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Discovering a beach “cemetery” of a seagrass *Posidonia oceanica* barrier reef: Search for clues to reconstruct its origins

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ABSTRACT

Barrier reefs are peculiar structures of high ecological importance formed by the Mediterranean seagrass *Posidonia oceanica* in very shallow areas through the accretion of biogenic *matte*. This study reports for the first time the multiple discovery of several *matte* blocks of *P. oceanica* stranded on the southern coast of Sicily (central Mediterranean) in front of a barrier reef. Unmanned Aerial Vehicle (UAV) mapping of the barrier reef and morphological analysis of the blocks made it possible to hypothesise that the original substrate of the stranded blocks was rocky, and that the colonisation of this substrate may have been facilitated by boring bivalve molluscs through a so far unexplored plant-animal interaction. Furthermore, the indirect estimation of the theoretical bathymetric origin of the blocks through a shoot density depth model, combined with the retrospective analysis of the time series of the wave regime prior to stranding, suggests that a severe storm caused this collective uprooting and stranding event from very shallow depths, raising new questions about the vulnerability of these important ecosystems to the increase in frequency and intensity of storms expected in the climate change scenarios.

1. Introduction

Posidonia oceanica (L.) Delile is an endemic, long-lived Mediterranean seagrass that forms extensive meadows providing multiple ecosystem services (Campagne et al., 2015). This species is also considered an ecosystem engineer due to its ability to reshape the environment by significantly modifying its physical, chemical and biological properties (Koch, 2001). In particular, *P. oceanica* is the only seagrass species that forms a biogenic structure called *matte*, which consists of the progressive burial of roots, rhizomes and attached leaf sheaths, together with entrapped sediment (Molinier and Picard, 1952; Boudouresque and Meinesz, 1982), representing a massive long-term carbon sink (Mateo et al., 2006). The vertical accretion of the *matte* determines the seabed elevation over time, which was estimated to average between 1.1 and 2.3 mm per year (Romero et al., 1994; Lo Iacono et al., 2008).

Under suitable conditions, *P. oceanica matte* accretion leads to the formation of biogenic structures called barrier reefs (*récif barrier sensu* Boudouresque and Meinesz, 1982), where outcropping *P. oceanica* leaves dampen hydrodynamics, dissipating wave energy (Molinier and Picard, 1952; Hemminga and Duarte, 2000) and creating lagoon-like environments on the landward side. In addition, the barrier reefs have a high morphological complexity due to the formation of cliffs, channels and *P. oceanica* atolls, which is also reflected at the structural and functional levels. Indeed, a high seagrass diversity has been observed in barrier reefs, with 75% of the native Mediterranean seagrass species co-occurring at a very small spatial scale, a rather unusual setting in the Mediterranean Sea where seagrass meadows are generally monospecific (Tomasello et al., 2020). Due to the complexity of the seascape and the long formation process of hundreds to thousands of years, *P. oceanica* barrier reefs are considered as "natural monuments" and require monitoring and conservation efforts (Pergent et al., 2014; Tomasello et al., 2020).

In recent decades, several authors have highlighted a regression

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trend of *P. oceanica* meadows throughout the Mediterranean Sea, although the extent of this phenomenon is still controversial, ranging from an almost stable to catastrophic scenarios (Boudouresque et al., 2021). Nevertheless, there is consensus that *P. oceanica* loss leads to sediment erosion and the consequent oxidation of buried carbon, transforming the dead *matte* from a sink to a source of carbon (Pergent et al., 2014; Boudouresque et al., 2016) although it has also been observed that the dead *matte* can retain its carbon storage capacity under certain conditions (*e.g.*, low hydrodynamics, colonisation by more opportunistic seagrass species or macroalgae) (Apostolaki et al., 2022).

However, it is clear that seagrass meadows are now threatened by multiple stressors (Stockbridge et al., 2020) and shallow meadows and barrier reefs, in particular, are especially vulnerable to storms, which are expected to increase in the near future as a consequence of climate change (IPCC, 2019). Particularly in the Mediterranean, one of the regions with the highest cyclogenesis in the world (Lionello et al., 2006), storms affect seagrass meadows through over-sedimentation (Gera et al., 2014) or physical damage, resulting in a halving of shoot coverage and the accumulation of detached vegetative material (leaves, shoots, small *matte* fragments) on the seabed or beaches, depending on the currents and local environmental conditions (Balestri et al., 2011; Oprandi et al., 2020). Although the accumulation of detached seagrass leaves and detritus is a common phenomenon along beaches (*e.g.*, Tomasello et al., 2022 and references therein), there are only two references in the literature that reportfindings of uprooted *matte* blocks after severe storms. In more detail, the former reported a *matte* block of about 30 cm width stranded in Corsica (France) after a storm (Boudouresque et al., 2016). In contrast, the latter described the finding of *matte* blocks with living shoots no longer anchored to the substrate between the lower and upper limits of a *P. oceanica* meadow on the Ligurian coast (Oprandi et al., 2020).

This study reports the discovery of multiple stranding of numerous *matte* blocks in front of a *P. oceanica* barrier reef in southern Sicily (Italy, central Mediterranean Sea), forming a sort of *P. oceanica* meadow "cemetery" along the coast. As far as known, *matte* blocks strandings of such magnitude have never been recorded before. This serendipitous discovery highlighted the need to investigate the vulnerability of *P. oceanica* barrier reef ecosystems using a multi-faceted approach. Firstly, the depth and sediment typology from which the *matte* blocks originated were estimated through field and laboratory analyses combined with Unmanned Aerial Vehicle (UAV) photogrammetry. In addition, a retrospective analysis of time series data of the wave regime prior to the stranding was carried out to infer the causes of these stranding events.

2. Materials and methods

2.1. Study area

Stranded blocks of *Posidonia oceanica matte* were discovered in November 2018 and 2019 at the Site of Community Importance (SIC ITA040015) Scala dei Turchi (Fig. 1a), a pocket beach along the Sicilian coast (Randazzo et al., 2021), east of the Punta di Maiata promontory. The Scala dei Turchi site is part of the Capo Rossello, Eraclea Minoa, Punta di Maiata, Punta Grande and Punta Piccola sections, all of which belong to a specific geological conformation of pelagic origin known as the Trubi Formation (Beltran et al., 2011). The geomorphology of the area is characterised by a series of cliffs with varying degrees of resistance to erosion, determined by the cyclic alternation of marls and marly limestones (Beltran et al., 2011), giving these rocks an iconic staircase landscape structure (Fig. 1b). In front of the Scala dei Turchi pocket beach, a *P. oceanica* meadow forms a barrier reef (Fig. 1c) growing on a *matte* and rocky substrate close to the shoreline (A. Tomasello pers. obs.).

