey tests).

The minimum current velocity needed to move seeds or seedlings at the bottom (threshold velocities) was lower for *Z. marina* seeds (mean \pm SE, 14 ± 0.01 cm s^{-1}) followed by *P. oceanica* seeds (which started at 20 ± 0.03 cm s^{-1}) and *C. nodosa* seeds (21 ± 0.01 cm s^{-1} ; $F_{2,27} = 2019.6$, $p < 0.001$; Fig. 4a). Regarding *P. oceanica* early life stages, 25 wk old seedlings were the first to move (4 ± 0.3 cm s^{-1}), followed by 8 wk old seedlings (7 ± 0.2 cm s^{-1}), 3 wk old seedlings (17.5 ± 0.04 cm s^{-1}) and seeds (20 ± 0.06 cm s^{-1} ; $F_{3,36} = 1893.6$, $p < 0.001$; Fig. 4b). Threshold velocities decreased linearly with drag coefficient for seeds of all species and for all developmental stages of *P. oceanica* (Fig. 5a).

Trapping differed across propagule types and substratum (significant interaction; Table 3). There was no trapping over sand for any of the life stages, and trapping differed across the other substratum types for every early life stage, except for the mattes with 75 and 150 rhizomes of 4 cm height, where trapping results were equal. Overall, while all *P. oceanica* seeds and seedlings went through the sand substratum without being trapped, trapping tended to decrease with flow velocity for all other substrata analysed, being maximum at flow velocities below 7 cm s^{-1} for all propagules. Seeds underwent higher trap-

Table 1. Mean \pm SE physical characteristics of *Posidonia oceanica*, *Cymodocea nodosa* and *Zostera marina* ($n = 10$). Tukey tests of a 1-way ANOVA comparing properties across seeds of the different species are shown. In all cases, results were significant at $p < 0.01$

Properties	<i>P. oceanica</i> (Po)	<i>C. nodosa</i> (Cy)	<i>Z. marina</i> (Zo)	$F_{2,27}$	Tukey test
Length (cm)	2.08 ± 0.67	1.02 ± 0.34	0.33 ± 0.07	2033.53	Po > Cy > Zo
Width (cm)	0.83 ± 0.10	0.64 ± 0.16	0.152 ± 0.04	6930.53	Po > Cy > Zo
Height (cm)	0.49 ± 0.07	0.14 ± 0.04	0.152 ± 0.04	6599.40	Po > Cy > Zo
Weight (g)	0.65 ± 0.02	0.078 ± 0.01	0.0073 ± 0.001	674.17	Po > Cy > Zo
Volume (cm^3)	0.58 ± 0.05	0.075 ± 0.001	0.007 ± 0.001	275.44	Po > Cy > Zo
Density (g cm^{-3})	1.12 ± 0.04	1.035 ± 0.001	1.065 ± 0.001	2 617 352	Po > Zo > Cy
Settling velocity (cm s^{-1})	9.73 ± 0.51	6.78 ± 0.124	7.44 ± 0.18	1865.28	Po > Zo > Cy
Frontal area (cm^2)	5.42 ± 0.06	0.147 ± 0.003	0.039 ± 0.001	10 023 886	Po > Cy > Zo
Drag coefficient	0.21 ± 0.03	0.18 ± 0.002	0.24 ± 0.005	474348.7	Zo > Po > Cy

Table 2. Mean \pm SE physical characteristics of *Posidonia oceanica* early life stages (n = 10). Tukey tests of a 1-way ANOVA comparing properties across early life stages are shown. In all cases, results were significant at $p < 0.01$

