

The effect of a centenary storm on the long-lived seagrass *Posidonia oceanica*

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Abstract

We used the disturbance resulting from a once in a 100-yr storm on the northwest Mediterranean coast to examine the extent of the disturbance, the tolerance thresholds to burial, and the medium-term response of the long-lived *Posidonia oceanica* seagrass. Sediment burial at 12 surveyed areas was particularly strong in shallow meadows, with 23% of their surfaces buried, on average, under more than 10 cm of sediment. In contrast, less than 5% of the meadow was affected at deeper locations. At three sites, we tracked short-term mortality along a gradient of sediment burial. Survival response to burial was clearly nonlinear, with a significant threshold at 4–5 cm, beyond which shoot mortality was 100%. To track medium-term potential recovery, we established permanent plots subject to three sediment burial levels (0–5, 5–10, and > 10 cm burial) in four meadows. Where the initial shoot mortality was 100%, we recorded no shoot recovery over the 4-yr period. In the remaining plots, where some shoots remained alive, we detected either further mortality or shoot recovery of 7% per year on average. Extreme storm events can result in sudden catastrophic losses of seagrass cover in shallow *P. oceanica* meadows. In the long term and due to the long return time of such storms, the species may still be able to recover despite its low recovery potential. However, added anthropogenic stressors, including climate change, may seriously test the ability of long-lived shallow seagrass ecosystems to resist high-intensity natural disturbances and may be critical for its persistence.

Ecosystems are, by and large, a product of the disturbance regimes within which they exist. Disturbance is a key habitat-structuring agent; communities are driven by the intensity and frequency of condition-altering forces and the relative abilities of their constituent species in dealing with these disturbances (Sousa 1984). While a raft of research has focused on the influence of small, frequent disturbances on ecosystem stability and recovery, we are far less certain of how systems respond to larger, more infrequent disturbances (Hughes 1994). Ecosystem responses may not scale up predictably with increasing disturbance intensity; large infrequent events may trigger qualitatively different effects on ecosystems compared to more frequent small-scale perturbations (Romme et al. 1998). This is because, while disturbance-prone systems may have endogenous feedback mechanisms to absorb regular disturbances, this natural resistance may have critical limits beyond which ecosystems may respond very differently (Holling 1973). Understanding if such discontinuities exist under natural field conditions, what these threshold values are, and how systems respond when thresholds are crossed requires considerably more empirical field data on system responses to large infrequent disturbances. However, their very unpredictability makes them difficult to study, except with opportunistic approaches in the wake of extreme events.

An extreme storm event, with a return time of ~ 100 yr, affected the northwest Mediterranean coast on 26 December 2008 (Sanchez-Vidal et al. 2012). The presence of a shallow depression over the Balearic Sea with a minimum

pressure of 1012 hPa and a high-pressure center over northern Europe (1047 hPa) generated an extreme storm with strong easterly winds and maximum wave heights of 14.4 m, maximum significant wave height (H_s) of 7.5 m, and a duration of 73 h. This event was the largest ever recorded (in terms of wave height) on the northwest Mediterranean coast (Costa Brava, Spain; Sanchez-Vidal et al. 2012). Storm action was not uniform, with the greatest effects (greatest wave power, heights, and shear stress) experienced in the northern third (which roughly corresponds to the rocky Costa Brava). South of this, wave power and shear stress decreased to around half (central Catalonia) and one-third (southern Catalonia) of the extreme northern storm conditions (see Fig. 1; Mateo and Garcia-Rubies 2012). The effects on the biota were severe, affecting several marine habitats, from superficial rocky algal beds to deep canyons (Mateo and Garcia-Rubies 2012; Sanchez-Vidal et al. 2012). The magnitude and rarity of this event provided a rare opportunity to examine the immediate response and subsequent recovery of subtidal *Posidonia oceanica* seagrass meadows to such high-intensity disturbances.

The long-lived endemic seagrass *P. oceanica* dominates sandy bottoms in the Mediterranean, extending to a depth of 35 m. It is considered one of the longest-living seagrass species in the world (Arnaud-Haond et al. 2012), and although characterized by extremely slow growth rates, it spreads almost exclusively through clonal growth, with successful sexual reproduction events being rare (Procaccini et al. 2001). An ecosystem dominant, *P. oceanica* is an important engineering species and plays a critical role in