2.2. Field and laboratory activities on stranded matte blocks

In November 2018, a *matte* block of *P. oceanica* was found on the beach of Scala dei Turchi completely upside down, with the roots exposed to the air and the top buried in the sand close to the sea. This unusual discovery was used to gather information on the morphology of the root system through detailed photographic images (Balestri et al., 2015). Numerous *matte* blocks were also found partially silted or colonised by terrestrial vegetation (online supplementary material, Fig. A1), further from the shore. On the other hand, the presence of *matte* blocks near the sea and in the intertidal zone was less frequent.

One year later, in November 2019, five more *matte* blocks were found on the same beach, but unlike the previous year, they were stranded with the leaf bundles facing upwards. This second finding was used for shoot density analysis, morphometric analysis and block size estimation.

2.2.1. Shoot density and theoretical bathymetric origin inference

Four of the five blocks of *P. oceanica matte* detected in November 2019 showed no necrotic tissue, allowing us to measure shoot density

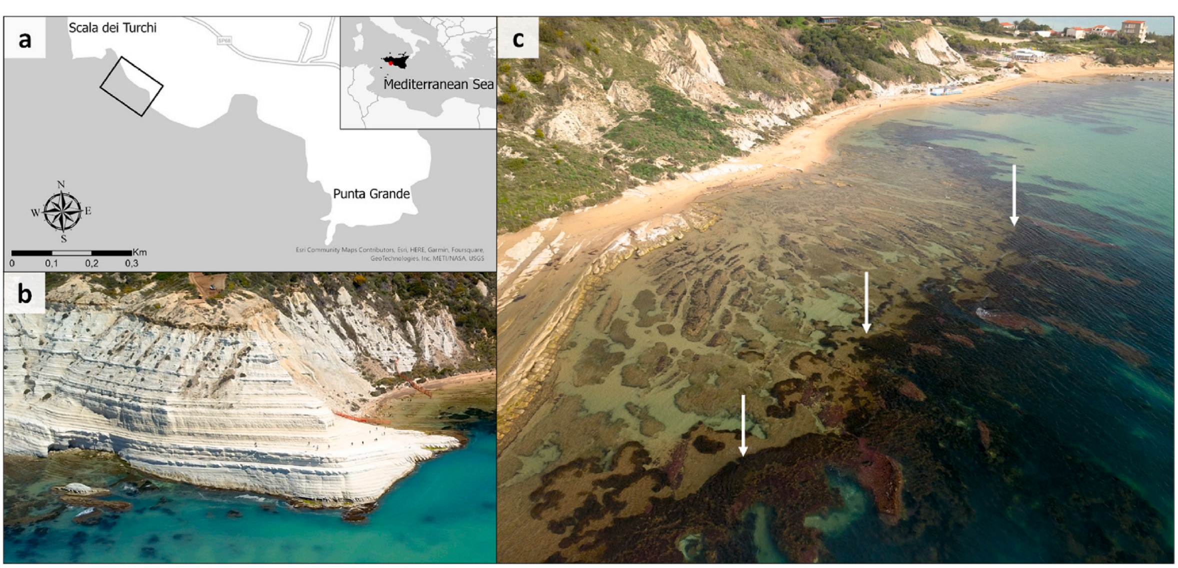

Fig. 1. a) Study area (southern Sicily, central Mediterranean Sea), b) Rocky ridge consisting of the Trubi Formation at Scala dei Turchi; c) *Posidonia oceanica* barrier reef marked by arrows. (ph A. Savona).

(Pergent et al., 1995). Conversely, the remaining block was excluded from these analyses as it showed clear signs of erosion at the top, with not perfectly distinguishable bundles and no leaf blades.

Shoots density was measured in the four selected blocks using a standard 40 cm × 40 cm quadrat (Panayotidis et al., 1981), or a 17 cm × 17 cm quadrat when the surface area of the blocks did not allow for proper placement of the standard quadrat (Supplementary material, Fig. A2). Shoot density was measured in triplicate for the largest blocks (*i.e.,* n. 1 and 3), and in two replicates for the smaller blocks (*i.e.,* n. 2 and 4). In all cases, density values were expressed as shoots m^{-2}.

The theoretical bathymetric origin of each *matte* block was estimated from shoot density values according to Pergent et al. (1995), who modelled the dependence of shoot density on depth using the following equation:

$$y = -254 \ln(x) + 1045.8 \quad \text{(Equation 1)}$$

where y is the number of shoots per square metre and x is the depth in metres.

Therefore, x is obtained by the following formula:

$$x = exp\ ((y - 1045.8) / 254) \quad \text{(Equation 2)}$$

2.2.2. Volume and mass measurements of the matte blocks

All the five blocks of *P. oceanica matte* detected in November 2019 were subjected to morphometry and size estimation. Where blocks were partially buried, the surrounding sand was removed with a shovel to isolate the blocks prior to measurements.

To calculate the volume of the *matte* blocks, the three dimensions of each block were measured directly in the field by using a folding rule. The shapes of all five blocks were then assimilated to regular polyhedra, following the approach used by Hendriks et al. (2010) and Montefalcone et al. (2015). Specifically, three geometric solid shapes were identified: i) quadrangular rhomboid prism (block 1); ii) quadrangular prism with rectangular base (blocks 2, 3, 5); iii) regular triangular prism (block 4) (Fig. 2).

Two/three subunits were randomly sampled from each of the five *matte* blocks (14 in total) using a hand saw and then transferred to the laboratory where they were stored at −20 °C until analysis. From each frozen subunits a vertical "block slice" (from the leaf bundle to the root layer) was obtained with an electric hacksaw. This method took into account the intrinsic mass variation of the *matte* blocks, which are characterised by three overlapping layers, i.e., leaf bundle, rhizomes and roots, from top to bottom (Supplementary material, Fig. A3). The slices were then sealed in plastic bags and immersed in plastic containers filled with distilled water to record the change in water volume used as a proxy for the slice volume, according to Archimede's principle. All slices were then weighed wet and oven dried at 105 °C to constant weight (48h) to obtain wet and dry weight respectively. Finally, the mass-volume relationship of the block slices was analysed by linear regression, and the regression coefficient represented the density.

