

# The Central Role of Dispersal in the Maintenance and Persistence of Seagrass Populations

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*Global seagrass losses parallel significant declines observed in corals and mangroves over the past 50 years. These combined declines have resulted in accelerated global losses to ecosystem services in coastal waters. Seagrass meadows can be extensive (hundreds of square kilometers) and long-lived (thousands of years), with the meadows persisting predominantly through vegetative (clonal) growth. They also invest a large amount of energy in sexual reproduction. In this article, we explore the role that sexual reproduction, pollen, and seed dispersal play in maintaining species distributions, genetic diversity, and connectivity among seagrass populations. We also address the relationship between long-distance dispersal, genetic connectivity, and the maintenance of genetic diversity that may enhance resilience to stresses associated with seagrass loss. Our reevaluation of seagrass dispersal and recruitment has altered our perception of the importance of long-distance dispersal and has revealed extensive dispersal at scales much larger than was previously thought possible.*

*Keywords: seagrass, long-distance dispersal, microsatellite DNA diversity, pollen, seed*

**T**he role of pollen and seed dispersal in the population dynamics and conservation of plant species is an emerging issue in plant ecology (Ouborg et al. 1999, Nathan 2006). Dispersal is fundamental to colonization, metapopulation dynamics, and plant migrations and will predictably be affected by human impacts and climate change in both terrestrial and aquatic environments (Cain et al. 2000). Interestingly, 41% of the world's most widely distributed plant species are aquatic, despite those species' representing fewer than 2% of all angiosperms (Cook 1996). Wide species distributions are attributed to efficient dispersal mechanisms and the capacity for long-distance dispersal (Les et al. 2003). Marine aquatic angiosperms are collectively known as *seagrasses* and are globally represented by a small number of species (72 species; Short et al. 2011). Seagrasses returned to the sea 100 million years ago, following the adaptation of their ancestors about 200 million years to terrestrial conditions (Les et al. 1997). These marine angiosperms are clonal plants that reproduce both vegetatively and sexually and that, with a combination of these reproductive modes, are able to persist and spread in dynamic nearshore environments. Important but unresolved areas in seagrass ecology include the influence of sexual reproduction in meadow maintenance, the way in which genetic variation can enhance

resilience to stresses, and the role of dispersal in colonization of new or previously inhabited areas.

Historically, seagrass researchers have focused largely on vegetative reproduction, because it appeared to be responsible for extensive and long-lived meadows that allow species to withstand adverse conditions. As a result, seagrass conservation has been focused on the prevention of losses of vegetative material or on the adoption of restoration strategies that use vegetative cuttings from existing meadows to ameliorate site disturbances (Paling et al. 2009). The role of other life-history stages has largely been ignored, with some exceptions (Orth et al. 1994, 2000, 2006a); however, the large investment of energy in producing flowers, fruits, and seeds and the high levels of genetic diversity among seagrass populations suggest that sexual reproduction contributes to the persistence and maintenance of meadows. Research on restoration techniques that use seeds to promote the successful recolonization of habitats is also justified (e.g., Marion and Orth 2010) and is critical to creating resilient, genetically diverse seagrass habitats.

Studies on other aquatic plants indicate that seed dispersal, in particular, plays a key role in shaping the distribution, structure, and resilience of aquatic plant populations (Les et al. 2003). Emerging results of molecular studies of

seagrasses support the claim that seed dispersal has a role in contributing to the genetic complexity of seagrass habitats, with high overall genotypic diversity and weak genetic structuring at large spatial scales within species. In the present article, we review the dispersal mechanisms of seagrasses, with a focus on their reproductive biology, adaptation to water pollination (*hydrophily*), and seed dispersal. We explore the patterns in spatial genetic variation that may give significant insight into long-distance dispersal and consider the implications that these patterns have on species distribution, habitat diversity, and resilience to environmental stress. As a result of our evaluation, we contend that sexual reproduction and dispersal are critically important to the ecological conservation and restoration of seagrasses. An awareness of these implications is essential for informing appropriate conservation and management strategies.

### Introducing seagrasses

Seagrasses are submerged aquatic flowering plants that are not directly related to terrestrial grasses. Seagrasses have evolved within the monocotyledon angiosperm group known as the Alismatidae (Les et al. 1997, Waycott et al. 2006). There are three or four separate major evolutionary events that resulted in contemporary seagrasses, which are currently placed within six taxonomic families (Waycott et al. 2006). The 72 seagrass species represent around two-hundredths of one percent of all flowering plants (Short et al. 2011). Worldwide, seagrasses have colonized only about 177,000 square kilometers (km<sup>2</sup>) of approximately 4.3 million km<sup>2</sup> of suitable habitat (Waycott et al. 2009).

Seagrasses have required dramatic modifications to facilitate their survival in and colonization of the submerged marine environment (Les et al. 1997). Apart from physiological changes to cope with salinity, the evolution of hydrophily is probably the most significant adaptation. The shift to hydrophily required severe modifications of typical angiosperm pollen to allow direct contact with seawater (Les et al. 1997). Most seagrasses (56% of all species) are dioecious (male and female flowers on different plants) (Les et al. 1997), which is an order of magnitude more common than among the angiosperms as a whole (4% of species; Richards 1986). Such unisexual flowers present further challenges for successful pollination and seed set, because pollen must reach small and often distant receptive female stigmas via a highly inefficient vector (water currents).

Once established, seagrass meadows are able to expand through vegetative clonal growth by rhizome extension. As a result, individual plants that arise from seed (*genets*) have the capacity to form large clones comprising many often physiologically disconnected shoots (*ramets*). In this respect, seagrasses are similar to many other rhizomatous terrestrial and aquatic monocotyledons. Because seagrasses have two major reproductive strategies (i.e., both sexual and vegetative), the formation of established seagrass meadows typically requires that the two strategies act in concert. For example, seeds or seedlings would logically represent the

primary mode of dispersal into new, uncolonized locations. However, once recruitment has occurred, the plants typically expand by rhizomatous growth. Therefore, the production and dispersal of sexual propagules and the subsequent establishment of seedlings are critical life-history stages for seagrasses. Despite their importance, these processes have received relatively little attention in studies in which the global resilience and survival of seagrass habitats were addressed (Waycott et al. 2006).

