# Seagrass on the rocks: *Posidonia oceanica* settled on shallow-water hard substrates withstands wave stress beyond predictions

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# Abstract

A multidisciplinary approach was applied to investigate the role of abiotic constrains in the settlement of *Posidonia oceanica* on shallow rocks in two coastal areas of the Ligurian Sea (Italy, NW Mediterranean). Meadows developed very shallow upper limits, at 1.5 m depth in both areas, and with a distinctive morphology of stripes growing on rocky outcrops orthogonal to the coastline. Application of a predictive model to individuate the reference condition zone for the meadow upper limit, already validated on meadows developing on soft-bottoms, was not adequate for these rocky substrata as the meadow upper limits were found shallower than model predictions (>5 m depth). Geological and geomorphological characteristics of the rocky shores were analysed through geomechanic and petrographic analyses (i.e. thin sections, SEM analyses, rock hardness tests) whilst the shape and the features of the meadows (i.e. shoot density and maximum leaf length) were assessed through scuba diving surveys. Among the different lithotypes occurring at the sites in the alternating and interbedded outcrops, *P. oceanica* was passively selected (i.e. due to the seedlings survival and settlement there) on the strongest lithotypes, whilst the comparatively weaker rocks remained unvegetated and covered by a layer of soft-sediments. *P. oceanica*, settling on specific rocky substrata with favourable lithological and geomechanical characteristics, is able to establish outside the theoretical reference zone predicted by the model for soft sediments due to greater attachment strength and possible resistance to hydrodynamic forces. Combining biological, ecological, petrological, geological and geomorphological approaches showed effective for explaining the primary role of substratum nature in the spatial variability of seagrass meadows, with geomechanical and lithological characteristics of the rocks being equally important abiotic factors than sedimentological features.

**Keywords**: *Posidonia oceanica*, Ligurian Sea, rocky substratum, modelling, lithology; biogeomorphology.

## Introduction

Biotic and abiotic components of coastal systems are inherently linked at various spatial and temporal scales through complex interactions and feedbacks. The term "geobiology" was coined to highlight the integration of biological and geological approaches in environmental sciences (Nealson and Ghiorse, 2001). Geomorphology, in particular, affects habitat structure and functioning, defining the boundaries of ecosystems and provides a framework for the location of ecological processes (Rovere et al., 2010 and references therein). A multidisciplinary approach, thus, is one of the major goal for effective study and management in both terrestrial and marine ecosystems, to understand ecological responses to environmental pressures (Rovere et al., 2011), and to translate processes observed over limited spatial and temporal scales to longer-term landscape change (Stallin, 2006).

Seagrass meadows are among the most productive habitats in coastal areas, delivering essential functions and providing high-value ecosystem services, such as water oxygenation, seafloor and beaches stabilisation, areas for nursery and refuge, etc. (Cullen-Unsworth and Unsworth, 2013; Vassallo et al., 2013). Loss of seagrass-vegetated areas is a worldwide concern, mainly in areas of intense human pressures (Duarte et al., 2008; Boudouresque et al., 2009; Pergent et al., 2014). Effective management interventions (as for instance transplanting activities) and conservation efforts on seagrasses could benefit from a greater knowledge of all the physical variables influencing meadow development. In addition, to ensure an integrated coastal zone management (Mokhtar and Aziz, 2003), the complex interplay between biotic and abiotic components should be taken into account and anthropogenic and natural processes should be discriminated (Montefalcone et al., 2010).

Most seagrass species thrive on soft substrates in wave-sheltered areas, the only exception being the members of the genus *Phyllospadix*, which attach to rocks exposed to high wave energy; a restricted number of seagrasses, however, may colonise both rock and sand (Green and Short, 2003). Among the latter, one of the most important species is the Mediterranean endemic *Posidonia oceanica* (L.)

Delile. It forms large meadows from the sea surface down to 40 m depth (Pergent et al., 2014), and has the unique ability to build its own substratum – a terraced structure, named 'matte', which consists of intertwined roots and rhizomes with sediment trapped among them (Molinier and Picard, 1952). As a foundation species, *P. oceanica* develops meadows with high (more than 6 m) and lignified matte giving rise to local seafloor elevation (Boudouresque et al., 2012).

The substratum, in turn, has been shown to influence plant morphology and meadow characteristics (Marbà and Duarte, 1998; Di Carlo et al., 2006; Giovannetti et al., 2008; Badalamenti et al., 2015; Balestri et al., 2015). For examples, when *P. oceanica* develops on rock, it shows reduced shoot size and higher density compared to meadows on sand and matte (Short, 1983; Giovannetti et al., 2008). Sedimentological features of the bottom are also known to control meadow development (Gacia et al., 1999; Cavazza et al., 2000; De Falco et al., 2000, 2008; Gacia and Duarte, 2001; Boudouresque et al., 2012); however, their role is less important in the shallowest portion of the shore, i.e. where the meadow upper limit usually develops and where wave breaking is the dominant hydrodynamic process (Smith, 2003). A number of studies highlighted the influence of coastal hydrodynamics on meadow distribution and state of health (Infantes et al., 2009; Vacchi et al., 2010, 2012), while others showed the impacts of rip-currents in creating erosive channels within a meadow (Lasagna et al., 2011; Ferrari et al., 2014). Predictive models have thus been proposed to determine the expected seaward and landward boundaries of a meadow, in absence of major human pressures, on the basis of physical parameters alone, namely wave climate and seafloor morphology (Vacchi et al., 2010, 2012; Ferrari et al., 2013). These models, to date validated only on meadows developing in soft-bottoms, individuate the region of the seafloor that can be identified as the baseline, i.e. the reference condition zone of development for the *P. oceanica* meadow under natural conditions. These predictive models have also been shown to be effective tools for disentangling the role of natural vs. human constrains on the health status of *P. oceanica* meadows (Vacchi et al., 2014a, b).