2.3. Extent of Posidonia oceanica barrier reefs

The extent of the *Posidonia oceanica* barrier reef was assessed using a DJI Mavic 1 drone equipped with a camera with a frame 1/2.3 CMOS sized 12.35 Mpx sensor (Tomasello et al., 2020). The focal length was 26 mm (35 mm format equivalent) and the flight height was 30 m, resulting in a ground sampling distance of 1 cm/pixel. In July 2019 (between 11:51 and 13:36 CET), 184 photographs were acquired and processed using the photogrammetry software Pix4Dreact (see below for details on data processing). The area of the reconstructed surface was 75,899 m^2, resulting in an average point density of approximately 3 cm equidistance.

Object Base Image Analysis (OBIA) was used to discriminate the *P. oceanica* meadow from the surrounding environment (Rende et al., 2020). Specifically, OBIA algorithms were combined with machine

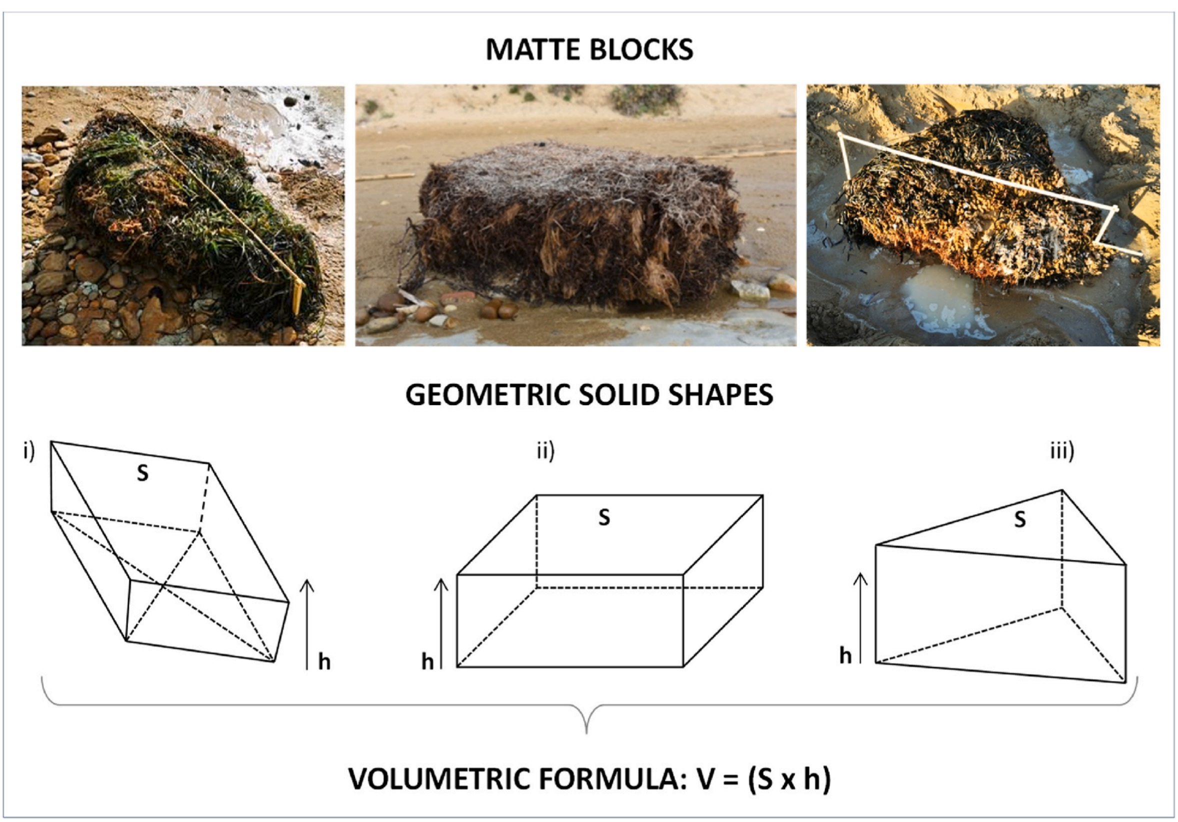

Fig. 2. *Matte* blocks and corresponding geometric solid shapes: (i) quadrangular rhomboid prism; (ii) quadrangular prism with rectangular base; (iii) regular triangular prism. The volumetric formula is also reported. V = volume, S = upper surface, h = height.

learning using eCognition Essentials software version 1.3. The data input consisted of the orthomosaic obtained by the UAVs – integrated with RGB bands. The EUNIS Habitat nomenclature was used to map the *P. oceanica* meadow, according to the following classes: 1) *Posidonia* beds, 2) Ecomorphosis of "barrier-reef" *Posidonia oceanica* meadows, 3) Sand, 4) Rock. The segmentation algorithm chosen was the Multi-resolution Segmentation which can create objects with as little internal heterogeneity as possible, representing significant elements of the area. Once the objects were created, 148 ground truth samples were used to train different types of classifiers available in the eCognition Essentials software and to classify the entire image. After classification, the vector of validation points was used to perform an accuracy assessment, again within eCognition Essentials, which generates an error matrix. The user and producer accuracy, overall accuracy and K index were therefore determined using 71 ground truth validation samples.

2.4. Significant wave height

Hydrodynamics conditions in the month (October 21, 2019–November 21, 2019) preceding the discovery of the second event of stranded *matte* blocks were reconstructed by analysing hourly significant wave height (H_s) data extracted from the Copernicus Marine Service Programme.

The information service provided is free and open to users (Copernicus Marine Service Programme, Korres et al., 2021). The spatial resolution was 0.042° × 0.042°.