Properties		Fruit (Fr)	Seed (Se)	Seedlings			$F_{3,36}$	Tukey
				3 wk	8 wk	25 wk		
Seed or fruit (cm)	Length	3.32 \pm 0.73	2.08 \pm 0.07	1.97 \pm 0.18	1.88 \pm 0.17	1.89 \pm 0.12	6448.40	Fr > Se > 3 > 8 = 25
	Width	1.24 \pm 0.30	0.83 \pm 0.05	0.83 \pm 0.01	0.92 \pm 0.05	0.97 \pm 0.08	6381.21	Fr > 25 > 8 > 3 = Se
	Height	1.33 \pm 0.32	0.49 \pm 0.02	0.52 \pm 0.04	0.61 \pm 0.03	0.58 \pm 0.01	2383.02	Fr > 8 > 25 > 3 = Se
Leaves	Area (cm ²)			1.04 \pm 0.04	7.52 \pm 0.72	25.8 \pm 2.73	322.76	25 > 8 > 3
	Max. length (cm)			1.24 \pm 0.04	3.57 \pm 0.29	13.0 \pm 1.31	578.96	25 > 8 > 3
Roots	Number			5.21 \pm 0.13	8.21 \pm 0.29	7.80 \pm 0.24	2733.08	8 > 25 > 3
	Total length (cm)			1.64 \pm 0.12	5.60 \pm 0.18	40.0 \pm 2.78	574.303	25 > 8 > 3
Whole propagule	Weight (g)	2.34 \pm 0.15	0.65 \pm 0.02	0.86 \pm 0.03	1.89 \pm 0.05	4.70 \pm 0.16	1532.79	25 > Fr > 8 > 3 > Se
	Volume (cm ³)	2.66 \pm 0.14	0.58 \pm 0.05	0.80 \pm 0.02	1.81 \pm 0.01	4.54 \pm 0.23	2509.94	25 > Fr > 8 > 3 > Se
	Density (g cm ⁻³)	0.87 \pm 0.01	1.12 \pm 0.04	1.11 \pm 0.03	1.09 \pm 0.01	1.08 \pm 0.03	1498.41	Se > 3 > 8 > 25 > Fr
	Settling velocity (cm s ⁻¹)		9.73 \pm 0.06	9.56 \pm 0.09	6.16 \pm 0.12	5.28 \pm 0.32	1478.65	Se > 3 > 8 > 25
	Frontal area (cm ²)		5.42 \pm 0.51	5.76 \pm 0.42	6.90 \pm 0.38	15.2 \pm 0.21	267.793.7	25 > 8 > 3 > Se
	Drag coefficient			0.21 \pm 0.03	0.24 \pm 0.02	0.86 \pm 0.05	1.17 \pm 0.05	546.11

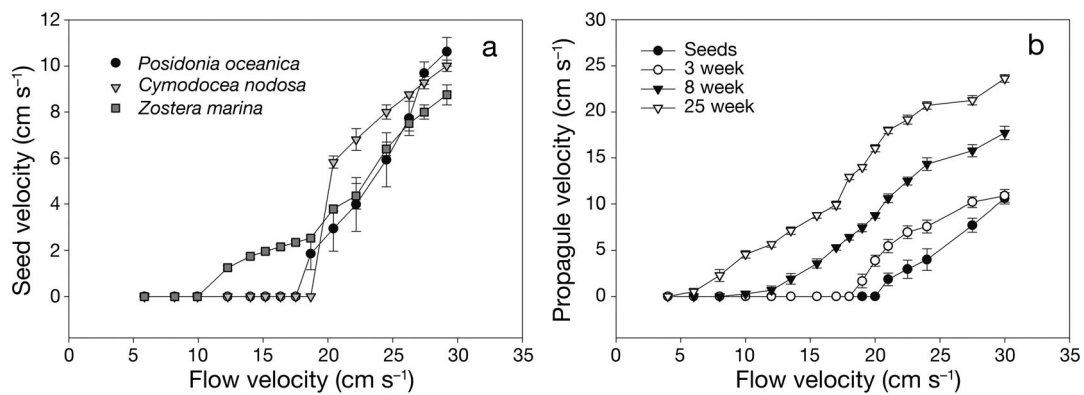


Fig. 4. Mean \pm SE threshold velocities of seeds of (a) *Posidonia oceanica*, *Cymodocea nodosa* and *Zostera marina*, and of (b) *P. oceanica* early life stages (seeds, and seedlings at 3, 8 and 25 wk of age)