According to seafloor characteristics, typology of substratum and hydrodynamics, meadows of *P. oceanica* may show different morphologies as categorized by Buia et al. (2004): i) uninterrupted and continuous meadow on soft bottoms; ii) terraced meadow on a continuous matte, which sometimes may be visible on the edge, and is typical in sites with considerable slope and intense hydrodynamics; iii) patches on rocks; iv) meadows with 'stripes', characterised by strips of meadow on matte that develop orthogonal to the coast, alternating with sandy channels of about 5 to 100 m in length and several meters in width; v) striped meadow that develops along wide-belted patches (with length of some kilometres and width of tens of meters) parallel to the coast and alternating with sandy areas; vi) hilly meadow characterised by small patches of matte that rise from the surrounding sandy, unvegetated areas; vii) atoll meadow on matte, with a typical ring shape, occurring in shallow and sheltered sites; viii) reef meadow showing a reef-like structure that rises up to the surface, sometimes with the formation of a small internal lagoon in very shallow and sheltered sites.

To date, few examples of studies using a geobiological approach are available on coastal marine environments (e.g. Rovere et al., 2011). The present paper aims at understanding the role of different abiotic constrains in the settlement of the Mediterranean seagrass *Posidonia oceanica*. A predictive model to individuate the theoretical depth of the meadow upper limit, already validated on soft-bottoms, was tested for the first time in rocky habitats. Geological, petrological and geomorphological characteristics of the rocky shores were investigated in two coastal areas of the Ligurian Sea (Italy, NW Mediterranean) where *P. oceanica* settled on rock, developing meadows whose upper limits show the distinctive morphology of stripes orthogonal to the coastline.

## Methods

### *Study area*

Two coastal areas along the Italian side of the Ligurian Sea (NW Mediterranean), both located in the western Ligurian Riviera, were investigated: Latte (LT) at Ventimiglia, close to the French border, and Capo Nero (CN) at Ospedaletti (Fig. 1). These two areas originated from different geological formations: Latte from the Provençal-Dauphinois Domain (Dallagiovanna et al., 2012), whilst Capo Nero from the Piedmont-Ligurian Domain (Giammarino et al., 2010). In the Latte area the outcrops are referred to the 'Flysch di Ventimiglia' Formation and consist of laminated sandstones interbedded by silty sandstones or silty claystones (Dallagiovanna et al., 2012). At Capo Nero the outcrops are referred to the 'Arenarie di Bordighera' Formation, which consist of siliciclastic, medium- to coarse-grained sandstones (up to conglomerates) interbedded with marlstones or claystones (see Giammarino et al., 2010 for a detailed description). In the two areas these rocks occur in subvertical stratification developed perpendicularly to the coastline.

The Ligurian coastline is mainly exposed to waves coming from the South (Ferrari et al., 2006; Cattaneo Vietti et al., 2010). SW is the dominant wave direction, with a fetch greater than 800 km and an off-shore wave height of more than 3 m, followed by the SE and the S wave directions. The former has a fetch of 200 km and waves of about 2 m, the latter has a fetch of 180 km and smaller waves (see Fig. 1 and Table 1).

Meadows of *Posidonia oceanica*, in both areas, develop between about 2 and 35 m of depth (Diviacco and Coppo, 2006). Lower limits appear in a good state of health and are positioned at depths compatible with the amount of light available on the bottom and the hydrodynamics of the two areas (Vacchi et al., 2012). Upper limits of the two meadows are very shallow and show the typical shape of stripes orthogonal to the coastline (Vetere et al., 1989; Diviacco and Coppo, 2006) (Fig. 2).

### *Data collection and analysis*

Field surveys were carried out to get information on the geomorphology and geological characteristics of the interbedded rocky outcrops from the backshore area to the upper limit of the two *P. oceanica* meadows. Strata position, i.e. measures of attitudes using a compass, and the seaward spatial continuity of emerged and submerged interbedded outcrops were assessed. Non destructive testing using a Schmidt hammer was performed to verify compressive strength of the different interbedded lithotypes identified in the emerged outcrops and to define their geomechanical characteristics. The test was replicated ten times at different points in each of the two areas and in correspondence of the lithotypes identified (see Results). The average measurement was calculated according to ASTM standards (ASTM, 2005): readings differing from the average of the 10 readings by more than 7 units were discarded and the average was then computed on the remaining readings. Data were combined in a Hoek & Bray chart to find the value of uniaxial compression strength in megapascal (MPa).

To confirm lithological classification, two rock samples were also taken from the emerged outcrops of each interbedded layer at each area: LT1 and LT2 at Latte and CN1 and CN2 at Capo Nero (see Fig. 2). The samples were studied in thin section under the polarizing microscope and were classified using Udden-Wentworth grain-size classification of terrigenous sediments (Wentworth, 1922). Samples of the rock in the submerged outcrops holding *P. oceanica* shoots have also been collected to be analysed with a scanning electron microprobe (SEM) using “SEM VEGA3 TESCAN” operated at 20 kV and equipped with the “EDAX-APOLLO_X DPP3” energy-dispersive (EDS) X-ray spectrometer.

Geometry, distribution, depth and distance from the coastline of the upper limit of the two meadows were assessed through scuba diving, and their typology was classified according to Buia et al. (2004). Observations were recorded along four underwater transects 300 m long laid on the bottom in each area, perpendicularly to the coast and separated about 50 m from each other (Montefalcone et al., 2006), starting from the shoreline and ending after the meadow upper limit in the middle portion of the meadow, at about 7 m depth at Latte and 10 m depth at Capo Nero. In correspondence with the meadow upper limit (on the belts) and at the end of each transect (within the meadow), the mean *P. oceanica* shoot density was measured using a 40 cm × 40 cm PVC frame in 5-replicated counts (Montefalcone, 2009) and the length of the leaf blade (indicatives of the meadow height) was measured using a rule, from 10-replicated measures of the longest leaf in each shoot. Differences in shoot density and leaf blade length values between meadow on belts and meadow at the end of the transects in the two areas were tested trough three-way ANOVAs. The model of the analyses consisted of three factors: sector (two levels: upper limit, end of transect) as fixed, meadow (two levels: LT and CN) as random and nested in sector, transect (4 levels: T1, T2, T3, T4) as random and nested in meadow, with $n$°=°5 observations per combination of factors levels for shoot density and $n$°=°10 for leaf blade length. Homogeneity of variance was tested by Cochran's test. When a treatment factor was significant, the differences between levels were determined using the Student–Newman–Keuls test (SNK test).

