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Evaluating the extent and impact of the extreme Storm Gloria on *Posidonia oceanica* seagrass meadows

Candela Marco-Méndez [a,*], Núria Marbà [c], Ángel Amores [c,d], Javier Romero [e], Mario Minguito-Frutos [a], María García [a], Jordi F. Pagès [a], Patricia Prado [f,g], Jordi Boada [a], José Luis Sánchez-Lizaso [h], Juan Manuel Ruiz [i], Gregori Muñoz-Ramos [j], Neus Sanmartí [e], Elvira Mayol [b], Xavier Buñuel [a], Jaime Bernardeau-Esteller [i], Pedro Clemente Navarro-Martinez [i], Lázaro Marín-Guirao [i], Carlos Morell [b], Marlene Wesselmann [b], Rita Font [b], Iris E. Hendriks [b], Xavier Seglar [j], Judith Camps-Castella [f], Eli Bonfill [k], Aurora Requena-Gutiérrez [k], Fabio Blanco-Murillo [h], Javier Aguilar-Escribano [h], Santiago Jimenez-Gutierrez [l], Joaquín Martínez-Vidal [l], Juan Eduardo Guillén [l], Maria Elena Cefalì [m], Marta Pérez [e], Marta Marcos [c,d], Teresa Alcoverro [a]

[a] *Center for Advanced Studies of Blanes (CEAB, CSIC), Carrer Accés Cala Sant Francesc, 14, 17300 Blanes, Girona, Spain*
[b] *Global Change Research Group, IMEDEA (CSIC-UIB) Institut Mediterrani d'Estudis Avançats, Miquel Marqués 21, c7190 Esporles, Spain*
[c] *Marine technologies, operational and coastal oceanography Group, IMEDEA (CSIC-UIB) Institut Mediterrani d'Estudis Avançats, Miquel Marqués 21, 07190 Esporles, Spain*
[d] *Department of Physics, University of the Balearic Islands, Cra. de Valldemossa km 7.5, 07122 Palma, Spain*
[e] *Departament de Biologia Evolutiva, Ecologia i Ciències Ambientals Secció d'Ecologia, Av. Diagonal, 643, 08028 Barcelona, Spain*
[f] *IRTA, Aquatic ecosystems, Sant Carles de la Ràpita, Ctra. Poble Nou km 5.5, 43540 Sant Carles de la Ràpita, Tarragona, Spain*
[g] *Institute of Environment and Marine Science Research (IMEDMAR-UCV), Universidad Católica de Valencia SVM, C/Explanada del Puerto S/n, 03710 Calpe, Alicante, Spain*
[h] *Department of Marine Science and Applied Biology, University of Alicante, Carretera San Vicente del Raspeig s/n, 03690 Alicante, Spain*
[i] *Centro Oceanográfico de Murcia, Instituto Español de Oceanografía, C/Varadero s/n, 30740 San Pedro del Pinatar, Murcia, Spain*
[j] *Escola del Mar, Ajuntament de Badalona, Spain*
[k] *Plàncton, Divulgació y Serveis Marins, Calle Número Vint-i-tres, 284, local 2 (Urb. Les 3 Cales), L'Ametlla de Mar, Spain*
[l] *Institut de Ecología Litoral, Carrer de Sta. Teresa, 50, 03560 El Campello, Alicante, Spain*
[m] *Estació d'Investigació Jaume Ferrer, Instituto Español de Oceanografía (IEO), Mahón, Spain*

* Corresponding author.
E-mail address: c.marco@ceab.csic.es (C. Marco-Méndez).

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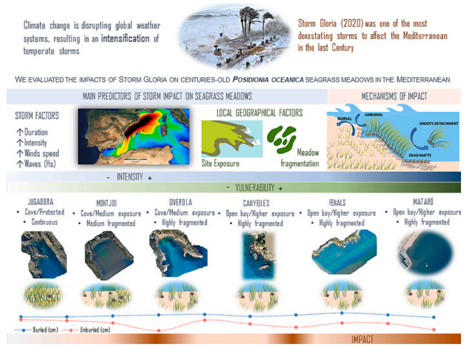
HIGHLIGHTS

- Climate change exposes temperate coastal systems to increasingly intense storms.
- We report impacts of Storm Gloria on long-lived Mediterranean seagrass meadows.
- Impacts aligned with storm strength causing widespread meadow burial and unburial
- Fragmented and exposed meadows were the most vulnerable to storm damage.
- Managing meadow integrity is vital to climate resilience as intense storms increase.

GRAPHICAL ABSTRACT

Graphical abstract showing main driving factors of the storm impact on *Posidonia oceanica* meadows. Conbined factors influencing level of burial and unburial are shown for six of the most affected meadows.



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ABSTRACT

Extreme storms can trigger abrupt and often lasting changes in ecosystems by affecting foundational (habitat-forming) species. While the frequency and intensity of extreme events are projected to increase under climate change, its impacts on seagrass ecosystems remain poorly documented. In January 2020, the Spanish Mediterranean coast was hit by Storm Gloria, one of the most devastating recent climate events in terms of intensity and duration. We conducted rapid surveys of 42 *Posidonia oceanica* meadows across the region to evaluate the extent and type of impact (burial, unburial and uprooting). We investigated the significance of oceanographic (wave impact model), geomorphological (latitude, depth, exposure), and structural (patchiness) factors in predicting impact extent and intensity. The predominant impact of Storm Gloria was shoot unburial. More than half of the surveyed sites revealed recent unburial, with up to 40 cm of sediment removed, affecting over 50 % of the meadow. Burial, although less extensive, was still significant, with 10–80 % of meadow cover being buried under 7 cm of sediment, which is considered a survival threshold for *P. oceanica*. In addition, we observed evident signs of recently dead matte in some meadows and large amounts of detached drifting shoots on the sea bottom or accumulated as debris on the beaches. Crucially, exposed and patchy meadows were much more vulnerable to the overall impact than sheltered or continuous meadows. Given how slow *P. oceanica* is able to recover after disturbances, we state that it could take from decades to centuries for it to recoup its losses. Seagrass ecosystems play a vital role as coastal ecological infrastructure. Protecting vulnerable meadows from anthropogenic fragmentation is crucial for ensuring the resilience of these ecosystems in the face of the climate crisis.

1. Introduction

As climate change disrupts global weather patterns, the current century is likely to see an increase in the strength and frequency of intense storms (Masson-Delmotte et al., 2019) leading to increased coastal flooding, exacerbated by rising sea levels (Jevrejeva et al., 2012; Masson-Delmotte et al., 2019; Levermann et al., 2013). Despite their short duration, episodic weather events can lead to dramatic changes in ecosystems if they are extreme in size (extent of area disturbed) and/or intensity (physical energy of the event per area per time, according to Turner et al., 1998). This raises serious concerns for the future of biological communities subject to these disturbances (Gillett et al., 2004; Ángel Gaertner et al., n.d.). Nearshore ecosystems, both on land and the sea, face the brunt of intense storms, even as they protect coastal areas from damage. Current climate projections suggest that many coastal ecosystems face an uncertain future given the mounting levels of stress they are likely to experience over the current century (Chapter 3 AR6 Working Group II, IPCC, 2021).

Seagrass meadows are the most widespread vegetated coastal ecosystems in the world, and occur along the coastal fringes of all continents except Antarctica (UNEP-WCMC & Short, 2021). They are vital for coastal protection (Christianen et al., 2013; James et al., 2019), attenuating the energy of nearshore waves (Fonseca and Fisher, 1986; Hansen and Reidenbach, 2012), reducing tidal currents (Gambi et al., 1990; Widdows et al., 2008) and protecting the seabed from erosion (Gacia and Duarte, 2001; Koch & Gust, 1999; Potouroglou et al., 2017). They are also responsible for a range of provisioning, regulatory, supporting and cultural services that directly benefit local communities (Cullen-Unsworth et al., 2014; Duarte et al., 2013; Ruiz-Frau et al., 2017). However, the integrity of these services can be severely disrupted by episodic storm events (Vacchi et al., 2017). Extreme storms and associated wind, tidal flow and sediment movement can bury seagrass shoots, expose roots and rhizomes, and even uproot entire plants (Frederiksen et al., 2004) resulting in sudden losses of seagrass cover (Gera et al., 2014). The effects of storms on seagrass meadows depend on the intensity and duration of the storm, and are typically mediated by sediment dynamics, particularly for shallow meadows (Gera et al., 2014; Oprandi et al., 2020). In addition, seagrass resilience can be further constrained by the biological features of the seagrass species, the characteristics of the meadow (i.e., shoot density, cover) and the biophysical environment (i.e., location, depth, level of exposure, fragmentation, etc.) (Unsworth et al., 2015). Given the current rate of loss in global seagrass area (Orth et al., 2006; Waycott et al., 2009; but see de los Santos et al., 2019), and the threats that these systems face in the near future (Hanley et al., 2020), any hope of maintaining the integrity of seagrass meadows is predicated on understanding how they respond to extreme weather events.