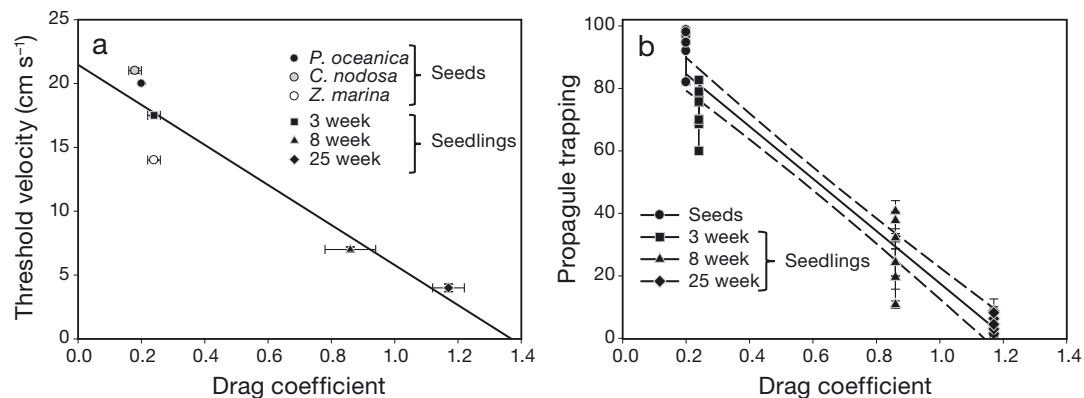


Fig. 5. (a) Mean \pm SE drag coefficient related to threshold velocities over a flat sandy bottom for seeds and seedlings of *Posidonia oceanica*, seeds of *Cymodocea nodosa* and seeds of *Zostera marina* ($y = 21.47x - 15.68$, $R^2 = 0.90$). (b) Trapping of the 4 stages of *P. oceanica* by each substratum at 20 cm s^{-1} ($y = 101.312x - 83.71$, $R^2 = 0.93$). Trapping was calculated by measuring the distance travelled by the propagules over a specific substratum type under different flow velocities. If the distance travelled was equal to the total length of the test section, the trapping was considered 0, while trapping was maximum (i.e. 100) if the propagule was retained at the beginning of the test section

Table 3. Factorial ANOVA evaluating early life stages (ELS) and substratum type (ST) effects on trapping. All results were significant at $p < 0.01$

Factor	df	MS	F
ELS	3	32 359.4	2467.67
ST	7	35 230.2	2686.59
ELS × ST	21	1810.7	138.08
Error	288	13.1	

ping than seedlings, and seedling trapping decreased with increasing age. Trapping of propagules by matte and coarse gravel decreased linearly ($y = 101.31x - 83.71$, $R^2 = 0.93$) with higher drag coefficients (Fig. 5b). Trapping increased with rhizome abundance and height (Fig. 6) and, over coarse gravel, all seeds and seedlings were trapped independently of flow velocity, except for the 25 wk old seedlings, which were not trapped at velocities above 16 cm s^{-1} (Fig. 7).

