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

2   ***Posidonia oceanica***

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13   **Running headline:** Extreme storms and long-lived seagrasses

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Acknowledgements

23   **Abstract**

24   We used the disturbance resulting from a once in a hundred year storm on the northwest

25   Mediterranean coast to examine the extent of the disturbance, the tolerance thresholds to

26   burial, and the medium-term response of the long-lived *Posidonia oceanica* seagrass.

27   Sediment burial at 12 surveyed areas was particularly strong in shallow meadows, with 23%

28   of their surfaces buried, on average, under more than 10 cm of sediment. In contrast, less than

29   5% of the meadow was affected at deeper locations. At three sites we tracked short-term

30   mortality along a gradient of sediment burial. Survival response to burial was clearly non-

31   linear, with a significant threshold at 4-5 cm, beyond which shoot mortality was 100%. To

32   track medium-term potential recovery, we established permanent plots subject to three

33   sediment burial levels (0-5, 5-10, >10 cm burial), in four meadows. Where the initial shoot

34   mortality was 100%, we recorded no shoot recovery over the 4 year period. In the remaining

35   plots, where some shoots remained alive, we detected either further mortality or shoot

36   recovery of 7% per year on average. Extreme storm events can result in sudden catastrophic

37   losses of seagrass cover in shallow *P. oceanica* meadows. In the long term, and due to the

38   long return time of such storms, the species may still be able to recover despite its low

39   recovery potential. However, added anthropogenic stressors, including climate change, may

40   seriously test the ability of long-lived shallow seagrass ecosystems to resist high intensity

41   natural disturbances and may be critical for its persistence.

42

43

Introduction

44   Ecosystems are, by and large, a product of the disturbance regimes within which they

45   exist. Disturbance is a key habitat-structuring agent; communities are driven by the intensity

46   and frequency of condition-altering forces and the relative abilities of their constituent species

47   in dealing with these disturbances (Sousa 1984). While a raft of research has focused on the

48   influence of small, frequent disturbances on ecosystem stability and recovery, we are far less

49   certain of how systems respond to larger, more infrequent disturbances (Hughes 1994).

50   Ecosystem responses may not scale up predictably with increasing disturbance intensity; large

51   infrequent events may trigger qualitatively different effects on ecosystems compared to more

52   frequent small-scale perturbations (Romme et al. 1998). This is because, while disturbance-

53   prone systems may have endogenous feedback mechanisms to absorb regular disturbances,

54   this natural resistance may have critical limits, beyond which ecosystems may respond very

55   differently (Holling 1973). Understanding if such discontinuities exist under natural field

56   conditions, what these threshold values are, and how systems respond when thresholds are

57   crossed, requires considerably more empirical field data on system responses to large

58   infrequent disturbances. However, their very unpredictability makes them difficult to study,

59   except with opportunistic approaches in the wake of extreme events.

60   An extreme storm event, with a return time of ca. 100 years, affected the northwest

61   Mediterranean coast on the 26 December 2008 (Sanchez-Vidal et al. 2012). The presence of a

62   shallow depression over the Balearic Sea with a minimum pressure of 1012 hPa and a high-

63   pressure center over northern Europe (1047 hPa), generated an extreme storm with strong

64   easterly winds and maximum wave heights of 14.4 m, maximum significant wave height (Hs)

65   of 7.5 m and a duration of 73 h. This event was the largest ever recorded (in terms of wave

66   height) on the northwest Mediterranean coast (Costa Brava, Spain) (Sanchez-Vidal et al.

68   2012). Storm action was not uniform, with the greatest effects (greatest wave power, heights,

69   and shear stress) experienced in the northern third (which roughly corresponds to the rocky

70   Costa Brava). South of this, wave power and shear stress decreased to around half (central

71   Catalonia) and one third (southern Catalonia) of the extreme northern storm conditions (*see*

72   Fig. 1 and Mateo and Garcia-Rubies 2012). The effects on the biota were severe, affecting

73   several marine habitats, from superficial rocky algal beds to deep canyons (Mateo and Garcia-

74   Rubies 2012; Sanchez-Vidal et al. 2012). The magnitude and rarity of this event provided a

75   rare opportunity to examine the immediate response and subsequent recovery of subtidal

76   *Posidonia oceanica* seagrass meadows to such high-intensity disturbances.