The impact of major coastal storms on shorelines is a result of a combination of strong winds, high waves, storm surges and intensified currents. When waves reach the coast, they transfer energy that triggers dynamic sedimentary processes, leading to the formation of sand waves and substantial movement of sediment. These processes have the potential to cause significant alterations to coastal ecosystems, including seagrass habitats (Kirkman and Kuo, 1990; Preen et al., 1995; Fourqurean and Rutten, 2004; Gera et al., 2014). The motion of sand waves (Marbà et al., 1994) and migration of barrier-islands (Cunha et al., 2005) can lead to sediment accretion (i.e., burial) or sediment loss (i.e., erosion). At the shoot level, seagrass burial can reduce the available photosynthetic surface, or deteriorate the basal meristem of leaves, which can lead to seagrass shoot mortality when a burial threshold is exceeded (Boudouresque et al., 1984; Marbà and Duarte, 1994, 1995; Duarte et al., 1998; Manzanera et al., 1998; Mills and Fonseca, 2003; Cruz-Palacios and Van Tussenbroek, 2005; Cabaço et al., 2008, Gera et al., 2014). Erosion, in contrast, exposes belowground seagrass biomass to waves and currents. In fact, since rhizomes and roots are generally less flexible than aboveground plant parts, once exposed, they can be easily detached (Cabaço et al., 2008). This reduces the anchoring capacity of the meadow, compromising its overall resilience. At the meadow level, patchiness and/or fragmentation can reduce plant stability, significantly affecting its resilience (Duarte et al., 2007). Exposure and water depth can also constrain meadow responses to storms by mediating the amount of surge energy they are subject to (Vacchi et al., 2012). In fact, seagrass meadows often preferentially colonize sheltered coastal coves that may be protected from stormy conditions. Under extreme storms, exposed meadows tend to experience more erosion and burial than protected meadows (Oprandi et al., 2020). However, the influence of water depth can vary, with the impacts either increasing or decreasing with depth depending on the behaviour of the storm (Gera et al., 2014; Oprandi et al., 2020).

The recognition that intense temperate storms are part of a suite of processes linked to anthropogenic climate change has been slow in coming. However, the increasing intensity of storm events particularly in the Mediterranean has been associated more clearly to climate drivers. Storms in the Mediterranean are have been classified by meteorologists as Mediterranean hurricanes or 'medicanes'. These storms are characterized as intense mesoscale cyclones exhibiting several similarities with tropical hurricanes notwithstanding latitudinal differences (Tous and Romero, 2013; Cavicchia et al., 2014; Ángel Gaertner et al., n. d.). Until the end of the last century, medicanes were considered rare but in the last few decades, their frequency has increased to recur annually during autumn (Onorato et al., 2011). Future projections of wave climate in the Mediterranean Sea indicate significant changes in the frequency of extreme events (Kapelonis et al., 2015). According to the sixth assessment report of the IPCC, a slightly increased frequency and amplitude of extratropical cyclones, strong winds and extratropical storms is projected for northern, central and western Europe by the middle of the century and beyond and for global warming levels of 2 °C or higher (medium confidence). While the frequency of Medicanes is projected to decrease (medium confidence), their intensity is projected to increase by mid-century and beyond and for global warming levels of 2 °C or more (AR6, IPCC, WGI; Howarth and Viner, 2022). Despite their growing importance as climate drivers, comparing to our understanding regarding the effects of hurricanes and tropical storms affecting coral reefs (e.g., Knowlton et al., 1981; Hughes, 1994; Gardner et al., 2005), there is little knowledge about how extreme storms affect benthic communities in temperate regions such as the Mediterranean Sea. This lack of knowledge may partially be explained by the rarity and stochastic nature of extreme storms in the Mediterranean Sea, combined with the scarcity of baseline data and long-term studies, making it difficult to study the effects of these events (Teixidó et al., 2013). As a result, most of what we know of how seagrasses respond to catastrophic meteorological events comes from hurricanes and tropical storms (Correia and Smee, 2022). These meadows are typically characterized by relatively short-lived species that grow in multispecies systems that are often highly dynamic. These tropical meadows are ecologically distinct from monospecific, long-lived temperate meadows, that may show patterns of decline and recovery quite different from tropical systems. This lack of information is unsurprising since evaluating the impact of storms on nearshore seagrass meadows is not straightforward. Even if adequate ecological baselines exist, sampling in the immediate aftermath of an intense storm presents challenges, since rough weather may persist for a while after the event. Often, by the time surveys are conducted, much of the directly attributable signs of impact may already have changed, as secondary processes take over – this is particularly true for dynamic soft-sediment communities. Additionally, matching the scale of assessments with the extent of the storm is often unfeasible. As a result, our knowledge of how Mediterranean seagrass meadows respond to intense storm events is patchy, based on a few opportunistic studies, often conducted at small spatial scales. Studies of two major storms (Coast of Catalonia, Spain 2008; Cost of Liguria, Italy 2018) show that extreme environmental events can result in major losses of *P. oceanica* meadows; the single-day loss of seagrass area and hence of associated services could equal chronic losses from more than a century of human impact (Gera et al., 2014; Oprandi et al., 2020). As these events increase, it becomes an urgent imperative to determine the nature and extent of these impacts to quantify the full scale of the loss.

Storm Gloria hit the Western Mediterranean coast from 19th to 23rd January 2020 and was considered one of the most extreme storm events in the last few decades due its extent, intensity and duration (Amores et al., 2020). The principal goal of this study was to determine the extent and nature of its impact on seagrass meadows of the Mediterranean endemic, dominant and slow-growing species *Posidonia oceanica* across the region of its influence. We employed a series of coordinated rapid surveys in 42 meadows in the path of the storm designed at quantifying the amount of burial, unburial and uprooting of the meadow in the wake of the event. We also explored if site-specific factors related to wave impact (simulated with oceanic models modified from Amores et al., 2020), location (latitude, depth and type of exposure) or meadow characteristics (i.e., continuity or patchiness of the habitat) help explain the observed effects.

2. Material & methods

2.1. Storm Gloria

From January 19th to 23th, the whole eastern part of the Iberian Peninsula suffered intense precipitation (up to 400 mm per day), accompanied by strong winds (mean values of 54 km/h and wind gusts of up to 140 km/h), storm surge (up to 0.7 m), record wave height that surpassed 14 m, and unusual wave mean periods (over 9 s) (see the online report of the Spanish Meteorological Agency AEMET at http://www.aemet.es/es/conocermas/borrascas/2019-2020/estudios_e_impactos/gloria, in Spanish only; see also ICM-CSIC report by Berdalet et al., 2020). The storm Gloria was characterized by high easterly winds and an extreme wave state in the western Mediterranean (beating historical records in significant wave height for some buoys moored in the region since the 1990s) (Sotillo et al., 2021; de Alfonso et al., 2021). The prolonged effect of strong easterly winds on the sea surface, generated wind-waves affecting coastal regions across the entire basin (see Fig. 1; storm evolution from January 19th to 23th). According to a statement released by the Spanish Council of Ministers, on January 28th of 2020, the combination of strong winds and heavy rain caused storm surge, inland flooding, and mudslides across the country, leaving 14 casualties and 3 missing people. The Copernicus Emergency Management Service (EMS) reported that Gandia and Valencia Harbors were closed to shipping traffic, that the storm surge swept 3 km inland, destroying rice paddies and coastal features in the Ebro River delta. Although erosion affected all beaches to some extent, it was particularly severe in open beaches oriented towards the east (Berdalet et al., 2020).

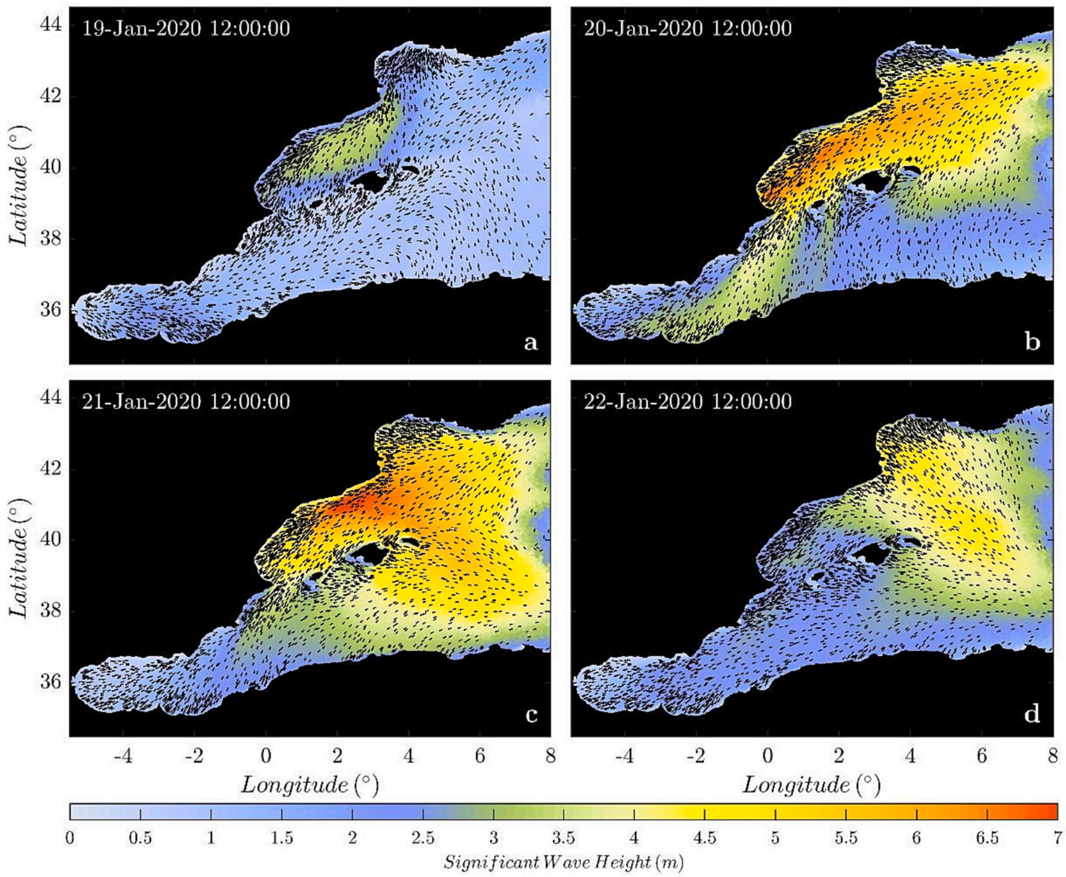

Fig. 1. Significant wave Height (m) evolution during Gloria storm (Amores et al., 2020).