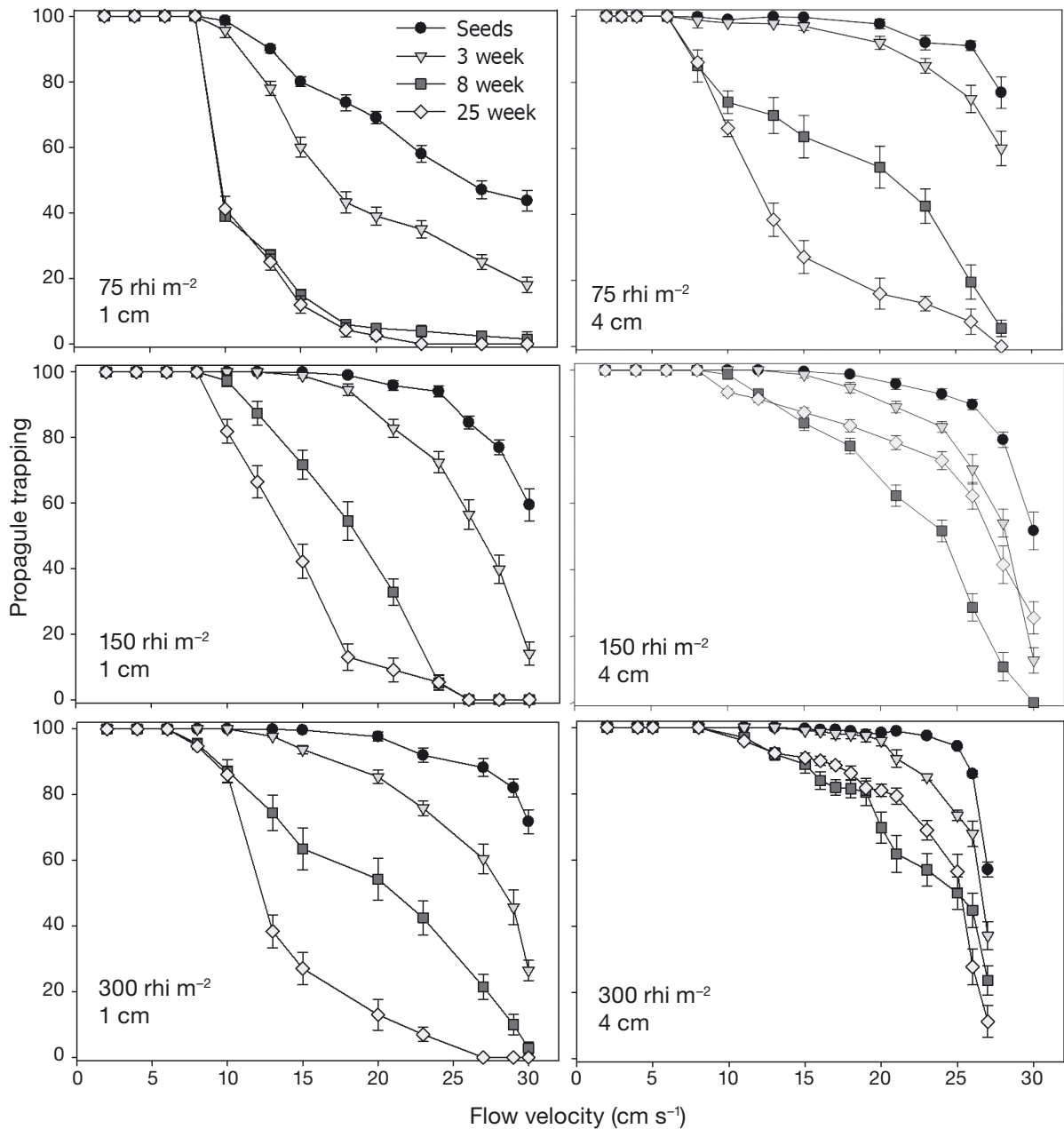


Fig. 6. Mean \pm SE trapping rates for the 4 stages of *Posidonia oceanica* over matte substrata of different dead shoot abundances (rhizomes m^{-2}) and heights (cm). See Fig. 5 for a brief explanation of how trapping was calculated

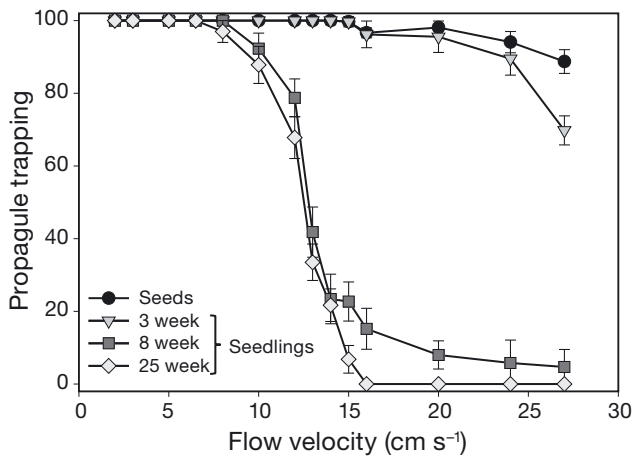


Fig. 7. Mean ± SE trapping rates for the 4 stages of *Posidonia oceanica* over coarse gravel substrata. See Fig. 5 for a brief explanation of how trapping was calculated