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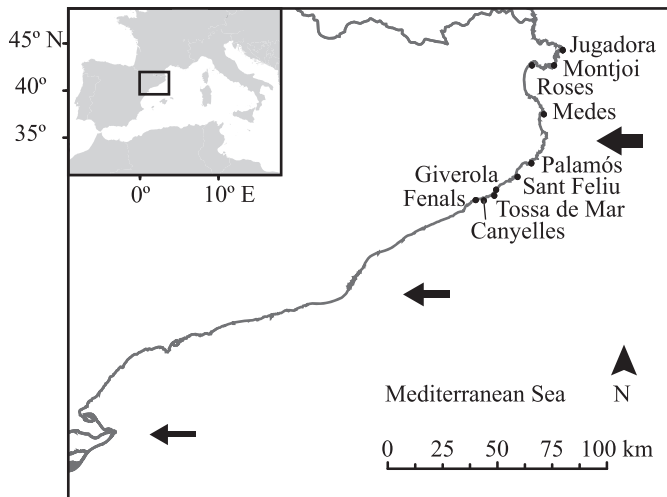


Fig. 1. Localities along the Catalan coast (northwestern Mediterranean) where the burial effect on *Posidonia oceanica* meadows was assessed (see Table 1 for meadows' details). The size of the arrows represents the wave power of the storm event along the coastal stretch investigated.

binding soft-sediment habitats with a dense network of rhizomes and roots (called the *matte*), significantly reducing sand movement within the meadow (Gacia and Duarte 2001). In addition, the long seagrass leaves and shoots create a structurally complex habitat that considerably attenuates wave and tidal action (Duarte et al. 2013). These factors, together with its large rhizome storage, may make healthy, unfragmented *P. oceanica* meadows more resistant to regular sand movement events than other seagrass species. For instance, it is known that, on coasts exposed to strong winds, storm surges, and tidal flows, sediment movements can bury seagrass shoots, expose roots and rhizomes, and even uproot entire plants (Frederiksen et al. 2004). In the face of this disturbance regime, several seagrass species are characterized by short life spans, increased investment in seed banks, sexual reproduction, fast recolonization and vertical shoot growth, a suite of life-history traits that enables them to thrive in disturbance-prone environments (Fourqurean and Rutten 2004). Unlike *P. oceanica*, these strategies are linked

more to ensuring a fast recovery after disturbance events rather than in resisting the disturbance itself.

The continued dominance and persistence of *P. oceanica* in most Mediterranean coastal waters over millennia (Mateo et al. 1997) has been attributed mainly to the species' ability to deal with low nutrient and good light conditions prevalent in Mediterranean waters as well as its ability to engineer its own low-disturbance regime in the normally dynamic soft sediments it inhabits (Ghisalberti and Nepf 2002). However, there are clear limits to this resistance. In fact, in shallow areas, *P. oceanica* is unable to cope with the persistently high hydrodynamic conditions present there, placing a natural upper boundary on meadow colonization (Infantes et al. 2009; Vacchi et al. 2010). The storm of 2008 subjected coastal waters to extreme hydrodynamic conditions, and our study was designed to document how *P. oceanica* meadows responded to this pulse event. We first determined the extent of the disturbance by measuring the amount of sediment burial in 12 randomly selected meadows, representing more than 50% of known seagrass meadows within the affected zone of the storm. In addition, at four of the affected meadows, we determined the sedimentation thresholds that plants can tolerate. Finally, in order to determine potential recovery trajectories of these meadows, we tracked shoot recovery for 4 yr after the initial pulse event.

Methods

Regional extent of storm burial—The storm of 2008 left a large part of the northern Catalan coast very badly affected. In order to monitor the regional extent of seagrass burial caused by this event, we surveyed 12 randomly chosen meadows 2 months after the event within the central affected zone of the storm (see Fig. 1; Table 1). Three of the meadows assessed were shallow (5–10 m), and the remaining nine were deep (15–25 m). This uneven distribution reflected the bathymetric distribution of *P. oceanica* meadows in the area and represented more than 50% of the known distribution of seagrass meadows in the area (Garcia et al. 2001). We estimated the extent of burial at each site in six randomly placed 50-m visual transects. We used a double-observer method in which two divers

Table 1. Regional extent of burial assessed using visual transects (mean \pm SE, $n = 3$ –6) in each of the different meadows along the northwest Mediterranean coast indicated in Fig. 1. Meadows with permanent recovery plots are marked with an asterisk (*).