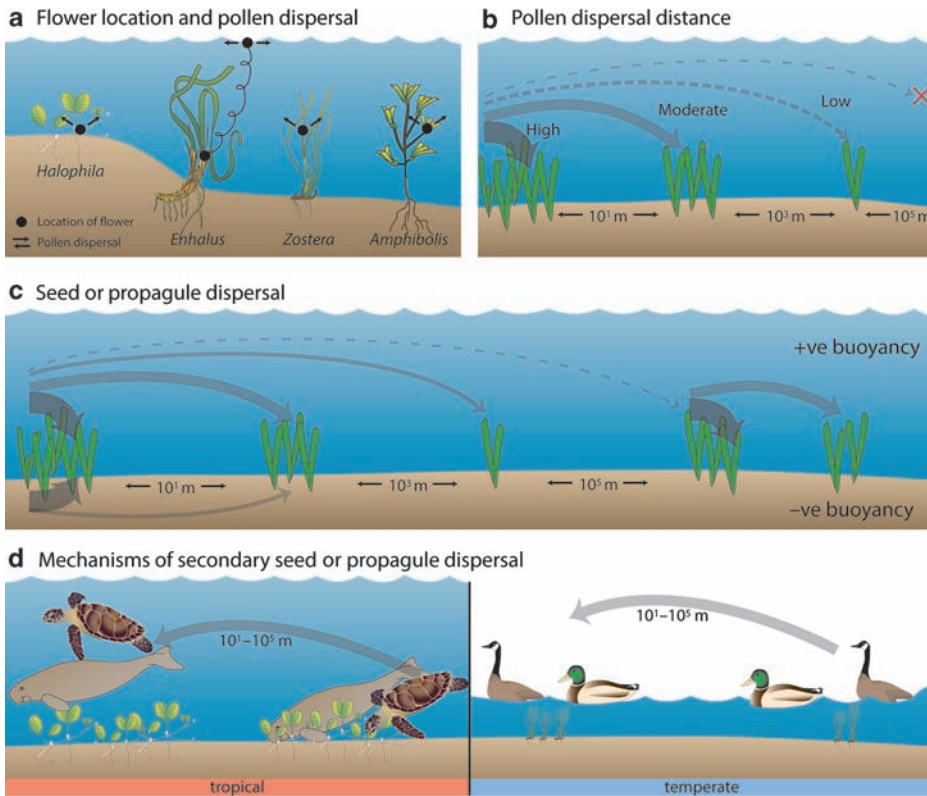
### Reproduction and flowering

Seagrass flowers develop within or above the canopy or at or below the sediment surface (figure 1). Flowers in the canopy are generally more robust than those at the sediment surface, which probably indicates an adaptation to hydrodynamic (wave and current) forces. Like many perennial plants, seagrasses must achieve a balance between resources allocated to flowering and those allocated to the ongoing production and maintenance of vegetative tissues (Obeso 2002). Although relative resource allocation to sexual reproduction has been poorly studied in seagrasses, the large variability in flowering rates and seed set among seagrass populations implies that some type of trade-off does occur (figure 2).

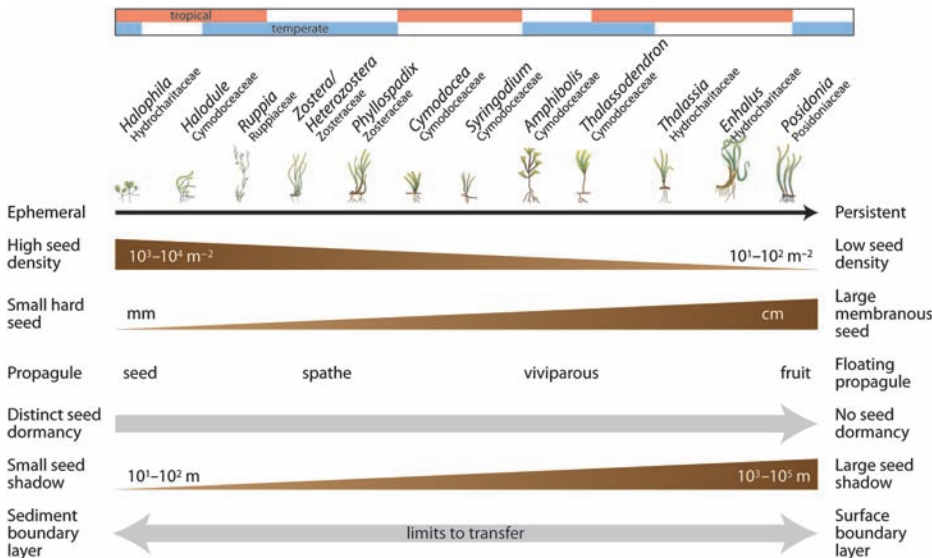
Flowering, much like vegetative growth, is regulated by temperature, light, and nutrients. For example, the temperate Australian species of *Posidonia* all typically flower in midwinter (Smith and Walker 2002), when water temperatures are lowest, day lengths are shortest, and storm frequency is highest. However, abnormally high sea temperatures can alter this pattern dramatically by inducing the onset of flowering in *Posidonia oceanica* (Diaz-Almela et al. 2006). Herbivory also appears to influence the timing of anthesis in some seagrass species. In the subtidal *Thalassia testudinum*, pollen is released within an hour of dusk, possibly to escape grazing by parrotfish (van Tussenbroek et al. 2008). The relationship between the onset of reproduction and pollen dispersal and storm frequency and the potential link between hydrodynamics and increased pollen-dispersal distances has not yet been studied quantitatively.

### Pollen dispersal in seagrasses

Pollen dispersal into seawater could provide a mechanism of long-distance dispersal, somewhat similar to that observed for wind-dispersed pollen. Unlike wind-dispersed pollen in terrestrial plants, seagrass pollen is generally very sticky and readily adheres to any surface that it encounters. In either case, pollen grains need to occur in sufficient numbers and proximity to the stigmas of the female flowers in order to enable successful reproduction (figure 1). The efficacy of seagrass pollination depends on the relative distribution of males and females within the population (i.e., the relative spatial distribution of genets); the morphology, viability, and adhesiveness of the pollen; stigmatic modifications that facilitate pollen capture; the location of pollen release (with respect to female flowers) in the canopy; canopy structure; and various hydrodynamic interactions (Inglis and Waycott



**Figure 1.** Conceptual diagrams for (a) flower location within seagrass canopies, (b) likelihood of pollen dispersal distance, (c) dispersal distance for positively and negatively buoyant seeds or propagules, and (d) mechanisms of secondary seed dispersal for tropical and temperate seagrass habitats. Abbreviation: m, meters.



**Figure 2.** Reproductive characteristics of tropical and temperate seagrasses, including reproductive effort, reproductive structures, and hydrodynamic interface driving seed or propagule dispersal. Abbreviations: m, meters; m<sup>-2</sup>, per square meter; cm, centimeters.

2001, Verduin et al. 2002, Ackerman 2006). The only exception to hydrophily in seagrasses is *Enhalus*, which disperses its pollen on the water surface, with floating male flowers

that release their pollen only after encountering a female flower also at the water surface (Les et al. 1997, Tanaka et al. 2004).

The extent of pollen-dispersal distances is determined in part by the position of the flowers in the seagrass canopy (figure 1a; Verduin et al. 2002). Pollen released at the base or at midcanopy is entrained locally within the meadow; therefore, there is a high probability of local mating success and a lower probability of long-distance dispersal. Several seagrasses (*Posidonia australis*, *Syringodium*, *Phyllospadix*, and *Zostera*) produce flowers toward the top of or even above the canopy (Ackerman 2006), where pollen and occasionally whole anthers are released into the water column (e.g., *Amphibolis*; McConchie and Knox 1989). The release of pollen above the canopy should facilitate the long-distance dispersal of some pollen, although much of the pollen is likely to become entrained locally because of synchronous leaf fluttering (known as *monami*) in a seagrass canopy in response to waves and currents (Grizzle et al. 1996).

