



## Review

## The impact of sediment burial and erosion on seagrasses: A review

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## ABSTRACT

The available information from experimental and descriptive studies on the effects of sediment burial and erosion on seagrasses was compiled to synthesize the information regarding the species-specific impacts and to relate them to plant characteristics. Burial thresholds (i.e. the burial levels causing 50% and 100% shoot mortality) and mortality-burial curves were estimated for the 15 seagrass species where the effects of experimental burial have been tested. All the species investigated reached 50% shoot mortality at burial levels ranging from 2 cm (*Halophila ovalis*) to 19.5 cm (*Posidonia australis*). *P. australis* was the most tolerant seagrass species to burial, while *Thalassia testudinum* was the most tolerant species to erosion. The relationships among plant size, growth, biomass and density with burial thresholds were examined. There were significant relationships between the burial thresholds and the shoot mass, the rhizome diameter, the aboveground biomass, the horizontal rhizome elongation and the leaf length of seagrass species. The leaf size and the rhizome diameter are the best predictors of the capacity of seagrasses to withstand burial. The burial thresholds estimated for seagrass species were in many cases in agreement with the burial impacts described by field observations (bioturbation), while in some cases was related to the species long-term colonization capacity (dune migration). Most human-induced impacts result in important changes of the sedimentary environment, with permanent negative effects on seagrass meadows (regression and complete destruction), whereas natural events, whether extreme (hurricane) or regular (dune migration), allow the recovery and/or adaptation of seagrasses to the burial/erosion sediment dynamics. The extent of the effects of burial and erosion on seagrasses is species-specific and strongly size-dependent.

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## 1. Introduction

Concerns about widespread seagrass loss have led to examination of the contribution of loss sources (e.g. Short and Wyllie-Echeverria, 1996; Duarte, 2002; Orth et al., 2006). Whereas the negative consequences of eutrophication are believed to be a major driver of losses, intense sediment dynamics involving excessive burial or erosion have also been identified as widespread causes of loss. Events such as hurricanes and storms induce intense sedimentary dynamics that may result in large-scale alteration of seagrass habitat (Kirkman and Kuo, 1990; Preen et al., 1995; Fourqurean and Rutten, 2004). The motion of sand waves (Marbà et al., 1994a) and migration of barrier-islands (Cunha et al., 2005) by currents can lead to burial and erosion. Sediment redistribution may also result from small-scale disturbances related to the activities of burrowing animals (Suchanek, 1983; Philippart, 1994; Duarte et al., 1997; Dumbauld and Wyllie-Echeverria, 2003; Fonseca et al., 2008), which affects seagrasses locally through the mobilization of sediments at small scales within meadows (Suchanek, 1983). Lastly,

global warming is leading to increased sea-level rise, with a parallel tendency for coastal erosion, causing seagrass loss (Short and Neckles, 1999).

Human activities in coastal areas may also affect sedimentary processes, severely affecting seagrass meadows. Coastal works (e.g. harbors, docks, breakwaters), beach stabilization, dredging and excess siltation from changes in land catchments, are examples of anthropogenic activities that result in changes of the sedimentary dynamics and consequent seagrass loss (Onuf, 1994; Terrados et al., 1998; Burdick and Short, 1999; Halun et al., 2002; Ruiz and Romero, 2003; Badalamenti et al., 2006). Frequently, such human-induced activities result in complete, perhaps irreversible, disappearance of seagrass meadows from coastal areas. The construction of permanent structures (e.g. harbors, Ruiz and Romero, 2003) and the local modifications of hydrodynamics and sedimentary dynamics (e.g. land reclamation, Meinesz et al., 1991) may exclude seagrasses through creation of unfavorable environments (Meinesz et al., 1991; Duarte, 2002).

The responses of seagrasses to sediment burial and erosion have been assessed through both experimental and descriptive studies, but a comparative analysis of the available information to provide a synthesis of the response of seagrass species to burial and erosion

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is still lacking. This study aims to compile the available information on species-specific impacts of burial and erosion disturbance to test whether the vulnerabilities of different seagrass species to burial and erosion are dependent on plant size, architecture and growth. Allometric relationships between these seagrass characteristics and experimentally determined burial thresholds were analyzed in order to identify which seagrass characteristics better predict the burial effects. These relationships will allow the prediction of the impacts of burial on seagrasses from consideration of architectural characteristics of each species.

## 2. Methods

### 2.1. Experimental effects of burial and erosion on seagrass species

Available data on the experimental effects of burial and erosion on seagrass species were compiled from both published literature and reports (Table 1). The experiments typically involved different treatments of burial pulses followed by the observation of the response of the seagrasses. Most experiments were conducted in the field, and involved several (3–6) burial treatments and, in some cases (4 species tested) an erosion treatment, as well as controls. Treatments were imposed using PVC cylinders or plots placed in the sediment to a height above the sediment equivalent to the corresponding burial treatment or at the maximum burial level tested.

Shoot mortality ( $M$ ), when not provided by the authors, was calculated as:

$$M(\%) = (d_i - d_f)/d_i \times 100$$

where  $d_i$  is initial shoot density and  $d_f$  is final shoot density. Shoot mortality of seagrass species was determined for each burial level tested and averaged for the overall experimental period, when the authors considered more than one sampling moment (e.g. Duarte et al., 1997). The burial thresholds of each seagrass species was defined as the burial levels causing 50% and 100% shoot mortality, and derived from information on changes in  $M$  with increasing burial, or interpolated from the data provided if necessary.

The plant size:burial ratio (SBR) was estimated as the ratio between the leaf length of each seagrass species and the maximum burial level tested. The plant size:erosion ratio (SER) was estimated as the ratio between the anchoring depth of each species and the maximum erosion level tested. The anchoring depth was calculated

as the sum of the leaf sheath length (which remain within the sediment), the length of the vertical rhizome (if present) and the diameter of the horizontal rhizome, as defined by Cruz-Palacios and van Tussenbroek (2005). The anchoring depth of *Zostera noltii* was calculated based on our own observations that only one-third of the sheath length is actually buried.

### 2.2. Scaling between burial threshold and seagrass characteristics

Seagrass characteristics (plant size, growth, biomass and density; Table 2) were derived from the information provided in the literature, compiled by Marbà and Duarte (1998), Duarte et al. (1998), Marbà and Duarte (2003), and amended, when necessary, with recently published information. Data on seagrass leaf length (minimum and maximum leaf length for each species) were obtained from Phillips and Meñez (1988) and Kuo and den Hartog (2001). The relationships between the burial thresholds ( $Y$ ) and seagrass characteristics ( $X$ ) were tested by fitting allometric equations of the form  $Y = a \times X^b$ , using least squares linear regression analyses on log-transformed variables (Niklas, 1994; Sokal and Rohlf, 1995).

### 2.3. Descriptive impacts of burial and erosion on seagrass meadows

The information from descriptive-field studies reporting the effects of natural- and human-induced changes of the sedimentary dynamics on seagrass meadows were compiled from the published literature to summarise the most important effects of burial and erosion for each species.

## 3. Results

### 3.1. Experimental effects of burial and erosion on seagrass species

#### 3.1.1. Experimental burial

The effects of experimental burial have been reported for 15 species, corresponding to about one-third of the seagrass flora (Table 1) and encompassing a broad size range. From all the seagrass species analyzed, including a wide range of plants size, some did not experience 100% mortality (*Cymodocea serrulata*, *Enhalus acoroides*, *Halodule uninervis*, *Posidonia australis*, *Posidonia sinuosa*, *Syringodium isoetifolium*, *Thalassia hemprichii*, *Thalassia testudinum*) even at the highest burial levels applied (16–30 cm, Table 3). Among those species, only *E. acoroides* does not have vertical rhizomes. The burial level causing total shoot loss varied between 2 cm for *Halophila ovalis*, and 15 cm for *Posidonia oceanica*. All species investigated showed 50% mortality within the time span of each experiment (Table 3). The corresponding burial threshold for 50% mortality ranged from 2 cm for *Cymodocea rotundata*, *C. serrulata*, *H. ovalis* and *Zostera noltii*, and 19.5 cm for *P. australis*, but most species experienced 50% mortality within the 2–4 cm range. *C. serrulata* and *E. acoroides* showed relatively low shoot mortality (ca. 40% and 20%, respectively) after 10 months under 16 cm of sediment, indicating a capacity to survive long-term burial (Fig. 1A and C).