Flow reduction was higher over substrata of higher complexity, such as 4 cm mat and coarse gravel. The flow reduction over sand was minimal, while over coarse gravel it was reduced between 20 and 90% in the first 3 cm above the bottom (Fig. 8a). Flow reduction over 1 cm mat varied between 10 and 40% in the first 2 cm above the bottom (Fig. 8b), while over 4 cm mat it varied between 10 and 60% in the first 5 cm (Fig. 8c). The boundary layer thickness (δ) increased with substratum complexity, reaching a value nearly 2 times higher over coarse gravel than over the other substrates (Table 4).

DISCUSSION

Our experiments highlight important inter- and intraspecific differences in how hydrodynamics and substratum type determine the movement of seagrass propagules. Such differences are strongly influenced by the different physical characteristics of the 3 species examined. Overall, trapping of seagrass propagules increases with bottom complexity and boundary layer thickness as the different substrata generate different flow reduction. The threshold velocities needed to start propagule movement decreased with developmental stage and drag coefficient. Furthermore, notable differences were observed between *Posidonia oceanica* seeds and seedlings, as drag coefficient increased with developmental stage, hampering trapping and indicating that younger stages have a lower frontal area and higher settling velocity in comparison to older stages (Table 2). Therefore, if *P. oceanica* seedlings cannot successfully colonize a new substrate in the first few days of development, their capacity for being trapped and thus their ability to become established might become limited by the modification of their physical characteristics as they grow.

The velocity of floating propagules (i.e. fruits and shoots) varies in proportion to the surface current velocity and differs between species. While reproductive shoots of *Zostera marina* move at nearly the same velocity as the surface current, *P. oceanica* fruits move slower than the surface current when