The potential of seagrass pollen for long-distance dispersal is enabled by its viability, which can extend to over 50 hours for *Posidonia* (Smith and Walker 2002) and to at least 8 hours for *Zostera* (Cox et al. 1992). At the upper end of this range, the period of pollen viability is comparable to that in other plants with long-distance dispersal: Insect-pollinated terrestrial plants can retain pollen viability for 36–48 hours, and some wind-pollinated terrestrial plants retain viability for more than 72 hours (e.g., Pacini et al. 1997).

However, seagrass pollen is not ideally designed for long-distance dispersal. The large size (up to 0.5 millimeters; Knox 1984) and elongate shapes that often characterize the pollen of subsurface pollinated species are not conducive to

distant transport in water, and the rafting chains of floating pollen rapidly disperse by wave action as the distance from their release point increases (Ackerman 1995). On the basis of its architecture, seagrass pollen appears better suited for local dispersal within meadows. The higher level of dioecy observed in seagrasses presumably functions to reduce within-genet pollination that might otherwise predominate as a result of near-neighbor pollination. Studies in mating systems and paternity assignment in *Zostera noltii* and *Zostera marina* suggest that, despite very high outcrossing rates, these species' pollen travels a maximum distance of 15 meters (m), which suggests that local environmental characteristics play a major role in dispersal (Zipperle et al. 2011).

### Dispersal potential of seeds and propagules

The dispersal of seagrass propagules occurs through abiotic transport by ocean waves and currents, through sediment movement, or potentially through transport by biotic vectors like manatee, dugong, turtles, and geese (figure 1). Similarly, the wide distributions of a large number of nonmarine aquatic plants have been achieved primarily through the transport of propagules by highly vagile birds, which are known to disperse seagrasses (Les et al. 2003). Terrestrial plants have a much wider array of biotic and abiotic dispersal agents available.

The response of seagrass propagules to waves and currents at a location will depend largely on the physical properties (especially buoyancy) of the seed, fruit, or vegetative bract (*spathe*) that surrounds the seeds (figure 2). Seagrass propagules are produced as two basic forms: positively buoyant (floating) fruit, spathe, and viviparous seedlings and neutrally or negatively buoyant seeds and viviparous seedlings. The seeds of seagrasses are generally neutrally or negatively buoyant, because they must settle on the substrate at considerable depth. However, seeds can be retained within positively buoyant structures such as fruits or spathes or can germinate as viviparous seedlings. All of these structures eventually sink, sometimes after being transported considerable distances.

Species that do not form floating structures release their seeds within the mother meadow and are dispersed locally by turbulence or rely on ingestion by herbivores (e.g., manatee, dugong, turtle) for dispersal over greater distances (figure 1). These different types of dispersal are well represented among seagrass genera (figure 2). *Posidonia*, *Enhalus*, and *Thalassia* produce floating fruits; *Zostera* and *Syringodium* produce floating rhipidia, spathes, and seeds; and *Thalassodendron* produces floating viviparous seedlings. *Cymodocea*, *Halophila*, and *Halodule* produce seeds that are neutrally or negatively buoyant, and *Amphibolis* produces negatively buoyant viviparous seedlings.

The farthest measured dispersal distances (300–400 kilometers [km]) have been recorded for those seagrass genera with floating fruit and rhipidia (figure 3; e.g., *Enhalus* and *Thalassia*). Floating may be viewed as a long-distance

dispersal strategy in cases in which dispersal distances are influenced by regional ocean-current systems. For example, the floating fruits of *T. testudinum* can be transported for more than 300 km when they are captured by offshore currents (van Dijk et al. 2009).

For negatively buoyant propagules, the potential scale of dispersal is limited by hydrodynamic processes occurring within the bottom boundary layer (figure 1b)—that is, those processes required for the vertical mobilization of propagules into the water column, where they can be transported horizontally by unidirectional currents. Interestingly, once they have settled onto the sediment surface, the seeds of *Zostera* require significant energy to be transported farther (Harwell and Orth 2002). However, even though primary seed dispersal may be localized when the seeds are in the sediment, there is the potential for secondary dispersal as sediments are resuspended and transported under high-energy storm conditions. Secondary dispersal may also occur through transport by herbivores like turtles, dugong, manatee, ducks and geese, although the viability of the seeds after ingestion requires further study (figure 1c, 1d). In *Halophila*, the seeds have been shown to be moved by bulk sediment transport during tropical storms and may also be transported in the guts of grazing dugongs and turtles (e.g., Heck et al. 2008).

The mobilization of negatively buoyant propagules also occurs when the shear stress at the bed (or at the canopy) exceeds some critical threshold. In coastal systems, where some wave energy is typically present, shear stresses induced by oscillatory wave motion are generally much greater (by a factor of 10–100) than those induced by unidirectional currents with equivalent flow speeds. Therefore, the dispersal distances of these propagules may ultimately depend on the amount of local wave energy available at a given site, and major dispersal events probably occur only during extreme wave events—for example, during cyclones (Hammerstrom et al. 2006). Species like *Cymodocea nodosa*, with seeds that are negatively buoyant or buried in the sediment, can persist in highly dynamic environments through recolonization of the substrate by the seeds after a perturbation (Marbà and Duarte 1995).

Conversely, the dispersal distance of positively buoyant propagules is most strongly influenced by processes occurring within the surface boundary layer (figures 1b and 2)—that is, subsequent to their release up to the surface of the water column. The floating fruits of *Thalassia* and *Enhalus* (e.g., Lacap et al. 2002, van Dijk et al. 2009), as well as the floating reproductive shoots of *Zostera* (e.g., Erfteimeijer et al. 2008, Källström et al. 2008), can attain large dispersal distances as a result of near-surface transport processes, especially when these processes are driven by local wind stresses. Although these floating propagules are transported directly by surface water currents, their transport rates also are influenced by winds (*windage effects*), which exert drag forces (Erfteimeijer et al. 2008, van Dijk et al. 2009). The direct transport of floating fruit or rhipidia by surface wave motions (e.g., Stokes drift) has yet to receive attention in the