Species lacking vertical rhizomes, such as *Zostera marina* and *Zostera noltii*, experienced high mortality (70–90%) under low burial levels (2–4 cm, Fig. 1D), while species with vertical rhizomes, such as *Posidonia* spp. showed high mortality only under high burial levels (>10 cm, Fig. 1E). However, some seagrass species with vertical rhizomes also showed high mortality under low burial levels of 4–5 cm (80% mortality, *Syringodium filiforme* and 60% mortality, *Halodule uninervis*, Fig. 1B). The estimated 0% mortality of *Halophila ovalis* (Fig. 1D) is not a consequence of the species high tolerance to burial, but rather reflects the great recovery capacity of this species. According to the authors (Duarte et al., 1997), this

**Table 1**

Seagrass species for which resistance to burial and erosion have been examined, and the corresponding sources

Species	Location	Reference
<i>Cymodocea nodosa</i>	Alfacs Bay, Spain (Lab)	Marbà and Duarte (1994)
<i>Cymodocea rotundata</i>	The Philippines <sup>a</sup>	Duarte et al. (1997)
<i>Cymodocea serrulata</i>	The Philippines <sup>a</sup>	Duarte et al. (1997)
<i>Enhalus acoroides</i>	The Philippines <sup>a</sup>	Duarte et al. (1997)
<i>Halodule uninervis</i>	The Philippines <sup>a</sup>	Duarte et al. (1997)
<i>Halophila ovalis</i>	The Philippines <sup>a</sup>	Duarte et al. (1997)
<i>Posidonia australis</i>	West Australia	Ruiz (personal communication)
<i>Posidonia oceanica</i>	NE Spain	Manzanera et al. (1998)
<i>Posidonia oceanica</i>	SE Spain	Ruiz (personal communication)
<i>Posidonia sinuosa</i>	West Australia	Ruiz (personal communication)
<i>Syringodium filiforme</i>	Caribbean, Mexico	Cruz-Palacios and van Tussenbroek (2005)
<i>Syringodium isoetifolium</i>	The Philippines <sup>a</sup>	Duarte et al. (1997)
<i>Thalassia hemprichii</i>	The Philippines <sup>a</sup>	Duarte et al. (1997)
<i>Thalassia testudinum</i>	Caribbean, Mexico	Cruz-Palacios and van Tussenbroek (2005)
<i>Zostera marina</i>	Beaufort, USA	Mills and Fonseca (2003)
<i>Zostera noltii</i>	South Portugal	Cabaço and Santos (2007)

<sup>a</sup> Mixed seagrass meadow.

**Table 2**  
Seagrass characteristics of the species examined. Mean aboveground biomass (AB, g DW m<sup>-2</sup>), shoot mass (SM, g DW), shoot density (SD, shoots m<sup>-2</sup>), leaf length (LL, cm), rhizome diameter (RD, mm), horizontal internodal length (HIL, mm), vertical internode length (VIL, mm), horizontal rhizome elongation rate (HE, cm yr<sup>-1</sup>), vertical rhizome elongation rate (VE, cm yr<sup>-1</sup>), internodes between shoots (IS, no. of internodes) and length between shoots (LS, cm). Data compiled from Marbà and Duarte (1998), Duarte et al. (1998) and Marbà and Duarte (2003). Leaf length range compiled from Phillips and Meñez (1988) and Kuo and den Hartog (2001). *Zostera noltii* data were updated with data from Cabaço and Santos (2007). –, Data not available

Species	AB	SM	SD	LL	RD	HIL	VIL	HE	VE	IS	LS
<i>C. nodosa</i>	245.7	0.090	2028.5	10–30	2.73	25.34	1.36	40.2	1.43	2.44	2.77
<i>C. rotundata</i>	27.1	0.065	215.5	7–15	2.44	28.75	1.97	209.9	1.53	7.61	4.80
<i>C. serrulata</i>	76.1	0.121	313.3	6–15	2.78	37.97	5.22	153.0	13.10	1.61	5.30
<i>E. acoroides</i> <sup>a</sup>	300.2	1.465	21.0	30–150	14.13	4.70		3.1		14.22	6.68
<i>H. uninervis</i>	297.9	0.027	71.5	6–15	1.37	20.97	4.95	101.2	4.10	5.17	270
<i>H. ovalis</i> <sup>a</sup>	39.0	0.016	1737.1	1–4	1.30	17.00		357.5		1.00	1.70
<i>P. australis</i>	241.3	0.875	605.0	30–60	7.21	14.90	–	9.3	1.42	7.36	6.00
<i>P. oceanica</i>	646.7	0.657	503.5	40–50	10.75	2.71	0.95	2.8	2.70	–	–
<i>P. sinuosa</i>	208.9	0.265	743.0	30–70	5.53	10.58	2.68	3.6	12.62	3.80	4.47
<i>S. filiforme</i>	185.4	0.037	4080.0	10–30	2.77	23.30	5.60	122.5	3.36	1.00	3.06
<i>S. isoetifolium</i>	52.0	0.038	1514.5	7–30	1.74	26.65	11.09	109.1	8.55	1.50	3.70
<i>T. hemprichii</i>	201.3	0.156	844.4	10–40	3.63	4.25	1.03	54.1	3.25	20.18	6.34
<i>T. testudinum</i>	907.1	0.238	1315.0	10–60	5.96	14.80	2.03	69.3	3.89	13.37	6.63
<i>Z. marina</i> <sup>a</sup>	418.9	0.323	852.6	–	3.50	10.58		26.1		5.59	6.08
<i>Z. noltii</i> <sup>a</sup>	122.1	0.011	7926.5	6–22	1.54	10.87		68.4		2.66	2.07

<sup>a</sup> Species without vertical rhizomes.

species must have experienced mortality immediately after burial, at least for burial levels >4 cm but rapidly recovered to densities of 4- to 5-fold higher than controls. This resulted in that no detrimental effects of burial were revealed by the analysis, even when a 2 months time-scale was considered. Similarly, the 0% mortality observed for *H. uninervis* at the 16 cm burial level (Fig. 1B) illustrates the species recovery, especially after 10 months, when density increased substantially (Duarte et al., 1997).

Increased shoot mortality was the main response found for seagrass species under experimental burial (Table 4), whether it was an immediate reaction, as was the case for *Cymodocea serrulata*, *Halodule uninervis* and *Syringodium isoetifolium*, or by the end of the experiment as found for *Enhalus acoroides*. An increase in the vertical internode length was also a common response among those species with vertical rhizomes, such as *Cymodocea nodosa*, *Cymodocea rotundata*, *Halodule uninervis*, *S. isoetifolium* and *Thalassia hemprichii*. However, no significant relationship was found between the vertical elongation rate of species and the

experimental burial thresholds. This suggests that the response of increasing internode length occurs at levels below the 50% mortality levels.

The length of the leaf sheath increased in response to burial in some species (*Cymodocea nodosa* and *Posidonia australis*) but decreased in others (*Posidonia oceanica*, *Posidonia sinuosa*, *Zostera marina* and *Zostera noltii*). Most of the species showed no response in leaf morphometry to changes in the sediment level (*Cymodocea rotundata*, *Cymodocea serrulata*, *Enhalus acoroides*, *Halodule uninervis*, *Halophila ovalis*, *Syringodium isoetifolium*, *Thalassia hemprichii*, *Z. marina* and *Z. noltii*, Table 4). On the other hand, a significant and positive relationship between the sheath length of plants at the 50% mortality burial level and the 50% burial threshold was found for species subject to experimental burial (Fig. 2).

### 3.1.2. Experimental erosion

The effects of experimental erosion were only tested for four seagrass species (Table 5). None of the tested species experienced

**Table 3**  
Details of the experimental design to test the effects of burial on seagrasses (burial levels tested, the duration of the experiments, the size:burial ratio (SBR)) and the resulting effect on seagrass survival summarised in the experimental burial levels causing 50% and 100% mortality. –, Total shoot loss did not occur for the tested burial levels

Species	Burial levels (cm)	Experimental period (days)	SBR	Burial level (cm)	
				50% Mort.	100% Mort.
<i>C. nodosa</i>	1, 2, 4, 7, 13, 16	35	0.6 <sup>c</sup>	4	13
<i>C. rotundata</i>	2, 4, 8, 16	60, 120, 300		2	8
<i>C. serrulata</i>	2, 4, 8, 16	60, 120, 300		2	–
<i>E. acoroides</i>	2, 4, 8, 16	60, 120, 300		4	–
<i>H. uninervis</i>	2, 4, 8, 16	60, 120, 300		4	–
<i>H. ovalis</i>	2, 4, 8, 16	60, 120, 300		2	2
<i>P. australis</i>	10, 15, 20, 30	50	1.3 <sup>d</sup>	19.5	–
<i>P. oceanica</i> <sup>a</sup>	5/7, 9/10, 13/14	250	1.4	14	14
<i>P. oceanica</i> <sup>b</sup>	3, 6, 9, 12, 15	45	1.3 <sup>e</sup>	10.2	15
<i>P. sinuosa</i>	10, 15, 20, 30	50	1.3 <sup>d</sup>	15.4	–
<i>S. filiforme</i>	3.5/4.5, 4/5, 6.5/7.5, 9/10	60	0.8	4.5	10
<i>S. isoetifolium</i>	2, 4, 8, 16	60, 120, 300		8	–
<i>T. hemprichii</i>	2, 4, 8, 16	60, 120, 300		4	–
<i>T. testudinum</i>	3.5/4.5, 4/5, 6.5/7.5, 9/10	60	1.2	5	–
<i>Z. marina</i>	4, 8, 12, 16	12, 24	1.0	4	12
<i>Z. noltii</i>	2, 4, 8, 16	7, 14, 28, 56	< 1 <sup>f</sup>	2	8

<sup>a</sup> Manzanera et al. (1998).

