Extending the life history of a clonal aquatic plant: Dispersal potential of sexual and asexual propagules of *Zostera noltii*

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ABSTRACT

The dispersal potential of sexual and asexual propagules of *Zostera noltii* was experimentally quantified in still water and under different currents in microcosm and mesocosm facilities. We estimated sinking rates of seeds and changes over time in shoot buoyancy, shoot viability, fragment breakage, shoot growth rate and spathe release rate of floating fragments. The fast sinking rates of detached *Z. noltii* seeds suggest a small spatial scale of dispersal insufficient to connect fragmented populations, whereas the traits of floating fragments, particularly shoot buoyancy and shoot survival (>55 d), suggest a potential for long distance dispersal (>2300 km) that could connect distant patches and allow colonization of new areas. We showed that the *Z. noltii* vegetative and reproductive fragments have the potential to extend the dispersal achieved by detached seeds alone.

1. Introduction

Dispersal is essentially any movement of an organism, or any of its propagules, that potentially leads to gene flow (sensu Ronce, 2007). It is a life history trait, most typically associated with sexual reproduction, whether postmeiotic or prezygotic (e.g. broadcast spawned gametes, haploid algal spores, plant pollen) or postzygotic (e.g. plant seeds or planktonic larvae). Compared to sexual dispersal, much less attention has been given to the evolutionary and ecological consequences of clonal dispersal, although it is widespread across many organisms, particularly in plants. Clonal dispersal can be defined as outward spreading of organisms or propagules from their point of origin or release (Lincoln, 1998), which also includes the shoot multiplication through rhizome extension. A unit of clonal dispersal is often a fragment of an adult organism, although other means of asexual dispersal are possible (e.g. apomixis). A dispersing fragment can be any unit capable of independent life. For clonal dispersal to occur, such a unit needs to get separated, either naturally as a consequence of maturation (Oróstica et al., 2012), or fragmented by any disturbance (Riis and Sand-Jensen, 2006), and survive temporarily during transport in an appropriate dispersal vector. Dispersal distance is, hence, a function of fragment viability and dispersal vector (Jackson, 1986). Clonal dispersal is especially advantageous as a mean of propagation under conditions in which sexual dispersal is not effective, such as in some species distributional ranges (e.g. Billingham et al., 2003; Tatarenkov et al., 2005).

Fragment separation is a process of creation of asexual propagules that has been considered to be under selection (Highsmith, 1982). There is evidence that some aquatic plants may disperse only by vegetative fragments (e.g. *Ranunculus lingua*; Johansson and Nilsson, 1993), others propagate mainly via vegetative fragments (e.g. *Elodea canadiensis* and *Myriophyllum spicatum*; Nichols and Shaw, 1986), while few spread via more specific dormant apices (e.g. *Potamogeton crispus*; Nichols and Shaw, 1986). Boedeltje et al. (2003) found that out of all the propagules of 12 submerged plant species found in a stream almost 99% were vegetative ones. For different species, buoyancy properties of the fragments define their dispersal pattern and fate. While e.g. *E. canadiensis* floats under the surface of the water, and can therefore get entangled to other submerged vegetation, *Ranunculus peltatus* fragments float on the surface and more often strand on shallow sediments (Riis and Sand-Jensen, 2006). Still, relatively few studies have addressed the relevance of fragmentation in marine vegetation, which have the potential to disperse over much longer distances via drifting

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fragments (Ceccherelli and Piazzi, 2001; McKenzie and Bellgrove, 2008). Some seagrass genetic studies explicitly discuss populations' genetic structure in the light of possible fragment dispersal paths (Reusch, 2002), but again emphasizing fragments as vectors carrying sexual propagules.

Fragmentation and dispersal in aquatic clonal vegetation are concurrently thought to play a role in diminishing the negative effect of selfing, commonly observed in terrestrial clonal plants (Charpentier, 2002). Furthermore, for species with higher dispersal of fragments, clonal reproduction is more common (Silvertown, 2008). Dispersal is therefore, particularly in aquatic clonal plants, likely to be a crucial process in shaping populations' distribution and structure.