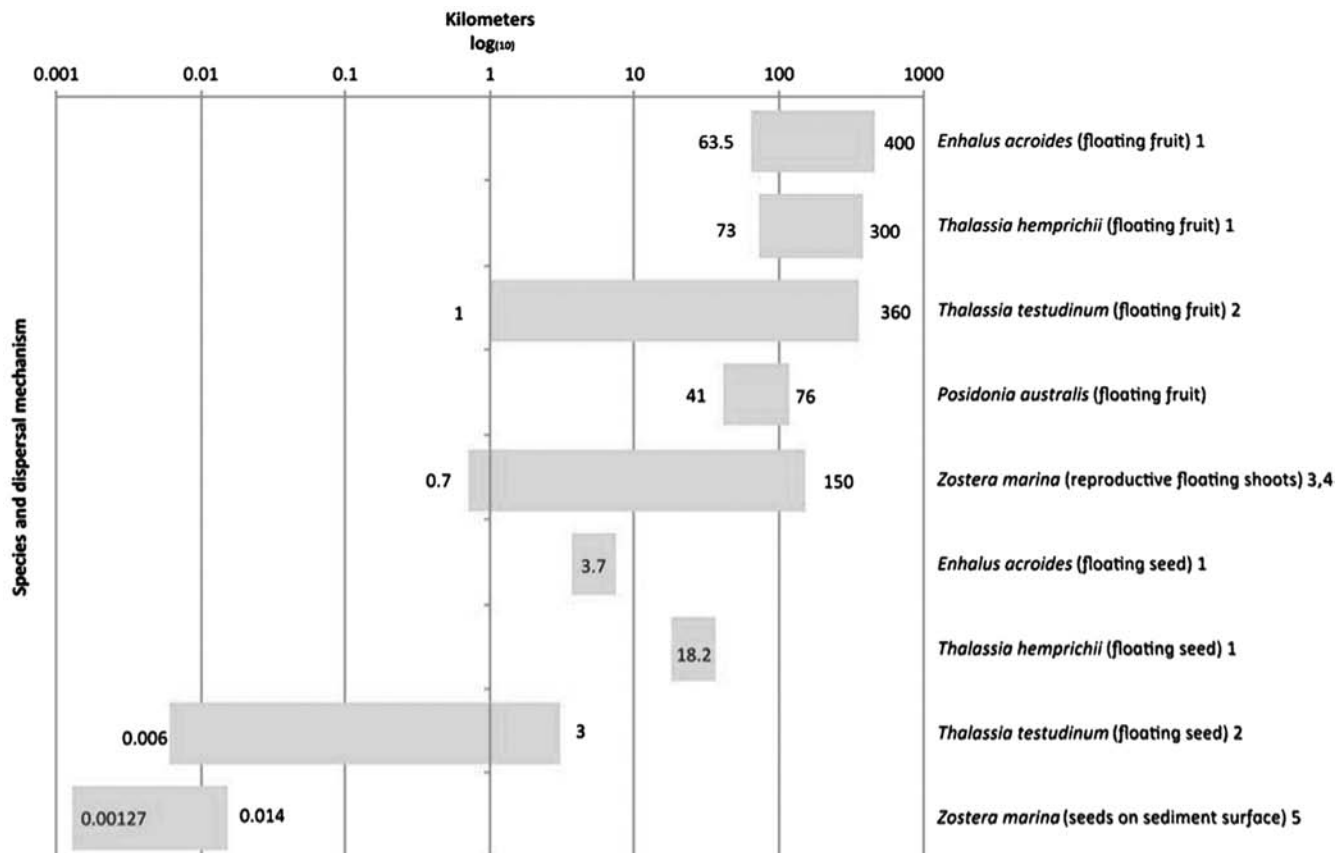


Figure 3. Ranges of seed dispersal reported for different seagrass propagules. Different methodologies have been used with each species, from direct tracking to genetic inferences. (1) Lacap and colleagues (2002), (2) Van Dijk and colleagues (2009), (3) Harwell and Orth (2002), (4) Reusch and colleagues (2000), (5) Orth and colleagues (1994).

seagrass literature; however, it could represent an important (or even dominant) transport mechanism in wave-dominated coastal environments.

Overall, long-distance dispersal in seagrasses appears far more likely to occur through seeds, fruits, viviparous seedlings, and vegetative fragments than by pollen. These structures have the capacity to move distances ranging from hundreds of meters to hundreds of kilometers. Seagrass dispersal has been directly and empirically addressed in few studies. In studies on *Z. marina*, Harwell and Orth (2002), Lacap and colleagues (2002), and Källström and colleagues (2008) concluded that long-distance dispersal to distances of 20–300 km were possible. In *T. testudinum*, van Dijk and colleagues (2009) similarly found that although the majority of the fruits in a meadow released their seed close to the parent plant, floating fruits occasionally had a much higher dispersal capacity, with distances of up to 8 km (Kinlan and Gaines 2003). Long-distance dispersal of vegetative fragments is possible, and the natural recruitment by dispersed floating vegetative fragments (which include rhizome fragments) has been reported (Di Carlo et al. 2005, Hall et al. 2006). However, few researchers have evaluated how effectively such floating, vegetative fragments can reestablish.

### Measuring dispersal in seagrasses with molecular markers

Molecular markers have provided several insights into the population genetic structure of seagrasses from which patterns and mechanisms of dispersal can be inferred. Population genetic studies have shown a trend whereby meadows at the extremes of a species range tend to show less genetic diversity (Waycott et al. 1997, Olsen et al. 2004, Arnaud-Haond et al. 2007, van Dijk et al. 2009). High genotypic diversity exists at all spatial scales within most species (table 1, and see the supplemental appendix S1, available online at <http://dx.doi.org/10.1525/bio.2012.62.1.10>). The full range of within-meadow genotypic diversity (from a single clone to no clonality detected) exists among seagrass meadows, even within close proximity (Ruggiero et al. 2002, Muñoz-Salazar et al. 2005, 2006, Alberto et al. 2006). Consequently, the processes affecting the dispersal of pollen, seed, and vegetative fragments at smaller spatial scales are complex and variable. The fixation index ( $F_{ST}$ ) and theta ( $\theta_{ST}$ ) measure genetic subdivision among populations, or genetic diversity. Low levels of spatial genetic subdivision (i.e., measured using the fixation index  $F_{ST} < 0.1$ ) are typical at local scales (less than 100 km; see table 1). These observations of high genetic diversity in many seagrass meadows and weak

**Table 1. Genetic diversity indices and sampling scales for seagrass species using microsatellite DNA markers.**

Species	Number of meadows	Sampling scale	Geographic sampling range (km)	Number of ramets	Number of genets	Number of genets/ramets	Mean $H_o$	Mean $H_e$	AMOVA or global $F_{ST}$	Reference
<i>Cymodocea nodosa</i>	10	Regional	15–300	373	255	0.68	—	0.43	0.18	Alberto et al. 2006
<i>Cymodocea nodosa</i>	47	Entire range	5500	1784	789	0.44	0.48	0.48	0.43	Alberto et al. 2008
<i>Thalassia testudinum</i>	16	Regional	1350	573	315	0.55	0.68	0.66	0.10	van Dijk and van Tussenbroek 2010, van Dijk et al. 2009
<i>Posidonia australis</i>	12	Local	80	587	348	0.59	0.49	0.48	0.11	
<i>Posidonia oceanica</i>	27	Entire range	3500	919	650	0.71	0.45	—	0.24	Serra et al. 2010
<i>Posidonia oceanica</i>	34	Entire range	3500	1217	875	0.72	0.43	—	0.23	Arnaud-Haond et al. 2007
<i>Posidonia oceanica</i>	4	Entire range	3500	307	218	0.71	—	—	—	Diaz-Almela et al. 2006
<i>Zostera marina</i>	6	Local	53	485	485	1.00	0.50	0.53	0.02	Oetjen and Reusch 2007
<i>Zostera marina</i>	6	Local	53	284	284	1.00	—	0.36	0.02	Oetjen et al. 2010
<i>Zostera marina</i>	12	Local	~80	281	242	0.86	0.61	0.62	0.14	Tanaka et al. 2011
<i>Zostera marina</i>	13	Regional	442	390	301	0.77	0.47	0.47	0.17	Becheler et al. 2010
<i>Zostera marina</i>	9	Regional	220–2300	328	328	1.00	0.55	0.57	0.16	Muñiz-Salazar et al. 2005
<i>Zostera marina</i>	12	Entire range	12–10000	545	371	0.68	0.47	0.48	0.29, 0.49	Reusch et al. 2000
<i>Zostera marina</i>	49	Entire range	10–10000	2139	1438	0.67	0.43	0.44	0.40	Olsen et al. 2004
<i>Zostera noltii</i>	8	Regional	60–1000	372	233	0.63	0.56	0.57	0.18	Diekmann et al. 2005
<i>Zostera noltii</i>	33	Entire range	2–8000	1706	1118	0.66	0.53	0.52	—	Coyer et al. 2004
<i>Zostera pacifica</i>	17	Regional	~300	783	291	0.37	—	0.13	—	Coyer et al. 2008