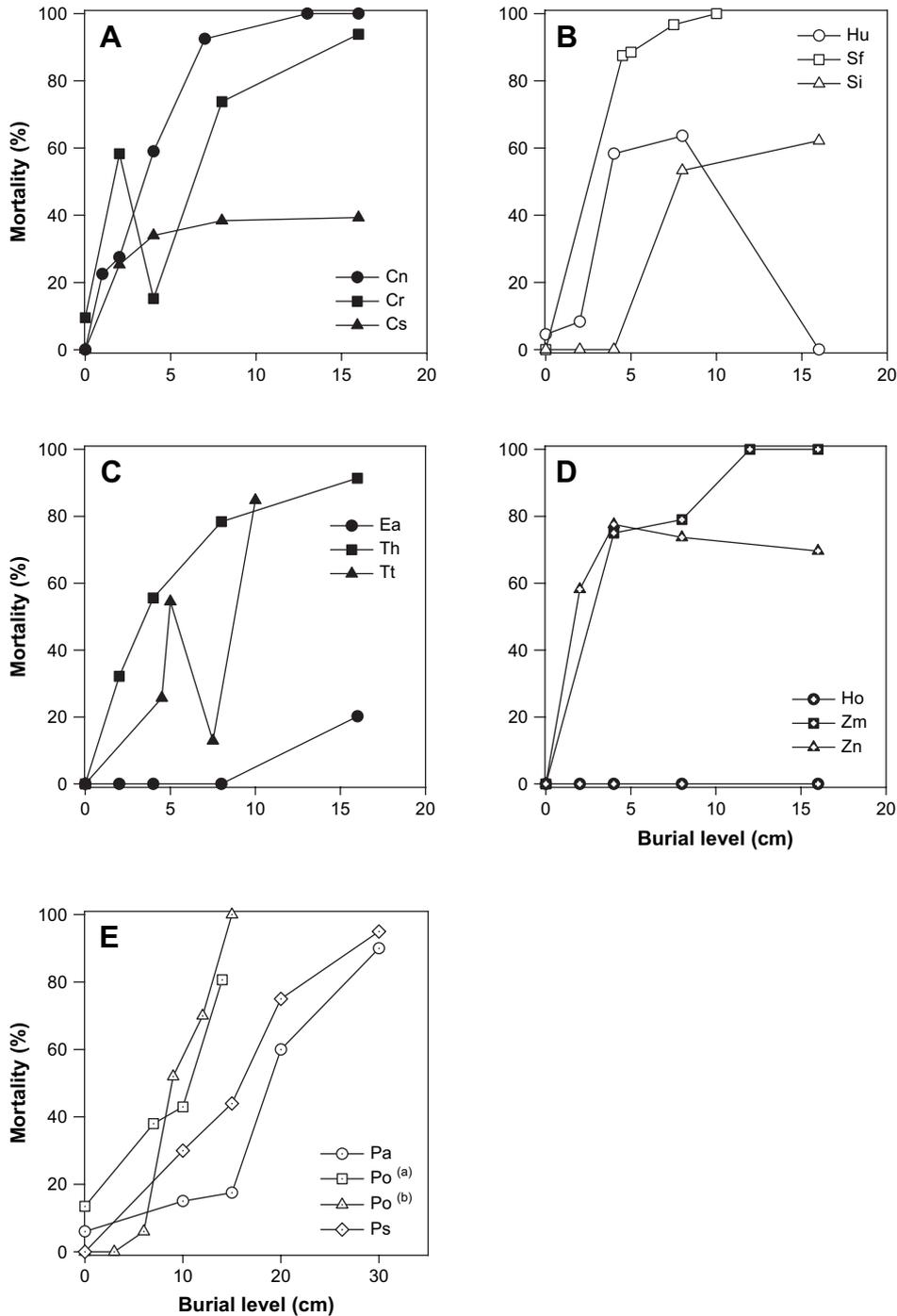
<sup>b</sup> Ruiz (personal communication).

<sup>c</sup> N. Marbà (personal communication).

<sup>d</sup> Leaf length from Smith and Walker (2002) for the same area.

<sup>e</sup> Leaf length from Manzanera et al. (1998).

<sup>f</sup> Intertidal species, leaves are buried even at low burial levels.



**Fig. 1.** The relationship between shoot mortality and burial levels in seagrasses subject to experimental burial. Cn, *Cymodocea nodosa*; Cr, *Cymodocea rotundata*; Cs, *Cymodocea serrulata*; Ea, *Enhalus acoroides*; Hu, *Halodule uninervis*; Ho, *Halophila ovalis*; Pa, *Posidonia australis*; Po, *Posidonia oceanica*; Ps, *Posidonia sinuosa*; Sf, *Syringodium filiforme*; Si, *Syringodium isoetifolium*; Th, *Thalassia hemprichii*; Tt, *Thalassia testudinum*; Zm, *Zostera marina*; Zn, *Zostera noltii*. (a) Manzanera et al. (1998), (b) Ruiz (personal communication).

100% mortality in response to erosion, even when deep erosion was applied (e.g. –10 cm for *Syringodium filiforme* and *Thalassia testudinum*). The maximum erosion levels tested exceeded the anchoring depth of *S. filiforme*, *T. testudinum* and *Zostera noltii* (SER < 1, Table 5). *S. filiforme* and *Z. noltii* experienced 50% mortality at erosion depths of –4.5 cm and –2 cm, respectively, whereas *Cymodocea nodosa* and *T. testudinum* showed relatively low mortality (< 30%) at –2 cm and –10 cm, respectively (Fig. 3). *T. testudinum* seemed to be the most tolerant species to erosion, as no responses

in shoot density and in the length of the horizontal rhizome were observed (Table 6). Moreover, the mortality–erosion relationship for this species showed that no mortality occurred until the erosion depth reached –5 cm. At the –7.5 cm erosion level, this species experienced 30% shoot loss (Fig. 3).

The main responses to experimental erosion of the seagrass species tested are summarised in Table 6. An increase in shoot mortality was a common response of *Cymodocea nodosa*, *Syringodium filiforme* and *Zostera noltii* to erosion. The plant morphometry

**Table 4**  
Summary of the main responses of seagrass species to experimental burial

Species	Main responses to burial
<i>C. nodosa</i>	<ul style="list-style-type: none"> <li>- Increased shoot mortality</li> <li>- Increased length of the youngest vertical internode (up to 4 cm of burial)</li> <li>- Increased leaf turnover rate (up to 2 cm of burial)</li> <li>- Increased vertical growth rate (up to 4 cm of burial)</li> <li>- Increased leaf sheath length (up to 4 cm of burial)</li> </ul>
<i>C. rotundata</i>	<ul style="list-style-type: none"> <li>- Shoot density decline</li> <li>- Increased vertical internode length (up to 4–8 cm of burial)</li> <li>- No changes in age distribution</li> <li>- No response of shoot size, sheath length and leaf specific weight</li> </ul>
<i>C. serrulata</i>	<ul style="list-style-type: none"> <li>- Initial shoot density decline in high burial levels (8 and 16 cm) followed by shoot density recovery</li> <li>- No response of vertical internode length</li> <li>- No changes in age distribution</li> <li>- No response of shoot size, sheath length and leaf specific weight</li> </ul>
<i>E. acoroides</i>	<ul style="list-style-type: none"> <li>- Shoot density decline only by the end of the experiment (300 days)</li> <li>- No response of shoot size, sheath length and leaf specific weight</li> </ul>
<i>H. uninervis</i>	<ul style="list-style-type: none"> <li>- Initial shoot density decline in high burial levels (8 and 16 cm) followed by shoot density recovery</li> <li>- Increased vertical internode length (up to 2 cm of burial)</li> <li>- Changes in age distribution</li> <li>- No response of shoot size, sheath length and leaf specific weight</li> <li>- Increased branching frequency (up to 8 cm of burial)</li> </ul>
<i>H. ovalis</i>	<ul style="list-style-type: none"> <li>- Early increase of shoot density at intermediate burial levels (4 and 8 cm of burial)</li> <li>- No response of shoot size, sheath length and leaf specific weight</li> </ul>
<i>P. australis</i>	<ul style="list-style-type: none"> <li>- Increased shoot mortality</li> <li>- Increased sheath length in 20 cm burial level</li> <li>- Decreased shoot biomass and leaf growth</li> <li>- Decreased leaf surface area</li> </ul>
<i>P. oceanica</i>	<ul style="list-style-type: none"> <li>- Increased shoot mortality</li> <li>- Decreased leaf growth and leaf length under moderate burial (6 cm)</li> <li>- Decreased shoot biomass and leaf no. per shoot in high burial levels (9 cm)</li> <li>- No response of sheath length</li> <li>- Decreased rhizome starch content in 3 cm burial level</li> <li>- Decreased leaf surface area</li> </ul>
<i>P. sinuosa</i>	<ul style="list-style-type: none"> <li>- Increased shoot mortality</li> <li>- Decreased leaf growth</li> <li>- Decreased sheath length and internode length under extreme burial (&gt; 30 cm)</li> <li>- No response of shoot biomass and leaf number per shoot</li> <li>- Decreased leaf surface area</li> </ul>
<i>S. filiforme</i>	<ul style="list-style-type: none"> <li>- Decreased shoot density</li> <li>- Decreased horizontal rhizome length</li> <li>- No response in the number of shoots per rhizome</li> </ul>
<i>S. isoetifolium</i>	<ul style="list-style-type: none"> <li>- Initial shoot density decline in high burial levels (8 and 16 cm) followed by shoot density recovery</li> <li>- Increased vertical internode length (up to 4 and 8 cm of burial)</li> <li>- Changes in age distribution (increase in recruitment of young shoots (&lt;1 yr))</li> <li>- No response of shoot size, sheath length and leaf specific weight</li> <li>- Increased branching frequency (up to 8 cm of burial)</li> </ul>