In each area, detailed bathymetric surveys were carried out with a single-beam echo-sounder (single frequency, error ± 0.1 m, 1 point every 5 seconds) and differential GPS to define the morphology of the seafloor where the meadow develops. A detailed 2D bathymetric map (1:5000) was produced for each area. From this map, combining the local wave climate parameters (Table 1 and Fig. 1), two hydrodynamic parameters were identified along the underwater beach profile: i) the breaking depth ($d_b$) is the depth where the wave breaks and is calculated using the formula $d_b = H_b/\gamma_b$, where $H_b = H_0 K_{sh} \sqrt{\varphi_o/\varphi_b}$ ($H_0$ = offshore wave height, $K_{sh}$ = shoaling coefficient, $\varphi_o$ and $\varphi_b$ = offshore and nearshore waves approach angle) and $\gamma_b = (b-a) \times (H_b/gT_0^2)$ ($a$ and $b$ being empirical coefficients depending on the slope of the beach, $g$ is the acceleration of gravity, $T_0$ is the period of the wave) (Smith, 2003); ii) the closure depth ($d_c$) is the depth where wave action on the seafloor becomes negligible and is computed using the formula $d_c = 6.75\ H_s$, where $H_s$ is the mean annual significant wave height (Sorensen, 2006). The annual offshore wave parameters (return time 1 year) was used in place of the daily average waves, as the latter can underestimate the effect of the annual extreme events on the meadow (Infantes et al., 2009; Vacchi et al., 2012).

To define the expected position of the upper limit of the *P. oceanica* meadows under natural conditions, the predictive model by Vacchi et al. (2010, 2014b), already validated for meadows developing on soft bottoms, was here applied in both areas. This model identifies the region of the seafloor where the upper limit of the meadow would be located according to the following two equations, which represent the minimum distance ($K_{min}$) and the maximum distance ($K_{max}$) in metres between the theoretical upper limit and the breaking depth:

$$K_{min} = 5.94 + 0.29\varepsilon$$

$$K_{max} = 17.83 + 0.41\varepsilon$$

$\varepsilon$ was computed using the equation $\varepsilon = a\omega^2/g \cdot \tan^2\beta$ (Jackson et al., 2005), where $a$ (breaker amplitude) $= H_0/2$ ($H_0$ = offshore wave height), $\omega$ (incident wave radian energy) $= 2\pi/T_0$ ($T_0$ = period of the wave), $g$ = acceleration of gravity, $\beta$ = the slope of the beach in the surf–zone. Finally, the predicted distances ($K_{min}$ and $K_{max}$) computed with the model in each meadow were compared with the measures taken during scuba surveys to verify the applicability of this model also on rocky bottoms.

## Results

Latte and Capo Nero were characterised by interbedded rocks that developed perpendicularly and sub-vertically to the coastline, from the backshore to a depth of about 7-10 m (Fig. 2). Two distinct lithotypes alternated in the interbedded outcrops. Samples CN2 at Capo Nero and LT2 at Latte appeared weaker than samples CN1 and LT1, respectively, due to the different minero-petrographic and geomechanical characteristics (Table 2 and Fig. 3). At both Latte and Capo Nero the morphology and lithology of the seafloor were in continuity with that of the backshore (see Fig. 2 and the schematic draw in Fig. 5). Underwater, the strongest lithotypes (corresponding to CN1 and LT1 samples) were also upraised relative to other sections of the seafloor to form rocky spurs that developed until the depth of about 7 m at Latte and 10 m at Capo Nero. These rocky spurs, at shallower depths, alternated with soft-sediments (gravels and sands) that covered the comparatively weaker rocks, whilst in a seaward direction (at depths greater than 7-10 m) medium- to fine-grained sands covered the underlying rocks.

In both areas *Posidonia oceanica* colonized only the strongest lithotypes rising-up from the seafloor on the rocky outcrops and was absent from the contiguous, and alternating, incoherent sedimentary grooves. At the end of these stripes, seaward, the meadow appeared homogeneous (Fig. 4). Analyses of variance showed that shoot density values of *P. oceanica* on the stripes (745±102 shoots $m^{-2}$ at LT and 750±73 shoots $m^{-2}$ at CN, at about 4 m depth) were higher ($p<0.0001$) than those recorded at the end of the transects (410±84 shoots $m^{-2}$ at LT and 405±72 shoots $m^{-2}$ at CN, at about 7 m depth) (Table 3). The mean length of the leaf blade on the belts (21±4 cm at LT and 33±12 cm at CN) was lower ($p<0.05$) than that at the end of the transects (68±13 cm at LT and 85±8 cm at CN) (Table 3).

The breaking depth and the closure depth were found at about 6 m and 9.5 m depth at Latte and at 4.5 m and 9.5 m depth at Capo Nero, respectively. At Latte the predictive model positioned the expected meadow upper limit in a zone between 62±13 m and 97±18 m of distance from the breaking depth, which corresponds to a zone between 6 m and 8 m depth, whilst at Capo Nero in a zone between 17±5 m and 34±7 m of distance from the breaking depth, which corresponds to a zone between 5 m and 6 m depth (Fig. 4).

## Discussion

Among the different morphologies displayed by the *Posidonia oceanica* meadow upper limit (Buia et al., 2004), the one developing with stripes orthogonal to the coastline has always been observed on soft-sediments (Vetere et al., 1989), where the vegetated stripes alternate with sedimentary channels and rise up from the bottom due to the continuous growth of the matte. In this paper we firstly described two *P. oceanica* meadows developing their upper limit with orthogonal stripes that grow on rocky spurs. The hypothesis that considered this morphology being due to the influence of strong rip-currents on the bottom, which create erosive channels inside the meadow (Boudouresque et al., 2012) does not hold in our meadows. At Latte and Capo Nero, this peculiar meadow morphology is due to the occurrence of sub-verticalized layers of rocks. Among the two different interbedded lithotypes outcropping in both areas, *P. oceanica* colonized only the strongest lithotype (i.e. that having subarkose composition with abundant sparry calcitic cement and higher values of uniaxial compression). On the contrary, the alternating lithotype is comparatively weaker and remains unvegetated and covered by a layer of soft-sediments (Fig. 5). Geomorphological and environmental features have been shown to control the development not only of *P. oceanica* meadows but also of other marine and near-shore vegetation communities, including other seagrass species (e.g. Adams et al., 2015; Vacchi et al., 2016).