Seagrasses are marine clonal plants that disperse through both sexual and asexual propagules (Orth et al., 1994). Both vegetative and reproductive fragments (i.e. fragments with flowering shoots composed of spathes containing flowers, fruits and seeds; Setchell, 1933) are important long distance dispersal vectors (Harwell and Orth, 2002; Hall et al., 2006). In some seagrass species, floating seeds or fruits are as well a type of long distance dispersal (e.g. *Enhalus acoroides* and *Thalassia hemprichii* (Lacap et al., 2002), *Posidonia oceanica* (Buia and Mazzella, 1991)), but seeds of most seagrass species are negatively buoyant (Pettit, 1984), and thus, unlikely to disperse far. Seagrass fragment formation, dispersal and establishment have rarely been studied and only for a few species, e.g. *Zostera marina* (Ewanchuk and Williams, 1996; Erftemeijer et al., 2008; Källström et al., 2008), *Thalassia testudinum* (Kaldy and Dunton, 1999) and *Posidonia oceanica* (Diaz-Almela et al., 2008).

Understanding the dispersal and colonization potential of seagrasses is valuable to predict the natural potential for self-restoration and colonization (Rasheed, 2004; Boese et al., 2009; Kendrick et al., 2012) and in that way essential for the continuous efforts to conserve and restore the existing meadows (Harwell and Orth, 2002). Studies focused on restoration methods (e.g. Harwell and Orth, 1999; Marion and Orth, 2009) have revealed limited establishment success (Orth et al., 2009; Paling et al., 2009). Improving our knowledge on seagrass dispersal process can therefore improve the success of restoration practices (Balestri et al., 2011). It can also help understand population connectivity, and their response to natural or human-induced disturbances. Most dispersal studies focused on dispersal of sexual propagules (Orth et al., 1994; Harwell and Orth, 2002; Erftemeijer et al., 2008; Källström et al., 2008; Koch et al., 2010), whereas less is known about the colonization potential of plant fragments (Barrat-Segretain and Bornette, 2000; Hall et al., 2006).

Zostera noltii is the smallest seagrass among the native European species (Kuo and den Hartog, 2001) exhibiting fast clonal growth rate (Peralta et al., 2005), with common flowering events and high seed production rates (Alexandre et al., 2006). The species inhabits mostly intertidal zones, even though some populations may develop in the subtidal, particularly where tides are very small. It is the dominant seagrass species in Ria Formosa lagoon, Southern Portugal, where it covers over 45% of the intertidal area (Guimarães et al., 2012). In this lagoon, intensive clam culturing and harvesting occurs in intertidal areas along the *Z. noltii* meadows (Guimarães et al., 2012). While the installation of clam beds removes local seagrass beds completely, clam digging within the remaining seagrass meadows decreases total biomass and shoot density (Alexandre et al., 2005; Cabaço et al., 2005). The latter activity leads to breakage and release of seagrass fragments, probably increasing the dispersal potential of the species. In the long term, such disturbed meadows invest more into reproductive shoots (Alexandre et al., 2005), which can also become detached and dispersed with the vegetative ones.

The aim of this study was to investigate the dispersal potential of sexual and asexual propagules of *Zostera noltii*. Here, we focus on clonal dispersal as the transport of a genetically identical vegetative fragment after breakage from the sessile clone, with potential to contribute to gene flow (Ronce, 2007). Dispersal potential was experimentally quantified for both spatial and temporal scales by measuring seed sinking rates and different properties of floating fragments, with and without reproductive structures, i.e. shoot buoyancy, shoot viability, fragment break down, shoot growth rate and spathe release rate. We hypothesize that both the vegetative and reproductive fragments play a crucial role in *Z. noltii* population maintenance in the Ria Formosa lagoon, allowing higher dispersal over larger spatial scales than detached seeds alone.

2. Material and methods

Seeds, vegetative and reproductive fragments were collected in summer 2011 during low tide from a *Z. noltii* meadow in Ria Formosa lagoon, South Portugal (37.01° N, 7.5° W). The dispersal potential of seeds, vegetative and reproductive fragments was evaluated in still water and under different currents in microcosm and mesocosm facilities.