Meadow	Latitude ($^{\circ}$ N)	Longitude ($^{\circ}$ E)	Orientation	Depth (m)	% Buried area
Canyelles*	41 $^{\circ}$ 41'59"	2 $^{\circ}$ 53'16"	Southeast	21	14 \pm 9
Fenals*	41 $^{\circ}$ 41'21"	2 $^{\circ}$ 49'42"	Southeast	9	30 \pm 3
Fenals	41 $^{\circ}$ 41'19"	2 $^{\circ}$ 50'12"	Southeast	24	6 \pm 5
Giverola*	41 $^{\circ}$ 44'10"	2 $^{\circ}$ 57'16"	Southeast	7	10 \pm 3
Jugadora	42 $^{\circ}$ 18'53"	3 $^{\circ}$ 18'52"	Southeast	20	0 \pm 0
Medes	42 $^{\circ}$ 02'46"	3 $^{\circ}$ 13'11"	Southwest	5	20 \pm 3
Medes	42 $^{\circ}$ 02'47"	3 $^{\circ}$ 13'08"	Southwest	15	0 \pm 0
Montjoi	42 $^{\circ}$ 14'48"	3 $^{\circ}$ 14'03"	Southeast	21	0 \pm 0
Palamós*	41 $^{\circ}$ 50'39"	3 $^{\circ}$ 07'00"	Southeast	16	1 \pm 1
Roses	42 $^{\circ}$ 14'18"	3 $^{\circ}$ 12'14"	South	22	0 \pm 0
St. Feliu	41 $^{\circ}$ 46'16"	3 $^{\circ}$ 01'33"	Southwest	22	0 \pm 0
Tossa	41 $^{\circ}$ 43'30"	2 $^{\circ}$ 56'41"	Southeast	14	10 \pm 3

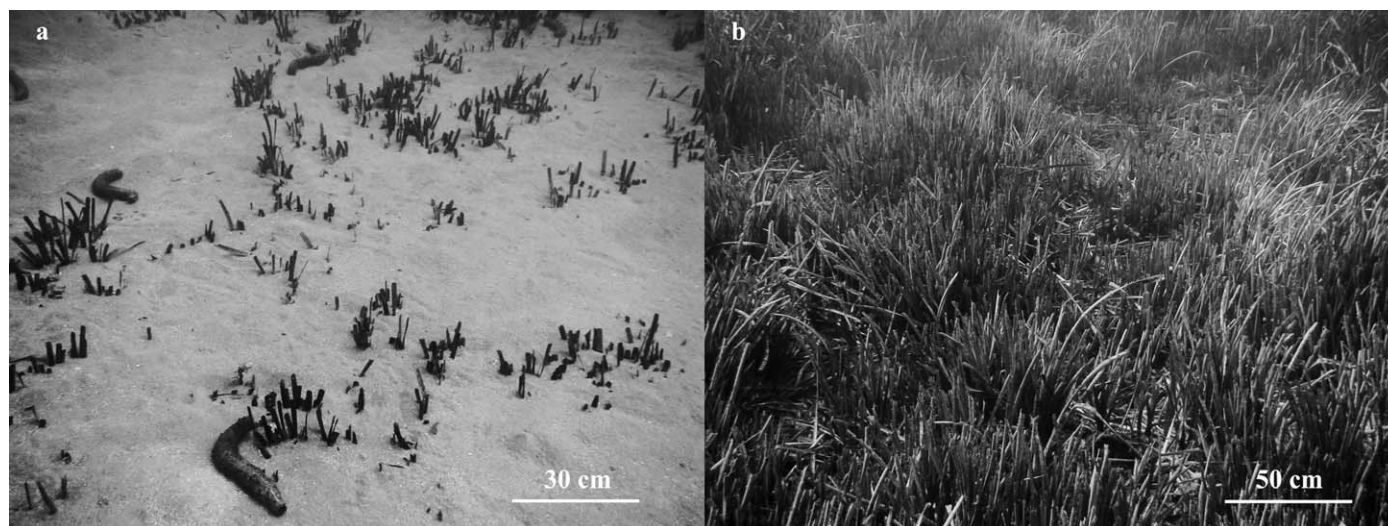


Fig. 2. Photographs showing (a) an area affected by sediment burial of more than 10 cm and (b) an area not affected.

independently scanned 5 m on either side of transect (total area surveyed per transect 500 m²) and assigned the area of the meadow that was buried under sand to five broad categories (0%, 25%, 50%, 75%, and 100% of the area of the transect with buried seagrass). All assessments were conducted with experienced seagrass researchers, and a prior uncertainty analysis conducted with the same observers showed that interobserver biases in visually assessing seagrass cover accounted for less than 2% of measurement error (calculated from Bennett et al. 2011 data set). Only areas with shoots covered with more than 10 cm of sediment, measured as the vertical distance between the sediment surface and the shoot ligula (i.e., a thin outgrowth at the junction of the leaf and the leaf base), were recorded as buried seagrass. This 10-cm sediment level was chosen based on known mortality thresholds for *P. oceanica* shoots (Cabaço et al. 2008; see also Results). This burial was clearly distinguished in the water because leaves were visibly trapped below the sediment and were at different stages of decomposition even 2 months after the storm (see Fig. 2 for examples of buried and unburied areas). Whenever we found large buried patches, we recorded their approximate area with a measuring tape (length \times width). These estimates of burial were relatively conservative since portions of the meadow with less than 10 cm of burial could also likely be lost (Manzanera et al. 2011). Additionally, we did not take into account areas of the meadow affected by abrasion, unearthing, and uprooting of plants, as this does not leave clear visible signs after the storm and is impossible to record unless spatially explicit baseline information is available.