Shallow soft-sediments, from tropical to temperate seas, are the preferential substrata colonized by most seagrass species, where they easily anchor and from which they take efficiently most of the nutrients (Touchette and Burkholder, 2000). On these sedimentary bottoms, the breaking depth (i.e. the still-water depth at the point where a wave breaks) represents the major constraint for the landward development of the meadows (Vacchi et al., 2010, 2012). At both Latte and Capo Nero, application of the predictive model showed that the upper limit of the two meadows should be located in the zone between the breaking depth and the closure depth (Vacchi et al., 2014b), i.e. at depths greater than 6 m and 5 m, respectively. However, we found the meadow upper limits at about 1.5 m depth in both areas: here the hard and strong rocky layers allowed the colonization of *P. oceanica* even in the more active hydrodynamic surf-zone. Colonization was instead prevented in the contiguous weaker layers, because wave action is too strong to ensure a solid anchorage of the plant on this kind of substratum (Vacchi et al., 2014b). Seagrass colonization on rock might be due to shoots pulled up by waves from the meadow below and forced into cracks and fissures of the rock, where they fix and survive, acting as pipings (Davico and Matricardi, 1995). *P. oceanica* can adjust root traits during plant development to maximize anchorage and substrate exploration efficiency (Balestri et al., 2015). An extensive presence of sticky hairs covering seedling roots has also been documented (Badalamenti et al., 2015): these adhesive root hairs are responsible for the anchorage strength displayed by seedlings settled on rocky substrates. Although *P. oceanica* is not specialised for rocky substrates, its plasticity allows for morphological and anatomical root adaptations similar to those of *Phyllospadix*, the only seagrass exclusive for rocky substrates in the surf zone (Cooper and McRoy, 1988). The strong anchorage of the plant on rock, consequent to the penetration of roots inside small cracks, is evident in the scanning electron microprobe images taken from the underwater rocky outcrops holding shoots of *P. oceanica* (Fig. 6).

On sedimentary bottoms the intense water movement may cause burial and displacement events, especially in the early stages of the plant life (Infantes et al., 2012). In both Latte and Capo Nero, the discontinuity in the seafloor morphology (due to interbedded lithologically and mechanically different layers) was likely to prevent displacement events, whilst the occurrence of the raised-up layers may help preventing shoot burial.

When *P. oceanica* develops on the strongest rocky layer, it shows reduced plant size and higher values of shoot density, as compared to the portions of the two meadows that develop on a sedimentary bottom. A reduced size of the aboveground system may reflect the obvious need for a better anchorage and the lower nutrient availability on rock (Giovannetti et al., 2008), which is an expression of the growth and size plasticity of seagrasses under stress conditions (Perez et al., 1994; Marbà and Duarte, 1998; Balestri et al., 2015). Strong hydrodynamics have also been shown to limit plant grow in shallow meadows (Koch et al. 2006; Infantes et al. 2009). Similarly, the high density is a strategy to compensate for the reduced aboveground size, to obtain maximum light energy and simultaneously optimize nutrient uptake (Short, 1983; Giovannetti et al., 2008).

Depth and morphology of the meadow limits have been recognized as efficient indicators of the state of health of *P. oceanica* meadows (Pergent-Martini et al., 2005) and may be spatially modelled to predict modifications of meadow distribution in response to human pressures (Vacchi et al., 2010, 2012, 2014b). Spatial modelling is an emerging approach to the management of coastal marine habitats, as it helps understanding and predicting the effects of global change (Valle et al., 2011; Downie et al., 2013; Vacchi et al., 2014a). Results of this study show the limited applicability of the predictive model to meadows developing on rocks (Vacchi et al., 2014b). In correspondence of rocks having particular and favourable lithological and geomechanical characteristics, settlement of *P. oceanica* can still occur under conditions of high wave energy and hydrodynamics, i.e. outside the theoretical reference condition zone individuated by the model, thanks for instance to trait morphological plasticity manifested in the roots (Badalamenti et al., 2015; Balestri et al., 2015). Notwithstanding the primary role of sedimentological features of the substrata in the settlement of *P. oceanica* meadows (Gacia et al., 1999; Cavazza et al., 2000; De Falco et al., 2000, 2008; Gacia and Duarte, 2001; Boudouresque et al., 2012), geomechanical and lithological characteristics of rocks are equally important factors to be taken into account, especially in the shallowest portions of the shore where hydrodynamics dictate seagrass meadow development.

## Conclusion

This study integrated distinct fields of research (i.e. biology, ecology, petrology, geology and geomorphology) through a collaborative effort of different specialists, thus offering new insights on the position of the upper limit of seagrass meadows. In the more active hydrodynamic surf-zone, seagrasses may colonize hard rock characterized by high values of compression strength. Under these conditions the plant is capable to settle where its development is usually prevented, as predicted by the model of Vacchi et al. (2014b). When the upper portion of the meadow is installed on sub-verticalized layers of rock, on which differential erosion acts, the arrangement of the strongest layers becomes the main element characterizing meadow geometry. This study showed how physical and biological phenomena play a central role in determining the overall geomorphology of the area and the development of the upper limit of *P. oceanica* meadows: further data, from other regions and/or different species, are needed to better clarify the role of mineralogical and petrographic characteristics of the substratum in seagrass settlement. In addition, future biogeomorphological studies to evaluate the crucial links between biological community dynamics and 'inorganic' earth surface processes are encouraged.