77   The long-lived endemic seagrass *Posidonia oceanica* dominates sandy bottoms in the

78   Mediterranean, extending to a depth of 35 m. It is considered one of the longest-living

79   seagrass species in the world (Arnaud-Haond et al. 2012), and although characterized by

80   extremely slow growth rates, it spreads almost exclusively through clonal growth, with

81   successful sexual reproduction events being rare (Procaccini et al. 2001). An ecosystem

82   dominant, *P. oceanica* is an important engineering species, and plays a critical role in binding

83   soft-sediment habitats with a dense network of rhizomes and roots (called the *matte*),

84   significantly reducing sand movement within the meadow (Gacia and Duarte 2001). In

85   addition, the long seagrass leaves and shoots create a structurally complex habitat that

86   considerably attenuates wave and tidal action (Duarte et al. 2013). These factors, together

87   with its large rhizome storage, may make healthy, unfragmented *P. oceanica* meadows more

88   resistant to regular sand movement events than other seagrass species. For instance, it is

89   known that, on coasts exposed to strong winds, storm surges and tidal flows, sediment

90   movements can bury seagrass shoots, expose roots and rhizomes, and even uproot entire

91   plants (Frederiksen et al. 2004). In the face of this disturbance regime, several seagrass

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92   species are characterized by short life spans, increased investment in seed banks, sexual

93   reproduction, fast re-colonization and vertical shoot growth, a suite of life-history traits that

94   enables them to thrive in disturbance-prone environments (Fourqurean and Rutten 2004).

95   Unlike *P. oceanica*, these strategies are linked more to ensuring a fast recovery after

96   disturbance events, rather than in resisting the disturbance itself.

97   The continued dominance and persistence of *P. oceanica* in most Mediterranean coastal

98   waters over millennia (Mateo et al. 1997) has mainly been attributed to the species' ability to

99   deal with low nutrient and good light conditions prevalent in Mediterranean waters as well as

100   its ability to engineer its own low-disturbance regime in the normally-dynamic soft sediments

101   it inhabits (Ghisalberti and Nepf 2002). However, there are clear limits to this resistance. In

102   fact, in shallow areas, *P. oceanica* is unable to cope with the persistently high hydrodynamic

103   conditions present there, placing a natural upper boundary on meadow colonisation (Infantes

104   et al. 2009; Vacchi et al. 2010). The storm of 2008 subjected coastal waters to extreme

105   hydrodynamic conditions, and our study was designed to document how *P. oceanica*

106   meadows responded to this pulse event. We first determined the extent of the disturbance by

107   measuring the amount of sediment burial in 12 randomly selected meadows, representing

108   more than 50% of known seagrass meadows within the affected zone of the storm. In

109   addition, at four of the affected meadows, we determined the sedimentation thresholds that

110   plants can tolerate. Finally, in order to determine potential recovery trajectories of these

111   meadows, we tracked shoot recovery for 4 years 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 two 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 independently scanned 5 m on either side of transect (total area surveyed per transect 500 m^2) and assigned the area of the meadow that was buried under sand to 5 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 inter-observer 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 also *see* 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

136 recorded their approximate area with a measuring tape (length x width). These estimates of

137 burial were relatively conservative, since portions of the meadow with less than 10 cm of

138 burial could also likely be lost (Manzanera et al. 2011). Additionally, we did not take into

139 account areas of the meadow affected by abrasion, unearthing and uprooting of plants, as this

140 does not leave clear visible signs after the storm and is impossible to record unless spatially

141 explicit baseline information is available.

142 Conducted in the immediate wake of this extreme storm, our measures of burial extent

143 were necessarily opportunistic and conducted at a time of the year when weather conditions

144 do not permit unrestricted access to the ecosystem. It was critical to assess seagrass burial

145 before sediment movement appeared again during the normally-stormy months after the

146 extreme storm. We could not know a-priori how the effect of the storm was distributed across

147 the meadows, and our sampling protocols were designed to assess these effects as rapidly and

148 accurately as possible.