Conducted in the immediate wake of this extreme storm, our measures of burial extent were necessarily opportunistic and conducted at a time of the year when weather conditions do not permit unrestricted access to the ecosystem. It was critical to assess seagrass burial before sediment movement appeared again during the normally stormy months after the extreme storm. We could not know a priori how the effect of the storm was distributed across the meadows, and our

sampling protocols were designed to assess these effects as rapidly and accurately as possible.

Plant burial tolerance—SCUBA divers assessed seagrass burial resistance thresholds in three meadows at different depths (Canyelles, 21 m; Giverola, 7 m; and Medes, 5 m; see Fig. 1). At each site, we identified meadow areas along a gradient of sediment burial (from 0-cm to 15-cm sediment level) after the storm event (4 months later). Burial was determined as the height from the ligula to the sediment surface; under normal conditions, the ligula stands a few cm (1 to > 5) above the sediment. The number of living and dead shoots was counted in small quadrats (15 \times 15 cm, n = 25–30) placed along the burial gradient. To determine the proportion of dead shoots under each burial level, we took advantage of the fact that even dead shoots (including leaves) remained in the buried area long after the storm (4 months at the time of sampling; see Fig. 2a for an example). After measuring burial in each quadrat, we carefully removed the sediment and counted all dead shoots (where the leaf base was completely necrotized). We also counted all shoots that remained alive, which, unlike dead shoots, had leaves with a healthy, light-green meristem. This method was unable to detect any potential loss of shoots directly uprooted by wave action. Therefore, our results represent a conservative estimate of the mortality caused by the storm and accounts for only the effects of storm burial, not uprooting.

Medium-term recovery potential—We established 40 \times 40 cm permanent quadrats in each of four *P. oceanica* meadows (Giverola shallow, 7 m; Fenals shallow, 9 m; Canyelles deep, 21 m; and Palamós deep, 16 m; see Fig. 1; Table 1) after the storm in order to determine the effect of burial (mortality) on the long-term survival (and potential recovery) of *P. oceanica* shoots. Three sets of plots with two replicates each (a total of six quadrats per site) were established at three burial levels (0–5, 5–10, and >10 cm, measured as explained above; n = 2 plots per treatment,

3 treatments per site). The number of shoots in each plot was counted (1) just after the storm (T_0 = beginning 2009) taking advantage of the fact that mortality by sediment burial takes several months to occur, (2) a year later (T_1 = beginning 2010), and (3) four years after the storm (T_4 = end of 2012). Shoot mortality was expressed as a percentage of the difference between the number of living shoots in the initial counts (S_0) and the counts 1 yr after the storm (S_1) divided by the initial counts (S_0):

$$\text{mortality} = \frac{S_0 - S_1}{S_0} \cdot 100 \quad (1)$$

Shoot recovery was established as a percentage of the difference between the number of living shoots in the counts 4 yr after the storm (S_4) and the counts 1 yr after the storm (S_1) divided by the initial counts (S_0):

$$\text{recovery} = \frac{S_4 - S_1}{S_0} \cdot 100 \quad (2)$$

Shoot recovery was then divided by 4 yr to obtain an annual rate of recovery for each location.

Statistical analyses—We assessed plant burial tolerance with data pooled from all sites and depths. Since our preliminary data observations suggested a threshold response to shoot burial, a change point detection method was run in R with the package *strucchange* (Zeileis et al. 2002; Andersen et al. 2009). The algorithm is based on assessing whether different parts of the data set require different parameters to fit a linear regression. Further, to assess the significance of every potential change point in the data set, an *F*-statistic (Chow test statistic) was also computed. Since these methods require data sets with one observation per burial level, we established burial intervals of 1 cm (i.e., grouping all shoots buried from 0 to 1 cm, from 1 to 2 cm, and so on), and we sampled one random observation from each interval 1000 times. Each of the 1000 sampling events resulted in a data set that was analyzed with an *F*-statistic and a change point estimator. We then plotted the mean *F*-statistic with its standard errors and the mean percentage mortality for each burial interval with the most probable change point and its confidence interval.