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Table 1. Main wave direction and local wave climate parameters characterizing the western Liguria. $H_0$ = offshore wave height (return time 1 year); $T_0$ = period of the wave (return time 1 year); $H_{S0}$ = mean annual significant offshore wave height. Data from Corsini et al. (2006) modified.

| Wave direction | $H_0$ (m) | $T_0$ (m) | $H_{S0}$ (m) |
|---|---|---|---|
| SW | 4.0 | 7.5 | 1.4 |
| S | 2.8 | 6.2 | 1.2 |
| SE | 2.6 | 5.8 | 0.9 |

Table 2. Minero-petrographic and geomechanical characteristics of the samples collected in Latte (LT) and Capo Nero (CN). See Figure 2 for sampling sites location.

| Samples | Maximum grain size (mm) | Sorting | Mean (±s.d.) uniaxial compression strength (MPa) | Composition |
|---|---|---|---|---|
| LT1 | 1 | poorly sorted | 43 ± 5 | Subarkose (quartz grains ≈ 80%, feldspars ≈ 15%, and subordinate lithics) with abundant fine-grained matrix. Some rare bioclasts and elongated mica flakes. Diffused sparry calcite cement. |
| LT2 | 0.25 | poorly sorted | 25 ± 5 | Fine-grained sandy siltstone with sub-angular quartz grains and calcitic cement. Some bioclasts and glauconite grains. |
| CN1 | 1 | moderately sorted | 57 ± 5 | Medium grained subarkose (quartz grains ≈ 85%, feldspars ≈ 10%, and subordinate lithics) with abundant sparry calcitic cement. The shape of the clasts is mostly subangular and subrounded. Lithic fragments are mainly represented by acid metavolcanics and gneisses; rare elongated mica flakes. |
| CN2 | 4 | poorly sorted | 15 ± 3 | Fine-grained siliciclastic conglomerate with arenaceous matrix, containing subrounded pebbles of polycrystalline quartz, feldspar, gneisses and acid metavolcanites (in order of relative abundance). Feldspars (both plagioclases and K-feldspar) partially altered. Poorly cemented by calcite. |

Table 3. Results of 3-way ANOVAs on meadow shoot density (shoot m$^{-2}$) and meadow height expressed as maximum length of the leaf blade (cm).

| | Shoot density | | | | Height | | | |
|---|---|---|---|---|---|---|---|---|
| Source of variation | df | MS | *F* | *p* | df | MS | *F* | *p* |
| Sector (S) | 1 | 2245840.2 | 7791.29 | 0.0001 | 1 | 98903.02 | 23.67 | 0.039 |
| Meadow (M) (SE) | 2 | 288.25 | 1.31 | 0.3050 | 2 | 4178.23 | 4285.36 | 0.000 |
| Transect (T) (S×M) | 12 | 219.49 | 0.03 | 1.0000 | 12 | 0.98 | 0.01 | 1.000 |
| Residual | 64 | 7503.4 | | | 144 | 102.69 | | |
| Total | 79 | | | | 159 | | | |
| Cochran's *C*-test | | n.s. | | | | n.s. | | |
| Transformation | | none | | | | none | | |

## Figure captions

Figure 1. Geographic location of the two study areas, Latte (LT) and Capo Nero (CN), in the western Liguria, with the relative annual wave climate (data from Corsini et al., 2006, modified). $H_{S0}$ is the mean annual significant offshore wave height (m) recorded by the La Spezia buoy (43°55’41.99” N; 09°49’36.01” E).

Figure 2. Aerial imageries (from Google Earth) of the two study areas, Latte (a) and Capo Nero (b), showing the morphology of the shallow portion of the two meadows. White boxes are blow up of Latte (c) and Capo Nero (d) coastal areas (from the Regione Liguria photographic database and available at http://www.regione.liguria.it/), where the main nearshore geomorphological features and the location of LT1, LT2, CN1, CN2 sampling sites are reported. White boxes are blow up of the detailed photographs collected at Latte (e) and Capo Nero (f), showing distinct interbedded lithotypes. The strong and weak layers are evidenced by selective erosion.

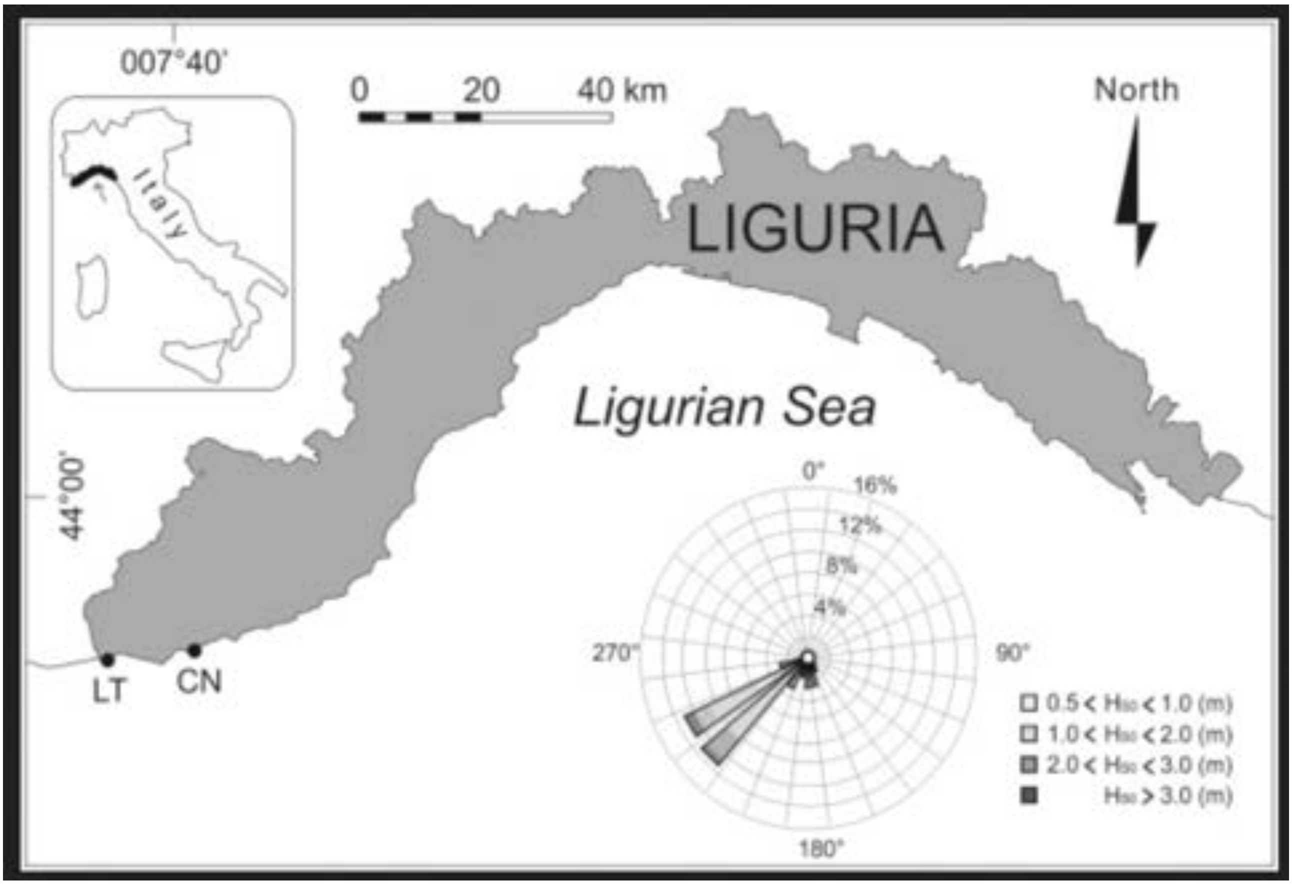
Figure 3. Microphotographs (under polarizing microscope, crossed polars) representative of the samples from Latte and Capo Nero. (a) LT1; (b) LT2; (c) CN1; (d) CN2.