2.1. Dispersal potential of seeds

Seeds of *Z. noltii* were obtained from flowering shoots that were collected, brought to the laboratory and placed in a seawater aquarium (20 L, 24 °C, 33‰) with moderate aeration (Cabaço and Santos, 2010). Seeds that naturally fell out from the spathes were collected every two days from the bottom of the aquarium. Forty-seven seeds were obtained over a period of four weeks.

The seed wet weight (precision of 0.1 mg) was determined after blotting each seed rapidly on a paper towel. The length and width of seeds were measured on photographs using the software ImageJ (Rasband, 1997). Seed density was calculated by dividing the seed weight by their volume; seed volume was estimated using a formula for an ellipsoid body:

$$V = \frac{4}{3}\pi\, abc$$

where a is half of width, b is half of thickness and c is half of length, assuming equality of width and thickness of the seed, independent of seed position along its longitudinal axis, as used by Koch et al. (2010) for seeds of similar shape. Seeds were kept separately in 1.5 mL tubes with autoclaved seawater until used in the still water and current dispersal experiments.

Sedimentation rate of seeds in still water was tested in a 40 cm tall seawater aquarium (24 °C, 33‰). Seeds were released immediately under the surface of the water to avoid an effect of surface tension on their sinking behavior. The time required for a seed to reach the bottom was recorded three times for each seed. The average time was used to calculate the sedimentation rate. Linear regression of biometric variables on sedimentation rate of seeds was used to determine if seed characteristics explain sinking behavior.

The distance traveled by seeds was measured under three distinct current velocities (1.5, 4.0 and 6.5 cm s^{-1}) in a flume tank (1.5 m long, 7 cm water column depth, with a thin layer of sandy sediment on the bottom) with re-circulating seawater (23 °C, 33‰). The current velocity was measured by releasing a colored liquid in the flow. Experimental current velocities were chosen based on preliminary measurements used to determine the highest current velocity allowing tracking and retrieving seeds. This current velocity was within the range of currents measured 6 cm above *Z. noltii* canopy in Ria Formosa lagoon (ca. 3.5–8.0 cm s^{-1}; Urs Neumeier, pers. comm.). Seeds were placed immediately below water surface to avoid the surface tension effect and aligned with the longer axis in the direction of the current. The distance traveled by seeds until they reach the bottom was measured. The same procedure was

repeated three times for each seed and the average distance was used.

In order to determine the critical current velocity causing seed transport along the bottom, batches of eight seeds were placed in a line across the bottom of the flume tank, far from the tank walls and from each other (ca. 5 cm). Water current was slowly increased and when an individual seed moved more than 1 cm, the current velocity was recorded. To avoid flow disturbance, seeds were only removed from the flume after all of them moved from the starting line. This procedure was repeated three times for each batch of seeds, and the average current velocity recorded.

Seed viability was tested at the end of the experiments, by soaking them in a 0.5% tetrazolium solution at 25 °C during 24 h (Conacher et al., 1994). Seeds were considered viable if the hypocotyl stained red and the radicle either red or brown. A *t*-test was used to investigate the difference in seed biometric characteristics and dispersal behavior between the viable and non-viable seeds, after checking for normal distribution. When *t*-test assumptions were not verified, the non-parametric Mann–Whitney *U* test was used (Lehman and D'Abrera, 2006). For the analysis of dispersal in current and critical current velocity for bottom transportation only the viable seeds were considered, as dispersal of non-viable seeds has no biological meaning.

2.2. Dispersal potential of vegetative fragments

To estimate the time period during which floating vegetative fragments of *Z. noltii* remain viable, a mesocosm experiment (still water) was conducted using 34 vegetative fragments. The length of the rhizomes was measured and the number of shoots was counted for each fragment. Fragments were on average ($\pm$SE) 15.7 ± 1.1 cm long and had 6.0 ± 0.5 shoots. They were marked individually using colored, numbered, adhesive tape that was loosely fixed around the rhizome (1 cm away) to avoid any type of damage. Marked fragments were placed in outdoor tanks (550 L) with low seawater renewal and covered with white plastic mesh to avoid overheating. Fragments were monitored after 5, 10, 15, 40 and 55 days for the number of shoots to estimate shoot production rate, as a proxy for growth. At the end of the experiment, the fragment production potential was evaluated by monitoring for tissue necrosis (brown-to-black colored leaves and rhizome with emphasis on meristems). Fragments were categorized as: growing (green leaves, without decaying tissue), stagnant (greenish-yellowish leaves with some decaying tissue) and dying (no green leaves, most of the tissue decaying).