149

150 *Plant burial tolerance*

151 SCUBA divers assessed seagrass burial resistance thresholds in three meadows at

152 different depths (Canyelles, 21 m; Giverola, 7 m; and Medes, 5 m; *see* Fig. 1). At each site we

153 identified meadow areas along a gradient of sediment burial (from 0 cm to 15 cm sediment

154 level) after the storm event (4 months later). Burial was determined as the height from the

155 ligula to the sediment surface; under normal conditions the ligula stands a few cm (1 to >5)

156 above the sediment. The number of living and dead shoots was counted in small quadrats (15

157 x 15 cm, *n* = 25-30) placed along the burial gradient. To determine the proportion of dead

158 shoots under each burial level, we took advantage of the fact that even dead shoots (including

159 leaves) remained in the buried area long after the storm (4 months at the time of sampling; *see*

160   Fig. 2a, for an example). After measuring burial in each quadrat, we carefully removed the

161   sediment, and counted all dead shoots (where the leaf base was completely necrotized). We

162   also counted all shoots that remained alive, which, unlike dead shoots, had leaves with a

163   healthy, light-green meristem. This method was unable to detect any potential loss of shoots

164   directly uprooted by wave action. Therefore, our results represent a conservative estimate of

165   the mortality caused by the storm, and only accounts for the effects of storm burial, not

166   uprooting.

167

168   *Medium–term recovery potential*

169   We established 40 x 40 cm permanent quadrats in each of four *P. oceanica* meadows

170   (Giverola shallow, 7 m; Fenals shallow, 9 m; Canyelles deep, 21 m; and Palamós deep, 16 m;

171   *see* Fig. 1 and Table 1) after the storm in order to determine the effect of burial (mortality) on

172   the long-term survival (and potential recovery) of *P. oceanica* shoots. Three sets of plots with

173   two replicates each (a total of 6 quadrats per site) were established at three burial levels (0-5

174   cm; 5-10 cm; >10 cm, measured as explained above; $n = 2$ plots per treatment, 3 treatments

175   per site). The number of shoots in each plot was counted 1) just after the storm ($T_0 = $

176   beginning 2009) taking advantage of the fact that mortality by sediment burial takes several

177   months to occur, 2) a year later ($T_1 = $ beginning 2010), and 3) four years after the storm ($T_4 = $

178   end of 2012). Shoot mortality was expressed as a percentage of the difference between the

179   number of living shoots in the initial counts (S_0) and the counts one year after the storm (S_1)

180   divided by the initial counts (S_0).

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

182   Shoot recovery was established as a percentage of the difference between the number of

183   living shoots in the counts four years after the storm (S_4) and the counts one year after the

184   storm (S_1) divided by the initial counts (S_0).

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

185   Shoot recovery was then divided by four years, to obtain an annual rate of recovery for

186   each location.

187

188   *Statistical analyses*

189   We assessed plant burial tolerance with data pooled from all sites and depths. Since our

190   preliminary data observations suggested a threshold response to shoot burial, a change point

191   detection method was run in R with the package *strucchange* (Zeileis et al. 2002; Andersen et

192   al. 2009). The algorithm is based on assessing whether different parts of the dataset require

193   different parameters to fit a linear regression. Further, to assess the significance of every

194   potential change point in the dataset, an *F*-statistic (Chow test statistic) was also computed.

195   Since these methods require data sets with one observation per burial level, we established

196   burial intervals of 1 cm (i.e., grouping all shoots buried from 0-1 cm, from 1-2 cm, etc.) and

197   we sampled one random observation from each interval 1000 times. Each of the 1000

198   sampling events resulted in a data set that was analyzed with an *F*-statistic and a change point

199   estimator. We then plotted the mean *F*-statistic with its standard errors, and the mean

200   percentage mortality for each burial interval with the most probable change point and its

201   confidence interval.