Figure 4. Maps of *Posidonia oceanica* meadows at Latte and Capo Nero from Diviacco and Coppo (2006) and the predicted reference condition zone (the red band) contained between the two boundaries $K_{min}$ (minimum distance in metres between the theoretical upper limit and the breaking depth) and $K_{max}$ (maximum distance in metres between the theoretical upper limit and the breaking depth). The black boxes include the sampling areas showed in Figure 2.

Figure 5. Schematic draw representing the interbedded rocky outcrops with belts of *Posidonia oceanica*. Ranges of the uniaxial compression strength (UCS, in MPa) defining strong and soft layers are reported with ranges of meadow shoot density (D, shoot $m^{-2}$) and meadow height

expressed as maximum length of the leaf blade (MH, in cm) found in correspondence of the strong layers.

Figure 6. Scanning electron microprobe (SEM) images of the interaction between *Posidonia oceanica* roots and hard rock from samples collected in the underwater rocky spurs. On the right is a blow up of the image within the white box.



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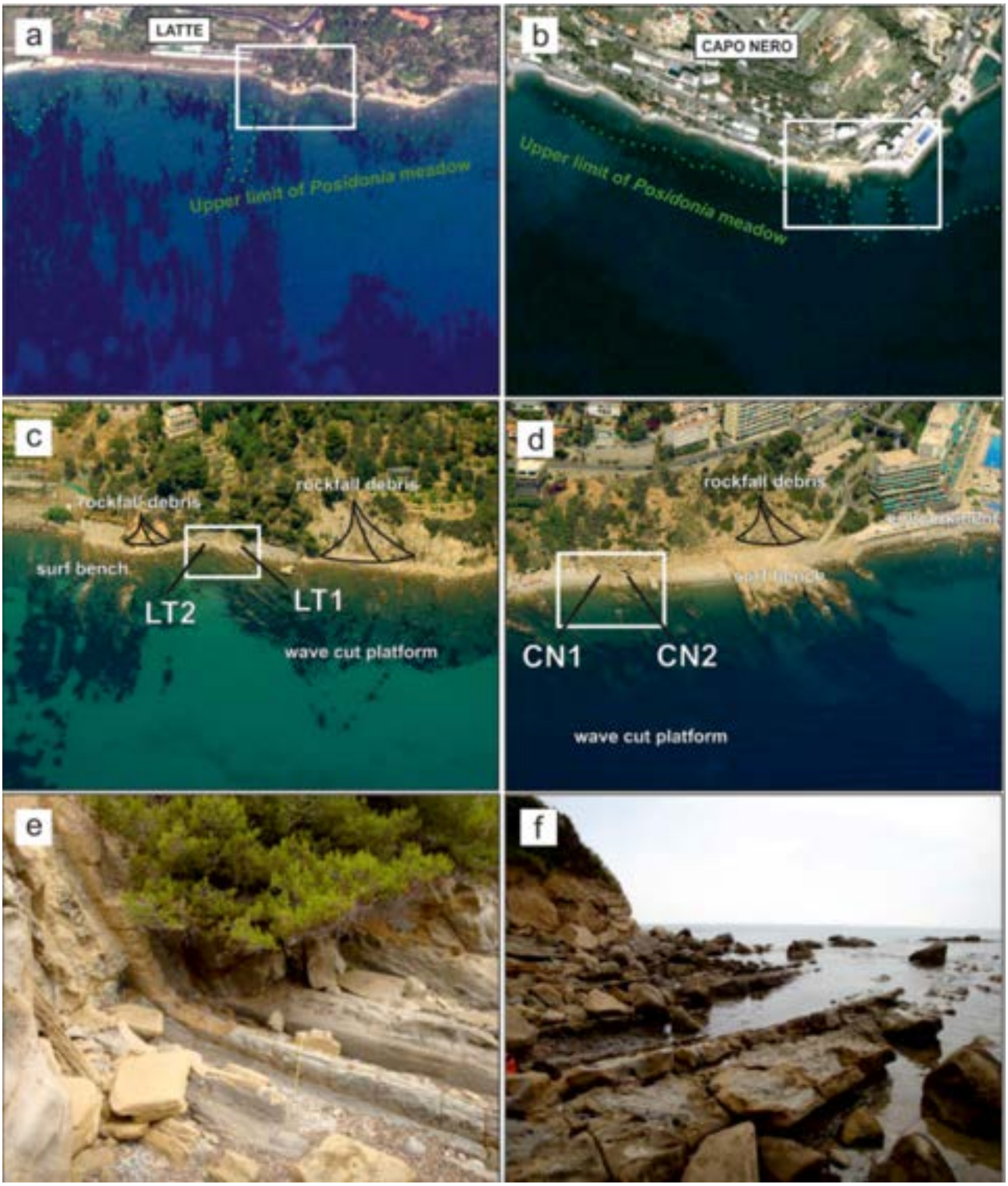