2.2. Sampling design

Storms are inherently unpredictable and can exhibit dynamic features such as geographical migration and evolving intensity. Consequently, employing a predefined experimental design, especially in the case of a dynamic event like Storm Gloria, presents challenges. Traditional Before-After-Control-Impact (BACI) designs, often used in disturbance studies, are not suitable for assessing the effects of such unexpected extreme events. Storms, being ubiquitous natural phenomena, do not emanate from a fixed source; instead, they distribute their impact as they move. To address this challenge, we adopted a gradient approach in our sampling design, which accommodated the evolving nature of the storm's impact. We sampled areas anticipated to be heavily affected by the storm and coastal zones expected to experience minimal or no impact. This methodology allowed us to investigate the influence of storm impact, as simulated by an oceanographic model of the storm (detailed in Section 2.4), in addition to assessing each site's exposure to hydrodynamics based on coastal geomorphology and the influence of prevailing winds.

Our approach was, therefore, to uniformly conduct a rapid assessment across all regions, enabling us to comprehensively capture both the scale and immediate impact of the storm. We specifically selected response variables related to sediment levels, which were easy to measure (see next section) and provided data reflecting the impact immediately after the storm occurred. Furthermore, sediment levels have long been recognized as critical determinants of seagrass health (e.g., Gera et al., 2014), making them suitable proxies for evaluating the ecological impact intensity of the storm on *P. oceanica* seagrass meadows (see Section 2.3).

2.3. Field measurements

The direct effects of Storm Gloria on *P. oceanica* meadows were evaluated in the first two months after the storm when recent sediment movement such as plant burial or unburial and signs of uprooting attributable to the storm were still visible. Given the extent of the coast impacted by the storm and the narrow time window available to observe the impact (burial or unburial), the sampling was designed to be quick, and was conducted by a collaborative network of several institutions with access to the areas. We surveyed 42 stations across the affected coastline (including regions of Catalonia, Valencia, Murcia and the Balearic Islands) at different water depths (encompassing the depth range of each seagrass meadow) (Table 1; Fig. 1). We estimated the extent of the impact on seagrass meadows using randomly placed transects, following the protocol developed by Gera et al. (2014). At each location, one observer deployed a 25 m transect tape (always within the meadow and avoiding edges), while the second recorded each change in category observed along the line (n = 4 transects per site). The categories recorded were: (i) healthy *Posidonia* (areas with no signs of burial or unburial caused by the storm), (ii) buried *Posidonia* (areas with evident signs of burial after the storm: e.g., shoots with >2–3 cm buried, relative to the ligula, see below and Figs. 2a, 3A), (iii) unburied *Posidonia* with evident signs of sediment erosion after the storm (corresponding to >5 cm unburied, relative to the ligula, see below and Figs. 2a, 3B, C) (iv) new dead matte, areas where shoots and roots had been recently detached (uprooted areas within the dead matte were identified soon after the impact in situ and were characterized by having fresh leaves still attached, or no leaves but dead black roots, Figs. 2b, 3D, E) (v) old dead matte, (vi) sand and (vii) rock (Fig. 2c). The linear distance of each benthic category relative to the total distance of the transect (25 m) was transformed to obtain the percentage cover for each

Table 1
Localities of study.

	Area of study	id	Latitude	Longitude	Depth (m)
1	North Calalonia	Cala Jugadora-5	42°19′01,8″N	3°18′44,4″E	5
2	North Calalonia	Cala Jugadora-15	42°18′56,4″N	3°18′48,5″E	15
3	North Calalonia	Cala Montjoi-7	42°14′48″N	3°14′03″E	7
4	North Calalonia	Medes G1-5	42°2′49,39″N	3°13′16,7″E	5
5	North Calalonia	Medes G1-14	42°2′48,06″N	3°13′14,2″E	14
6	North Calalonia	Medes G2-6	42°2′40,88″N	3°13′5,8″E	6
7	North Calalonia	Medes G2-10	42°2′39,29″N	3°13′2,8″E	10
8	North Calalonia	Cala Giverola-4	41°44′10,0″N	2°57′16,0″E	4
9	North Calalonia	Tossa de mar-23	41°43′26,6″N	2°56′45,2″E	23
10	North Calalonia	Canyelles-5	41°42′09,8″N	2°53′0,7″E	5
11	North Calalonia	Canyelles-21	41°42′01″N	2°53′20,7″E	21
12	North Calalonia	Cala Frares-8	41°41′54″N	2°51′38″E	8
13	North Calalonia	Fenals-8,1	41°41′22,5″N	2°49′42,9″E	8
14	North Calalonia	Fenals-15	41°41′15,0″N	2°50′08,5″E	15
15	North Calalonia	Fenals-22	41°41′15,0″N	2°50′08,5″E	22
16	North Calalonia	Port de Blanes-13	41°40′20,9″N	2°48′05,8″E	13
17	North Calalonia	Mataro II-19	41°31′35,9″N	2°27′57,3″E	19
18	North Calalonia	Mataro I-12	41°31′33,0″N	2°28′15,2″E	12
19	South Calalonia	Cala Llobeta-5	40°55′28,5″N	0°50′56,5″E	5
20	South Calalonia	Cala Llobeta-9	40°55′28,5″N	0°50′56,5″E	5
21	South Calalonia	Calafato-6	40°55′14,1″N	0°50′29,9″E	6
22	South Calalonia	Cala Vidre-2	40°54′40,4″N	0°49′48,8″E	2
23	South Calalonia	L'estany Podrit-3	40°51′28,4″N	0°46′11,7″E	3
24	Mallorca (Balearic Islands)	Cala Millor-19	39°53,792′N	3°05,523′E	19
25	Mallorca (Balearic Islands)	Pollença-4	39°53,792′N	3°05,523′E	4
26	Menorca (Balearic Islands)	La Mola-12	39°51′50,6″N	4°18′50,6″E	12
27	Mallorca (Balearic Islands)	Cala Millor-9	39°36,373′N	003°24,385′E	9
28	Mallorca (Balearic Islands)	Cala Millor-7	39°36,070′N	003°23,573′E	7
29	Mallorca (Balearic Islands)	Cala Murada-6	39°26,605′N	003°16,695′E	6
30	Mallorca (Balearic Islands)	Cala Murada-10	39°26,582′N	003°16,701′E	10
31	Valencian community	Denia-10	38°52′20,4″N	0°05′30,0″E	10
32	Valencian community	Denia-6	38°51′42,6″N	0°05′37,6″E	6
33	Valencian community	Javea-12	38°47′56,1″N	0°11′30,4″E	12
34	Valencian community	Javea-6	38°47′58,7″N	0°11′29,4″E	6
35	Valencian community	Cala mina-10	38°33′58,7″N	0°03′10,5″W	10
36	Valencian community	Cala mina-5	38°33′56,9″	0°03′11,4″W	5
37	Valencian community	Tabarca-12	38°10′16,35″N	0°28′43,58″W	12
38	Murcia	TM_5	37°44′24,92″N	0°43′14,995″W	5
39	Murcia	IG_32m	37°44′13,14″N	0°41′14,931″W	32
40	Murcia	IG_5m	37°43′45,63″N	0°42′44,202″W	5
41	Murcia	IG20m	37°43′41,828″N	0°42′14,355″W	20
42	Murcia	CAU_IG_12m	37°43′30,112″N	0°42′38,473″W	12

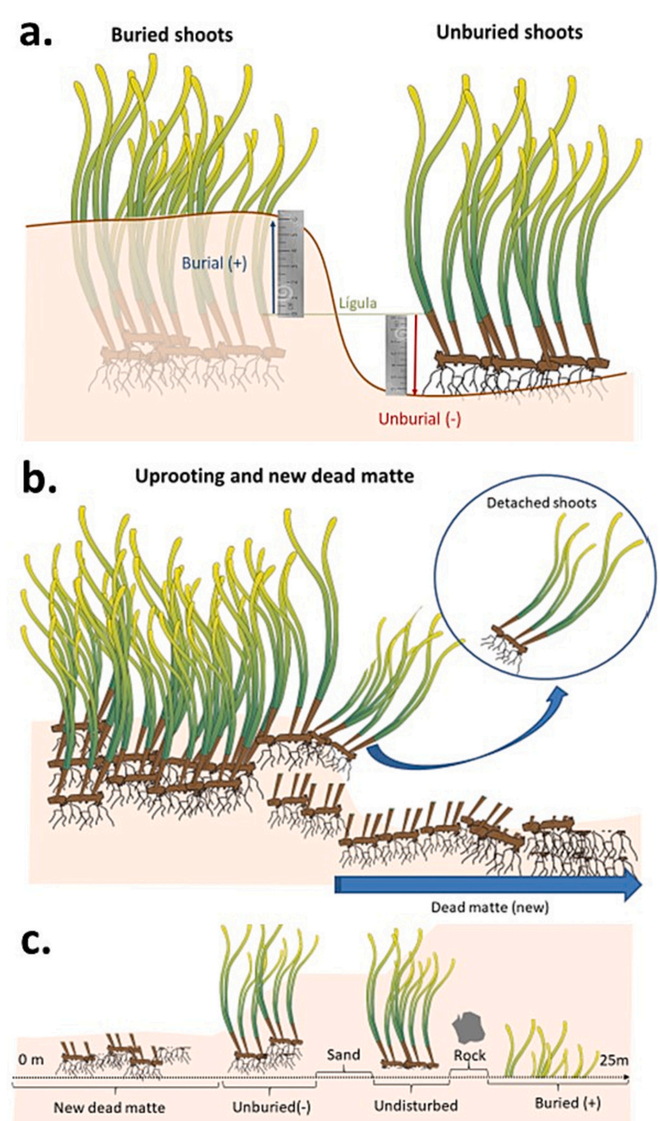

Fig. 2. a. Mechanism of impact by sediment burial and unburial, b. impact by shoots detachment and consequent new dead matte and c. transect methodology to estimate cover.