202   To determine the factors influencing medium-term shoot mortality (obtained from the

203   fixed quadrats) we performed a 3-way nested ANOVA to test the effect of the fixed factors

204   'burial' (3 levels: 0-5 cm; 5-10 cm; >10 cm), 'depth' (2 levels: shallow (5-10 m) and deep

205   (15-25 m)) and their interaction (burial x depth), with 'site' (2 levels: Fenals and Giverola

206   shallow meadows; Canyelles and Palamós deep meadows) as a random factor nested in

207   'depth'. Before analysis, data were tested for normality and homoscedasticity using the

208   Shapiro–Wilk's and Bartlett's test, respectively. Whenever an ANOVA was significant, a

209   multiple range contrast test was applied (Tukey's Honestly Significant Difference) to

210   determine differences among burial levels. We could not test the effects of burial on medium-

211   term recovery, since we recorded zero recovery in most of the fixed quadrats (*see* results) and

212   we only discuss trends.

213

Results

215   *Regional extent of burial*

216   The effects of the 26 December 2008 extreme storm was strongest in the shallow

217   meadows (5-10 m depth) we surveyed (Fig. 3, Table 1). These meadows were heavily

218   affected by burial, with a mean of $20 \pm 6\%$ of their total area covered with more than 10 cm of

219   sediment (Fig. 3). In contrast, deep meadows (15-25 m depth) showed relatively low levels of

220   burial, with an average of $3 \pm 2\%$ of their total area under sand (Fig. 3). For the most part,

221   burial occurred in patches of ca. 10 m^2 or more, and was more frequent at the edges of

222   meadows.

223

224

225 *Plant burial tolerance*

226   Four months after the storm, shoot mortality increased substantially as a result of sediment

227 burial in the three meadows studied. While zones that had been buried from 0 to 3 cm showed

228 relatively low shoot mortality after the storm event, mortality increased substantially at higher

229 burial levels. Indeed, this increase was non-linear, with a sharp rise at 4-5 cm, and near-total

230 mortality at burial levels of 8-9 cm and above (Fig. 4a). The burial interval of 4-5 cm was

231 found to be a significant change point of plant tolerance (Fig. 4a,b).

232

233 *Medium–term recovery potential*

234   The medium-term monitoring plots confirmed mortality patterns documented in the plant

235 burial tolerance measurements (*see* previous section). A year after the storm, most plots with

236 more than 10 cm of burial showed 100% mortality, while in plots with 0-5 cm of burial the

237 mortality was significantly lower (Table 2), but with signs of delayed mortality (negative

238 trajectories even 4 years after the storm, Table 3). There was some variability in the response

239 of plots with intermediate burial levels (5-10 cm), with mortality values of 52 ± 14% (mean ±

240 standard error (SE), $n = 8$ [2 quadrats per 4 sites]).

241   In tracking potential recovery, we did not observe shoot recruitment in the majority of

242 quadrats from both shallow and deep meadows four years after the storm, confirming the low

243 recovery capacities of *Posidonia oceanica* (Table 3). Indeed, from a total of 24 quadrats (2

244 per 3 levels per 4 sites), recovery was observed only in 5 quadrats. In these plots (most of

245 them from the 5-10 cm burial level), the average annual shoot recovery rate was 7 ± 3%

246 relative to pre-storm conditions. In plots where the initial shoot mortality was 100%, we

247 documented no recovery at all (Table 3).

248

Discussion

250   The storm of 2008 was among the most intense on record, with a return time of 100 years.

251   The *Posidonia oceanica* seagrass meadows we tracked in the wake of this extreme event

252   declined significantly in cover across the northern Catalan coast. Although storm effects were

253   relatively modest in deep meadows (ca. 3% of areal losses), they were dramatic in shallow

254   waters, with an average of 23% areal losses across the affected region. This is most likely a

255   conservative estimate, since they are based only on measured losses caused by sediment

256   burial and do not account for uprooting of seagrass shoots as a result of the large shear forces

257   generated by the storm. Compared to many smaller, fast-growing species, *Posidonia oceanica*

258   showed a moderate resistance to burial; plants appeared to tolerate sediment burial up to a

259   clear threshold of 4-5 cm, beyond which shoot mortality increased sharply. We observed that

260   burial levels above 8-9 cm resulted in the total mortality of shoots both in our extensive post-

261   disturbance surveys of plant burial tolerance, as well as in the permanent plots we tracked to

262   assess potential recovery. Four years after the disturbance, shoot recruitment was only

263   observed in the few plots that had not suffered total mortality as a consequence of the storm;