To evaluate the damage occurring during exposure to currents, we mimicked the conditions observed in Ria Formosa lagoon where drifting patches of *Z. noltii* fragments get entangled in the canopies of semi-submerged vegetation or physical structures set by humans; the flow of water current over these stationary fragments can cause breakage. To estimate the rate of fragment breakage, vegetative fragments were exposed to three distinct current velocities of 15, 30 and 40 cm s^{-1}. Batches of 30 fragments per treatment were placed in a flume tank (7 m long, re-circulating water, 23 °C, 33‰) with a plastic net (1 cm mesh) at the end of the working section to hold the fragments, exposing them to continuous water flow. The current velocity in the tank was monitored using an Acoustic Doppler Velocimeter (ADV). The current was measured 15 cm upstream of the working area and the probe was removed before fragment release. Fragments were released together, at the beginning of the tank and were exposed to the current during 2 h. To synthesize our observations we categorized fragments in interval classes of number of shoots. All the fragments placed in the tank had more than three shoots, meaning that all fragments with one, two or three shoots at the end of experiment were a consequence of damage caused by the current. Therefore,

Table 1
Biometric characteristics and dispersal behavior of viable and non-viable seeds of *Zostera noltii* (mean $\pm$ SE).

Characteristics (units)	Viable seeds	Non-viable seeds
Length (mm)	2.3 ± 0.2	2.3 ± 0.2
Width (mm)	0.9 ± 0.1	0.9 ± 0.1
Weight (mg)[**]	1.4 ± 0.5	1.0 ± 0.4
Density (mg mm^{-3})[*]	0.92 ± 0.36	0.74 ± 0.43
Sedimentation rate (cm s^{-1})[***]	2.5 ± 0.8	0.9 ± 0.6
Critical current for bottom transportation (cm s^{-1})	8.2 ± 1.2	N/A
Percentage (n)	66 (31)	34 (16)

[*] $p < 0.05$.
[**] $p < 0.01$.
[***] $p < 0.0001$.

we defined the first category to have three or less shoots and kept the range in shoot number for all other categories equal. Change rate of fragments in each shoot number class was calculated as: $(N_a/N_b) - 1$, where N_a is the number of fragments in a given shoot number class after the exposure to the current and N_b is the number of fragments in the same class at the start. Positive change rate indicated an increase of fragments in a particular shoot number class, due to the damage of fragments from bigger size classes. Negative change indicated breakage of fragments in that shoot number class and their reclassification into a smaller shoot number class.

2.3. Dispersal potential of reproductive fragments

Twenty fragments with flowering shoots were kept in a seawater aquarium (20 L, 24 °C, 33‰, as described in Section 2.1), and monitored for the natural release of the spathes and seeds in still water for 30 days. We assumed that reproductive fragments have the same dispersal potential as the vegetative ones, because there are no structural differences between them except for the presence of spathes in 1–2 shoots.

To test the damage caused by water current on the reproductive fragments, spathe release from the flowering shoots was quantified after 2 h of current exposure (15, 30 and 40 cm s^{-1}) using the same experimental design as described for vegetative fragments (see Section 2.2). The change rate in the number of spathes per flowering shoot after exposure to current was used to quantify the damage imposed by water current. Change rate was calculated as before (see Section 2.2). Positive change rate was caused by the increase in number of fragments with target spathe–shoot ratio. As no new spathes could have been produced, this was indicative of spathe release for fragments with more spathes per shoot than the observed group. Negative change rate was considered to be indicative of spathe release in fragments of observed group.