To determine the factors influencing medium-term shoot mortality (obtained from the fixed quadrats) we performed a three-way nested ANOVA to test the effect of the fixed factors “burial” (three levels: 0–5, 5–10, and > 10 cm), “depth” (two levels: shallow [5–10 m] and deep [15–25 m]) and their interaction (burial \times depth), with “site” (two levels: Fenals and Giverola shallow meadows and Canyelles and Palamós deep meadows) as a random factor nested in “depth.” Before analysis, data were tested for normality and homoscedasticity using the Shapiro–Wilk’s and Bartlett’s test, respectively. Whenever an ANOVA was significant, a multiple range contrast test was applied (Tukey’s honestly significant difference) to determine differences among burial levels. We could not test the effects of burial on medium-term recovery since we recorded zero recovery in most of the fixed quadrats (see Results), and we discuss only trends.

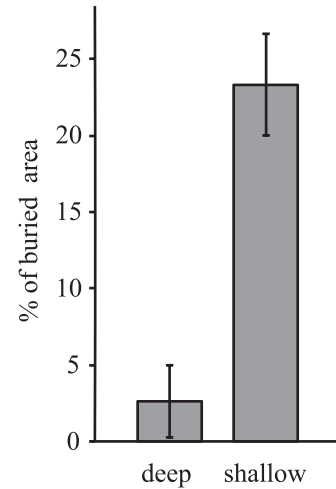


Fig. 3. Regional extent of burial. Estimated percentage of buried area (>10 cm) in deep ($n = 9$) and shallow meadows ($n = 3$) assessed with visual transects (see Table 1 for meadow details; mean \pm SE).

Results

Regional extent of burial—The effects of the 26 December 2008 extreme storm was strongest in the shallow meadows (5–10 m depth) we surveyed (Fig. 3; Table 1). These meadows were heavily affected by burial, with a mean of $20\% \pm 6\%$ of their total area covered with more than 10 cm of sediment (Fig. 3). In contrast, deep meadows (15–25 m depth) showed relatively low levels of burial, with an average of $3\% \pm 2\%$ of their total area under sand (Fig. 3). For the most part, burial occurred in patches of $\sim 10 \text{ m}^2$ or more and was more frequent at the edges of meadows.

Plant burial tolerance—Four months after the storm, shoot mortality increased substantially as a result of sediment burial in the three meadows studied. While zones that had been buried from 0 to 3 cm showed relatively low shoot mortality after the storm event, mortality increased substantially at higher burial levels. Indeed, this increase was nonlinear, with a sharp rise at 4–5 cm and near-total mortality at burial levels of 8–9 cm and above (Fig. 4a). The burial interval of 4–5 cm was found to be a significant change point of plant tolerance (Fig. 4a,b).

Medium-term recovery potential—The medium-term monitoring plots confirmed mortality patterns documented in the plant burial tolerance measurements (see previous section). A year after the storm, most plots with more than 10 cm of burial showed 100% mortality, while in plots with 0–5 cm of burial, the mortality was significantly lower (Table 2) but with signs of delayed mortality (negative trajectories even 4 yr after the storm; Table 3). There was some variability in the response of plots with intermediate burial levels (5–10 cm), with mortality values of $52\% \pm 14\%$ (mean \pm standard error [SE], $n = 8$ [two quadrats per four sites]).

In tracking potential recovery, we did not observe shoot recruitment in the majority of quadrats from both shallow