264   in contrast, in plots where shoot mortality had been 100%, we did not record any recovery at

265   all. The role of high-intensity low-frequency disturbances has rarely been considered an

266   important driver of seagrass decline, perhaps because their long return times make them

267   difficult to track (but *see* Larkum and West 1990; Fourqurean and Rutten 2004; Van

268   Tussenbroek et al. 2014). Nevertheless, our results indicate that, despite their rarity, such

269   infrequent disturbances may profoundly influence seagrass meadow dynamics. In this study,

270   the storm resulted in a reduction of nearly one-fourth of its effective cover in shallow areas,

271 from which recovery is likely to be protracted – potentially requiring several decades to return

272 to pre-disturbance conditions.

273   The ability of *P. oceanica* to resist this high intensity disturbance appears to be moderate

274 when compared to smaller, fast-growing species (Cabaço et al. 2008), which tend to suffer

275 higher shoot mortalities due to burial, but show a faster subsequent recovery (Cabaço et al.

276 2008). Unsurprisingly, our results show that shallow meadows were the most heavily affected

277 by the disturbance. Shallow meadows are often more subject to areal losses than deep

278 meadows since the intensity of physical disturbances generally attenuate rapidly with depth.

279 The high-energy waves and sediment transport generated by storms is experienced most

280 strongly in the first few meters of the water column and decreases considerably with depth

281 (Ruiz et al. 2009). These regular storm events have already been identified as critical in

282 determining the upper depth limit of seagrass distribution in the Mediterranean Sea (Infantes

283 et al. 2009; Vacchi et al. 2010), and *P. oceanica* can only colonize shallower areas in the most

284 protected bays (Ruiz et al. 2009). Below these limits however, the shallow meadows we

285 monitored are remarkably persistent in the wake of frequent small-scale disturbances, having

286 been present in shallow coastal waters for centuries and possibly millennia (Mateo et al.

287 1997). The fact that a single large storm event could cause such a dramatic reduction in

288 meadow cover suggests that high-intensity low-frequency disturbances, though rare, are

289 potentially critical structuring agents of these nearshore ecosystems. In addition, given the

290 long life span of this slow-growing species, these events can have important, and long-lasting

291 demographic consequences for *P. oceanica*. Nearshore marine ecosystems like seagrass

292 meadows can be particularly prone to these high-intensity disturbances, with long-term

293 consequences for these systems as has been documented in the wake of hurricanes in Florida

294 and the Caribbean (Fourqurean and Rutten 2004; Van Tussenbroek et al. 2014) or after the

295   combined effects of storms and anthropogenic engineering on the Australian coast (Larkum

296   and West 1990).

297   The ability of *P. oceanica* to withstand sediment burial showed a sharp threshold around

298   4-5 cm; beyond 8-9 cm, shoot mortality was nearly 100% in all three studied meadows. A

299   similar pattern of tolerance was identified by earlier experimental burial studies for the

300   species (Manzanera et al. 2011). A comprehensive review of sedimentation responses to

301   burial suggested that seagrass species have an average critical burial limit for vertical rhizome

302   growth of around 10 cm, which causes a 50% shoot reduction (Cabaço et al. 2008). This limit

303   is highly species-specific and while some small, fast-growing species cannot tolerate more

304   than 2 cm of burial, larger plants, particularly those with vertical rhizomes and large rhizome

305   diameters (i.e., with more reserves), appear better able to counteract burial (Cabaço et al.

306   2008). However, although *P. oceanica* is one of the largest seagrass species, with high

307   structural complexity, the quantity of sediment this storm deposited on these meadows clearly

308   tested the plant's sediment tolerance, resulting in the dramatic losses we recorded. While, as

309   this study documents, storms can result in the direct burial of large stretches of seagrass

310   meadow, these events can reduce meadow conditions through several other pathways

311   including directly uprooting plants or temporarily decreasing light transparency, among others

312   (Frederiksen et al. 2004; Sanchez-Vidal et al. 2012). We did not directly assess uprooting or

313   light reduction (caused by sediment resuspension) although these are likely to be significant

314   additional pathways of meadow loss. At the only station where data on meadow patch area