3. Results

3.1. Dispersal potential of seeds

Sixty-six percent of *Z. noltii* seeds were viable, and viable seeds had higher density and weight than the non-viable ones (*t*-test, $p < 0.05$, Table 1). Viable seeds showed a significant ($p < 0.0001$), three–fold faster sedimentation rate than the non-viable ones (2.5 ± 0.8 and 0.9 ± 0.6 cm s^{-1} respectively). The seed weight had a significant effect on still water sedimentation rate ($R^2 = 0.35$, $p < 0.0001$); whereas the other biometric variables explained a smaller proportion of the variation ($R^2 < 0.15$, e.g. seed density, $p = 0.01$). The critical resuspension current velocity for viable seeds was 8.2 cm s^{-1}.

The distance traveled by *Z. noltii* seeds increased with increasing currents (Fig. 1); seeds dispersed 2.3, 10.4 and 15.5 cm in current
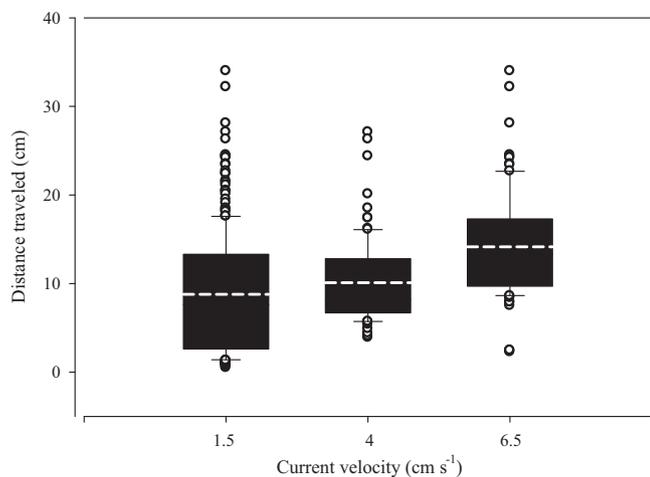
Fig. 1. Observed *Zostera noltii* seed dispersal in experimental current velocities of 1.5, 4.0 and 6.5 cm s^{-1}. Dashed line inside the box shows the mean value, open circles represents outliers; the boundary of the box closest to zero indicates the 25th percentile, and the boundary of the box farthest from zero indicates the 75th percentile. Whiskers above and below the box indicate the 90th and 10th percentiles, respectively.

velocities of 1.5, 4.0 and 6.5 cm s^{-1}, respectively. Seed dispersal distance was significantly related to the seed weight in currents of 4.0 and 6.5 cm s^{-1} ($p < 0.05$), but the association was poor (R^2: 0.26 and 0.22, respectively; data not shown).

3.2. Dispersal potential of vegetative fragments

Z. noltii fragments floating in still water showed almost no change during the first five days of experiment, i.e. after the detachment from the sediment (Fig. 2). Most of the fragments tested (68%) were viable and growing (0.40 shoots d^{-1}) after 15 days. After 40 days, half of the fragments were decaying although at a lower rate (−0.02 shoots d^{-1}) than the ones growing (0.11 shoots d^{-1}). At the
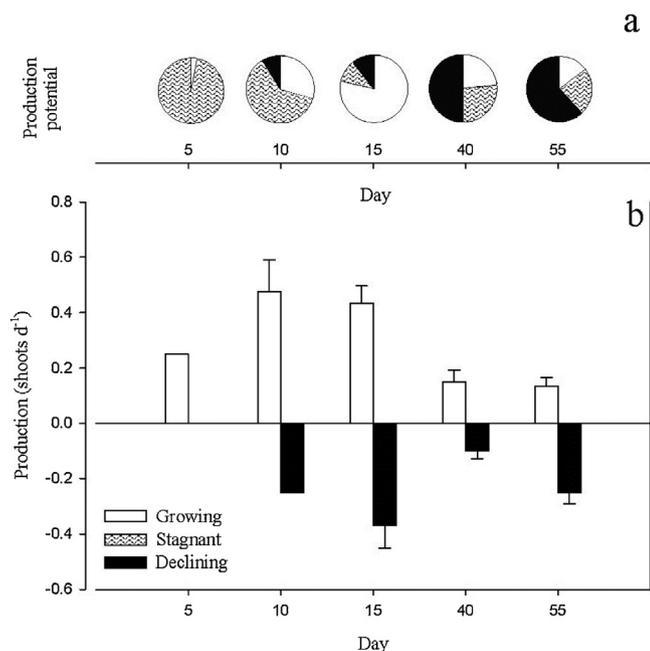
Fig. 2. *Zostera noltii* capacity to produce new shoots while floating in still water ($n = 34$). (a) Production capacity and (b) Production of shoots per day; whiskers indicate standard error.
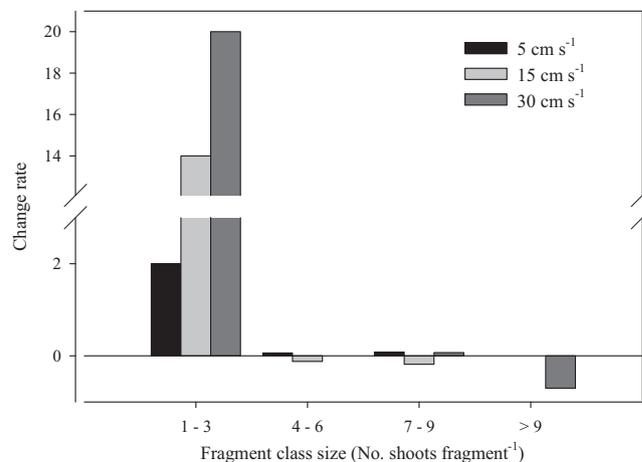
Fig. 3. Change in size of *Zostera noltii* fragments after 2 h exposure in current velocities of 5, 15 and 30 cm s^{-1}. *X*-axis shows the fragments' size class.