Note: Entire range represents the entire geographic distribution of the species.

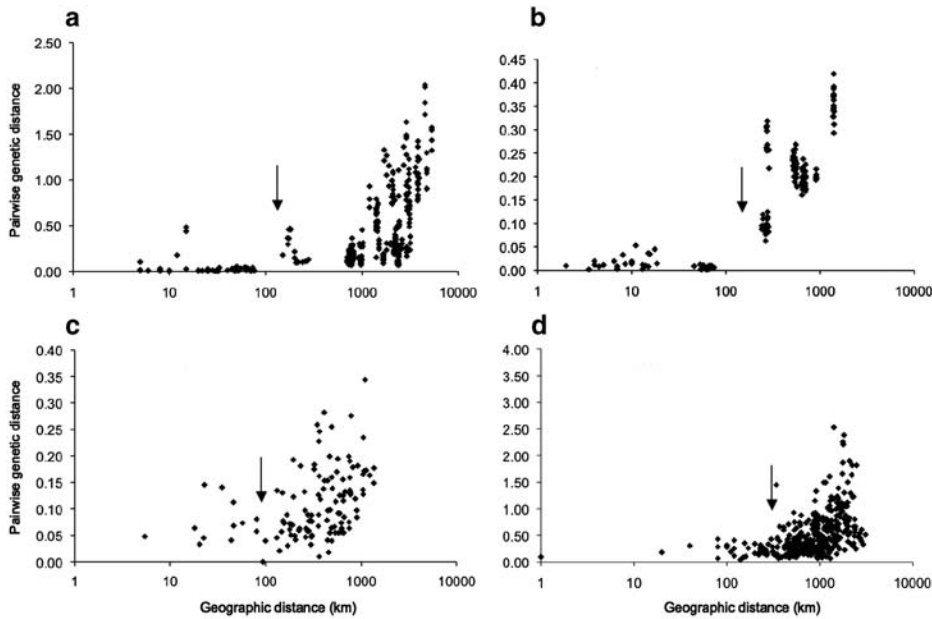
AMOVA, analysis of molecular variance;  $H_o$ , observed heterozygosity;  $H_e$ , expected heterozygosity;  $F_{ST}$ , measure of genetic subdivision; km, kilometers.

spatial genetic structuring among meadows suggest that sexual reproduction in seagrasses is more important than was previously thought and that seagrass population structure is not always dominated by clonal processes.

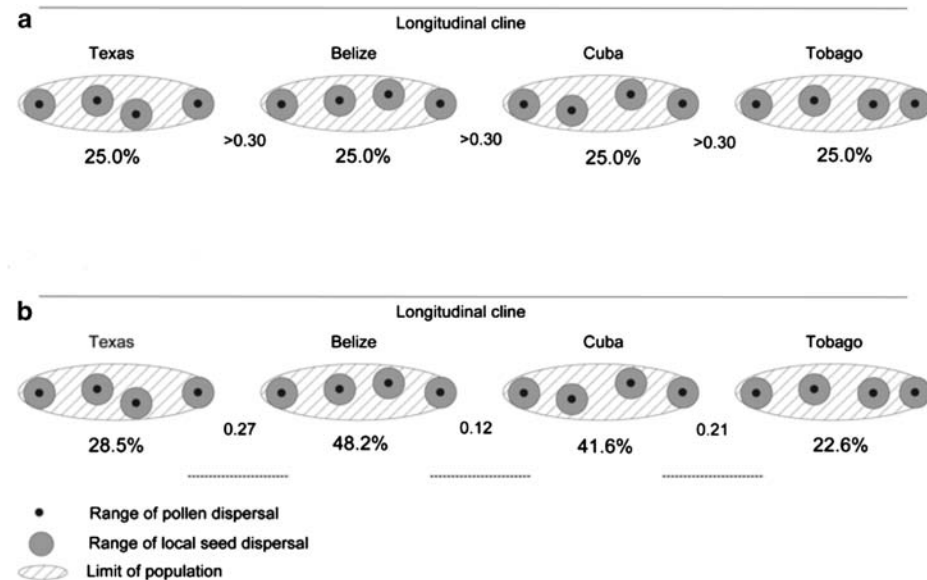
Patterns of spatial genetic variation in widespread seagrasses assessed over broad geographical ranges have also revealed significant insights into long-distance dispersal. Extensive, range-wide genetic studies typically show pairwise population genetic distances increasing proportionally with geographical distance at broad scales (hundreds of kilometers) but show weak relationships or no significant relationship at more regional scales (less than 200 km) (figure 4a–4d). Significantly, these genetic data strongly suggest a general threshold long-distance dispersal distance at hundreds of kilometers for widespread seagrass species—a distance that coincides with some directly observed seed-dispersal distances (Harwell and Orth 2002).

Physical (e.g., local currents) and biological (e.g., mating systems) factors play additive or antagonistic roles in

the patterns of genetic structuring that add complexity to a simple relationship between spatial scale and population genetic differentiation (Olsen et al. 2004). Further studies of isolating mechanisms, such as currents and geography, at small and large spatial scales, in combination with more-detailed molecular studies in which dispersal is assessed both directly and indirectly, will be necessary to better understand the complexities of long-distance dispersal in seagrasses. Some ecological studies that have evaluated or modeled the physical ability of seeds to move through a marine landscape (e.g., Källström et al. 2008) have been supplemented by genetic studies designed to characterize realized long-distance dispersal either directly or indirectly. For example, direct observations of floating-propagule-dispersal distances of up to 360 km for *T. testudinum* were consistent with results from genetic analyses, which indicated a panmictic area of 350 km—a much greater extent of gene flow than would be predicted by estimates based simply on local pollen- and seed-dispersal ranges (figure 5;



**Figure 4.** Plots showing the relationship between pairwise genetic distance derived from microsatellite DNA data, for the fixation index ( $F_{ST}$ ) and theta ( $\theta_{ST}$ ) that measure genetic subdivision among populations, measured by  $F_{ST}/(1 - F_{ST})$  (for panels a and c) or  $\theta_{ST}/(1 - \theta_{ST})$  (for panels b and d) and geographic distance (in kilometers [km]) for (a) *Zostera marina* (Olsen et al. 2004), (b) *Zostera noltii* (Coyer et al. 2004), (c) *Thalassia testudinum* (van Dijk et al. 2009), and (d) *Posidonia oceanica* (Arnaud-Haond et al. 2007). The arrows indicate geographic distance thresholds, below which there was no significant interaction of genetic isolation and geographic distance.