315   was available before the storm (Fenals shallow, *see* Table 1), we measured an areal loss due

316   to uprooting of less than 5% after the storm, compared to the 30% loss by burial (Table 1,

317   manuscript in prep.). In a parallel study conducted in the same region, we have shown that

318   even low-intensity storms (significant wave heights ca. 2 m) can result in an 80% reduction in

319   light availability for between 2 to 3 days (Roca et al. 2014). The storm of 26 December 2008

320 was considerably more intense, and we would expect a much more severe and lasting light

321 reduction in its wake (Sanchez-Vidal et al. 2012). Light reduction associated with storms can

322 substantially reduce the photosynthetic performance and carbon storage of seagrass species

323 and can even result in extensive shoot mortality (Cabello-Pasini et al. 2003). While we have

324 not evaluated these factors, we cannot discount them as potential co-acting drivers of shoot

325 mortality along with burial.

326   Extrapolating from our four-year meadow recovery rates of affected meadows, it appears

327 that *P. oceanica* has the ability to recover areal losses well within the return time of the storm.

328 Using annual recovery rates estimated from shoot growth documented from the few

329 monitored plots that showed some recovery, we estimate that the affected meadows could be

330 recolonized by clonal growth within approximately 30 years if uninterrupted by additional

331 disturbances. This is considerably faster than the projected return time of high-intensity

332 storms. While, at first glance, this may appear encouraging, it is important to note that this

333 recovery was restricted to a very limited number of plots (5 plots out of 24) where a few stray

334 shoots had been spared the initial burial. Where burial caused complete shoot mortality, plots

335 showed no signs of recovery, at least within the 4 year window of our observation. In

336 addition, in the vast majority of our monitored plots (15 out of 24) the few shoots that

337 survived the initial burial (from 0-5 cm and 5-10 cm burial levels) showed a clear trajectory of

338 continued mortality even 4 years after the event. This lag indicates that even if shoots survive

339 the initial burial, they may still be subject to a negative carbon balance, precipitating further

340 mortality when they exhaust their reserves. Our results suggest that these meadows may rely

341 heavily on vegetative growth for recolonizing disturbance gaps. Recovery from completely

342 bald patches of meadow may be much more protracted since they may depend on colonization

343 events by sexual propagules. Flowering events in *P. oceanica* are very rare, specially in

344 northern Mediterranean meadows, and when they occur, are coupled with low reproductive

345   success. This is reflected in a very low genetic diversity in *P. oceanica* at a global scale

346   (Procaccini et al. 2001). However, the species has also been reported to show very infrequent

347   alternate sexual strategies like pseudo-vivipary (Ballesteros et al. 2005) or massive successful

348   recruitment events (Balestri and Lardicci 2008). In terrestrial grasses like bamboo, these mass

349   seeding strategies have been considered to be evolutionary adaptations to equally infrequent

350   disturbances (Schaller 2007). These occasional reproductive events, together with slow

351   vegetative expansion from neighboring areas (growth rate of horizontal rhizomes between 1

352   and 6 cm per year; Marbà and Duarte 1998) may accelerate recovery process from barren

353   patches at scales of centuries (Kendrick et al. 2005). Given enough time, large gaps of *P.*

354   *oceanica* meadow have been shown to recover over even decadal time scales (Meinesz and

355   Lefevre 1984). Taken together, it is likely that occasional pulsed recruitment events, together

356   with clonal growth and horizontal growth from neighboring areas may be sufficient for *P.*

357   *oceanica* to spearhead a full recovery. The very persistence of *P. oceanica* in these waters

358   (Mateo et al. 1997; Arnaud-Haond et al. 2012) suggests that this species may be able to

359   recover from occasional pulse disturbances, even when they are as destructive as the 2008

360   storm,

361   A more worrying uncertainty is how anthropogenic stresses can disrupt these natural

362   dynamic processes. At regional scales, coastal modifications have dramatically changed the

363   dynamics of sedimentation in most human-dominated areas (González-Correa et al. 2009).