**Table 4** (continued)

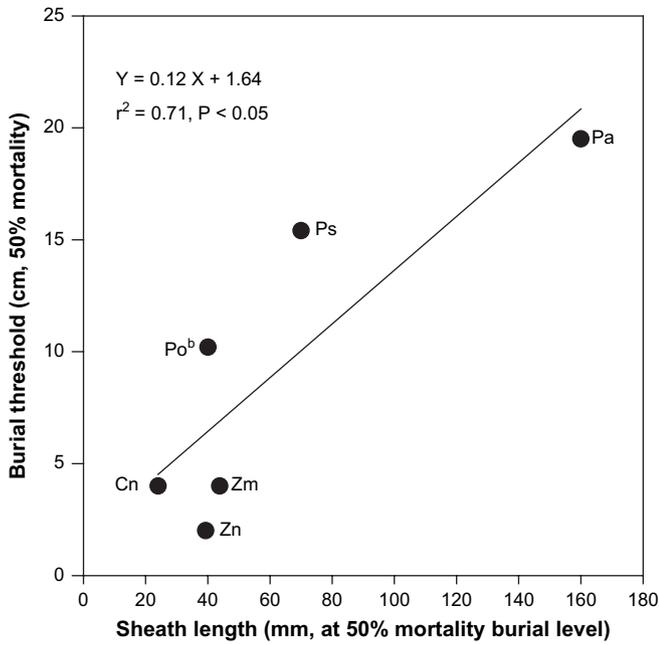
Species	Main responses to burial
<i>T. hemprichii</i>	<ul style="list-style-type: none"> <li>- Shoot density decline</li> <li>- Increased vertical internode length (up to 8 cm of burial)</li> <li>- Changes in age distribution (selective loss of young shoots (&lt; 1 yr) and reduced recruitment)</li> <li>- No response of shoot size, sheath length and leaf specific weight</li> <li>- Increased branching frequency (up to 4 cm of burial)</li> </ul>
<i>T. testudinum</i>	<ul style="list-style-type: none"> <li>- Decrease or no response of shoot density</li> <li>- No response in horizontal rhizome length</li> <li>- No response in the number of shoots per rhizome</li> </ul>
<i>Z. marina</i>	<ul style="list-style-type: none"> <li>- Increased mortality</li> <li>- Decreased productivity</li> <li>- No changes in sheath length</li> <li>- Decreased leaf length and leaf surface area</li> </ul>
<i>Z. noltii</i>	<ul style="list-style-type: none"> <li>- Decreased shoot density</li> <li>- No response of flowering shoot density</li> <li>- No response of leaf length and sheath length</li> <li>- Increased horizontal internode length</li> <li>- Decreased leaf and rhizome C content in high burial levels (4 cm, 8 cm and 16 cm)</li> <li>- Decreased leaf N content and simultaneous increase in rhizomes</li> <li>- Increased leaf sugar content in intermediate burial level (4 cm)</li> <li>- No response of leaf and rhizome starch content</li> </ul>

showed no general trend in response to erosion, but three out the four species tested experienced reduced rhizome growth, as *C. nodosa* and *S. filiforme* showed a decrease in the vertical internode length and of the horizontal rhizome length, respectively; whereas *Z. noltii* showed an increase of the horizontal internode length (Table 6).

### 3.2. Scaling between burial thresholds and seagrass characteristics

The capacity of seagrass species to withstand sediment burial was strongly size-dependent (Figs. 4 and 5). Both burial thresholds, 50% and 100% mortality, were significantly related to the shoot mass, the rhizome diameter, the aboveground biomass, the horizontal elongation rate and the size of leaves, and their scaling allometric slopes were similar across species. The 50% and 100% burial thresholds were scaled to, respectively, the 0.31 and 0.28 power of the shoot mass (Figs. 4A and 5A), the 0.57 and 0.59 power of the rhizome diameter (Figs. 4B and 5B), the 0.39 and 0.41 power of the aboveground biomass (Figs. 4C and 5C), the -0.34 and -0.26 power of the horizontal elongation rate (Figs. 4D and 5D), the 0.60 and 0.51 power of minimum leaf length (Figs. 4E and 5E) and the 0.81 and 0.77 power of maximum leaf length (Figs. 4F and 5F).

This scaling relationships indicate that large species, with high shoot mass, high aboveground biomass, thick rhizomes, low horizontal rhizome elongation rates and long leaves, such as *Posidonia* spp., have a great capacity to withstand sediment burial, but that the capacity to withstand burial increases more slowly than plant size (allometric slopes < 1). Mortality rates of 50% and 100% were only observed under high burial levels (Table 3). On the other hand, small seagrass species, such as *Cymodocea rotundata*, *Cymodocea serrulata*, *Halophila ovalis* and *Zostera noltii*, characterised by low shoot mass, low aboveground biomass, thin rhizomes, high horizontal rhizome elongation and small leaves, are more sensitive to burial disturbance. Low burial levels down to 2 cm resulted in 50% mortality for the first three species, while for *H. ovalis* mortality attained 100% (Table 3). The burial thresholds for seagrass species were independent ( $P > 0.05$ ) of the vertical and horizontal



**Fig. 2.** The relationship between the burial threshold causing 50% mortality and the length of the leaf sheath at the 50% mortality burial level in seagrasses with above-ground sheaths subject to experimental burial. Legends as in Fig. 1.

internode length, of the vertical elongation rate, of the number of internodes and distance between shoots, and of the shoot density.

3.3. Descriptive impacts of burial and erosion on seagrass meadows

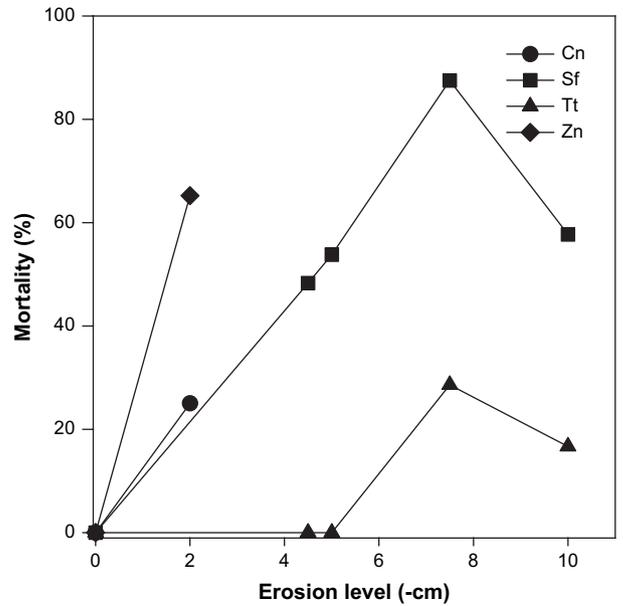
Field observations on the impacts of burial and erosion events, whether natural or human-induced, have been described for several seagrass species worldwide (Table 7).