The term "significant wave height" (H_s) refers to a well-defined and standardised statistical method of expressing the characteristic height of random waves in a sea state (Thomsen, 2014). More specifically, it indicates the average height of the third highest sea surface wave generated by wind and swell and describes the vertical distance between the crest and trough of the wave (European Centre For Medium Range Weather Forecast, Holthuijsen, 2007). For instance, a record of a significant wave height of 2 m is likely to be an average value, as waves of about twice that height can occur, albeit rarely (Thomsen, 2014). Through H_s it is possible to estimate the maximum height (H_{max}) of waves hitting the coast (Consorzio LAMMA, Holthuijsen, 2007) using the following formula

$$H_{max} = H_s \bullet 2 \quad \text{(Equation 3)}$$

3. Results

3.1. Characteristics of the stranded matte blocks

The upside-down *matte* block found in November 2018 near the shore was peculiar in terms of the spatial configuration of the roots. In particular, the roots of the outermost part formed a very dense and compact network due to the numerous intertwined growth axes, which however assumed a predominant coplanar orientation defining a rather flat and regular surface (Fig. 3a). Exceptions were areas where the roots change direction by emerging from the surface plane formed by the surrounding roots through small subspherical or truncated cylindrical outgrowths with transversely broken roots (Fig. 3b), or by forming depressions (Fig. 3c). In addition, the outermost roots along the flat surface of the block were often broken along the longitudinal axis for most of their length (Fig. 3d).

Field measurements of the five stranded *matte* blocks found in November 2019 showed high variability in size, with surface area (S) ranging from 0.14 to 0.72 m^2, height (h) from 0.19 to 0.38 m, and the corresponding total volume varying from 0.03 to 0.27 m^3 (Table 1).

The relation between the mass and volume of the block slices allowed the estimation of wet and dry density (Fig. 4, Table 1), which in turn were used to estimate the wet and dry mass of the whole *matte*

Table 1
Morphometry and total mass of the stranded *matte* blocks. S = upper surface, h = height, V = volume.

Matte block	S (m^2)	h (m)	V (m^3)	wet density (kg/m^3 ww)	dry density (kg/m^3 dw)	wet mass (kg ww)	dry mass (kg dw)
1	0.50	0.33	0.17			98	48
2	0.27	0.35	0.09			52	26
3	0.72	0.38	0.27	577.0	284.3	156	77
4	0.14	0.23	0.03			17	9
5	0.26	0.19	0.05			29	14

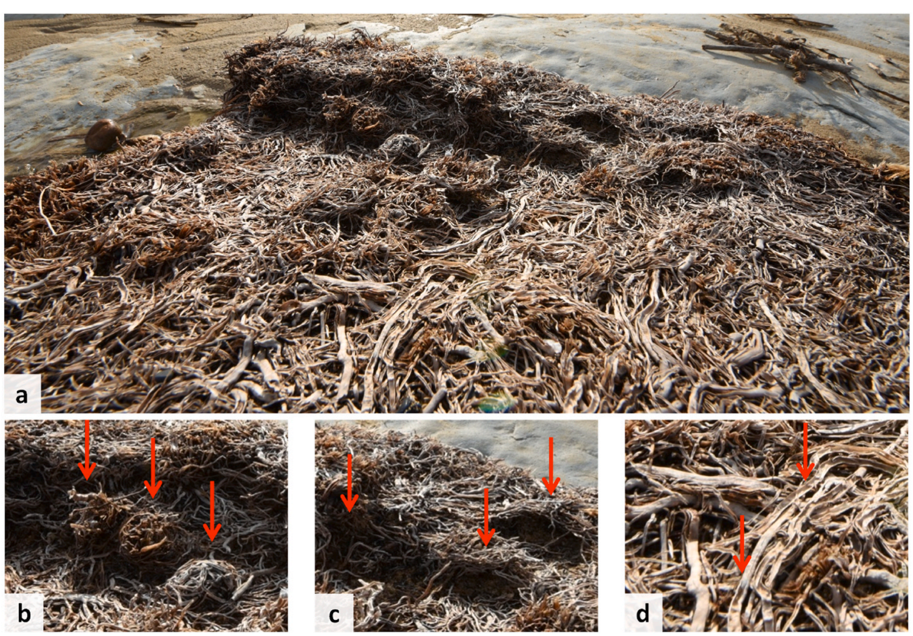

Fig. 3. a) Photographs of the upside-down block showing a) roots growing almost parallel to the surface and b) roots aggregating into emerging subspherical or truncated cylindrical structures; c) depressions in the surface root system; d) broken roots along longitudinal sections parallel to the block surface.

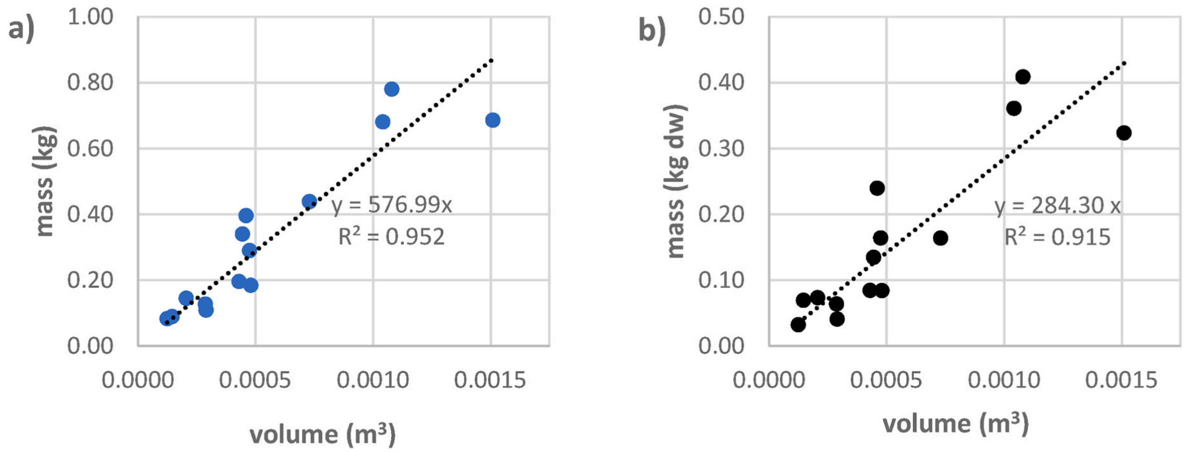

Fig. 4. Relationship between wet mass (kg ww) (a) and dry mass (kg dw) (b) and volume (m^3) of *matte* blocks.

blocks, which ranged from 17 to 156 kg w.w. and from 9 to 77 kg d.w., respectively (Table 1), with an average water content of about 50%.