category. Whenever buried or unburied patches were observed along the transect, we also measured the sediment level with a ruler as the distance in cm between the ligula and the sediment surface (we measured at least 6 shoots per patch found along the transect, Figs. 2, 3A, B). Burial

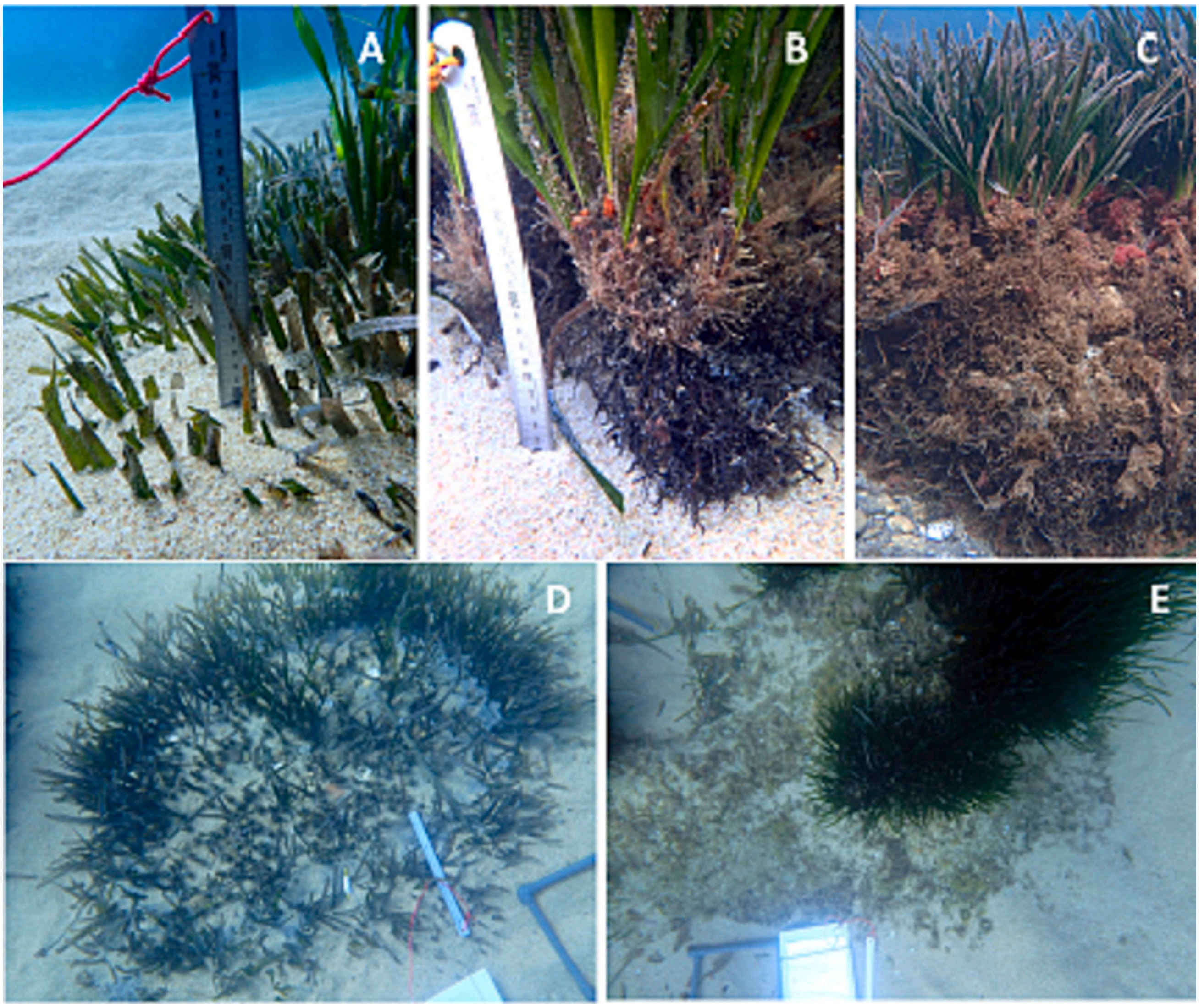

Fig. 3. Images of impacted meadows: A. Buried shoots (Fenals, shallow meadow); B and C. unburied shoots (Fenals and Montjoi shallow meadow); D. buried patch with shoots mortality and E: dead matte (new) at Fenals shallow meadow.

values were assigned positive values (e.g., shoot ligula buried under 3 cm of sediment: sediment height = +3 cm), while unburied values were assigned negative values (e.g., shoot ligula 10 cm above the sediment surface: sediment height = −10 cm). As indices of the **extent** of the storm impact, we used the following response variables: (i) the percentage of meadow that was buried under sediment along the transects (above +2–3 cm distance between ligula and sediment height), (ii) the percentage of meadow unburied along the transect (below −5 cm distance between ligula and sediment height). In addition, as an index of the **intensity** of burial and unburial, we used the average values of *P. oceanica* (iii) burial (positive) or (iv) unburial (negative) in cm of sediment height for each transect obtained from the measurements with the ruler. In addition, we constructed an index of **combined impact** based on burial and unburial values known to cause significant impacts or mortality in *P. oceanica*. For this, we used a subset of data where only values higher than +4 cm for burial and below −10 cm for unburial were included, corresponding to sediment heights at which shoot mortality reaches 60 % and 50 %, respectively (Gera et al., 2014, unpublished results). For some of the meadows included in this "subset", unburial values before the storm were: among −4.2 ± 0.4 cm (2014), −4.9 ± 0.3 cm (2016), −4.6 ± 0.3 (2018), which makes reasonable the threshold we chose (Hereu et al., 2018). Then we calculated the overall impact of the storm on meadow where shoots were buried (A) and unburied (B) as a simple multiplication of extent and intensity:

$$unburial\ impact\ A = \frac{unburied\%(below - 10cm) \times 100}{Total\ meadow} \times [abs(unburied_{cm})]$$

$$burial\ impact\ B = \frac{buried\%(above + 4cm) \times 100}{Total\ meadow} \times buried_{cm} (1) Total\ meadow\ (\%) = Posidonia\ healthy\ (\%) + Unburiedp\ (\%) + Buriedp\ (\%)$$

where "*unburied% (below −10 cm)*" and "*buried% (above +4 cm)*" are the percentage of the meadow with shoots unburied >10 cm and with shoots buried >4 cm, respectively; "*[abs(unburied$_{cm}$)]*" and "*buried$_{cm}$*" the average sediment height (in cm) eroded or buried, respectively; and "*total meadow*" the percent of transects in the meadow with *Posidonia* cover (including healthy, buried and unburied *Posidonia*).

Finally, we summed A and B as a proxy of "combined impact" (v):

$$\text{Combined impact} = \text{unburial impact A} + \text{burial impact B}$$

2.4. Explanatory variables

To determine the factors influencing the impact of Storm Gloria in seagrass meadows (response variables, see Section 2.2) we measured several potential explanatory variables, including: Latitude of the meadow, meadow depth (m), degree of shelter/exposure to wave action, meadow patchiness (% of sand in the transect) and modelled wind-waves arriving at the meadow (see next paragraph for details on the wave model). Longitude and latitude were obtained with a GPS, depth was measured using dive computers and the type of substrate was obtained from the transects. Degree of exposure to storm Gloria was obtained by analyzing the orientation of each location with the Google Earth gridlines tool (https://earth.google.com. Google Earth Pro 7.3.2.549, July 23, 2018. Spain, Eye alt 800–500 m. Access: March 15, 2021). Since Gloria winds were mostly easterlies (Amores et al., 2020; Berdalet et al., 2020; de Alfonso et al., 2021), therefore, meadows oriented towards dominant winds were considered more exposed than the north west oriented (N, NW and W: 0; NE and SW: 0.5; S and E:1 and SE: 3). In addition, in this rank, meadows located in open bays were considered more exposed than meadows located in sheltered coves (based on coastal damages reported in ICM-CSIC-report by Berdalet et al., 2020). Therefore, the degree of exposure was the sum of all wind components that could impact each location based to their orientation and geomorphology (rank from 0 to 6).

The wind-wave generated cumulative impact from 5 to 35 km off the coast was calculated following Amores et al. (2020), and integrated for the entire duration of the storm. The generated storm surge and wind-waves were simulated for the entire duration of storm activity (17–26 January 2020) with a SCHISM model (Semi-implicit Cross-scale Hydroscience Integrated System Model; Zhang et al., 2016) in its 2DH barotropic mode, fully coupled with the spectral wave model WWM-III (Roland et al., 2012), with an average resolution between 1 and 2 km along the coastlines and outputs every 30 min. Further details of the model configuration, its performance and the complete study of Storm Gloria can be found in Amores et al. (2020). Figs. S1, S2 and S3 details the computational procedure used to obtain the cumulative storm impact index for seagrass meadows located near Lloret de Mar (Fenals, S1), Mataró (S2) and Dénia (S3) (red dot in panel a). For the three figures, panel (a) shows the significant wave height (H_s) field on January 21th at 08:00 (Fenals and Mataró) and January 20th at 06:00 (for Dénia), when the storm was at its peak at each of the analyzed points. The first step was to consider only those parts of the ocean where waves were travelling straight (with a tolerance of ±10°) towards the target point (panel b). Then, a spatial mask of possible locations from which the waves could affect the point was applied (grey zone in panel c). In this example, the areas behind the Balearic Islands are filtered out because waves from there could never reach the target point. We then used the maximum significant wave height inside a circle with a radius of 0.5° as a measure of the impact at that time step (blue circle in panel c). This procedure was repeated for all time steps resulting in a time series of maximum significant wave heights directly affecting the studied point from all physically possible directions (panel d).