The natural disturbances ranged from small-scale events, such as bioturbation, to large-scale changes, such as barrier-island migration and hurricanes (Table 7). Such disturbances resulted in different magnitudes of burial, ranging from around 6 cm of burial as in the case of bioturbation (Suchanek, 1983) to more than 70 cm of burial as in the case of hurricanes (Marbà et al., 1994b). Disturbance due to barrier-island migration and hurricanes resulted in extensive change in local sediment distribution and drastic decline of seagrass communities. Even so, seagrass meadows often are able to recover, depending on the magnitude of burial. Fourqurean and Rutten (2004) reported that seagrass meadows may recover within a few months, from surviving shoots, from a few centimeters of sediment deposition to years, through recolonization, when buried

**Table 5**

Details of the experimental design to test the effects of erosion on seagrasses (erosion levels tested, the duration of the experiments and the size:erosion ratio (SER) and the resulting effect on seagrass survival summarised in the experimental erosion levels causing 50% and 100% mortality. –, Shoot loss did not occur for the erosion levels tested

Species	Erosion levels (cm)	Experimental period (days)	SER	Erosion level (cm) causing	
				50% Mort.	100% Mort.
<i>C. nodosa</i>	-2	35	1.1	-	-
<i>S. filiforme</i>	-3.5/-4.5, -4/-5, -6.5/-7.5, -9/-10	60	0.4	-4.5	-
<i>T. testudinum</i>	-3.5/-4.5, -4/-5, -6.5/-7.5, -9/-10	60	0.9	-	-
<i>Z. noltii</i>	-2	7, 14, 28, 56	0.9	-2	-



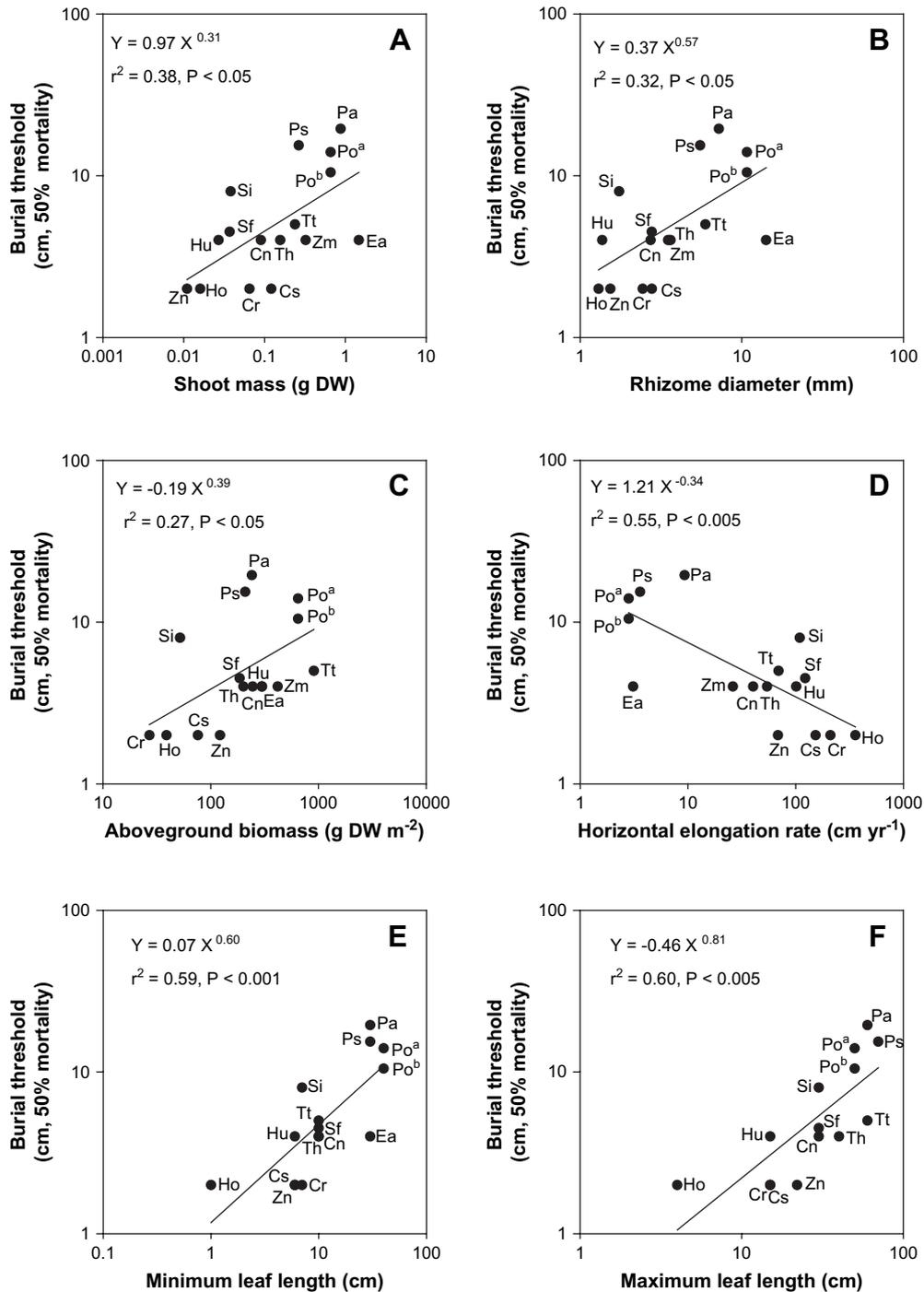
**Fig. 3.** The relationship between shoot mortality and erosion levels in seagrasses subject to experimental erosion. Legends as in Fig. 1.

50 cm after the passage of a category 2 hurricane (Table 7). Extensive recovery of *Halophila decipiens* from seed recruitment was reported in the following year after a hurricane (Bell et al., 2008; Fonseca et al., 2008). Cunha et al. (2005) reported that *Zostera noltii* meadows recovered, through recolonization, 10 years after the passage of a sand-barrier island over them. Marbà and co-workers report that recovery from the burial by sand-waves involved recolonization from horizontally-branching rhizomes of a few surviving shoots that managed to grow vertically to reach the sediment surface from the 10–20 cm burial affecting a *Cymodocea nodosa* stand (Marbà and Duarte, 1995) and the more than 70 cm burial affecting a *Thalassia testudinum* buried by the migration of mega-ripples displaced by a hurricane (Marbà et al., 1994b). On the other hand, the effects of burrowing animals (bioturbation) on seagrasses, although at a small-scale, resulted in the decrease of seagrass cover, abundance and growth (Table 7), and may play an

**Table 6**

Summary of the main responses of seagrass species to experimental erosion

Species	Main responses to erosion
<i>C. nodosa</i>	- Increased shoot mortality - Decreased vertical internode length and vertical growth rate
<i>S. filiforme</i>	- Decreased leaf turnover rate and leaf sheath length - Decreased shoot density - Decreased horizontal rhizome length in high erosion level (-9 cm)
<i>T. testudinum</i>	- No response in the number of shoots per rhizome - No response of shoot density - No response of horizontal rhizome length and number of shoots per rhizome length
<i>Z. noltii</i>	- Decreased shoot density - No response of flowering shoot density - No response of leaf length and sheath length - Increased internode length - No response of leaf and rhizome C and N content - Increased leaf sugar content, but no response of rhizome sugar content - No response of leaf starch content, but decrease of rhizome starch content



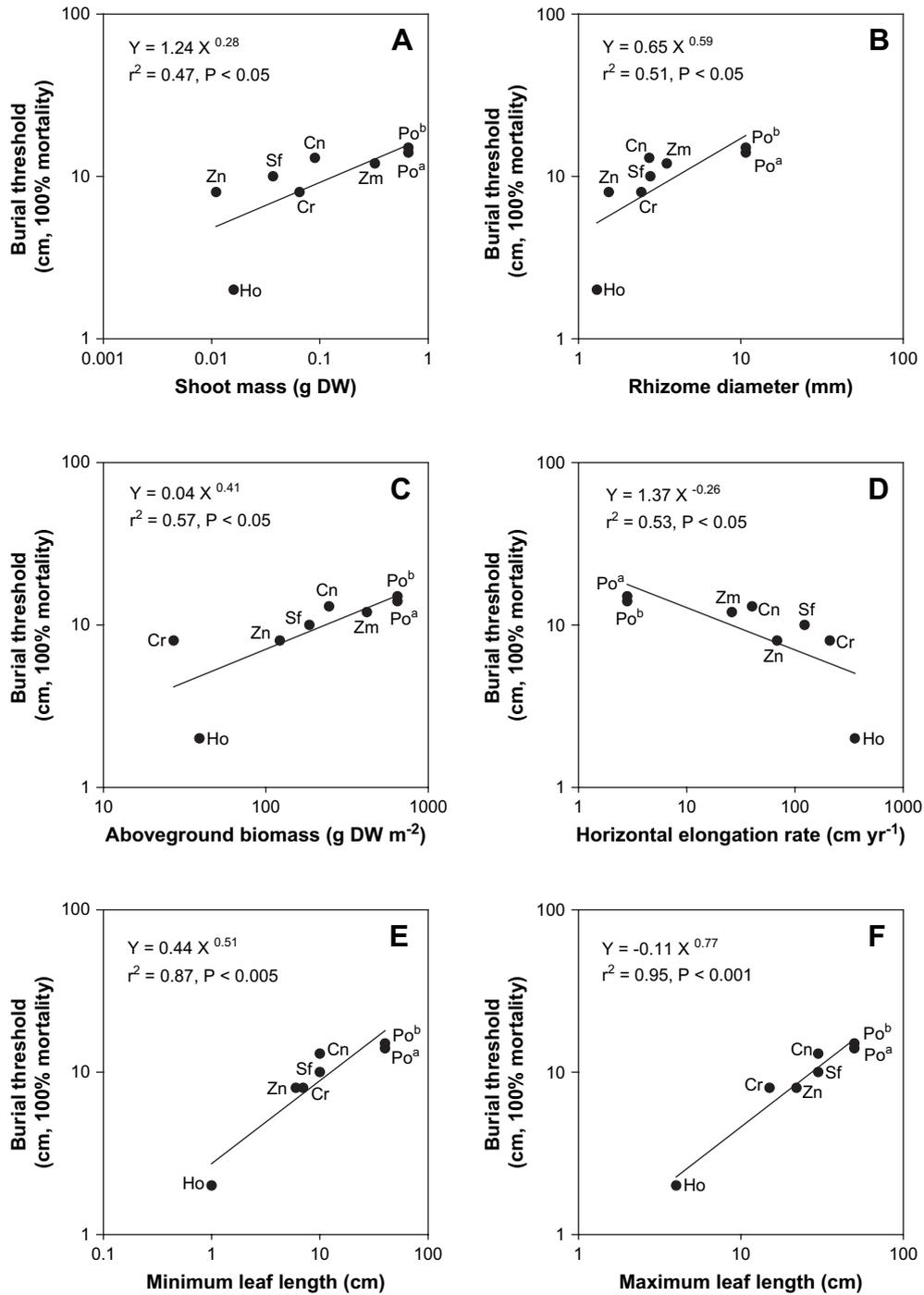
**Fig. 4.** Allometric relationships between the burial threshold causing 50% mortality and (A) the shoot mass, (B) the rhizome diameter, (C) the aboveground biomass, (D) the horizontal rhizome elongation, (E) the minimum leaf length and (F) the maximum leaf length of seagrass species. Legends as in Fig. 1.