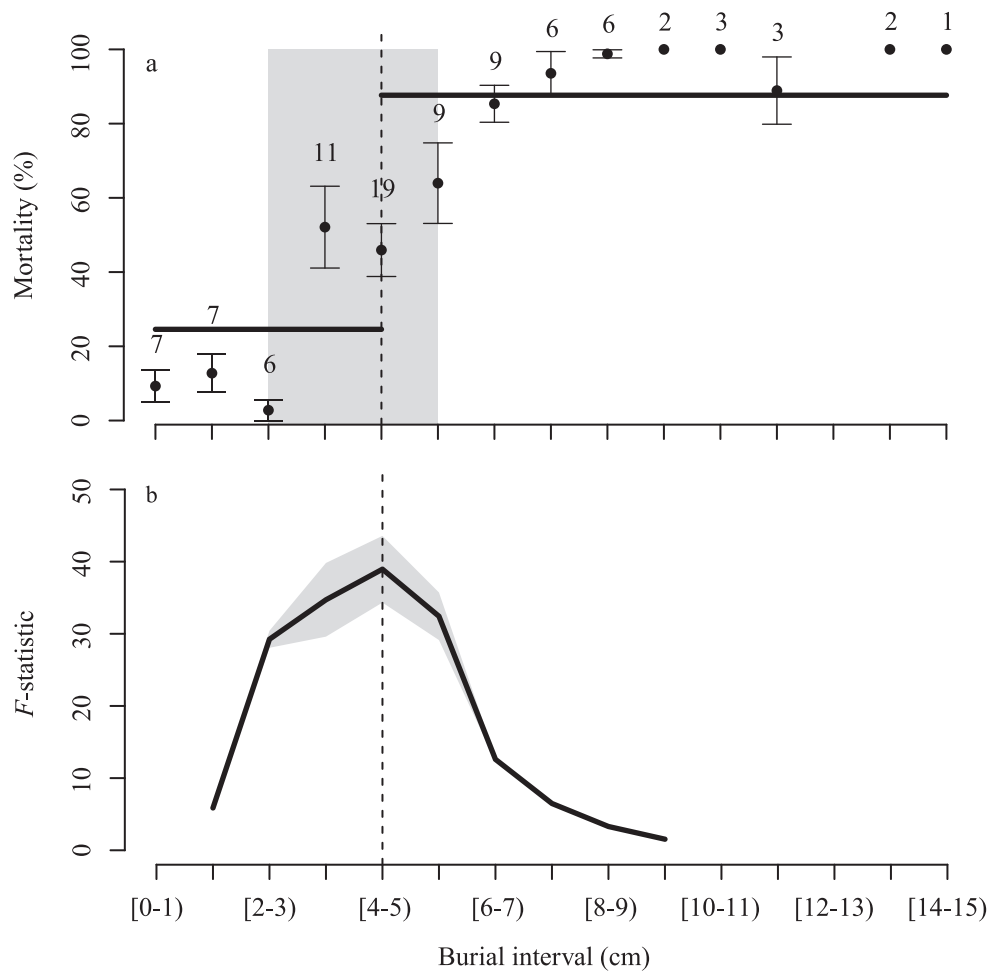


Fig. 4. Plant burial tolerance. (a) Shoot mortality as a function of sediment burial assessed in 15 × 15 cm quadrats ($n = 23$) placed extensively within the affected meadows. Note the presence of an evident change point at a burial level of (4–5) cm (dashed line). The confidence interval around the change point is indicated in grey, and solid black lines correspond to the mean shoot mortality before and after the change point. The sample size is indicated in numbers above each point. (b) Mean F -statistic \pm error ($n = 1000$ samples; see Methods) in order to assess the significance of the potential change points. The method indicates the most significant change point as a peak (see the dashed line).

and deep meadows 4 yr after the storm, confirming the low recovery capacities of *P. oceanica* (Table 3). Indeed, from a total of 24 quadrats (two per three levels per four sites), recovery was observed in only five quadrats. In these plots

(most of them from the 5–10 cm burial level), the average annual shoot recovery rate was $7\% \pm 3\%$ relative to prestorm conditions. In plots where the initial shoot mortality was 100%, we documented no recovery at all (Table 3).

Table 2. Effects of sediment burial on shoot mortality. Results from F -tests for the dependent variable “shoot mortality” with “burial” and “depth” as fixed factors and “site” nested in depth. Significant value ($p < 0.05$) is presented in bold; ns, not significant; df, degrees of freedom; SS, sum of squares; F , F -statistic.

Variable	Source of variation	Effect	df	SS	F	p
Shoot mortality	Burial	Fixed	2	24,681	12.3	< 0.001
	Depth	Fixed	1	293	0.2	ns
	Burial × depth	Fixed	2	283	0.1	ns
	Site (depth)	Random	2	3183	1.6	ns
	Error		14			

Table 3. Medium-term (4 yr) recovery potential (see Eq. 2) in quadrats with (< 100% shoots lost) and without (100% shoots lost) surviving shoots after the storm. For each category, the mode of burial values found is reported (cm). Note that most of the quadrats do not recover, and those that do recover do so at slow rates.