Finally, the cumulative storm impact index was defined as:

$$I = \frac{1}{t_{end} - t_{start}} \int_{t_{end}}^{t_{start}} H_{s,max}(t) \cdot dt$$

Table 2
Index of wave impact (IWI). For each locality, the model can create a large number of impact variables combining the distance ratio from the source (from 5 km to 45 km) and the arc degree set (from 10 to 50). Here we present the 45 combination we used to create a single Index of wave Impact (IWI) for the selected distances.

Index of wave impact					
Arc (±°)	Distance ratio from source (km)				
	5	15	25	35	45
10	m510	m1510	m2510	m3510	m4510
15	m515	m1515	m2515	m3515	m4515
20	m520	m1520	m2520	m3520	m4520
25	m525	m1525	m2525	m3525	m4525
30	m530	m1530	m2530	m3530	m4530
35	m535	m1535	m2535	m3535	m4535
40	m540	m1540	m2540	m3540	m4540
45	m545	m1545	m2545	m3545	m4545
50	m550	m1550	m2550	m3550	m4550
Arc (averaged)	IWI_5	IWI_15	IWI_25	IWI_35	IWI_45

This definition considers not only how hard each location was hit by storm-generated waves, but also for how long they were affected, and only by those waves coming from physically possible locations. Sensitivity tests were performed to fix the tolerance value of the possible incoming directions and the maximum allowed distance from the source point to select the maximum significant wave. The model was set to calculate the cumulative storm impact index (hereinafter: Index of Wave Impact or IWI) from 5 to 45 km ratio of distance from the source point (each station) and from 10° to 50° giving 45 different combinations (Table 2). We worked with IWI-5 km, IWI-15 km, IWI-25 km and IWI-35 km for statistical analyses.

2.5. Data analyses

The effect of the storm on seagrass meadows was assessed using five response variables: (1) the percentage cover of meadow buried and (2) unburied obtained from each transect (% of meadow buried >2–3 cm or unburied >5 cm with respect to the total meadow cover along the transect), (3) *Posidonia oceanica* buried (cm) (4) and unburied (cm), obtained from random measurements in the areas of the transect where burial or unburial was detected (in cm), and the combined impact (5).

We ran five Generalized Linear Models (GLM) to assess if the predictors latitude, depth, meadow patchiness (that was obtained as the percentage of sand within the meadow), degree of exposure and the Index of Wave Impact (IWI) influenced any of the five response variables describing the effects of the storm on *P. oceanica* seagrass meadows (Table 2). For model 1 (response: burial_cm), model 2 (response: unburial_cm) and model 5 (response: combined impact) we used a Gaussian distribution (with a logarithmic link function). In model 3 (response: % burial) and 4 (response: % unburial) we used a Quasi-Poisson distribution. Quasipoisson is generally recommended when data are overdispersed counts, as ours was. We applied the 'round' function to convert any decimals to whole numbers, as required for this distribution (Zuur 2009). All explanatory variables were introduced into the model as fixed continuous variables. In all cases, the model selection was based on the Akaike's Information Criterion (AIC) and log-likelihood ratio tests (Zuur et al., 2009). Data were checked for normality by visually inspecting plots of residuals and fitted values. All data were analyzed with the packages MASS (Venables and Ripley, 2002) and stats in the statistical software R (R Development Core Team, 2012).

To provide context for our results regarding baseline sediment levels, we conducted a GLM analysis to evaluate the differences in unburial levels for a subset of six seagrass meadows. These meadows had measurements taken both before the storm, thanks to long-term monitoring programs spanning from 2014 to 2020, and after the storm using data from this study. Our analysis revealed significantly higher unburial levels in seagrass meadows after Gloria (our data, 2020-G in S5a, b) than those obtained before the storm by the long-term monitoring program (see 2014_C, etc.… S5a, b). However, it is important to note that the differences in unburial levels were less pronounced in monitoring data alone (excluding the data from this study) before and after the storm. This discrepancy may be attributed to the common practice of avoiding sampling near the edges of the meadows in most long-term monitoring programs, while these edge areas are the most impacted during storm events. Therefore, when comparing our results to those from long-term monitoring programs, it is advisable to exercise caution. Despite of this, meadows such as Cala Jugadora-15 and Mataró I-12 proved to be the most affected after the storm, recording higher values of unburial in both 2020-C and 2020-G (see S5a). We hope that this information could help to better understand the decision we made concerning sampling design, the threshold of impact (burial/unburial) we chose (see Section 2.4) and the interpretation of results.

3. Results

3.1. Storm impacts on seagrass meadows

Storm Gloria was particularly intense across the entire northwestern Mediterranean coast explored from the north of Catalonia (42° N) to Murcia (37° N), and the Balearic Islands. At the beginning of the storm, the maximum wave height value was reached in Gulf of Valencia, but the impact shifted to northern latitudes in Catalonia, where extreme wave heights lasted longer (Fig. 1). The principal nature of its impact on *Posidonia oceanica* was in the form of shoot unburial. Of the 42 localities studied, half showed >50 % of the meadow unburied, and eight of these meadows had >70 % of the area unburied (at least 10 cm unburial). Six of these severely affected meadows were located in the northern sector of the studied area (north of Catalonia, e.g., Cala Jugadora-5, Medas I-5, Medas II-10, Tossa-23, Mataró II-19, Cala Llobeta-9) and two in the central sector (Valencia, e.g., Cala Mina-10 and Tabarca-12) (Figs. 4, S4). The level of unburial (mean ± SE in cm) had the highest average values in Cala Giverola-4 (−43.5 ± 11.7 cm), Canyelles-21 (−21.1 ± 4.23 cm), Fenals-8 (−32 ± 1.4 cm) and Mataró I-12 (−40.3 ± 5.2 cm) all located in the northern coast (Figs. 4, 5). Apart from unburial, several meadows also had extensive areas buried under the sediment (Figs. 4, 5). The meadows most affected by burial were Canyelles-5 (78 %), Fenals-22 (47 %), Denia-10 (32 %) and Jávea-6 (42 %) (Figs. 4, S4). The intensity of burial (i.e., the amount of sediment above the shoots' ligula, in cm) was variable across the coast. Eleven location showed isolated measures above 10 cm, but only three of them (e.g., Canyelles-5, Fenals-15 and Cala Vidre-2) (Fig. 4 top and bottom) showed averaged measures >7 cm of burial (mean ± SE cm of burial), which is known to cause >80 % of shoot mortality (Gera et al., 2014). We also observed signs of recent uprooting of shoots, which in some meadows affected >30 % of their area: Cala Jugadora-15, Canyelles-21, Mataró I-12, Cala Vidre-2, Cala Murada-10, TM-5, IG-12 and Cala Montjoi-7. These meadows were often characterized by a high level of patchiness, with sand cover and dead matte representing >50 % of the meadow (Fig. S4).

3.2. Model output: Index of Wave Impact (IWI)

The Index of Wave Impact (IWI) obtained from the model at increasing distances from each locality showed similar trends. All IWIs showed that the highest impact by wave action (integrated for the entire duration of the storm) was concentrated in the northern coast of Catalonia, between Medes II and Mataró I (IWI values 3–4) (Figs. 5, S1 and 2). Another maximum was recorded in the southern coastline at Denia-10, Denia-6, (IWI values around 3) (Figs. 5, S3). Although the highest H_s was recorded for Denia on January 20 (8 m), the Index of Wave Impact (which included the entire duration of the storm) showed that the northern coast of Catalonia was the area most heavily affected by Storm Gloria.

3.3. General Linear Models (GLMs)

Results from all GLMs with different combination of factors showed that latitude, degree of exposure of the meadow and meadow patchiness (percentage of sand within the meadow) were the most significant factors influencing the amount (in cm) of unburial and burial of *P. oceanica* meadows ($p < 0.001$ and $p < 0.5$ respectively; Fig. 6a and b, Table 3). The area affected by unburial (% unburial cover) was best explained by latitude and meadow patchiness (percentage of sand within the meadow, $p < 0.01$ and $p < 0.001$ respectively. Table 3; Fig. 7a), with a moderate influence of depth ($p < 0.05$, Table 3). Buried cover was significantly influenced by the Index of Wave Impact (IWI) at 5 and 25 km distance from the source ($p < 0.001$; Table 3; Fig. 7b). Analyses of the combined impact variable concurred with these overall results, identifying exposure as the most significant drivers of cumulative impact recorded along the affected coastline (Table 3).

4. Discussion

As global weather patterns get disrupted with climate change, large infrequent disturbances are becoming more intense and frequent. Historically extreme storms like Gloria are increasingly common, testing the integrity of the ecological infrastructure of coastal systems. For 5 days between the 19th and 23rd of January 2020, Storm Gloria was active over >5 degrees of latitude across the Iberian Peninsula from the north of Catalonia to Murcia (overall ca. 3000 km of coastline) and the Balearic Islands (overall ca. 1000 km of coastline). The event was unusual not merely in its extent but also its intensity. Within a few weeks after the storm, *Posidonia oceanica* meadows showed three types of impacts: burial, unburial and uprooting. The storm resulted in significant sediment movement, as evidenced by nearly all surveyed meadows showing signs of unburial. This indicated that Storm Gloria had a greater erosive than rather than accretive impact. The worst of this impact, both in the extent and intensity of unburial, was borne by meadows in the northern sector of the coastline, where exposure to the storm was highest (based on their orientation and geomorphological features), and where meadows were patchiest. The intensity of burial (cm) was similarly influenced by latitude and exposure, while its extent (burial cover) was mostly influenced by wave impact (IWI-5 and IWI-25). These northern meadows also had frequent signs of uprooting, often with detached, drifting shoots still present in the meadow at the time of sampling (personal observation). These results were well-predicted by our hydrodynamical model – the impact of the storm on *P. oceanica* meadows mapped closely with the energy input along the coastline. Our results indicate that while there was a distinct regional signature to the storm's impact, the vulnerability of affected meadows was strongly influenced by local exposure and patchiness.