**Figure 5.** Schematic representation of genetic composition of *Thalassia testudinum* (a) predicted by the limited pollen and seed-dispersal ranges and (b) based on observed frequencies of 137 microsatellite alleles for nine loci. The numbers below the populations refer to the percentage of the total alleles; the numbers between the populations are fixation index ( $F_{ST}$ ) values that are a measure of genetic subdivision or genetic diversity. The broken lines indicate probable long-distance dispersal events.

van Dijk et al. 2009). Similarly, genetic data for *Z. marina* (Olsen et al. 2004) supported predictions based on experimental modeling (Källström et al. 2008), which indicated that dispersal distances of as much as 150 km are possible for this species.

The spatial distribution of genetic variation within and among populations of seagrasses provides considerable insight into dispersal vectors at smaller spatial scales (e.g., Waycott et al. 2006, van Dijk and van Tussenbroek 2010). For example, in *T. testudinum*, the occurrence of identical shared multilocus genotypes over 230 m suggests that rhizomes can extend over large distances or that vegetative fragments can successfully recruit (van Dijk and van Tussenbroek 2010). In contrast, for *Posidonia australis*, no multilocus genotypes (clones) were shared among sampled meadows along an 80-km stretch of coastline ( $N = 587$ ), which supports the suggestion that sexually produced seeds, rather than vegetative fragments, are the main source of long-distance dispersal.

In terrestrial plants, the vast majority of seeds disperse close to their parent plant, and the very few long-distance dispersal events are usually due to “non-standard” vectors that are different from those responsible for local dispersal (Nathan 2006). Although it remains unclear whether a similar pattern applies to marine environments, where habitats can be more highly connected, a fundamental difference from terrestrial plant dispersal is that the standard vector of ocean currents remains responsible for both local dispersal and long-distance dispersal. In addition, it might be expected that stochasticity associated with long-distance dispersal, which is high in terrestrial plants (Nathan 2006), is substantially lower in

seagrasses, leading to more regular dispersal events and an erosion of spatial genetic structure at large spatial scales (figure 4). The maximum dispersal distances in sedentary marine species appear to exceed the maximum estimates for terrestrial plants by at least one to two orders of magnitude (Kinlan and Gaines 2003). Although seagrasses were not considered by Nathan (2006) or by Kinlan and Gaines (2003), patterns of broad-scale genetic structure for widespread seagrass species (figure 4) support this observation.

The recent development of gene-linked microsatellites derived from expressed sequence tag libraries (EST-microsatellites) in *Z. marina* and *P. oceanica* (Wissler et al. 2009) highlight exciting future opportunities to further assess the genetic importance of long-distance dispersal and, therefore, the ability of species to shift ranges, as well as their genetic capacity to adapt to changing environmental conditions. For example, genome scans in *Z. marina* have shown divergent selection among subtidal versus intertidal meadows, showing evidence for habitat-specific selection (Oetjen and Reusch 2007, Oetjen et al. 2010), with consequences for realized dispersal in the face of rapid climate change.

#### Implications for managing disturbance to seagrass ecosystems

Seagrasses inhabit some of the most threatened coastal ecosystems in the world (Orth et al. 2006b, Waycott et al. 2009), and a more thorough understanding of the nature and extent of their dispersal is essential for implementing appropriate management and restoration strategies under predominantly anthropogenic conditions (Orth et al. 2006b). A better understanding of the relationships between the frequency and the range of pollen, seed, and propagule dispersal, with respect to particular spatial scales of disturbance, should help managers decide whether to actively enhance recruitment into a disturbed area (e.g., rehabilitation) or to manage an area for natural recruitment. In genera such as *Halophila*, existing seed banks can facilitate recovery following a disturbance (Marbà and Duarte 1995) and should allow natural recovery from small- to medium-scale disturbances, as long as the habitat quality (such as water quality, sediment quality, and geomorphology) is maintained. Conversely, genera such as *Posidonia*, which flower only once a year and do not form seed banks, are characterized by a small window of recruitment opportunity and would require more active management, through restoration, to remediate losses. In cases in which restoration would involve the deliberate introduction of propagules, it is important to understand patterns of genetic diversity and dispersal thoroughly in order to determine the most appropriate provenance for propagule sources. In cases in which seed dispersal is widespread and genetic subdivision is low among populations, seed stocks representing a broad provenance should have minimal negative restoration consequences. The development of restoration methods using seeds provides a better opportunity to maintain genetic

diversity within restored sites while dramatically reducing the impact on donor sites.

#### Conclusions

Seagrasses represent several specialized groups of monocotyledons, which have adapted successfully to colonize the shallow coastal seas and estuaries of the world. This review has described several unique aspects of flowering and pollination, the dispersal of reproductive propagules, and seedling recruitment across this group. The flowers occur at the sediment surface, within the canopy, and above the canopy. Seagrass pollen is among the largest for all angiosperms and is modified for water pollination in its shape, buoyancy characteristics, and size. In many seagrasses, pollination appears to occur predominantly at a local scale, within meadows, because most pollen is trapped within the canopy when released. In species that release pollen above the canopy, the potential for long-distance dispersal is enhanced. Ultimately, the power of molecular markers for paternity studies is required for a true understanding of the realized patterns of pollen dispersal within seagrasses.

Seagrasses possess diverse dispersal mechanisms that include floating fruits, rhipidia, and viviparous seedlings that are capable of long-distance dispersal and can potentially be transported over considerable distances in marine systems. In contrast, some seagrass species produce their seeds within the sediment or on the sediment surface, and dispersal away from the parental plants is minimal unless the sediments as a whole are moved by major disturbances (e.g., cyclones and extreme storms). Similar processes have been described for terrestrial plants (Nathan et al. 2008).

Our reevaluation of seagrass dispersal and recruitment has altered our fundamental understanding of seagrass resilience in several ways. It is evident that seagrasses are resilient and have persisted in a physiologically challenging submerged environment because they have broad realized niches. However, it now is apparent that the local persistence of seagrasses has been achieved not only by clonal growth but also by recruitment from sexually derived propagules. Seagrasses invest significant amounts of energy in sexual reproduction producing seeds with a high capacity for long-distance dispersal that enables them to colonize distant new locations. Although the frequency, extent, influences, and consequences of long-distance dispersal are still poorly known for many seagrass species, recent assessments of range-wide population genetic variation in widespread seagrass species have revealed extensive dispersal at scales much larger than was previously thought possible. Molecular studies in combination with ecological and hydrological assessments offer exciting new opportunities for a more-detailed understanding of long-distance dispersal in seagrasses.