end of the experiment, after 55 days, 15% of the fragments were still viable and growing (0.13 shoots d^{-1}).

The proportion of damaged fragments increased with current velocity (Fig. 3). Ten percent of the fragments were damaged at 5 cm s^{-1} velocity, as indicated by the small positive change rate of the smallest shoot number class. A similar level of damage of 52 and 58% was observed for the current velocities of 15 and 30 cm s^{-1}, respectively, visible as higher positive change rates of the smallest shoot number class (Fig. 3). The damage caused by currents on *Z. noltii* vegetative fragments caused mostly the separation of single shoots, mainly in the older (terminal) part of the plant.

3.3. Dispersal potential of reproductive fragments

Spathe release in still water occurred exclusively for the spathes carrying mature seeds, which had decaying tissues. The tissue decay precluded the precise quantification of the number of spathes released from the flowering shoots. None of the immature spathes was released from the flowering shoots during the whole experiment.

When the flowering shoots were exposed for 2 h to currents of 5 and 15 cm s^{-1} a similar low spathe release (3%) was observed. However, spathe release increased to 15% after 2 h exposure to 30 cm s^{-1} current. An increase in the number of flowering shoots with only one spathe per shoot (50% in 5 cm s^{-1}, 20% in 15 cm s^{-1} and 83% in 30 cm s^{-1}) was observed for the three tested currents, resulting from the transfer of flowering shoots from higher classes that lost all spathes except one. The release of spathes was strongest in fragments with more spathes per flowering shoot at the beginning of the experiment as shown by the negative change rate for the group of 5–7 spathes per flowering shoot (Fig. 4).

4. Discussion

Our results showed that floating asexual propagules of the seagrass *Z. noltii* have a dispersal potential (in the order of thousands of km) that is not comparable to the dispersal of seeds (in the order of cm). Considering that fragments were still viable and growing after 55 days, that the average current velocity in Ria Formosa is about 50 cm s^{-1} (Duarte et al., 2008) and assuming unidirectional and constant flow for the whole period and no wind effect in enhancing the transport of fragments, the potential dispersal of *Z. noltii* fragments would be 2300 km. However, it is important to consider reestablishment success of floating fragments to assess effective dispersal. In any case, considering the *Z. noltii* fragments
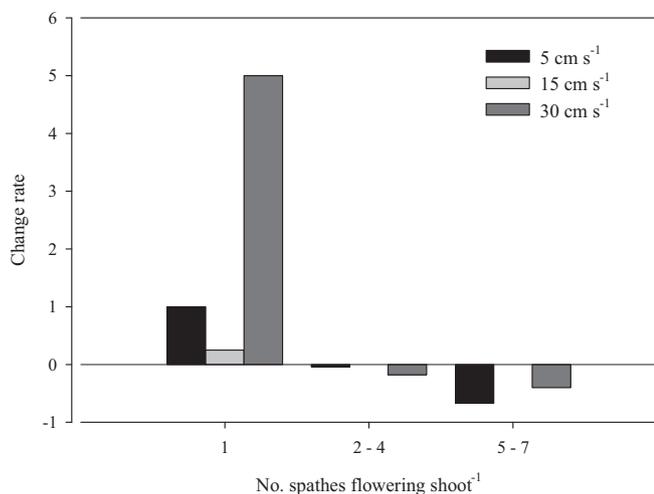
Fig. 4. Change in number of spathes per flowering shoot of *Zostera noltii* reproductive fragments after 2 h exposure in current velocities of 5, 15 and 30 cm s^{-1}. The *X*-axis shows the number of flowering shoots class in relation to their number of spathes.