Our model simulations showed that while the overall maximum wave heights were recorded in the region of Valencia (offshore from the city of Denia), the highest cumulative wave impact (for the entire duration of the storm) was experienced on the Catalonia coast (IWI = 3–4) (see S2; S3). This is concurrent with other studies which also reported that extreme wave heights (over a threshold) lasted longer in Catalonia (de Alfonso et al., 2021). The impact along the coastline caused strong beach erosion, flooding in many coastal sections, and the destruction of coastal infrastructures (breakwaters, etc.) (ICM-CSIC report by Berdalet et al., 2020), even in areas not exposed to maximum wave heights (e.g., Cala Millor). The magnitude of the storm's erosive impact on the coast was driven not merely by the physical characteristics of the storm itself, but also by coastal features that determined coastal exposure and vulnerability to waves and storm surge (see S3 diagram). Indeed, some localities in the northern part of the surveyed coastline with the highest cumulative wave impact indices were also highly exposed either because of their orientation (e.g., Cap de Creus), because they were open bays or non-enclosed beaches (Fenals, Mataró), or because the type of substrate (sand vs rocks or pebbles). This agrees

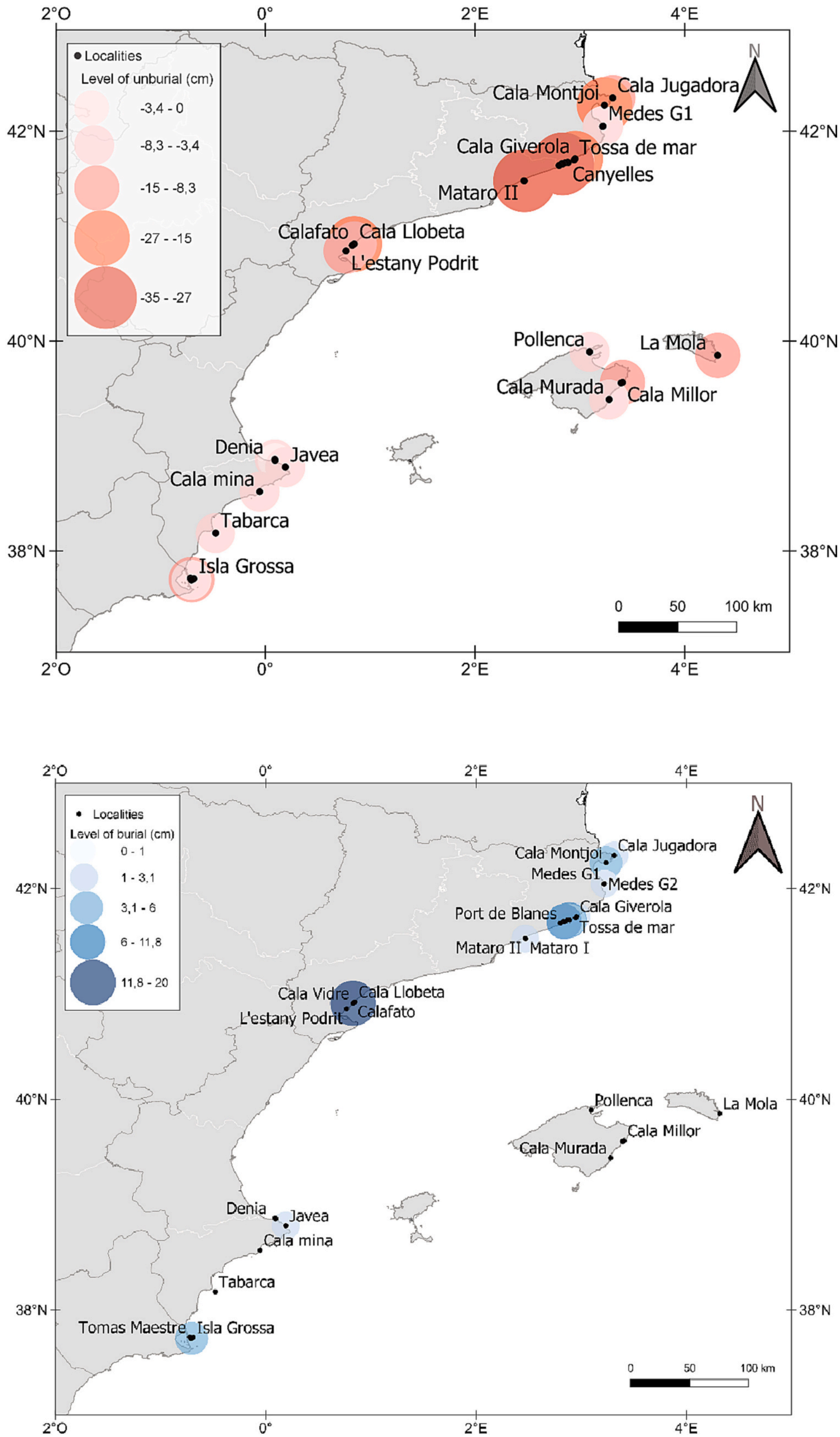

Fig. 4. Map of the Impact: unburial (top); burial (bottom).

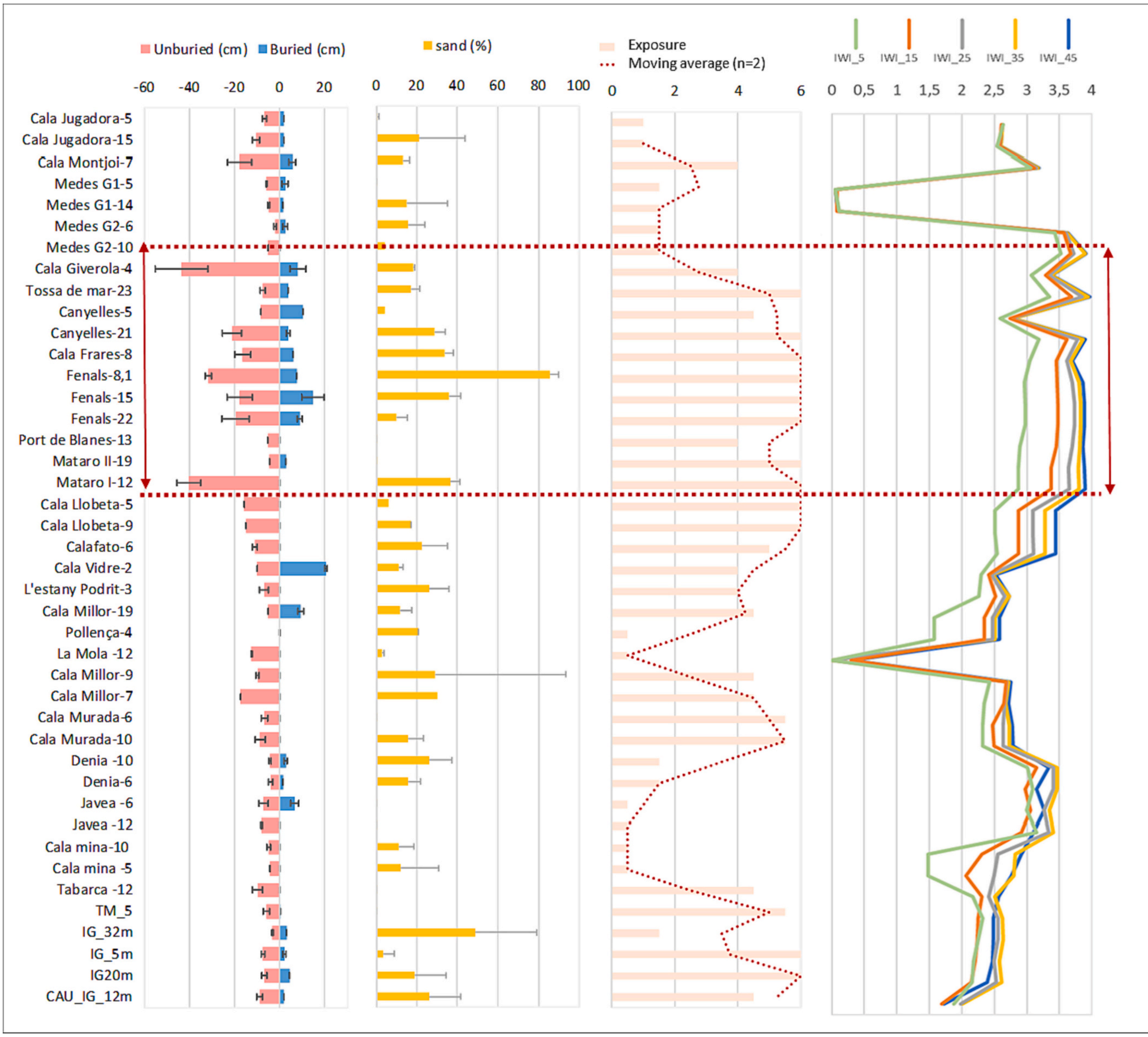

Fig. 5. Average level of unburial vs burial (cm) for the different location (ordered from North to South) and Index of Wave Impact (IWI) obtained for distance from 5 to 45 km. Colored lines indicate the different arc degree used on the model. Red dashed lines and arrows indicates locations with the highest values of unburial (cm) which concur with highest IWI at all distances.

with a report published months after the storm, that showed that the Catalan coast was significantly affected by erosion, particularly open beaches facing east and northeast (ICM-CSIC report by Berdalet et al., 2020).