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## References cited

- Ackerman JD. 1995. Convergence of filiform pollen morphologies in seagrasses: Functional mechanisms. *Evolutionary Ecology* 9: 139–153.
- . 2006. Sexual reproduction of seagrasses: Pollination in the marine context. Pages 89–110 in Larkum AWD, Orth RJ, Duarte CM, eds. *Seagrasses: Biology, Ecology and Conservation*. Springer.
- Alberto F, Arnaud-Haond S, Duarte CM, Serrão EA. 2006. Genetic diversity of a clonal angiosperm near its range limit: The case of *Cymodocea nodosa* in the Canary Islands. *Marine Ecology Progress Series* 309: 117–129.
- Alberto F, Massa S, Manent P, Diaz-Almela E, Arnaud-Haond S, Duarte CM, Serrão EA. 2008. Genetic differentiation and secondary contact zone in the seagrass *Cymodocea nodosa* across the Mediterranean–Atlantic transition region. *Journal of Biogeography* 35: 1279–1294.
- Arnaud-Haond S, Migliaccio M, Diaz-Almela E, Teixeira S, van de Vliet MS, Alberto F, Procaccini G, Duarte CM, Serrão EA. 2007. Vicariance patterns in the Mediterranean Sea: East–west cleavage and low dispersal in the endemic seagrass *Posidonia oceanica*. *Journal of Biogeography* 34: 963–976.
- Becheler R, Diekmann OE, Hily C, Moalic Y, Arnaud-Haond S. 2010. The concept of population in clonal organisms: Mosaics of temporally colonized patches are forming highly diverse meadows of *Zostera marina* in Brittany. *Molecular Ecology* 19: 2394–2407.
- Cain ML, Milligan BG, Strand AE. 2000. Long-distance seed dispersal in plant populations. *American Journal of Botany* 87: 1217–1227.
- Cook CDK. 1996. *The Aquatic Plant Book*. SPB Academic Publishing.
- Cox PA, Laushman RH, Ruckelshaus MH. 1992. Surface and submarine pollination in the seagrass *Zostera marina* L. *Biological Journal of the Linnean Society* 109: 281–291.
- Coyer JA, Diekmann OE, Serrão EA, Procaccini G, Milchakova N, Pearson GA, Stam WT, Olsen JL. 2004. Population genetics of dwarf eelgrass *Zostera noltii* throughout its biogeographic range. *Marine Ecology Progress Series* 281: 51–62.
- Coyer JA, Miller KA, Engel JM, Veldsink J, Cabello-Pasini A, Stam WT, Olsen JL. 2008. Eelgrass meadows in the California Channel Islands and adjacent coast reveal a mosaic of two species, evidence for introgression and variable clonality. *Annals of Botany* 101: 73–87.
- Diaz-Almela E, Marbà N, Álvarez E, Balestri E, Ruiz-Fernández JM, Duarte CM. 2006. Patterns of seagrass (*Posidonia oceanica*) flowering in the western Mediterranean. *Marine Biology* 148: 723–742.
- Di Carlo G, Badalamenti F, Jensen AC, Koch EW, Riggio S. 2005. Colonisation process of vegetative fragments of *Posidonia oceanica* (L.) Delile on rubble mounds. *Marine Biology* 147: 1261–1270.
- Diekmann OE, Coyer JA, Ferreira J, Olsen JL, Stam WT, Pearson GA, Serrão EA. 2005. Population genetics of *Zostera noltii* along the west Iberian coast: Consequences of small population size, habitat discontinuity and nearshore currents. *Marine Ecology Progress Series* 290: 89–96.
- Erfteimeijer PLA, van Beek JKL, Ochieng CA, Jager Z, Los HJ. 2008. Eelgrass seed dispersal via floating generative shoots in the Dutch Wadden Sea: A model approach. *Marine Ecology Progress Series* 358: 115–124.
- Grizzle RE, Short FT, Newell CR, Hoven H, Kindblom L. 1996. Hydrodynamically induced synchronous waving of seagrasses: ‘Monami’ and its possible effects on larval mussel settlement. *Journal of Experimental Marine Biology and Ecology* 206: 165–177.
- Hall LM, Hanisak MD, Virnstein RW. 2006. Fragments of the seagrasses *Halodule wrightii* and *Halophila johnsonii* as potential recruits in Indian River Lagoon, Florida. *Marine Ecology Progress Series* 310: 109–117.
- Hammerstrom KK, Kenworthy WJ, Fonseca MS, Whitfield PE. 2006. Seed bank, biomass, and productivity of *Halophila decipiens*, a deep water seagrass on the west Florida continental shelf. *Aquatic Botany* 84: 110–120.
- Harwell MC, Orth RJ. 2002. Long-distance dispersal potential in a marine macrophyte. *Ecology* 83: 3319–3330.
- Heck KL, Carruthers TJB, Duarte CM, Hughes AR, Kendrick G, Orth RJ, Williams SW. 2008. Trophic transfers from seagrass meadows subsidize diverse marine and terrestrial consumers. *Ecosystems* 11: 1198–1210.
- Inglis GJ, Waycott M. 2001. Methods for assessing seagrass seed ecology and population genetics. Pages 123–140 in Short FT, Coles RG, eds. *Global Seagrass Research Methods*. Elsevier.
- Källström B, Nyqvist A, Åberg P, Bodin M, André C. 2008. Seed rafting as a dispersal strategy for eelgrass (*Zostera marina*). *Aquatic Botany* 88: 148–153.
- Kinlan BP, Gaines SD. 2003. Propagule dispersal in marine and terrestrial environments: A community perspective. *Ecology* 84: 2007–2020.
- Knox RB. 1984. Pollen–pistil interactions. Pages 508–608 in Linskens HF, Heslop-Harrison J, eds. *Cellular Interactions*. *Encyclopedia of Plant Physiology*, vol. 17. Springer.
- Lacap CDA, Vermaat JE, Rollon RN, Nacorda HM. 2002. Propagule dispersal of the SE Asian seagrasses *Enhalus acoroides* and *Thalassia hemprichii*. *Marine Ecology Progress Series* 235: 75–80.
- Les DH, Cleland MA, Waycott M. 1997. Phylogenetic studies in Alismatidae, II: Evolution of marine angiosperms (seagrasses) and hydrophily. *Systematic Botany* 22: 443–463.
- Les DH, Crawford DJ, Kimball RT, Moody ML, Landolt E. 2003. Biogeography of discontinuously distributed hydrophytes: A molecular appraisal of intercontinental disjunctions. *International Journal of Plant Science* 164: 917–932.
- Marbà N, Duarte CM. 1995. Coupling of seagrass (*Cymodocea nodosa*) patch dynamics to subaqueous dune migration. *Journal of Ecology* 83: 381–389.
- Marion SR, Orth RJ. 2010. Innovative techniques for large-scale seagrass restoration using *Zostera marina* (eelgrass) seeds. *Restoration Ecology* 18: 514–526.
- McConchie CA, Knox RB. 1989. Pollen–stigma interaction in the seagrass *Posidonia australis*. *Annals of Botany* 63: 235–248.
- Muñiz-Salazar R, Talbot SL, Sage GK, Ward DH, Cabello-Pasini A. 2005. Population genetic structure of annual and perennial populations of *Zostera marina* L. along the Pacific coast of Baja California and the Gulf of California. *Molecular Ecology* 14: 711–722.
- . 2006. Genetic structure of eelgrass *Zostera marina* meadows in an embayment with restricted water flow. *Marine Ecology Progress Series* 309: 107–116.
- Nathan R. 2006. Long-distance dispersal of plants. *Science* 313: 786–788.
- Nathan R, Schurr FM, Speigel O, Steinitz O, Trakhtenbrot A, Tsoar A. 2008. Mechanisms of long-distance seed dispersal. *Trends in Ecology and Evolution* 23: 638–647.
- Obeso JR. 2002. The costs of reproduction in plants. *New Phytologist* 155: 321–348.
- Oetjen K, Reusch TBH. 2007. Genome scans detect consistent divergent selection among subtidal vs. intertidal populations of the marine angiosperm *Zostera marina*. *Molecular Ecology* 16: 5156–5167.
- Oetjen K, Ferber S, Dankert I, Reusch TBH. 2010. New evidence for habitat-specific selection in Wadden Sea *Zostera marina* populations revealed by genome scanning using SNP and microsatellite markers. *Marine Biology* 157: 81–89.
- Olsen JL, et al. 2004. North Atlantic phylogeography and large-scale populations differentiation of the seagrass *Zostera marina* L. *Molecular Ecology* 13: 1923–1941.