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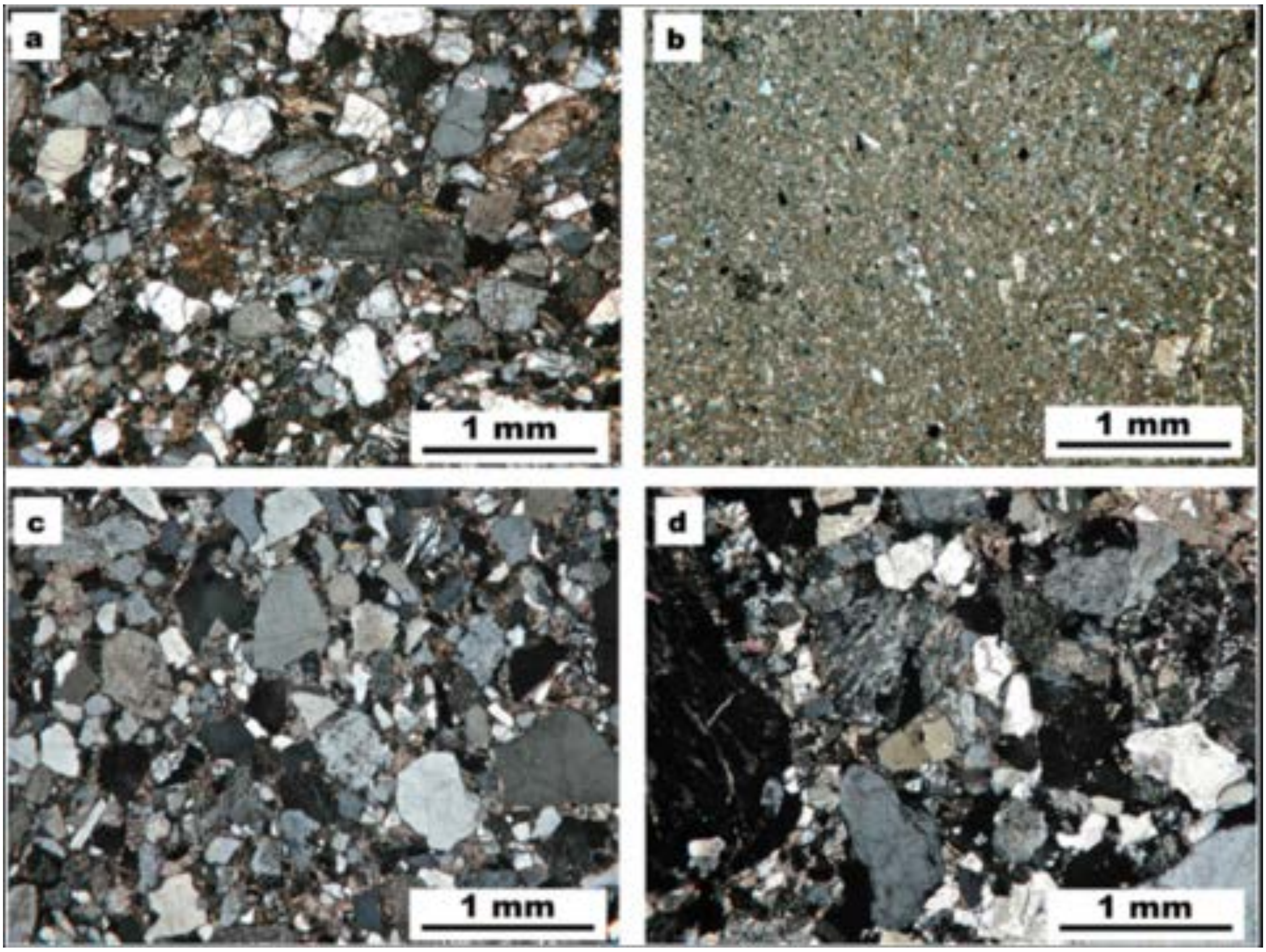

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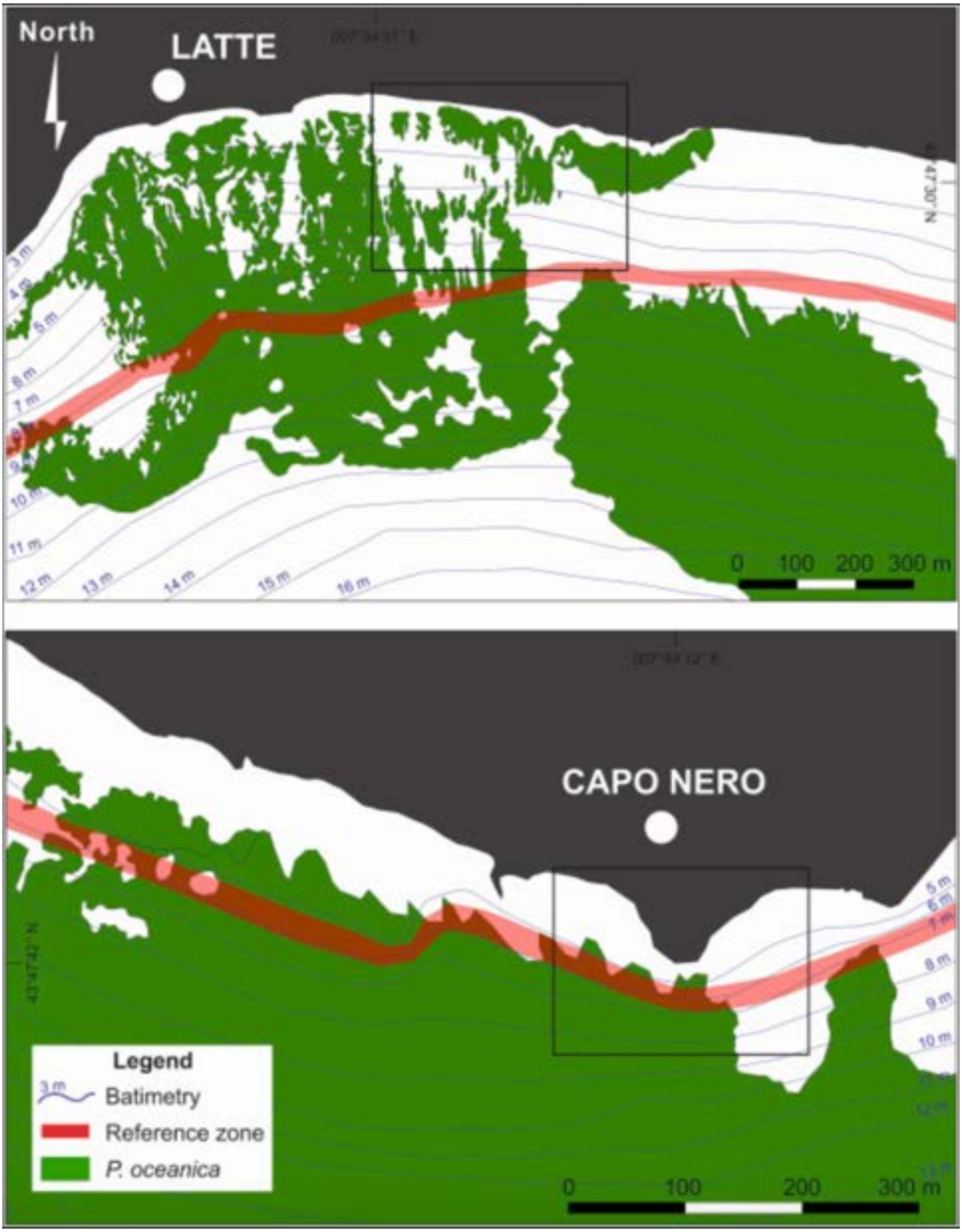