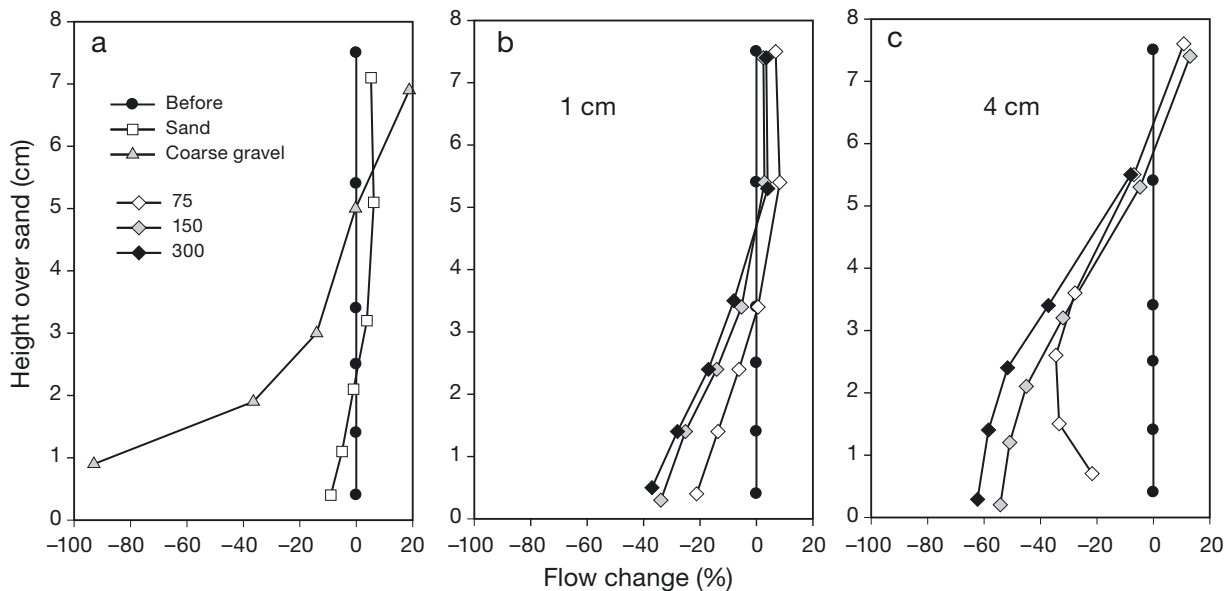


Fig. 8. Percentage of flow reduction in a 20 cm s⁻¹ flow compared between (a) sand and coarse gravel, (b) rhizomes of 1 cm height and (c) rhizomes of 4 cm height. Three rhizome abundances were used (75, 150 and 300 dead shoots m⁻²). ‘Before’ represents the flow over sand at the beginning of the flume

Table 4. Boundary layer thickness (δ) at 1 m downstream for the different substratum types: sand, the 6 combinations of matte substrata (given as rhizome abundance in shoots m^{-2} and [rhizome height in cm]) and coarse gravel. Velocity flow in all experiments was 20 cm s^{-1}

Substratum type	δ (cm)
Sand	3.24
75 [1]	3.33
150 [1]	3.42
300 [1]	3.39
75 [4]	3.49
150 [4]	3.68
300 [4]	3.85
Coarse gravel	5.83

flow velocities are low ($<10 \text{ cm s}^{-1}$). Such a reduction may occur because part of the fruit emerges from the sea surface while part of it is submerged, therefore interacting with the sea–air boundary layer and decreasing the overall speed. Velocities achieved by *Z. marina* and *P. oceanica* propagules might be related to their different interaction with the surface boundary layer, with the fruits of *P. oceanica* more emerged than *Z. marina* shoots, and therefore having lower velocities. We did not manipulate wind conditions, but in addition to the current velocity, wind also contributes to propagule dispersal, allowing fruits to move faster than the surface currents, which allows fruits to be transported at rates ca. 2–4 % of the wind velocity (Harwell & Orth 2002, Källström et al. 2008, Ruiz-Montoya et al. 2012). Further research is necessary to assess the combined effects of wind, waves and currents on floating propagules in order to further assess dispersal of floating propagules.

The threshold velocity for seeds of *Z. marina* has been estimated to be 8 cm s^{-1} over a flat sandy bottom (Orth et al. 1994), which is nearly half the velocity that we measured (14 cm s^{-1}). Such differences may be explained by the fact that during the measurements by Orth et al. (1994), only some of the *Z. marina* seeds tested started to move, and it was not a continuous movement. Moreover, the substratum that they used was slightly different from ours, i.e. a false bottom composed of sandpaper and sand (0.4–0.425 mm in diameter). We used bare sand in order to compare different levels of substratum complexity. Nevertheless, if we had simulated the interface created by benthic organisms in soft sediments such as sand, it would probably have modified the bottom roughness, and our results may therefore have been different (Graf & Rosenberg 1997).

Interestingly, *P. oceanica* and *Cymodocea nodosa* seeds required about 50 % higher threshold veloci-

ties than *Z. marina*, and this pattern is likely explained by the difference in seed physical characteristics (e.g. frontal area exposed to the flow) of the 3 species, providing *Z. marina* with a higher drag coefficient than *P. oceanica* or *C. nodosa*. The higher floating velocities of reproductive spathes and the lower threshold velocities of seeds could contribute to explain the wide geographical range that *Z. marina* colonizes in comparison to the other 2 species (Green & Short 2003). Furthermore, under current and future scenarios of local and global human stressors (e.g. eutrophication, climate change), these physical traits may provide an advantage, as this species may be able to colonize more places and may thus have a larger potential for escaping to other areas with better environmental conditions. Nevertheless, Orth et al. (1994) observed that when mature seeds of *Z. marina* are released from reproductive shoots in the field, they fall to the bottom while transported by water currents, often dispersing only up to a few metres.