important role in the long-term decline of seagrasses, particularly when compounded with other disturbances (e.g. *Z. noltii* in the Dutch Wadden Sea, Philippart, 1994). However, bioturbation may also have positive effects on seagrasses. Fonseca et al. (2008) reported that the excavation mounts of *Callinassa* shrimps brought the *H. decipiens* seeds to the sediment surface, stimulating the seed germination and enhancing the species recruitment.

These observations suggest that burial disturbances derived from events that have a return time sufficient for seagrass recovery allow the maintenance of patchy seagrass meadows, through the coupling of the plant population dynamics to the sediment disturbance. The

patch dynamics of *Cymodocea nodosa* was reported to be coupled with the migration rate of subaqueous dunes that arrested the population in a continuous colonization process yielding a patchy landscape (Marbà et al., 1994a; Marbà and Duarte, 1995). A similar process at a decadal time scale was described by Cunha et al. (2005) for *Zostera noltii* experiencing burial loss from a barrier-island migration and subsequent recolonization.

The field observations on the effects of human-induced disturbances that result in burial and erosion events were mainly related to coastal construction and dredging activities (Table 7). Most of these impacts were reported for *Posidonia oceanica*, a Mediterranean



**Fig. 5.** Allometric relationships between the burial threshold causing 100% mortality and (A) the shoot mass, (B) the rhizome diameter, (C) the aboveground biomass, (D) the horizontal rhizome elongation, (E) the minimum leaf length and (F) the maximum leaf length of seagrass species. Legends as in Fig. 1.

threatened species, whose meadows have been destroyed and altered (e.g. reduction of shoot density, biomass and productivity), not only due to the direct effects of the sediment redistribution, but also due to the associated effects of the increased water turbidity (Guidetti, 2001). In some cases, seagrass recovery was apparent after 2–3 years of human-induced disturbances such as the deposition of dredged materials (Eldridge et al., 2004; Sheridan, 2004), whereas complete destruction of seagrass meadows or continuous meadow regression were identified as a consequence of continuous disturbances related to coastal construction and use (Ruiz and Romero, 2003; Badalamenti et al., 2006).

**4. Discussion**

*4.1. Experimental burial and erosion*

The comprehensive analysis of the available literature on the experimental effects of burial and erosion on seagrasses confirms that seagrasses are highly vulnerable to changes in sediment level. All species studied showed at least 50% mortality when subject to experimental burial. Moreover, in most of these species this level of mortality was induced by low burial levels (2–4 cm, Table 3). However, some seagrass species are able to survive relatively high

**Table 7**

Field observations of the natural and human-induced impacts of burial and erosion events on seagrasses

Species	Disturbance	Factors/Intensity	Effects on seagrasses
Natural disturbances			
<i>Cymodocea nodosa</i>	Dune migration (Marbà et al., 1994a; Marbà and Duarte, 1995)	<ul style="list-style-type: none"> <li>- Sand dunes height of 0.22 m (0.07–0.65 m)</li> <li>- Dune migration of 13 m yr<sup>-1</sup> (5.4–32.3 m yr<sup>-1</sup>)</li> <li>- Period between successive dunes of 1.5 yrs</li> </ul>	<ul style="list-style-type: none"> <li>- Patchy landscape with scattered meadows at migrating slope and exposed dead rhizomes at regressing slope</li> <li>- Period of denuded sediment of 3–9 mo</li> </ul>
<i>Halophila decipiens</i>	Bioturbation (Fonseca et al., 2008)	<ul style="list-style-type: none"> <li>- Excavation mounds</li> <li>- Seeds to the sediment surface</li> </ul>	<ul style="list-style-type: none"> <li>- Stimulation of seed germination</li> <li>- Enhanced seagrass recruitment</li> </ul>
<i>Halophila decipiens</i>	Hurricane (Bell et al., 2008; Fonseca et al., 2008)	<ul style="list-style-type: none"> <li>- Bottom currents of 2.4 m s<sup>-1</sup></li> <li>- Sand burial and erosion of bottom communities</li> <li>- Seed dispersal</li> </ul>	<ul style="list-style-type: none"> <li>- Dramatic reduction of species abundance (greater frequency, but lower density cover)</li> <li>- Extensive cover in the following year (seed recruitment)</li> </ul>
<i>Posidonia oceanica</i>	Dune migration (Boudouresque et al., 1984)	<ul style="list-style-type: none"> <li>- Regular and small sand dunes</li> </ul>	<ul style="list-style-type: none"> <li>- Rhizome growth related to the sedimentation rate</li> </ul>
<i>Thalassia testudinum</i>	Hurricane (Wanless et al., 1988; Gallegos et al., 1992; Marbà et al., 1994b; van Tussenbroek, 1994)	<ul style="list-style-type: none"> <li>- Changes in sediment dynamics: erosion, deposition and sediment redistribution</li> </ul>	<ul style="list-style-type: none"> <li>- High mortality, burial of shoots and exposure of rhizomes</li> <li>- Increased vertical growth in buried shoots and decrease in eroded ones</li> <li>- Decreased shoot density and increase of flowering intensity</li> </ul>
	Bioturbation (Suchanek, 1983; Valentine et al., 1994)	<ul style="list-style-type: none"> <li>- Extensive burrow construction</li> <li>- Increase of sediment transport (4 g m<sup>-2</sup> d<sup>-1</sup>) and siltation over shoots</li> </ul>	<ul style="list-style-type: none"> <li>- Decline of area covered (regression &gt;1 m in 7 mo)</li> <li>- Decreased shoot density and productivity</li> <li>- Complete burial in high bioturbation areas</li> </ul>
<i>Zostera japonica</i>	Bioturbation (Dumbauld and Wyllie-Echeverria, 2003)	<ul style="list-style-type: none"> <li>- Burial of shoots, and dispersal and burial of seeds</li> </ul>	<ul style="list-style-type: none"> <li>- Decreased shoot density, seeds and germination</li> <li>- Decreased sprout survival and growth</li> </ul>
<i>Zostera marina</i>	Storm (Cabello-Pasini et al., 2002)	<ul style="list-style-type: none"> <li>- Sediment resuspension</li> <li>- Periods of light limitation</li> </ul>	<ul style="list-style-type: none"> <li>- Decreased survival and population loss</li> <li>- Increased internode length</li> <li>- Decreased sugar and starch levels</li> </ul>
<i>Zostera noltii</i>	Bioturbation (Philippart, 1994)	<ul style="list-style-type: none"> <li>- Cover of seagrass shoots by burrowing materials (sediment layer of 26 cm yr<sup>-1</sup>)</li> </ul>	<ul style="list-style-type: none"> <li>- Decline of seagrass meadows and shoot density</li> <li>- Decreased seagrass growth and survival</li> <li>- Decreased rhizomes, seeds and seedlings survival</li> </ul>
	Barrier-islands inlet migration (Cunha et al., 2005)	<ul style="list-style-type: none"> <li>- Change of sedimentary dynamics and hydrodynamics</li> <li>- Natural inlet migration of 119–187 m yr<sup>-1</sup></li> </ul>	<ul style="list-style-type: none"> <li>- Change in landscape coinciding with inlet migration</li> <li>- Increased patch number and area with the sediment stabilization due to the acceleration of the inlet migration</li> </ul>
<i>Zostera novazelandica</i>	Bioturbation (Woods and Schiel, 1997)	<ul style="list-style-type: none"> <li>- Burrows within meadows (9.4 burrows m<sup>-2</sup>), decreasing in abundance towards the centre</li> </ul>	<ul style="list-style-type: none"> <li>- Destabilization and loss of meadows (22.5% in 6 mo)</li> <li>- Increased meadow erosion</li> <li>- Decreased shoot density</li> </ul>
Seagrass meadows <sup>a</sup>	Dune migration (Patriquin, 1975)	<ul style="list-style-type: none"> <li>- Erosion of seagrass meadows</li> <li>- Seagrass-free depressions (blowouts)</li> </ul>	<ul style="list-style-type: none"> <li>- Exposure of rhizomes</li> <li>- Changes of seagrass landscape</li> <li>- Close interaction between seagrasses and sand dunes</li> </ul>
Seagrass meadows	Sand movement (Kirkman, 1978)	<ul style="list-style-type: none"> <li>- Rapid increase in sand deposition</li> </ul>	<ul style="list-style-type: none"> <li>- Re-stabilization of a blowout after 5–15yrs</li> <li>- Seagrass decline</li> </ul>