4.1. Mechanisms of impact on seagrass meadows: unburial, burial and uprooting

The most visible sign of Storm Gloria's erosive force was the dramatic damage it wreaked on coastal infrastructure and the region's many beaches (ICM-CSIC report by Berdalet et al., 2020). Below water as well, as our results indicate, its impact on nearshore systems was also dominated by strong erosive processes. Sediment displacement is one of the main mechanisms of storm influence on seagrass ecosystems (Marbà et al., 1994; Cunha et al., 2005). The movement of sediment brings with it a host of related stressors that together test the integrity and optimal functioning of meadows. Apart from increasing turbidity and reducing light availability, sediment movements also cause the burial or unburial/uprooting of shoots, roots and rhizomes (Frederiksen et al., 2004). This lead to alteration or destruction of the meadows (e.g., reduction of overall abundance with concomitant reductions in 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). The extensive unburial of *Posidonia oceanica* shoots in most of the localities we surveyed (half of them with >50 % of their cover unburied), left seagrass roots and rhizomes highly exposed. Although this unburial does not translate to mortality in the short term, over time, unburied shoots will see a gradual erosion of the anchoring capacity of the species, reducing the meadow's ability to resist even low-intensity storm surge events in the future (Cabaco and Santos, 2014). From our preliminary evaluations of the short-term effects of unburial based on data collected immediately after the storm, beyond 10 cm of unburial, *P. oceanica* meadows start to show signs of mortality. Beyond 20 cm of unburial the studied meadows showed 100 % mortality

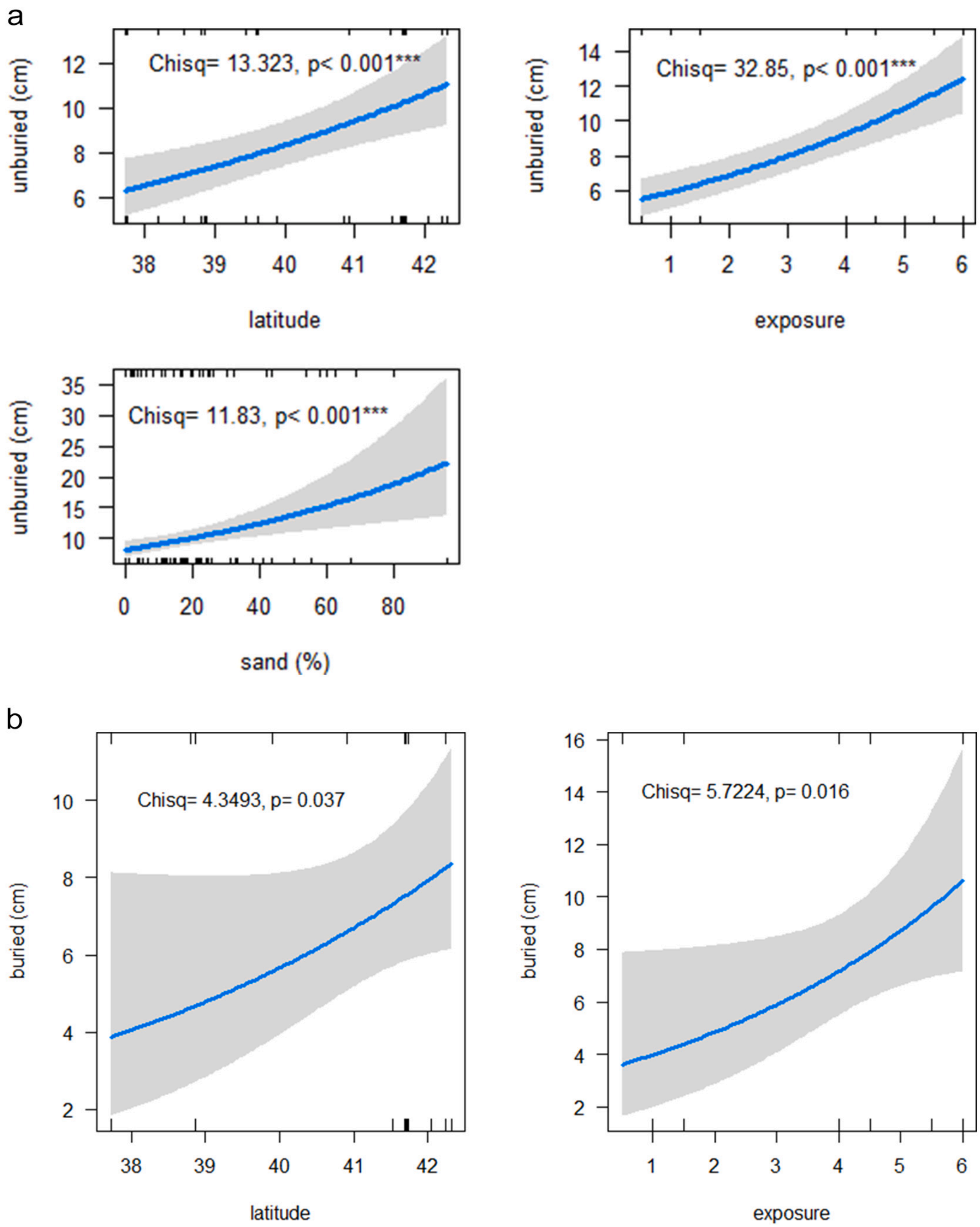

Fig. 6. a: General Linear model plots for response variable, unburial (cm) and the significant explanatory variables: latitude, depth and exposure. The grey areas represent confidence bands.
b: General Linear model plots for response variable, burial (cm) and significant explanatory variables latitude and exposure. The grey areas represent confidence bands.

(Marco-Méndez et al., in prep.).

At some meadows, apart from unburial, plant uprooting (fully detached from the ground) was also widespread, with cover values as high as 30 % in some localities. Several weeks after the event, large amounts of detached shoots were still drifting on the sea bottom or had accumulated as debris on the beaches, and meadows had large tracts of newly formed matte. This uprooting represents a significant, and potentially long-term change to meadow structure, altering its continuity and making it vulnerable to a host of other flow-on edge effects. The unusually high impact that accrued on northern meadows is a synergy between: i) the high intensity and duration of waves impact (IWIs); ii) high exposure due to meadow orientation (the direction of the facing waves) and iii) meadow patchiness. As with unburial, some of the meadows most impacted by uprooting were highly patchy before the storm (Pagès et al., 2014), attesting to the vulnerability of fragmented meadows to physical disturbance (Fonseca and Bell, 1998). Between burial and uprooting, these patchy meadows could see a rapidly accelerating loss of patch size and cover with each new storm.

While erosive processes were widespread along the path of the storm, sediment deposition also contributed significantly to the observed impact on meadows. The effects of burial directly translate to mortality in just a few weeks. *P. oceanica* can withstand sediment burial until a sharp threshold of around 4–5 cm; beyond 8–9 cm, shoot mortality rises to ~100 % (Boudouresque et al., 1984; Marbà and Duarte, 1994, 1995;

Table 3
General Linear Model analyses for the different response variables investigated and the effects tested. Model distribution and transformation are indicated for each variable. Final GLM model after AIC adjustments, p-values and level of significance are indicated (*p < 0.05, **p < 0.01, ***p < 0.001, ns: no significant). Significant predictors are highlighted in bold.

Response variable	Effects tested	Family model (GLM)	Response transf.	Final model	Chisq	Df	p-Value		vif
P. oceanica unburied (cm)	Latitude	Gaussian	Model 1: Log	**Latitude**	**13,323**	**1**	**0,000**	***	**1049**
	Depth			Depth	2799	1	0,094	ns	1142
	exposure			**Exposure**	**32,856**	**1**	**0,000**	***	**1119**
	Sand			**Sand**	**11,827**	**1**	**0,000**	***	**1175**
P. oceanica buried (cm)	IWI_5 to IWI_35 (each IWI distance was tested separately)		Model 2: Log	**Latitude**	**4349**	**1**	**0,037**	*	1079
				Depth	2693	1	0,100	ns	1.495
				Exposure	**5722**	**1**	**0,017**	*	**1.500**
P. oceanica unburied (%)		Quasi Poisson	Model 3: Round	**Latitude**	**6826**	**1**	**0,008**	**	**1011**
				Depth	4157	1	0,041	*	1062
				Sand	**30,687**	**1**	**0,000**	***	**1062**
P. oceanica buried (%)			Model 4a: Round	Latitude	0,865	1	0,352	ns	1298
				Sand	0.213	1	0,644	ns	1025
				IWI_5	**19,931**	**1**	**0,000**	***	**1270**
			Model 4b: Round	Latitude	0,564	1	0,452	ns	1545
				Sand	0,813	1	0,367	ns	1054
				IWI_25	**14,563**	**1**	**0,000**	***	**1564**
Combined impact[a]		Gaussian	Model 5: sqrt	**Exposure**	**13,747**	**1**	**0,000**	***	

[a] This variable was created as a combination of the four variables investigated (see Material and methods section).

Duarte et al., 1998; Manzanera et al., 1998; Mills and Fonseca, 2003; Cruz-Palacios and Van Tussenbroek, 2005; Cabaço and Santos, 2007, 2012; Gera et al., 2014). Burial of the leaf meristem (and maybe also of the vegetative apex of the rhizome) could reduce oxygen availability for the tissues, and expose them to toxic compounds such as sulfide (Manzanera et al., 1998), a compound shown to be very toxic, even at low concentrations (Carlson et al., 1994). Some meadows surveyed in this study had large areas buried under >7 cm of sediment, which we expect will lead rapidly to widespread shoot mortality. Although shoot mortality was not directly assessed in this study, preliminary results show that burial levels of 6–7 cm caused 100 % shoot mortality across the studied meadows (manuscript in prep.). The intensity and extent of meadow burial intensity was linked to wave impact, latitude and exposure, clearly implicating the storm as a major agent of sediment movement.