Regarding *C. nodosa* seeds, they are formed at the base of the shoots buried in the sediment and normally are retained there, contributing mainly to the maintenance of already established meadows (Buia & Mazzella 1991). However, if seeds are over soft sediments, such as sand, they could be resuspended and moved tens of metres, contributing to the formation of new meadows. Under these circumstances, seeds could be accumulated in bottom depressions like subaqueous sand dunes (Marbà & Duarte 1995). In addition, Terrados (1993) found relatively few seeds of *C. nodosa* inside shallow meadows, but did note some low-density patches originating from seeds in the surroundings, apparently formed by seeds which were re-suspended, transported and accumulated there.

Seeds of *P. oceanica* required higher threshold velocities than older seedlings, likely as a result of their lower drag coefficient. The threshold velocity decrease observed from seeds to seedlings has also been reported for other aquatic macrophytes such as *Ruppia maritima*, *Potamogeton perfoliatus* and *Stuckenia pectinata* (Koch et al. 2010), and the values are of the same order of magnitude as the ones we have determined for *P. oceanica*. These species increase their drag after germination and consequent organ development, and some seedlings actually acquire buoyancy, hampering their establishment (Koch et al. 2010).

Drag coefficient is a good proxy for propagule movement, since a higher value results in decreasing the propagules' threshold velocities and trapping success, yet estimations of drag coefficient still re-

main scarce for most species of marine vascular plants (Backhaus & Verduin 2008, Infantes et al. 2011a, Ruiz-Montoya et al. 2012).

The positive correlation between substratum of different complexities and trapping indicates that complex substrata, such as 4 cm height matte and coarse gravel, are more capable of retaining propagules. Indeed, sand (which we had given a value of 0 complexity) was not able to retain propagules at any of the tested velocities, while matte and coarse gravel, with higher complexity, were able to trap some of them depending on current velocity and propagule characteristics (Fig. 9).

Our first trapping measurements over matte were conducted at shoot abundances of 300 m^{-2} , which is equivalent to a highly degraded and/or deeper meadow (Pergent et al. 1995), and we observed seed and seedling trapping of almost 100%. On account of these results, we decreased rhizome abundance and modified rhizome height to evaluate the trapping by matte at further stages of deterioration. Here we provide the first experimental evidence of the trapping variability of *P. oceanica* propagules by matte depending on its complexity, and our results highlight that rhizome height contributes more strongly to trapping than the actual shoot numbers, suggesting that even highly degraded meadows could allow for

recovery if enough complexity is provided by matte. Indeed, matte is considered a favourable substratum for the establishment of *P. oceanica* seedlings, both naturally and for transplanting (Balestri et al. 1998, Piazzzi et al. 1999, Terrados et al. 2013). In comparison to sand, coarse gravel was the substratum with the highest complexity, and almost all propagules were trapped independently of the flow velocity. While *P. oceanica* seedlings are able to establish in gravel, they do not appear to survive on this substrate in the long term, probably because of damage and abrasive action caused by the gravel particles (Piazzzi et al. 1999). Similarly, *P. oceanica* seedlings are also able to establish in sand (Balestri & Lardicci 2008), but their survival over the long term is unclear (Infantes et al. 2011a). In consolidated substrata such as matte or rocks, higher survivorship of *P. oceanica* seedlings is often observed in nature (Balestri et al. 1998, Piazzzi et al. 1999, Alagna et al. 2013, Terrados et al. 2013), which is in accordance with our results of higher trapping.

In addition to substratum type and its associated complexity, we also found that other factors are important in influencing the transport and trapping of seagrass propagules. A relevant finding was the positive correlation between flow reduction over complex substrata and propagule trapping. At high substratum complexity, propagule trapping is highly independent of its physical characteristics. Conversely, at lower substratum complexity, propagule trapping depends on the propagules' physical characteristics, because the effect of substratum on flow is weaker. Therefore, the drag coefficient is a strong predictor of trapping, particularly for substrata of low, but some, complexity (i.e. not sand).