SE-Asia seagrass meadows <sup>b</sup>	Siltation (Gacia et al., 2003)	<ul style="list-style-type: none"> <li>- Sediment deposition (also trapped by seagrasses)</li> <li>- Deterioration of light and sediment conditions</li> </ul>	<ul style="list-style-type: none"> <li>- Detrimental effects for seagrasses</li> <li>- Sediment deposition within meadows is species-specific</li> <li>- Sediment deposition by seagrasses is small compared to the deposition by the water column</li> </ul>
Seagrass meadows <sup>c</sup>	Hurricane (Fourqurean and Rutten, 2004)	<ul style="list-style-type: none"> <li>- Sediment deposition (&lt;1 to 50 cm) and erosion</li> </ul>	<ul style="list-style-type: none"> <li>- Severe loss of seagrasses</li> <li>- Rapid seagrass recovery under few cm of burial, but slow recovery (&gt;3 yr) of 50 cm buried meadows</li> <li>- Slowest recovery of eroded seagrass meadows</li> </ul>
Human-induced disturbances			
<i>Posidonia oceanica</i>	Coastal construction and engineering (Meinesz et al., 1991; Guidetti and Fabiano, 2000; Guidetti, 2001; Ruiz and Romero, 2003; Badalamenti et al., 2006)	<ul style="list-style-type: none"> <li>- Changes of sedimentary dynamics and hydrodynamics</li> <li>- Increase of sediment deposition</li> <li>- Resuspension of silty sediments and increase of water turbidity</li> <li>- Irreversible replacement of the natural environment</li> </ul>	<ul style="list-style-type: none"> <li>- Destruction or severe alteration of seagrass meadows</li> <li>- Significant mortality and meadow regression</li> <li>- Decline in seagrass density, biomass and productivity</li> <li>- Burial-induced vertical growth responses</li> <li>- Changes in photosynthetic activity</li> <li>- Decreased rhizome carbohydrates reserves</li> </ul>
<i>Thalassia testudinum</i>	Dredging (Eldridge et al., 2004)	<ul style="list-style-type: none"> <li>- Sediment deposition in seagrass meadows (dredged material burial of 7–10 cm)</li> <li>- Reduction of water transparency</li> <li>- Addition of organic matter to sediments</li> <li>- Lethal sulphide levels and increased ammonium in sediment</li> </ul>	<ul style="list-style-type: none"> <li>- Continued reduction in biomass</li> <li>- Unsuitable sediment conditions for seagrass recolonization (up to 2.5 yrs)</li> </ul>
<i>Zostera noltii</i>	Dredging (inlet relocation) (Cunha et al., 2005)	<ul style="list-style-type: none"> <li>- Change of sedimentary dynamics and hydrodynamics</li> <li>- Deposition of sand over seagrass meadows</li> </ul>	<ul style="list-style-type: none"> <li>- Dramatic changes in seagrass landscape</li> <li>- Decreased landscape cover and increase of patch fragmentation</li> </ul>
Seagrass meadows <sup>d</sup>	Coastal construction (Clarke, 1987)	<ul style="list-style-type: none"> <li>- Sediment movement</li> <li>- Erosion</li> </ul>	<ul style="list-style-type: none"> <li>- Seagrass burial and uprooting</li> <li>- Death of seagrasses</li> </ul>
Seagrass meadows <sup>e</sup>	Dredging (Larkum and West, 1990)	<ul style="list-style-type: none"> <li>- Sand patches within meadows (blowouts)</li> <li>- Increase of wave height</li> <li>- Erosion of seagrass meadows</li> </ul>	<ul style="list-style-type: none"> <li>- Substantial seagrass decline</li> <li>- Long-term deterioration of seagrass meadows</li> <li>- Decreased seagrass cover</li> <li>- Fragmentation of meadows</li> <li>- Decreased leaf biomass after a storm event</li> </ul>
Seagrass meadows	Dredging deposits (Sheridan, 2004)	<ul style="list-style-type: none"> <li>- Deposition of dredged materials (0.14–18.7 ha) over seagrass meadows</li> <li>- Increased water turbidity</li> </ul>	<ul style="list-style-type: none"> <li>- Decreased seagrass cover</li> <li>- Seagrass recovery, as increased biomass, noticeable after 2 yrs and widespread after 3 yrs</li> </ul>

<sup>a</sup> *Thalassia testudinum* and *Syringodium filiforme*.

<sup>b</sup> Mixed meadows of *Enhalus acoroides*, *Cymodocea rotundata*, *Cymodocea serrulata*, *Halodule uninervis*, *Thalassia hemprichii*.

<sup>c</sup> Dominant seagrass: *Thalassia testudinum*, other seagrasses: *Syringodium filiforme*, *Halodule wrightii*, *Halophila decipiens*, *Halophila engelmanni*.

<sup>d</sup> *Amphibolis*, *Halophila*, *Heterozostera* and *Posidonia*.

<sup>e</sup> *Posidonia australis* and *Zostera capricorni*.

burial levels, and they did not experience 100% mortality under experimental burial. The burial tolerance was more evident in large seagrass species with vertical rhizomes, while the small-size seagrasses lacking vertical rhizomes were most sensitive to burial. An exception to this pattern was *Enhalus acoroides*, a large seagrass that does not have vertical rhizomes. This species is one of the most tolerant species to burial (20% mortality along 10 months under 16 cm of burial, Fig. 1), probably due to the large size of its leaves, which can exceed 1 m in length. Despite the high sensitivity to burial showed by some species, such as *Cymodocea serrulata* (50% mortality burial threshold of 2 cm), their great recovery capacity (Duarte et al., 1997) results in a long-term ability to cope with burial. *Posidonia australis* was the most tolerant seagrass species to burial, not reaching 100% mortality for the burial levels tested (up to 30 cm), and reaching 50% of mortality only at 19.5 cm of burial. On the other hand, *Zostera noltii*, *Halophila ovalis*, *Cymodocea rotundata* and *C. serrulata* were the less tolerant species to burial, with a burial threshold of 50% mortality at the 2 cm burial level. Among these, *Halophila ovalis* was the most sensitive species to burial, experiencing 100% mortality under 2 cm of burial (Table 3).

The available data does not show any significant relationship between the vertical rhizome elongation and the burial thresholds, even though the stimulation of the vertical rhizome growth by sediment accretion was experimentally demonstrated for several seagrass species. Marbà and Duarte (1998) reported that the seagrass vertical elongation rate is species-specific, but it is independent of seagrass size. This explains why no correlation was found between the vertical elongation rate, which is size-independent, and the burial thresholds, which were found to be size-dependent.

Seagrasses were also vulnerable to sediment erosion. The capacity of seagrasses to sustain erosion disturbance was also dependent on plant size, specifically with the size of the below-ground modules, which determine the anchoring depth of species. *Thalassia testudinum* was the species most resistant to erosion disturbance among those tested (Fig. 3). This species has the deepest anchorage system (around –8.5 cm), and shows woody rhizomes and sturdy, unbranched roots (Cruz-Palacios and van Tussenbroek, 2005), which certainly play an important role in its capacity to survive erosion.

#### 4.2. Scaling between burial thresholds and seagrass characteristics

The burial thresholds were strongly size-dependent, scaling with the plant shoot mass, rhizome diameter, aboveground biomass, horizontal elongation rate and leaf length (Figs. 4 and 5). The leaf length is the best predictor of the vulnerability to burial (Figs. 4 and 5). The rhizome diameter, which is a very conservative trait within species (Marbà and Duarte, 1998) closely related to plant size (Figs. 4 and 5), was also found to be a good predictor of the vulnerability of seagrass species to burial. The rhizome diameter is also related to the resource storage capacity (Duarte and Chiscano, 1998; Marbà and Duarte, 1998), and therefore to the capacity of seagrasses to withstand burial. Sediment burial results in the reduction of the available photosynthetic area of seagrass leaves, forcing the plants to use stored resources to survive (Alcoverro et al., 1999). Cabaço and Santos (2007) reported a decrease in carbon and carbohydrates content of *Zostera noltii* rhizomes as a consequence of the burial-induced light deprivation. Species with high storage capacity, as indicated in thicker rhizomes, are better able to survive burial disturbance. The robust relationships described indicate that the vulnerability of seagrasses to sediment burial decreases with increasing leaf length and rhizome diameter. Whereas the species for which sediment burial thresholds have been experimentally determined comprise only a third of the seagrass flora, the allometric relationships developed here allow

predictions on the vulnerability to sediment burial to be formulated from easily determined architectural traits of yet untested seagrass species.