3.2. Shoot density and theoretical bathymetric origin

Shoot density measured in four of the five blocks varied from 911.1 to 2011.1 shoots m^{-2} with a mean (± SE) value of 1550.0 ± 134.4 shoots m^{-2} (Fig. 5). According to Equation (2), the theoretical bathymetric origin ranged from 0.02 to 1.7 m, with most values corresponding to very shallow areas (< 1 m) (Fig. 5).

3.3. Reef extension

The photomosaic of the reef showed very clearly the distribution of *Posidonia oceanica* (Fig. 6a) due to the high transparency and the shallowness. The *P. oceanica* meadow is present above several more or less continuous clear rock outcrops, arranged orthogonally to the horizontal axis of the image and interspersed with channels, often covered by sand or rock, with no *P. oceanica* plants above. Proceeding towards the shoreline, the typical multi-arc atolls (*sensu* Tomasello et al., 2020) can be recognised, beyond which the lagoon occurs, and the meadow disappears completely (Fig. 6b and c). According to the Kappa Nearest Neighbour (KNN) algorithm, the following thematic classes were identified, with the corresponding area: *Posidonia* beds: 2.07 ha, Ecomorphosis of "barrier-reef" *Posidonia oceanica* meadows: 0.73 ha, Sand: 2.37 ha, Rock: 1.7 ha (Fig. 6d). The obtained classification had an overall accuracy of 83.10% and a Kappa Index of 0.81 (Table 2).

3.4. Significant wave height

In the first half of the month preceding the discovery of the five *matte* blocks in 2019, two medium-intensity storms (wave height of about 2 m) were recorded. In the second half of the month, instead, several storms of slightly higher intensity occurred, characterised by a significant wave height between 2 and 3 m. In particular, around the 13th of November, *i. e.*, 7 days before the discovery of *matte* blocks, an extreme event occurred, with a significant wave height of more than 4 m (Fig. 7). Applying the formula given in Equation (3), it was estimated that waves of more than 8 m occurred off the coast studied.

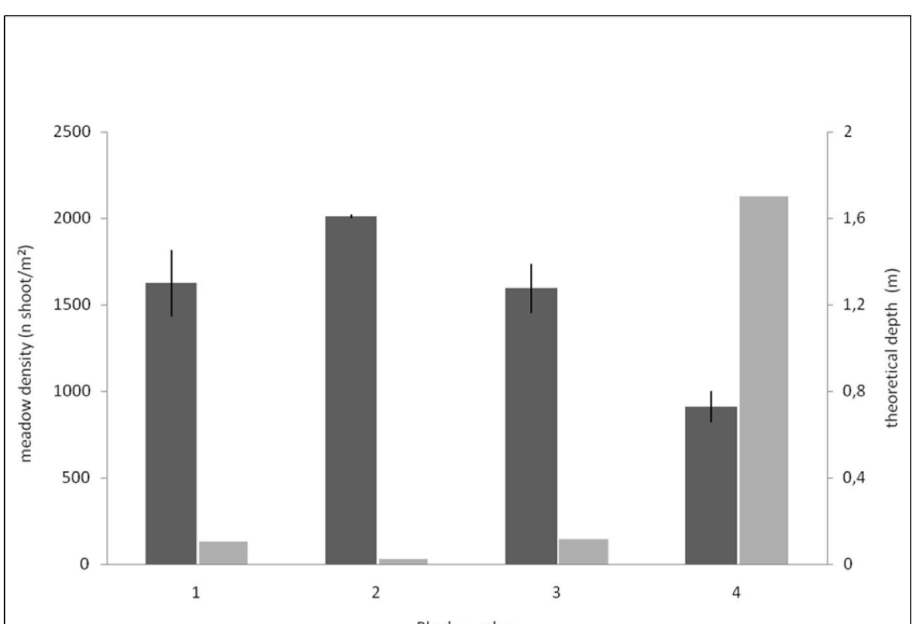

Fig. 5. Mean shoot density (±SE) and theoretical depth of four stranded *matte* blocks.