364   The additive effects of natural disturbances like storms and anthropogenic coastal

365   interventions such as beach nourishment or sand dredging have already resulted in sediment

366   being deposited periodically on seagrass meadows (Larkum and West 1990; Erftemeijer and

367   Lewis 2006). In fact, Mediterranean seagrass meadows have been contracting steadily over

368   the last century, a decline attributed to a range of mostly anthropogenic factors operating at

369   different scales (Marbà et al. 2014). Additionally, projections of future scenarios under

370   climate change for the Mediterranean region remain equivocal (Intergovernmental-Panel-on-

371   Climate-Change 2013), with most studies predicting a decrease in storm conditions (Lionello

372   et al. 2008), but with other models predicting a slight increase or even an increased risk of

373   Mediterranean cyclones (the so-called 'medicanes', Romero and Emanuel 2013). While slow-

374   growing *P. oceanica* seagrass meadows may be able to offset the effects of high-intensity,

375   low-frequency disturbances, whether the *ecosystem* will be able to cope with these events

376   while additionally dealing with an increasingly anthropogenized Mediterranean sea is still

377   uncertain.

378

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484

Tables

Table 1. Regional extent of burial assessed using visual transects (mean ± 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 (ºN)	Longitude (ºE)	Orientation	Depth (m)	% buried area
Canyelles*	41°41'59"	2°53'16"	southeast	21	14 ± 9
Fenals*	41°41'21"	2°49'42"	southeast	9	30 ± 3
Fenals	41°41'19"	2°50'12"	southeast	24	6 ± 5
Giverola*	41°44'10"	2°57'16"	southeast	7	10 ± 3
Jugadora	42°18'53"	3°18'52"	southeast	20	0 ± 0
Medes	42°02'46"	3°13'11"	southwest	5	20 ± 3
Medes	42°02'47"	3°13'08"	southwest	15	0 ± 0
Montjoi	42°14'48"	3°14'03"	southeast	21	0 ± 0
Palamós*	41°50'39"	3°07'00"	southeast	16	1 ± 1
Roses	42°14'18"	3°12'14"	south	22	0 ± 0
St. Feliu	41°46'16"	3°01'33"	southwest	22	0 ± 0
Tossa	41°43'30"	2°56'41"	southeast	14	10 ± 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 values ($p < 0.05$) are 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	24681	12.3	**<0.001**
	depth	fixed	1	293	0.2	ns
	burial x depth	fixed	2	283	0.1	ns
	site[depth]	random	2	3183	1.6	ns
	error		14			

Table 3. Medium–term (4 years) 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.

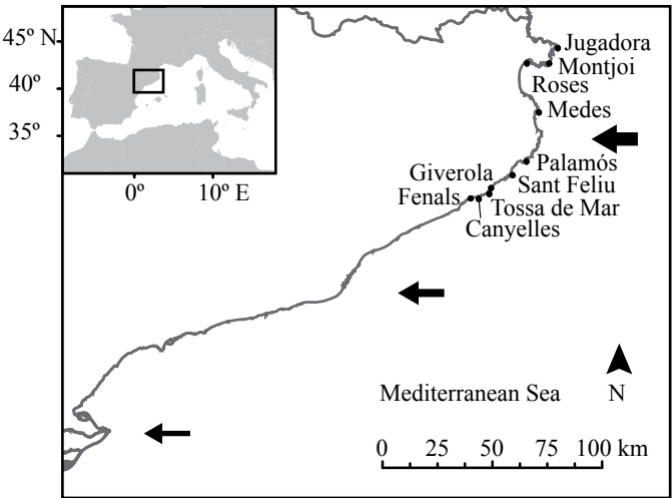| Shoots lost	Burial (mode)	Trajectory	Number of plots	Recovery
100%	10-15 cm	stable	4	no
<100%	5-10 cm	positive	5	7 ± 3%
<100%	0-5 cm	negative	15	no

Figure legends

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.

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

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 ± SE).

Fig. 4. Plant burial tolerance. (a) Shoot mortality as a function of sediment burial assessed in 15 x 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 ± 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).

45° N

40°

35°

0°   10° E

Jugadora
Montjoi
Roses
Medes

Giverola
Fenals

Palamós
Sant Feliu
Tossa de Mar
Canyelles

Mediterranean Sea

N

0   25   50   75   100 km

a

b

30 cm

50 cm