viability and the elevated number of fragments always floating in Ria Formosa it is expected that fragment dispersal is important for population connectivity. Other estimates obtained here, such as the fragment temporal viability, breakage and decay parameters, can provide valuable information to parameterize a hydrodynamic-based transport model that will allow a more accurate estimation of dispersal.

The observed long–term viability, survival and growth of *Z. noltii* vegetative fragments was similar to results found for *Zostera marina* with ca. 60% of fragments being viable six weeks after detachment (Ewanchuk and Williams, 1996). Prolonged viability of detached fragments is also frequently observed in macroalgae (e.g. Coleman and Brawley, 2005; Macaya et al., 2005; McKenzie and Bellgrove, 2008), with reports of kelp viable propagules almost 18 weeks after detachment (Hernández-Carmona et al., 2006). This prolonged viability indicates that floating fragments are a common dispersal vector in macrophytes (McKenzie and Bellgrove, 2008) and that fragmentation can be considered part of their life history, as is considered for corals (Highsmith, 1982). Survival capacity of *Z. noltii* fragments observed in this study was larger than that of other seagrasses, such as *Halophila johnsonii* and *Halodule wrightii* (Hall et al., 2006). This higher survival may be related to the species adaptation to the dynamic intertidal habitat, where tidal currents and waves can easily brake off fragments, enhancing plant fragmentation and release of propagules. Seagrass fragmentation by hydrodynamic forces or human disturbances such as trampling or clam harvesting therefore appears to be an important factor mediating the species dispersal. To cope with habitat disturbances, *Z. noltii* may have been selected to promote fragmentation of the older parts of the clone, far from the apical shoot where clonal growth occurs. As such, the plant can still maintain its physiological integration (Marbà et al., 2002) and also keep the meristem intact, increasing the chances of survival. Indeed, Cabaço et al. (2005) showed that damage had negative, significant effect on plant growth and survival only when the apical shoot was removed. Due to these mechanisms, even with high fragment damage (up to 58% in currents of 30 cm s^{-1}), the potential colonization capacity of *Z. noltii* fragments does not seem to be diminished. Even though in this study all the fragments were >10 cm long, which was described as the species' minimal functional length for clonal integration (Marbà et al., 2002), variable success (growing vs. decaying) was observed.

The small dispersal capacity of individual *Z. noltii* seeds (<30 cm) was similar to what has been observed for other *Zostera* species

(Orth et al., 2000), suggesting that seeds falling from the spathes within a meadow are not likely to be exported to other areas. Other seagrass species generally have larger and heavier seeds, with faster sinking rates than *Z. noltii* (e.g. *Enhalus acoroides* and *Thalassia hemprichii*; Lacap et al., 2002). Even in comparison to other submerged angiosperm species of similar seed size (e.g. *Ruppia maritima*, *Potamogeton perfoliatus* and *Stuckenia pectinata*; Koch et al., 2010), viable *Z. noltii* seeds showed lower density, lower sinking rate and higher critical re-suspension velocities. The *Z. noltii* seed sedimentation rate in still water was partially explained by the seed weight (35%), as observed for some freshwater species by Koch et al. (2010), and both were significantly related to seed viability, suggesting that seed weight can be used as a quick, non-destructive proxy of seed viability. Seed weight explained 26% of variance in dispersal distance at higher current velocities. This is probably due to the fact that the drag force is directly related with the surface exposed to the current and not to the weight of the seed (Denny, 1988). According to our observations, the current velocity at critical resuspension approached the level necessary to resuspend sandy sediment particles, which may bury the seeds and prevent their further dispersal.