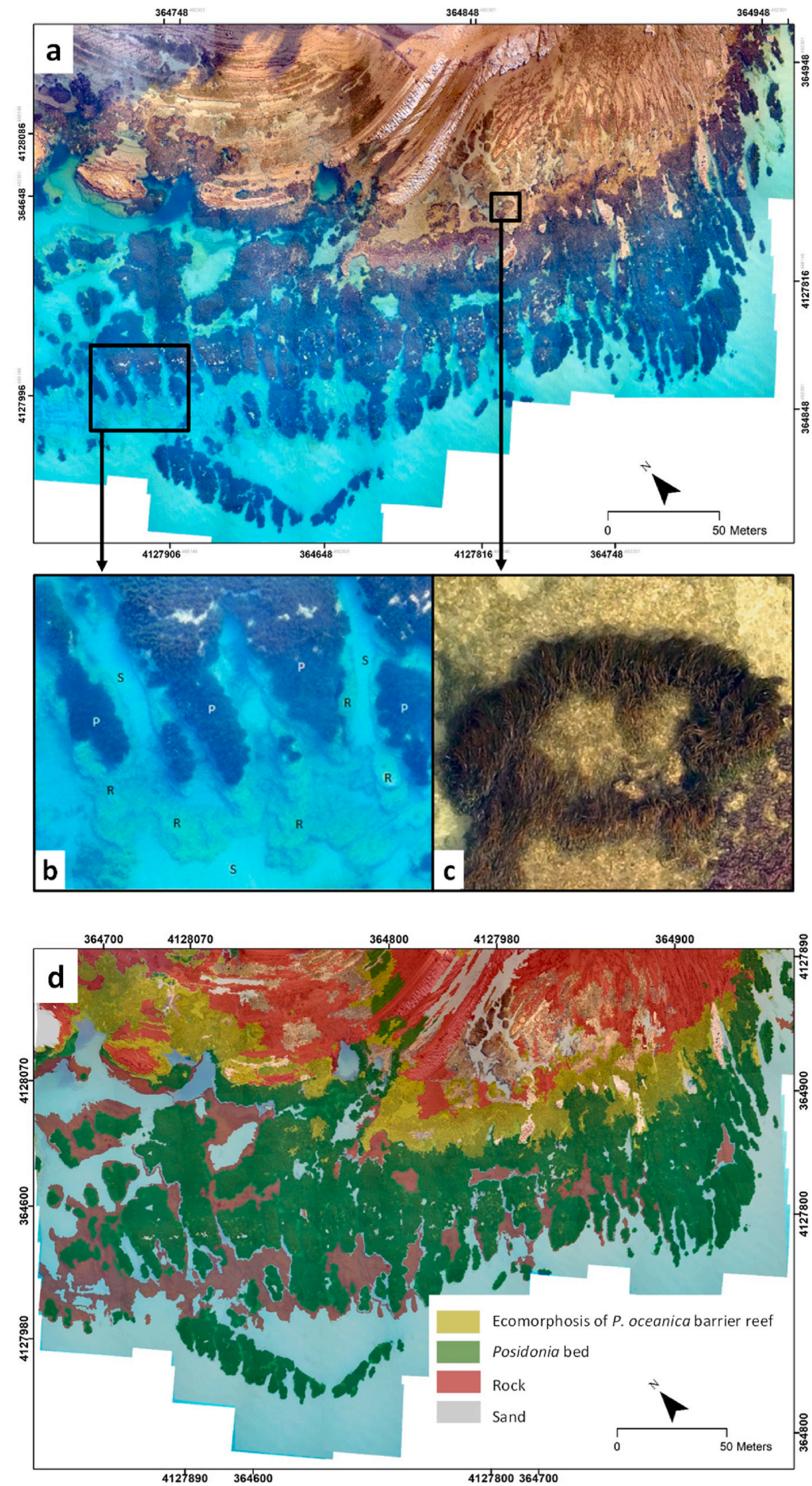

Fig. 6. a) Photomosaic of the reef showing very clearly the distribution of *Posidonia oceanica*, with focus on b) *P. oceanica* growing on rocks (P= *Posidonia*, S = sand, R = rock) and c) multi-arc atoll formed (sensu Tomasello et al., 2020). d) Object-based Image Analysis (OBIA) classification and thematic classes detected by means of Kappa Nearest Neighbour (KNN) algorithm classification.

Table 2
Accuracy of the KNN algorithm classification systems.

KNN overall accuracy: 83.1%; K = 0.81		
Class	User's accuracy	Producer's accuracy
Ecomorphosis of *P. oceanica* barrier reef	100%	66.7%
P. oceanica bed	92.3%	100%
Rock	100%	71.4%
Sand	83%	100%

4. Discussion

4.1. Theoretical substratum origin of Posidonia oceanica matte blocks

Morphological analysis of the stranded *matte* blocks coupled with the photogrammetric analysis of the adjacent *P. oceanica* barrier reef allowed the substratum from which the blocks originated to be inferred. In more detail, the peculiar morphological structure of the *matte* blocks stranded on the beach suggested that they had entirely detached from the substrate. Indeed, the block sections revealed the presence of intact rhizomes in the epigeal and hypogeal layers and the clearly separated root layer further down. Additionally, the root system of all stranded blocks exhibited visible high biomass, dense clustering and horizontal orientation. These are the typical characteristics of *P. oceanica* roots growing on rocky substrates (Di Carlo et al., 2007; Balestri et al., 2015; Tomasello et al., 2018) which have been attributed to the exploratory strategy of *P. oceanica* to find cracks into which roots can penetrate to strengthen their anchorage (Montefalcone et al., 2016), further enhanced by the mechanical and adhesive properties of the polymorphic root hairs (Badalamenti et al., 2015; Tomasello et al., 2018; Zenone et al., 2020).

At the same time, the acquisition and processing of the UAV images allowed the extent and morphology of the barrier reef formed by *P. oceanica* to be determined. Shallowness of the meadow and aerial view with very high resolution combined with optimal water transparency, made it possible to assess that in the outermost part of the meadow the reef occurred only on rocks while sandy bottoms were bare. This finding confirms that the development of *P. oceanica* meadows often occurs on rocky bottoms (Calvo et al., 1995; Badalamenti et al., 2015), especially in very shallow coastal areas with high hydrodynamics (Montefalcone et al., 2016; Tomasello et al., 2020).

This is further confirmed by the clear flat shape of the root system of the first *matte* block which was discovered in an inverted position, faithfully reproducing the morphology of the Trubi Formation, the typical substrate of the study area. The Trubi Formation contains a compact clayey marl (grain size class < 0.004 mm), which is susceptible to erosion by the sea, resulting in a typically flat and smooth surface. Under these circumstances, the plasticity of roots in changing the direction of growth (Balestri et al., 2015), combined with the adhesive strength of the root hairs (Zenone et al., 2022) grouped in gelatinous pads distributed along the radical axis at the points of contact with the substrate (Tomasello et al., 2018), enables the roots to adhere to the surface and assume its shape. However, the regularity of the flat surface