Shoots lost	Burial (mode) (cm)	Trajectory	No. of plots	Recovery
100%	10–15	Stable	4	No
< 100%	5–10	Positive	5	7% ± 3%
< 100%	0–5	Negative	15	No

Discussion

The storm of 2008 was among the most intense on record, with a return time of 100 yr. The *P. oceanica* seagrass meadows we tracked in the wake of this extreme event declined significantly in cover across the northern Catalan coast. Although storm effects were relatively modest in deep meadows (~ 3% of areal losses), they were dramatic in shallow waters, with an average of 23% areal losses across the affected region. This is most likely a conservative estimate since they are based only on measured losses caused by sediment burial and do not account for uprooting of seagrass shoots as a result of the large shear forces generated by the storm. Compared to many smaller, fast-growing species, *P. oceanica* showed a moderate resistance to burial; plants appeared to tolerate sediment burial up to a clear threshold of 4–5 cm, beyond which shoot mortality increased sharply. We observed that burial levels above 8–9 cm resulted in the total mortality of shoots both in our extensive postdisturbance surveys of plant burial tolerance and in the permanent plots we tracked to assess potential recovery. Four years after the disturbance, shoot recruitment was observed only in the few plots that had not suffered total mortality as a consequence of the storm; in contrast, in plots where shoot mortality had been 100%, we did not record any recovery at all. The role of high-intensity, low-frequency disturbances has rarely been considered an important driver of seagrass decline, perhaps because their long return times make them difficult to track (but see Larkum and West 1990; Fourqurean and Rutten 2004; Van Tussenbroek et al. 2014). Nevertheless, our results indicate that, despite their rarity, such infrequent disturbances may profoundly influence seagrass meadow dynamics. In this study, the storm resulted in a reduction of nearly one-fourth of its effective cover in shallow areas, from which recovery is likely to be protracted, potentially requiring several decades to return to predisturbance conditions.

The ability of *P. oceanica* to resist this high-intensity disturbance appears to be moderate when compared to smaller, fast-growing species (Cabaço et al. 2008), which tend to suffer higher shoot mortalities due to burial but show a faster subsequent recovery (Cabaço et al. 2008). Unsurprisingly, our results show that shallow meadows were the most heavily affected by the disturbance. Shallow meadows are often more subject to areal losses than deep

meadows since the intensity of physical disturbances generally attenuate rapidly with depth. The high-energy waves and sediment transport generated by storms is experienced most strongly in the first few meters of the water column and decreases considerably with depth (Ruiz et al. 2009). These regular storm events have already been identified as critical in determining the upper depth limit of seagrass distribution in the Mediterranean Sea (Infantes et al. 2009; Vacchi et al. 2010), and *P. oceanica* can colonize shallower areas only in the most protected bays (Ruiz et al. 2009). Below these limits however, the shallow meadows we monitored are remarkably persistent in the wake of frequent small-scale disturbances, having been present in shallow coastal waters for centuries and possibly millennia (Mateo et al. 1997). The fact that a single large storm event could cause such a dramatic reduction in meadow cover suggests that high-intensity, low-frequency disturbances, though rare, are potentially critical structuring agents of these nearshore ecosystems. In addition, given the long life span of this slow-growing species, these events can have important, long-lasting demographic consequences for *P. oceanica*. Nearshore marine ecosystems like seagrass meadows can be particularly prone to these high-intensity disturbances, with long-term consequences for these systems, as has been documented in the wake of hurricanes in Florida and the Caribbean (Fourqurean and Rutten 2004; Van Tussenbroek et al. 2014) or after the combined effects of storms and anthropogenic engineering on the Australian coast (Larkum and West 1990).

The ability of *P. oceanica* to withstand sediment burial showed a sharp threshold around 4–5 cm; beyond 8–9 cm, shoot mortality was nearly 100% in all three studied meadows. A similar pattern of tolerance was identified by earlier experimental burial studies for the species (Manzanera et al. 2011). A comprehensive review of sedimentation responses to burial suggested that seagrass species have an average critical burial limit for vertical rhizome growth of around 10 cm, which causes a 50% shoot reduction (Cabaço et al. 2008). This limit is highly species specific, and while some small, fast-growing species cannot tolerate more than 2 cm of burial, larger plants, particularly those with vertical rhizomes and large rhizome diameters (i.e., with more reserves), appear better able to counteract burial (Cabaço et al. 2008). However, although *P. oceanica* is one of the largest seagrass species, with high structural complexity, the quantity of sediment this storm deposited on these meadows clearly tested the plant's sediment tolerance, resulting in the dramatic losses we recorded. While, as this study documents, storms can result in the direct burial of large stretches of seagrass meadow, these events can reduce meadow conditions through several other pathways, including directly uprooting plants or temporarily decreasing light transparency, among others (Frederiksen et al. 2004; Sanchez-Vidal et al. 2012). We did not directly assess uprooting or light reduction (caused by sediment resuspension), although these are likely to be significant additional pathways of meadow loss. At the only station where data on meadow patch area was available before the storm (Fenals shallow; see Table 1),