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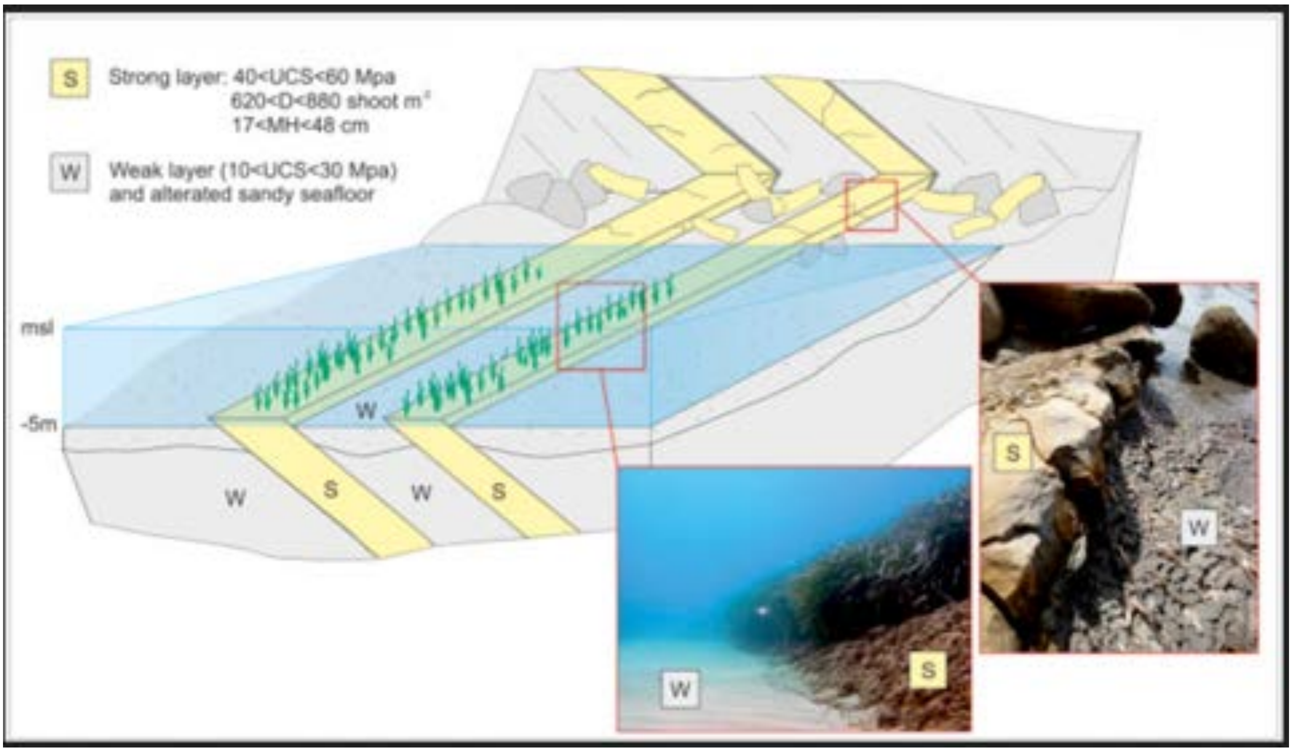

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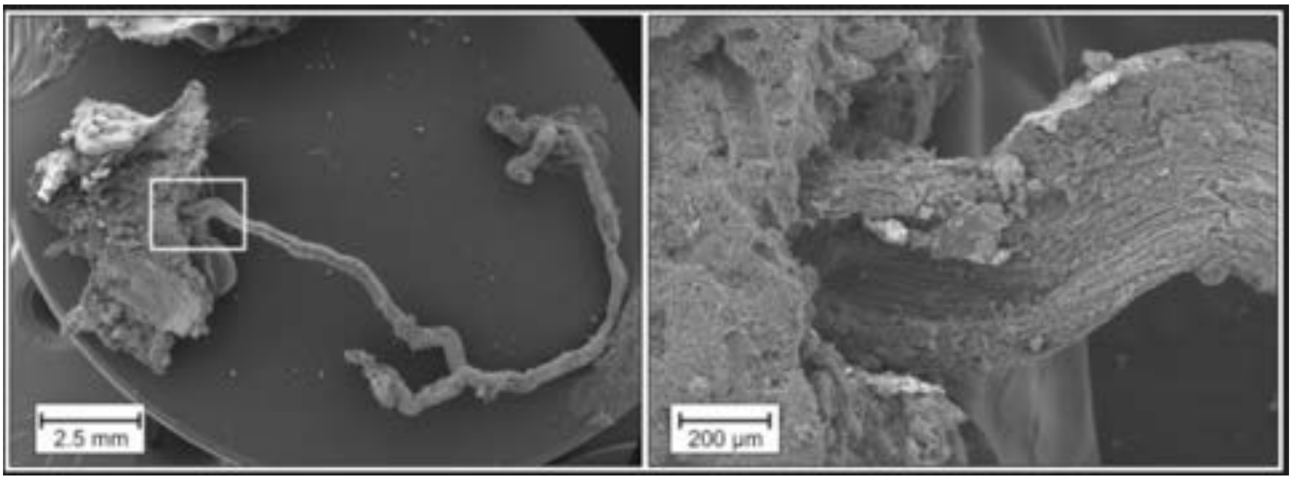

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