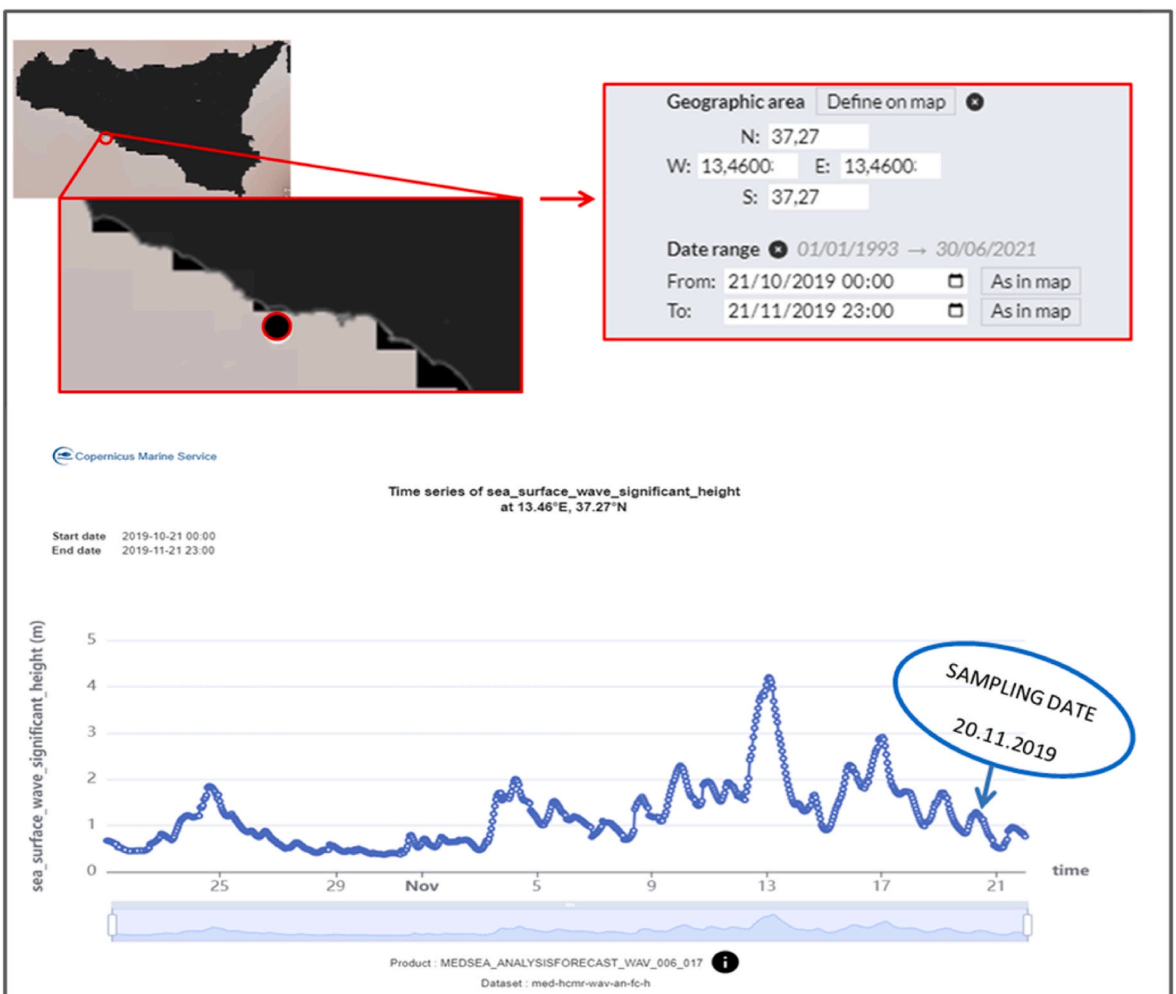

Fig. 7. Time series of significant wave height in the month preceding the discovery of the five *matte* blocks.

of the root system was interrupted by subspherical, tubular or conical root aggregates emerging orthogonally from the (inverted) block surface. Such peculiar structures, never observed before as far as is known, allowed to hypothesise that they may represent the casts formed by roots growing inside the burrows of two species of boring bivalves that are common in the study area (Consoli et al., 2016): the date mussel *Lithophaga litophaga* (Linnaeus, 1758) and the common piddock *Pholas dactylus* (Linnaeus, 1758). This hypothesis was corroborated by the recent and occasional finding of an additional small, stranded block at the same site (December 11, 2023), including *P. oceanica* plants along with the rocky substrate (Fig. 8), an event that is more unique than rare in nature.

The date mussel is a long-lived (> 50 years) endolithic species with elongated oval shells (> 90 mm long) (Peharda et al., 2015) that chemically erode carbonate rocks creating tunnels that are typically 1.5 times larger than the organism itself (Galinou-Mitsoudi and Sinis, 1995). The tunnels are mainly excavated from the vertical face of the rock and can be interconnected, further increasing the available colonisable area within the rock substrate (El-Menif et al., 2007). At the same time, the common piddock, whose mean density in the study area was estimated as 1348 ± 672 ind. m^{-2} with a mean length of 36.8 ± 22.8 mm (Consoli et al., 2016), is a very effective bioeroder, capable of removing up to 10.1 cm^3 of substrate over a 12-year lifespan (Pinn et al., 2005). However, the size of the holes produced varies greatly with age with 1-year-old piddocks creating burrows with an aperture of 4.4 ± 1.9 mm in diameter, a measure that increases by approximately 1.6 mm per year (Pinn et al., 2005). Based on these estimates, the total internal surface area of the burrows can appreciably modify the architecture of the initial flat surface area of the rocky substrate, significantly changing the relationship that *P. oceanica* can establish with it, shifting from two- to three-dimensional. The possibility that empty burrows become available for colonisation by other organisms is well known (Pinn et al., 2005), as is the ability of *P. oceanica* roots to penetrate holes and crevices in rocks (Mazzella et al., 1993; Hemminga and Duarte, 2000). The presence of very small holes in consolidated substrates is crucial as it facilitates mechanical interlocking, enabling roots to penetrate and anchor firmly in rocky substrates by thickening and lignifying their tips and walls (Zenone et al., 2024). However, to the best of current knowledge, a link between these two processes, suggesting the existence of a specific plant-animal interaction, has never been hypothesised, let alone described. Nevertheless, the findings of this study suggest that the presence of shape burrows created by bioeroders may facilitate the anchoring of plant roots on flat rocky substrates that would otherwise be challenging to colonise due to their low roughness, which is a limiting factor for *P. oceanica* establishment (Zenone et al., 2020). Further field and experimental studies with *P. oceanica* seedlings and shoots are required in order to gain a deeper understanding of the role of boring invertebrates in the plant-substrate relationship.

4.2. Theoretical bathymetrical origin and stranding causes of the matte blocks

The size and integrity of the blocks naturally detached and transported from the sea to the shore made it possible to assess their theoretical bathymetrical origin. Measurements of the density of the shoots growing on the stranded blocks, incorporated into the suitably adapted *P. oceanica* density-depth statistical model, were used to infer the theoretical bathymetry of the shoots prior to stranding. It was assessed that, prior to detachment and stranding, the shoots on the blocks were theoretically living at an average depth of 0.5 m, but in most cases were only a few centimetres below the water surface. This corresponds to the upper limit of *P. oceanica* forming the barrier reef in the study area (author's personal observation) and is also consistent with the findings of a recent study reporting a 3D centimetre reconstruction of another *P. oceanica* reef found on the southern coast of Sicily (upper limit mean depth: 0.27 m), where *P. oceanica* shoots were also found settled directly, or through a *matte* layer, on rocky outcrops or stones (Tomasello et al., 2020). Therefore, since the maximum recorded thickness of the stranded blocks found in this study ranged from 19 to 38 cm, the depth of the substrate to which the blocks were anchored prior to detachment would theoretically have been less than 1 m.