After release by floating fruits, *P. oceanica* seeds sink and, depending on the hydrodynamic conditions and substratum type, are trapped or transported along the bottom until a microhabitat which facilitates their trapping is encountered. Given that seeds lack dormancy, if they cannot establish in the first few days after fruit dehiscence, trapping may be hampered because their development modifies their physical characteristics. Once retained in a safe recruitment microhabitat, the presence of adhesive root hairs (Badalamenti et al. 2015) reinforces establishment and facilitates persistence over consolidated substrata, explaining the prevalence in rocky substrata a few years after establishment (Alagna et al. 2013). In addition to the adhesive properties of root hairs, the complexity of the substratum facilitates seedling anchoring (Alagna et al. 2015). Additionally, our observations of seedling movement in the flume suggest

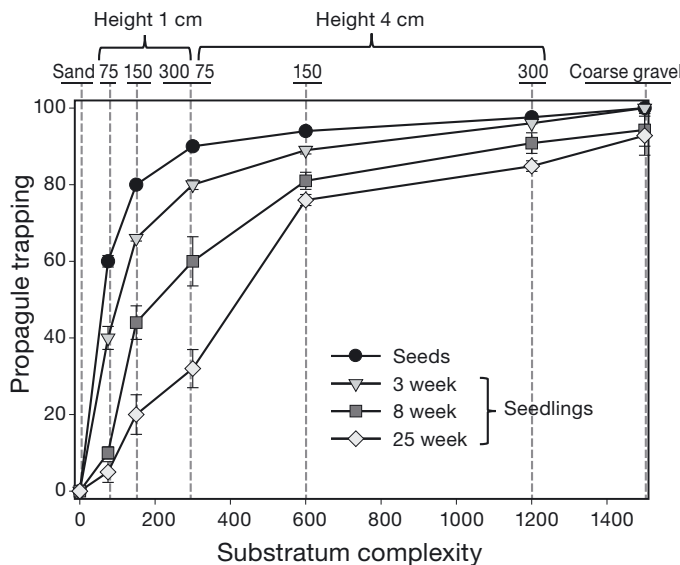


Fig. 9. Relation between trapping of *Posidonia oceanica* seeds and seedlings and substratum complexity in a 20 cm s^{-1} flow. Three rhizome abundances were used (75, 150 and $300 \text{ dead shoots m}^{-2}$, at heights of 1 and 4 cm). Matte complexity was calculated as the number of rhizomes $\text{m}^{-2} \times$ rhizome height (cm). For coarse gravel, complexity was calculated as the number of gravel pieces $\text{m}^{-2} \times$ gravel height. Complexity assigned to sand was 0

that roots, which are somewhat rigid and show an apparent negative phototropism, might become anchoring structures that could facilitate propagule trapping and establishment. The primary root (first root produced at the distal end of the seed) frequently grows curved, resembling a hook (Fig. 1a) that could possibly enhance trapping. Indeed, anchor-like structures that are suggested to contribute to trapping have been described in propagules of *Phyllospadix* and *Amphibolis* spp. (Kuo & den Hartog 2006).

Our study provides important insights into the drivers of seagrass dispersal recruitment, which could be applicable for numerical hydrodynamic dispersal models and restoration efforts. The structure and function of seagrasses in many ecosystems is affected by anthropogenic and natural disturbances that have caused their strong decline worldwide (Waycott et al. 2009), prompting a renewed interest in seagrass restoration (Orth et al. 2006b, Ganassin & Gibbs 2008, Renton et al. 2011). Hydrodynamic exposure (Orth et al. 2006a, Bos & van Katwijk 2007, van Katwijk et al. 2009) and the availability of a suitable substratum (Infantes et al. 2011b, Rivers et al. 2011) frequently determine restoration success. More complex substrata such as coarse gravel areas or dense and high mattes of *Posidonia oceanica* may facilitate the retention and establishment of seagrass propagules, and therefore substratum complexity could be an additional criterion in the site selection process during restoration. Further data are needed to better understand the role played by rocky substrata.

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