we measured an areal loss due to uprooting of less than 5% after the storm, compared to the 30% loss by burial (Table 1). In a parallel study conducted in the same region, we have shown that even low-intensity storms (significant wave heights ~ 2 m) can result in an 80% reduction in light availability for between 2 and 3 days (Roca et al. 2014). The storm of 26 December 2008 was considerably more intense, and we would expect a much more severe and lasting light reduction in its wake (Sanchez-Vidal et al. 2012). Light reduction associated with storms can substantially reduce the photosynthetic performance and carbon storage of seagrass species and can even result in extensive shoot mortality (Cabello-Pasini et al. 2003). While we have not evaluated these factors, we cannot discount them as potential coacting drivers of shoot mortality along with burial.

Extrapolating from our 4-yr meadow recovery rates of affected meadows, it appears that *P. oceanica* has the ability to recover areal losses well within the return time of the storm. Using annual recovery rates estimated from shoot growth documented from the few monitored plots that showed some recovery, we estimate that the affected meadows could be recolonized by clonal growth within approximately 30 yr if uninterrupted by additional disturbances. This is considerably faster than the projected return time of high-intensity storms. While, at first glance, this may appear encouraging, it is important to note that this recovery was restricted to a very limited number of plots (five plots out of 24) where a few stray shoots had been spared the initial burial. Where burial caused complete shoot mortality, plots showed no signs of recovery, at least within the 4-yr window of our observation. In addition, in the vast majority of our monitored plots (15 out of 24), the few shoots that survived the initial burial (from 0–5 cm and 5–10 cm burial levels) showed a clear trajectory of continued mortality even 4 yr after the event. This lag indicates that even if shoots survive the initial burial, they may still be subject to a negative carbon balance, precipitating further mortality when they exhaust their reserves. Our results suggest that these meadows may rely heavily on vegetative growth for recolonizing disturbance gaps. Recovery from completely bald patches of meadow may be much more protracted since they may depend on colonization events by sexual propagules. Flowering events in *P. oceanica* are very rare, especially in northern Mediterranean meadows, and, when they occur, are coupled with low reproductive success. This is reflected in a very low genetic diversity in *P. oceanica* at a global scale (Procaccini et al. 2001). However, the species has also been reported to show very infrequent alternate sexual strategies, such as pseudovivipary (Ballesteros et al. 2005) or massive successful recruitment events (Balestri and Lardicci 2008). In terrestrial grasses like bamboo, these mass seeding strategies have been considered to be evolutionary adaptations to equally infrequent disturbances (Schaller 2007). These occasional reproductive events, together with slow vegetative expansion from neighboring areas (growth rate of horizontal rhizomes between 1 and 6 cm per year; Marbà and Duarte 1998) may accelerate recovery process from barren patches at scales of centuries

(Kendrick et al. 2005). Given enough time, large gaps of *P. oceanica* meadow have been shown to recover over even decadal time scales (Meinze and Lefevre 1984). Taken together, it is likely that occasional pulsed recruitment events, together with clonal growth and horizontal growth from neighboring areas, may be sufficient for *P. oceanica* to spearhead a full recovery. The very persistence of *P. oceanica* in these waters (Mateo et al. 1997; Arnaud-Haond et al. 2012) suggests that this species may be able to recover from occasional pulse disturbances, even when they are as destructive as the 2008 storm.

A more worrying uncertainty is how anthropogenic stresses can disrupt these natural dynamic processes. At regional scales, coastal modifications have dramatically changed the dynamics of sedimentation in most human-dominated areas (González-Correa et al. 2009). The additive effects of natural disturbances, such as storms, and anthropogenic coastal interventions, such as beach nourishment or sand dredging, have already resulted in sediment being deposited periodically on seagrass meadows (Larkum and West 1990; Erftemeijer and Lewis 2006). In fact, Mediterranean seagrass meadows have been contracting steadily over the past century, a decline attributed to a range of mostly anthropogenic factors operating at different scales (Marbà et al. 2014). Additionally, projections of future scenarios under climate change for the Mediterranean region remain equivocal (Intergovernmental Panel on Climate Change 2013), with most studies predicting a decrease in storm conditions (Lionello et al. 2008) but with other models predicting a slight increase or even an increased risk of Mediterranean cyclones (the so-called medicanes; Romero and Emanuel 2013). While slow-growing *P. oceanica* seagrass meadows may be able to offset the effects of high-intensity, low-frequency disturbances, whether the *ecosystem* will be able to cope with these events while additionally dealing with an increasingly anthropogenized Mediterranean sea is still uncertain.

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