Analysis of the time series of the sea surface significant wave heights revealed that the study area was affected by intense storm events in the weeks immediately preceding the discovery of the *P. oceanica matte*

Fig. 8. a) Block of rocky substrate belonging to the Trubi Formation stranded at Scala dei Turchi following a storm. Cylindrical holes in the block and bundles of *Posidonia oceanica* with fresh leaves on the block are visible; (b) details of the root aggregates of *P. oceanica* associated with the block: truncated cylindrical root aggregates on the inside (red arrows) and outside (white arrows) of the block holes, intact cylindrical root aggregate on the outside of the hole in which it had grown, as indicated by the rounded apex (black arrow); c) details of roots growing in all directions inside the block holes, adhering to the walls and filling the space available inside. (ph F.P. Cassetti, A. Tomasello). (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

blocks. In particular, the Copernicus satellite system recorded a significant wave height of about 4 m just 9 days prior to the survey, suggesting that waves of up to 8 m may have occurred at about 2.5 km off the barrier reef. The energy of these swell waves may have exceeded the anchoring strength of the root system to the substrate, despite the improved anchoring provided by the colonisation of the burrows no longer occupied by piddocks, causing several blocks to be uprooted from the seabed and pushed towards the beach, including two very large blocks with masses of about 100 and 150 kg, which covered a distance of at least 80 m (*i.e.*, the minimum distance between the stranding point and the barrier reef mapped).

The detrimental effects of storm surges on seagrass meadows are well known, especially in shallow areas (Balestri et al., 2011; Oprandi et al., 2020), where the survival of the meadows is already compromised by their proximity to the sea surface and the higher intensity of physical disturbance (Paillard et al., 1993). Indeed, shallow seagrass meadows are known to be more vulnerable to mass loss than deeper meadows because the intensity of physical disturbance increases rapidly with decreasing depth (Gera et al., 2014). On the other hand, the high fragmentation of the meadows, caused by the detachment of entire *matte* blocks rather than individual shoots, in turn increases their exposure and vulnerability to hydrodynamics through positive feedback mechanisms (Oprandi et al., 2020). Therefore, this type of disturbance is expected to have a major impact on the resilience of the meadow (Duarte et al., 2007).

Although the results of this study show that high-magnitude storms affected *P. oceanica* barrier reef, it is not currently possible to quantify the total extent of the damage caused. Considering that uprooted blocks with alive shoots were also observed between the lower and upper limits of a *P. oceanica* meadow along the east coast of Liguria after a severe storm (Oprandi et al., 2020), it is likely that a similar phenomenon could have occurred at the Scala dei Turchi reef with a theoretical overall impact greater than that inferred from the stranding event alone. Furthermore, it should be noted that only a short time series of hydrodynamic conditions was considered in this study, while longer and more detailed investigations are needed to perform a more robust analysis and to confidently estimate the occurrence and impact of extreme storm events (Meucci et al., 2020). This is particularly relevant today, as climate models predict an increase in significant wave height due to the expected higher occurrence of extreme storm events under climate change scenarios (Menéndez et al., 2008; Izaguirre et al., 2010; Duarte et al., 2013).

5. Conclusions

As far as is known, this study provides the first documented evidence of erosion of shallow *Posidonia oceanica* reef resulting in the detachment and stranding of numerous and, in some cases very large, *matte* blocks after a severe storm, forming a sort of "cemetery" on the beach. The opportunity offered by this discovery combined with the methodological framework adopted allowed some aspects of the vulnerability of *P. oceanic*a barrier reef systems to be explored. First, UAV photogrammetric mapping of the barrier reef coupled with the morphological analysis of the *matte* blocks stranded on the beach let us to deduce that they were entirely detached from a rocky substrate. In addition, the overall flat morphology of the root system that was interrupted by digitate protuberances reproduced the peculiar three-dimensional outline of the adjacent rocky substrate, led to the hypothesis about a possible facilitating role of the boring bivalves *Pholas dactylus* and *Litophaga litophaga,* common in the study area for the anchoring of *P. oceanica*. Such a hypothesis, which would shed light on an unexplored plant-animal interaction, deserves further investigation. Second, this study found that the physical disturbance caused by extreme storms had a greater impact on the very shallow meadow, resulting in the destruction of entire sections of the barrier reef. However, it was not possible to assess the severity of the overall impact of these events, as it cannot be ruled out that detached blocks may have been also transported offshore. Concluding, the discovery of the *P. oceanica* reef "cemetery", along with the large volume of stranded *matte* blocks, represent a "wake-up call" as extreme climatic events are expected to become more frequent due to ongoing climate change. Further research in the same area and on other barrier reefs will help to understand the extent to which *P. oceanica* is threatened by extreme storms and the plant's mechanisms to counteract the intensity of storm surges, in order to identify mitigation and adaptation measures to ensure the survival of these unique natural monuments.

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CRediT authorship contribution statement

Agostino Tomasello: Writing – review & editing, Writing – original draft, Supervision, Resources, Methodology, Investigation, Funding acquisition, Conceptualization. **Geraldina Signa:** Writing – review & editing, Writing – original draft, Visualization, Methodology, Investigation. **Federica Paola Cassetti:** Writing – review & editing, Writing – original draft, Methodology, Investigation, Data curation. **Sante Francesco Rende:** Writing – review & editing, Writing – original draft, Visualization, Software, Formal analysis, Data curation. **Giovanna Cilluffo:** Writing – review & editing, Methodology, Formal analysis, Data curation. **Vincenzo Pampalone:** Writing – review & editing, Formal analysis, Data curation. **Salvatrice Vizzini:** Writing – review & editing, Supervision, Resources, 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.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.ecss.2025.109164.

Data availability

Data will be made available on request.

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