- Orth RJ, Luckenbach M, Moore KA. 1994. Seed dispersal in a marine macrophyte: Implications for colonisation and restoration. *Ecology* 75: 1927–1939.
- Orth RJ, Harwell MC, Bailey EM, Bartholomew A, Jawad JT, Lombana AV, Moore KA, Rhode JM, Woods HE. 2000. A review of issues in seagrass seed dormancy and germination: Implications for conservation and restoration. *Marine Ecology Progress Series* 200: 277–288.
- Orth RJ, Harwell MC, Inglis GJ. 2006a. Ecology of seagrass seeds and dispersal strategies. Pages 111–134 in Larkum AWD, Orth RJ, Duarte CM, eds. *Seagrasses: Biology, Ecology and Conservation*. Springer.
- Orth RJ, et al. 2006b. A global crisis for seagrass ecosystems. *BioScience* 56: 987–996.
- Ouborg NJ, Piquot Y, van Groenendael JM. 1999. Population genetics, molecular markers and the study of dispersal in plants. *Journal of Ecology* 87: 551–568.
- Pacini E, Franchi GG, Lisci M, Nepi M. 1997. Pollen viability related to type of pollination in six angiosperm species. *Annals of Botany* 80: 83–87.
- Paling EI, Fonseca M, van Katwijk MM, van Keulen M. 2009. Seagrass restoration. Pages 687–713 in Perillo G, Wolanski E, Cahoon D, Brinson M, eds. *Coastal Wetlands: An Integrated Ecosystem Approach*. Elsevier.
- Reusch TBH, Stam WT, Olsen JL. 2000. A microsatellite-based estimation of clonal diversity and population subdivision in *Zostera marina*, a marine flowering plant. *Molecular Ecology* 9: 127–140.
- Richards AJ. 1986. *Plant Breeding Systems*. Chapman and Hall.
- Ruggiero MV, Turk R, Procaccini G. 2002. Genetic identity and homozygosity in North-Adriatic populations of *Posidonia oceanica*: An ancient, post-glacial clone? *Conservation Genetics* 3: 71–74.
- Serra IA, et al. 2010. Genetic structure in the Mediterranean seagrass *Posidonia oceanica*: Disentangling past vicariance events from contemporary patterns of gene flow. *Molecular Ecology* 19: 557–568.
- Short FT, et al. 2011. Extinction risk assessment of the world's seagrass species. *Biological Conservation* 144: 1961–1971.
- Smith NM, Walker DI. 2002. Canopy structure and pollination biology of the seagrasses *Posidonia australis* and *P. sinuosa* (Posidoneaceae). *Aquatic Botany* 74: 57–70.
- Tanaka N, Uehara K, Murata J. 2004. Correlation between pollen morphology and pollination mechanisms in the Hydrocharitaceae. *Journal of Plant Research* 117: 265–276.
- Tanaka N, Demise T, Ishii M, Shoji Y, Nakaoka M. 2011. Genetic structure and gene flow of eelgrass *Zostera marina* populations in Tokyo Bay, Japan: Implications for their restoration. *Marine Biology* 158: 871–882.
- Van Dijk JK, van Tussenbroek BI. 2010. Clonal diversity and structure related to habitat of the marine angiosperm *Thalassia testudinum* along the Atlantic coast of Mexico. *Aquatic Botany* 92: 63–69.
- Van Dijk JK, van Tussenbroek BI, Jiménez-Durán K, Márquez-Guzmán GJ, Ouborg J. 2009. High levels of gene flow and low population genetic structure related to high dispersal potential of a tropical marine angiosperm. *Marine Ecology Progress Series* 390: 67–77.
- Van Tussenbroek BI, Wong JGR, Márquez-Guzmán J. 2008. Synchronized anthesis and predation on pollen in the marine angiosperm *Thalassia testudinum* (Hydrocharitaceae). *Marine Ecology Progress Series* 354: 119–124.
- Verduin JJ, Backhaus JO, Walker DI. 2002. Estimates of pollen dispersal and capture within *Amphibolis antarctica* (Labill.) Sonder and Aschers. *Ex Aschers. Meadows. Bulletin of Marine Science* 71: 1269–1277.
- Waycott M, James SH, Walker DI. 1997. Genetic variation within and between populations of *Posidonia australis*, a hydrophilous, clonal seagrass. *Heredity* 79: 408–417.
- Waycott M, Procaccini G, Les DH, Reusch TBH. 2006. Seagrass evolution, ecology and conservation: A genetic perspective. Pages 25–50 in Larkum AWD, Orth RJ, Duarte CM, eds. *Seagrasses: Biology, Ecology and Conservation*. Springer.
- Waycott M, et al. 2009. Accelerating loss of seagrasses across the globe threatens coastal ecosystems. *Proceedings of the National Academy of Sciences* 106: 12377–12381.
- Wissler L, Dattolo E, Moore AD, Reusch TBH, Olsen JL, Migliaccio M, Bornberg-Bauer E, Procaccini G. 2009. Dr. Zompo: An online data repository for *Zostera marina* and *Posidonia oceanica* ESTs. Database 2009. doi:10.1093/database/bap009
- Zipperle AM, Coyer JA, Reise K, Stam WT, Olsen JL. 2011. An evaluation of small-scale genetic diversity and the mating system in *Zostera noltii* on an intertidal sandflat in the Wadden Sea. *Annals of Botany* 107: 127–134.

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