4.2. Seagrass meadows and climate change

Seagrasses have suffered large-scale declines at alarming rates in response to increasing stressors mainly imputable to human activities and the consequent environmental changes they induce (Orth et al., 2006; Waycott et al., 2009; Marbà et al., 2014). All these severe impacts can affect the overall capacity of seagrasses to recover from disturbance. Damages to large slow-growing species, such as the Mediterranean *P. oceanica*, are viewed with particular concern since they rely mainly on vegetative clonal growth and their colonization is likely to occur over centuries (Duarte, 1995; Collier and Waycott, 2009; Erftemeijer and Robin Lewis, 2006; Jarvis et al., 2014). However, it is evident that the ability of seagrass to recover and the rate of recovery are largely dependent on the nature of the disturbance, its duration and spatial extent (O`Brien et al., 2018). In areas of the meadow where rhizomes survive, recovery can potentially proceed more rapidly (Collier et al., 2009). This is why maintaining meadows intact becomes of prime importance in a climate change age. Given the increased vulnerability of patchy meadows to storm damage, every subsequent disturbance is likely to accelerate processes of fragmentation, leading to a spiralling feedback of meadow loss because of physical losses and increased edge effects (Yarnall et al., 2022). These patchy fragmented meadows may have a reduced capacity to face future climatic events such as: frequent low intensity storms, infrequent high intensity storms or even other global-scale environmental changes (e.g., sea surface temperature, sea level rise and changes in salinity from altered rainfall patterns) (Connolly, 2012, Saunders et al., 2013; Connolly et al., 2018). This would mean a rapid unravelling of the coastal defense function that seagrasses like *P. oceanica* provide, with significant costs to coastal economies as tourist beaches erode more rapidly and nearshore infrastructure faces increased wave forces.

5. Conclusions

What do these results tell us about our ability to manage nearshore ecosystems in the face of climate change? For a start, we have to acknowledge that local geography will always render some habitats more vulnerable than others. Ecosystems growing on exposed capes and promontories are always going to experience the brunt of storm forces when they blow. However, this makes it all the more imperative to ensure that local action works to maintain ecosystems in as contiguous a state as possible, reducing anthropogenic fragmentation and habitat loss as much as possible. The recovery of these slow-growing systems is largely dependent on the return time of large storms and the role that local conditions may play in promoting site-specific recovery capacities. Here again local management can help promote seagrass recovery by maintaining water quality and preventing further physical damage of affected meadows. The return time of large storms is a big unknown. Although climate change scenarios indicate a general weakening of regular storms for this region, intense Gloria-like storms may actually

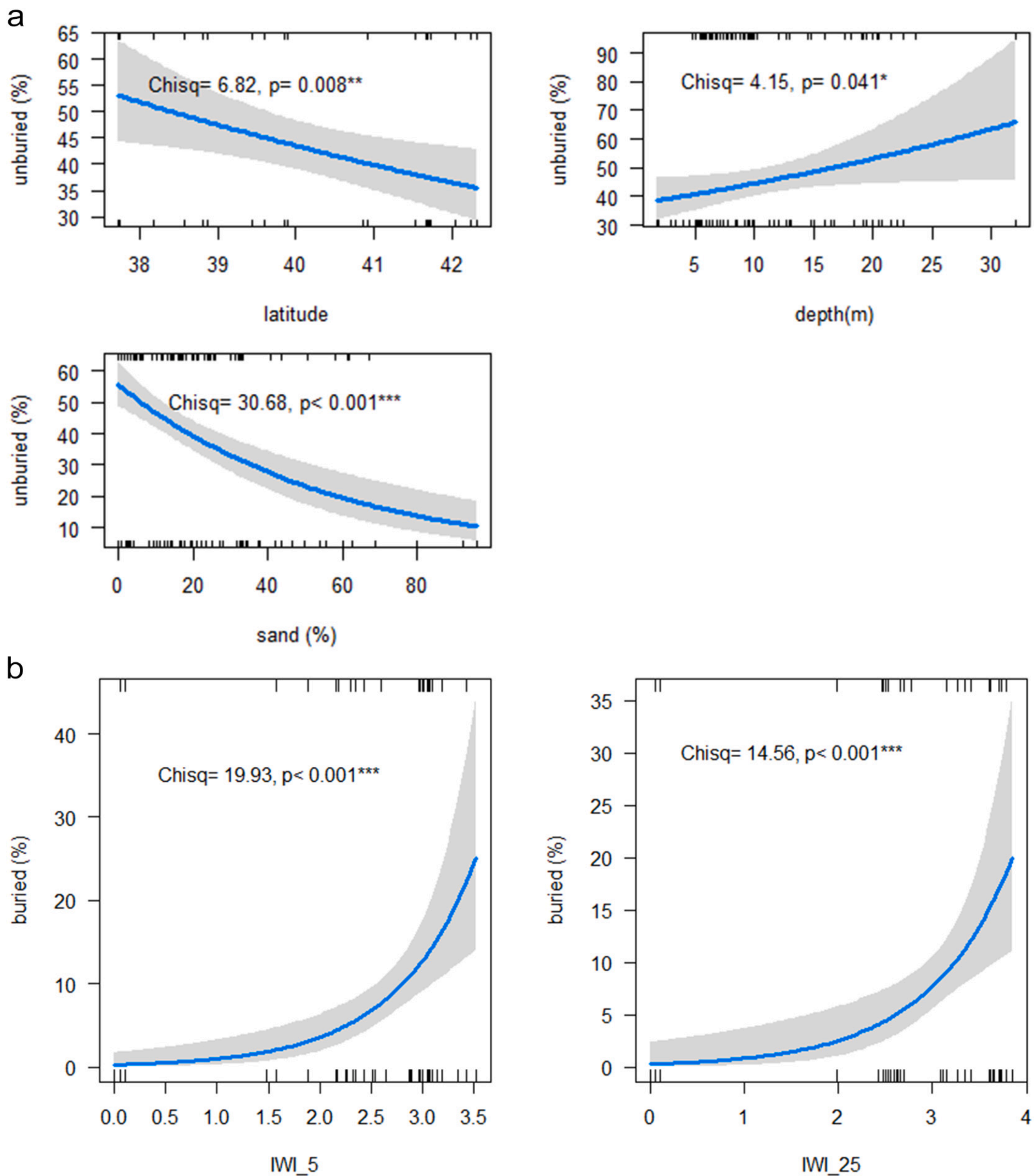

Fig. 7. a: General Linear model plots for response variable, unburial (%) and the significant explanatory variables: latitude, depth and sand. The grey areas represent confidence bands.
b: General Linear model plots for response variable burial (%) and the significant explanatory variables Index of Wave impact (IWI) at 5 and 25 km distance. The grey areas represent confidence bands.

increase over the next century. In the final analysis, if we need to get beyond symptomatic solutions, we need the global scale of the problem of climate change to be tackled with equally global solutions. While avoiding fragmentation is the best we can do locally, unless global climate change reverts, there is little that can be done to reverse the storm-driven declines of seagrass meadows.

CRediT authorship contribution statement

Candela Marco-Méndez: Writing – review & editing, Writing – original draft, Visualization, Supervision, Software, Resources, Project administration, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Núria Marbà:** Writing – review & editing, Writing – original draft, Validation, Supervision, Resources, Project administration, Methodology, Investigation, Funding acquisition, Conceptualization. **Ángel Amores:** Writing – review & editing, Writing – original draft, Visualization, Validation, Supervision, Software, Resources, Methodology, Investigation, Formal analysis. **Javier Romero:** Writing – review & editing, Resources, Investigation. **Mario Minguito-Frutos:** Writing – review & editing, Resources, Investigation. **María García:** Writing – review & editing, Resources, Investigation. **Jordi F. Pagès:** Writing – review & editing, Software, Resources, Investigation. **Patricia Prado:** Writing – review & editing, Resources, Investigation. **Jordi Boada:** Writing – review & editing, Resources, Investigation. **José Luis Sánchez-Lizaso:** Writing – review & editing, Resources, Investigation. **Juan Manuel Ruiz:** Writing – review & editing, Resources, Investigation. **Gregori Muñoz-Ramos:** Writing – review & editing, Resources, Investigation. **Neus Sanmartí:** Writing – review & editing, Resources, Investigation. **Elvira Mayol:** Writing – review & editing, Resources, Investigation. **Xavier Buñuel:** Writing – review & editing, Resources, Investigation. **Jaime Bernardeau-Esteller:** Writing – review & editing, Resources, Investigation. **Pedro Clemente Navarro-**

Martinez: Writing – review & editing, Resources, Investigation. **Lázaro Marín-Guirao:** Writing – review & editing, Resources, Investigation. **Carlos Morell:** Writing – review & editing, Resources, Investigation. **Marlene Wesselmann:** Writing – review & editing, Resources, Investigation. **Rita Font:** Writing – review & editing, Resources, Investigation. **Iris E. Hendriks:** Writing – review & editing, Resources, Investigation. **Xavier Seglar:** Writing – review & editing, Resources, Investigation. **Judith Camps-Castella:** Writing – review & editing, Resources, Investigation. **Eli Bonfill:** Writing – review & editing, Resources, Investigation. **Aurora Requena-Gutiérrez:** Writing – review & editing, Resources, Investigation. **Fabio Blanco-Murillo:** Writing – review & editing, Resources, Investigation. **Javier Aguilar-Escribano:** Writing – review & editing, Resources, Investigation. **Santiago Jimenez-Gutierrez:** Writing – review & editing, Resources, Investigation. **Joaquín Martínez-Vidal:** Writing – review & editing, Resources, Investigation. **Juan Eduardo Guillén:** Writing – review & editing, Resources, Investigation. **Maria Elena Cefalì:** Writing – review & editing, Resources, Investigation. **Marta Pérez:** Writing – review & editing, Resources, Investigation. **Marta Marcos:** Writing – review & editing, Writing – original draft, Validation, Supervision, Resources, Methodology, Investigation. **Teresa Alcoverro:** Writing – review & editing, Writing – original draft, Validation, Supervision, Resources, Project administration, Methodology, Investigation, Funding acquisition, Conceptualization.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be made available on request.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.scitotenv.2023.168404.

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