The limited seed dispersal of *Z. noltii* suggests that reproductive fragments are necessary vectors for long distance seed dispersal, as observed for *Z. marina*, (e.g. Orth et al., 1994), and reinforces the importance of fragments as seagrass dispersal propagules. Currents had a positive effect on the spathe release from the flowering shoots and, consequently, on the seed release to the bottom, as shown by the change in the number of spathes per flowering shoot subjected to high currents (positive change rate for fragments with only one spathe per flowering shoot after 2 h exposure to 30 cm s^{-1} current). More spathes were released during exposure to current in flowering shoots that had initially more spathes, independently of the current velocity. This may be related to the reproductive biology of *Z. noltii*, i.e. the successive spathe production within the flowering shoot (Eichler, 1875), which results in presence of spathes of different age and maturation stage in the same flowering shoot. Hence, flowering shoots with more spathes probably carry spathes in advanced stage of maturation, which naturally start to decay and release the ripe seeds. The higher release of spathes from the more developed flowering shoots with increasing current velocity, highlights currents as an important factor for the species dispersal. Previous studies showed that seagrass flowering fragments could travel up to 150 km and for periods of almost a month (Källström et al., 2008), but the importance of flowering shoot dispersal is reduced by the limited flowering season and the low persistence of the spathes on the flowering shoots, which is dependent on their maturation stage (Alexandre et al., 2006). Hence, considering that the difference between reproductive and vegetative fragments is the presence of flowering shoots, the potential dispersal of reproductive fragments can only be equal or lower than that of vegetative ones, which are present all year around. In addition, this study showed fragments can stay viable for a prolonged period of time. This may be common in seagrasses, as Balestri et al. (2011) found that *Posidonia oceanica* fragments can stay viable for three years without losing the capacity to root and grow. Considering this, we can conclude that the dispersal of vegetative fragments plays an important role for the species' dispersal and future research should reveal how this dispersal translate into migration.

The considerably higher dispersal potential of asexual propagules of *Z. noltii* in comparison to that of detached seeds is of fundamental relevance for the classical interpretation of the species life history, and likely to be extended to other seagrasses or other clonal aquatic plants (Gliddon et al., 1987; Fischer and van Kleunen, 2002). The sexual component producing dispersal vectors in the form of pollen and seeds are classically considered as the component that can reach areas beyond the close neighborhood of the

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parental plant, despite substantial evidence for clonal dispersal across long distances to potentially outreach sexual propagules in many taxa (Highsmith, 1982; Johansson and Nilsson, 1993).

While addressing the importance and maintenance of clonal life history, studies have focused primarily on population level topics, such as phenotypic plasticity (Alpert and Simms, 2002; Bergamini and Peintinger, 2002; Donohue, 2003), foraging strategy and micro-habitat variability (De Kroon and Hutchings, 1995; Poor et al., 2005), and density dependence effects on the balance of clonal versus sexual allocation (Ikegami et al., 2012). In our study, by experimentally replicating the conditions clonal fragments face naturally, we showed that broken fragments are viable for long periods of time (more than 50 days), are able to grow and produce shoots, and can carry and release seeds for long distances. These traits are likely to increase the chances of effective asexual dispersal (i.e. migration). If the fragments establish in new area after the dispersal they will become a part of the dispersal strategy of the plant (Hall et al., 2006). Therefore, these could be adaptive dispersal traits that play a role in the ultimate causes explaining the maintenance of clonal growth. Our findings should attract attention to processes that go beyond the local population in order to understand the evolutionary implications of clonal growth. To the best of our knowledge our study was the first comparison of the sexual and vegetative dispersal capacities of a clonal marine plant species. However, additional research is necessary to understand the probability of rooting and growth of seagrass fragments after dispersal and settlement.

Acknowledgements

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