Although fast growing species, such as *Halophila ovalis* and *Zostera noltii*, were extremely sensitive to sediment burial with relatively low burial thresholds, the high horizontal elongation rate of these species allows a fast recovery after burial. However, such recovery also depends on the scale of the burial disturbance. The horizontal rhizome elongation rate, which is largely species-specific and is strongly size-dependent (Marbà and Duarte, 1998), is the main mechanism involved in space occupation. As the horizontal rhizome elongation is negatively scaled to the burial thresholds, it provides valuable information on the recovery capacity of each species after burial disturbance. Seagrass characteristics that are independent of plant size, such as the vertical elongation rate and the vertical and horizontal internode length (Marbà and Duarte, 1998), were not significantly related to the burial thresholds, which proved to be a strongly size-dependent trait.

#### 4.3. Descriptive studies

Both natural and human-induced disturbances may lead to drastic changes in the sedimentary dynamics that seriously impact seagrass meadows. Whereas recovery typically follows after natural disturbances, such as inlet migration and hurricanes (Fourqurean and Rutten, 2004; Cunha et al., 2005) that typically involve pulses of sediment redistribution, human-induced disturbances, such as coastal works (Clarke, 1987; Meinesz et al., 1991; Guidetti and Fabiano, 2000; Guidetti, 2001; Ruiz and Romero, 2003; Badalamenti et al., 2006) often lead to permanent loss. Human-induced disturbances generally result in long-lasting changes in the sedimentary environment that preclude seagrass recovery.

Seagrass recovery from large pulses of burial and erosion following natural disturbances is relatively independent of their specific burial thresholds, depending strongly on their longer-term colonization capacity and patch dynamics. Two examples are presented in the literature. The first one is related to the regular, periodic pattern of some natural disturbances, such as the migration of subaqueous dunes, which allows *Cymodocea nodosa* to adapt its life strategy to this particular sedimentary environment (Marbà et al., 1994a; Marbà and Duarte, 1995). Even though, the burial thresholds estimated for *C. nodosa* of 4 cm (50% mortality) and 13 cm (100% mortality) are well below the mean height of the sand dunes studied (22 cm), the progressive process of dune migration allows the plants to couple its patch dynamics to the sedimentary dynamics in a continuous colonization process. The coupling between the species flowering frequency and the dynamics of dune progression (Marbà et al., 1994b; Marbà and Duarte, 1995) also supported the species adaptation to this natural disturbance.

The second example is the coupling of *Zostera noltii* patch dynamics to the effects of inlet migration and relocation in Ria Formosa lagoon, southern Portugal (Cunha et al., 2005). The low burial thresholds estimated for *Z. noltii*, of 2 cm (50% mortality) and 8 cm (100% mortality), are in a completely different scale to the dramatic changes caused by the artificial inlet migration and relocation in this landscape. However, the long-term patch dynamics of the species was coupled to the burial caused by the passage of the lagoon inlet over the seagrass meadows (10 years).

Small-scale disturbances, such as the impacts resulting from the burrowing animal activities, should not be neglected. Regression of seagrass meadows and a decrease of plant growth and survival were reported as a consequence of bioturbation (Table 7). The negative effects of bioturbation on the *Thalassia testudinum* cover and abundance are clearly explained by the 50% mortality burial threshold of the species (5 cm), which was similar to the mean

height (5.46 cm) of the sediment mounds built by ghost shrimps (Suchanek, 1983).

The indirect effects originated by the changes of the sedimentary dynamics also play an important role in the adverse effects related to the burial and erosion events. The decline of *Posidonia oceanica* meadows reported in the Mediterranean basin as a consequence of human-induced changes of the sedimentary dynamics (e.g. coastal works), were often accompanied by events of increased turbidity (Table 7). Even though the direct burial disturbance involved considerable changes of the sediment level, this species has a relatively high capacity to sustain burial, with burial thresholds of 10.2–14 cm for 50% mortality, and 14–15 cm for 100% mortality. This suggests that the increased water turbidity may have been responsible for the reported decline.

#### 4.4. Mechanisms of seagrass mortality upon sediment burial or erosion

Disturbance of seagrass meadows upon sediment burial and erosion has direct and indirect components. Indirect or secondary effects associated with post-disturbance processes, such as increased turbidity, can greatly affect seagrasses. The sediment redistribution by currents, wind and tides, is often involved in such processes, which may last from several months (Guidetti and Fabiano, 2000) to years (Eldridge et al., 2004). The resuspension of sediment, particularly of fine sediment particles, results in increased turbidity of coastal waters, which limits the light availability for seagrass photosynthesis (Ruiz and Romero, 2003). The decrease of carbohydrate reserves and the increase of shoot mortality may follow if the light limitation extends for long periods (Alcoverro et al., 1999). The capacity of seagrasses to endure under such circumstances depends on the storage capacity of each species (Duarte and Chiscano, 1998).

Sediment redistribution can also involve the modification of the sediment attributes, resulting in unsuitable conditions for seagrasses. The addition of organic matter due to the deposition of dredging materials (Eldridge et al., 2004), or the erosion of the bottom exposing sediment layers depleted of oxygen (Hemminga and Duarte, 2000) may result in anoxic conditions. Such anoxic sediments may be detrimental to seagrasses by promoting growth inhibition and mortality (Terrados et al., 1999). Increased levels of toxic compounds, such as sulfides, may also be associated with this process and impact seagrasses, especially when in lethal concentrations. Sulfide has been considered a major contributing factor in seagrass diebacks (Koch and Erskine, 2001) and a limiting factor in seagrass recovery (Eldridge et al., 2004). In such cases, the sediment disturbance caused the community to shift to a new, stable state (Sutherland, 1974) and thus the reverse to the former state may be difficult.

Plant burial results in the reduction of the available photosynthetic biomass, which may negatively affect the growth and survival of plants. Substantial shoot mortality and increase of the vertical growth of the shoots are the main effects/responses described for several species (Boudouresque et al., 1984; Marbà and Duarte, 1994; Marbà and Duarte, 1995; Duarte et al., 1997; Manzanera et al., 1998; Mills and Fonseca, 2003; Cruz-Palacios and van Tussenbroek, 2005; Cabaço and Santos, 2007). Changes in plant morphometry, such as longer leaves and leaf sheaths (e.g. Marbà and Duarte, 1994), and longer internodes (e.g. Duarte et al., 1997), have also been reported as a response to burial. Burial may also increase the probability of exposure of the leaf meristems, which may be buried in the sediments, to anoxic conditions, which has been shown to lead to seagrass mortality (Borum et al., 2005).

Erosion exposes belowground tissues to the colonization by organisms, and drilling organisms can penetrate the rhizomes, disrupting gas flow and affecting seagrass survival. In addition, erosion exposes the belowground components to waves and

currents that can, because these elements are not flexible like leaves, be broken and advected out.

The results presented here show that the effects of burial on seagrasses are strongly dependent on plant size. In a mixed seagrass meadow, Duarte et al. (1997) described a pattern of species loss after burial-induced disturbance, in which mortality increased with decreasing seagrass size. The size of seagrass modules, the resource allocation within modules, and the life-strategy of each species result in a differential capacity of seagrass species to sustain burial disturbance.

## 5. Conclusions

Changes of the sediment level related to sediment burial and erosion were revealed to be detrimental to seagrasses. The impacts of sediment erosion on seagrass survival and on the plant allometric responses are different than those caused by burial. Whereas burial results in the decrease of the available photosynthetic area, erosion leads to the exposure of the belowground parts of the plants. Such a situation affects the anchoring capacity of the species, and consequently the plants may be more easily detached from the substrate. The extent of the burial and erosion effects is species-specific and depends on the magnitude and on the frequency of disturbance. Large seagrass species are less susceptible to burial, whereas small, fast-growing species showed to be very sensitive to burial. *Posidonia australis* was the most tolerant seagrass species to burial, while *Thalassia testudinum* was the most tolerant species to erosion. The capacity of seagrasses to withstand sediment burial is strongly size-dependent. The leaf size and the rhizome diameter are the best predictors of the burial impact on seagrasses. Both natural and human-induced changes of the sediment level may seriously impact seagrasses. However, many natural events allow the recovery and/or adaptation of seagrasses to the sediment burial/erosion, as a consequence of the natural sediment redistribution occurring after disturbance. In contrast, most human-induced disturbances related to coastal construction and dredging activities strongly affect the sedimentary dynamics, and also result in increased water turbidity. These often result in the regression and permanent destruction of seagrass meadows. The burial thresholds estimated for seagrass species are generally in accordance with the burial impacts reported by the field descriptive studies. In some cases (e.g. *Halophila ovalis*), the recovery of seagrasses was related to the long-term meadow dynamics, rather than to their specific burial thresholds, highlighting the importance of separating the effects on individual mortality and on population mortality.

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