

# The sedimentary facies of *Posidonia oceanica* seagrass meadows from the central Mediterranean Sea

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**Abstract** Sedimentary facies of seven *Posidonia oceanica* meadows of western Mediterranean Sea were investigated. Five meadows are located in the Tyrrhenian coast, two are placed in the western coast of Sardinia and Corsica. These meadows develop on soft and hard substrates, often forming “*mattes*”, in areas characterized by different oceanography, morphology, and terrigenous inputs produced by coastal erosion and fluvial runoff. A total of five sedimentary facies have been recognized ranging from pure terrigenous to bioclastic: terrigenous sand to gravelly sand, bioclastic sands, skeletal gravelly sands, mixed siliciclastic–carbonate sands, well to moderately sorted skeletal siliciclastic sands. All of the sedimentary facies associated with *P. oceanica* are in the sand grain size. The gravelly fraction is generally subordinated and variable, whereas the muddy fraction is generally low. The very low frequencies of the muddy fraction can be attributed to re-suspension processes and to

the lack of carbonate mud production. The rate of epiphytic carbonate production obtained by two of the investigated meadows averages  $400 \text{ g m}^{-2} \text{ year}^{-1}$ . This value is in the range of temperate Mediterranean as well as of tropical and subtropical seagrasses. The epiphytic carbonate production plus the calcareous biota living on seagrass substrate contributes to form mixed siliciclastic–carbonate sediments of the nearshore environment of the Mediterranean. Lastly, the carbonate production associated with seagrass was derived by biota belonging to the heterozoan assemblage, where aphotic organisms are dominant, together with oligophotic biota such as coralline algae and symbiont-bearing foraminifera. Consequently, in the well-illuminated seagrass settings, the prevalent skeletal assemblages is represented by the heterozoan association while the components of the photozoan assemblages are absent or subordinate. This a key point for the paleoenvironmental reconstruction of the photic zone in the fossil record. Because the skeletal components of many seagrass dwellers greatly contribute to the carbonate sediment production of photic shallow-water environments, the seagrass meadows became substantial places of carbonate production and C (organic and inorganic) sequestration during the Cenozoic.

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**Keywords** Skeletal carbonate production · Heterozoan · Tyrrhenian shelf · Coastal systems · Mixing carbonate-siliciclastic

## Introduction

Seagrasses are marine angiosperms developing in the photic zone of rocky or loose substrate along temperate to tropical shelves worldwide (Green and Short 2003; Short et al. 2007). These plants have been integral components

of shallow-marine ecosystems since their appearance in the Late Cretaceous (Brasier 1975; Ivany et al. 1990). Moreover, marine angiosperms are a keystone in the carbonate platform with heterozoan factories corresponding to a conspicuous skeletal production in the euphotic zone (Mateu-Vicens et al. 2012). Seagrass plays an important role in the sedimentary processes occurring in the coastal environments by binding and trapping both autochthonous and allochthonous sediments through the rhizome action that, in turn, prevents the erosion effect during storm events (Koch et al. 2006). Furthermore, the dense rhizomatic meshwork inhibits sediment resuspension, which favors light penetration and ensures the meadow development within the euphotic zone (Short and Short 1984; Ward et al. 1984). Seagrass meadows are determinant for trophic balance of the coastal environment because of their relatively rapid uptake of nutrients from the water column both by the plant and their epiphytes. Successively, once the plant decays, through a process of decomposition and consumption these nutrients can be slowly released, thereby reducing problems of eutrophication and binding organic pollutants (Hemminga and Duarte 2000; Short et al. 2007).

Seagrass meadows have become substantial places of carbonate production and C (organic and inorganic) sequestration in the Cenozoic since many seagrass dwellers contribute significantly to the sediment bulk of photic shallow-water environments (Brandano et al. 2016). These plants remove carbon dioxide from the atmosphere and bind it as organic matter. The carbon (C) incorporated in vegetated coastal ecosystems, specifically mangrove forests, seagrass beds, and salt marshes, has been termed “blue carbon” (Nellemann et al. 2009). Blue carbon is sequestered over the short term (decennial) in biomass and over longer (millennial) time-scales in sediments (Duarte et al. 2005; Lo Iacono et al. 2008). Carbon is stored above ground in leaves, below ground in roots and rhizomes, and in sediments in organic and inorganic forms, the latter represented by carbonate skeletal grains.

Seagrass meadows present in the Mediterranean are mainly of the genus *Posidonia*, and at lesser extent of genera *Cymodocea*, *Zostera*, *Ruppia*, and *Halophila*. *P. oceanica* is endemic to the Mediterranean where it forms extensive meadows in the bathymetric range from the surface to 30–40 m depth in clear waters (Pergent et al. 1995; Betzler et al. 1997), meadows show different types of coverage pattern, from continuous to patchy, in row distributions (Molinier and Picard 1952; Borg et al. 2005); with shoot densities ranging from very sparse, between 150 and 300 shoots  $m^{-2}$  to dense ( $>700$  shoots  $m^{-2}$ ) with exceptionally high values of ca. 1500 shoots  $m^{-2}$  (Giraud 1977). Seagrasses and in

particular *P. oceanica* build a complex 3D structure (*matte*, Boudouresque and Meinesz 1982; Mateo et al. 1997) that results from vertical growth of orthotropic rhizomes in response to sedimentation rates, and the expansion of horizontal (plagiotropic) rhizomes. This architectural display is very effective in trapping and accumulating both allochthonous and autochthonous sediments.

*P. oceanica*, as other seagrass species, hosts a significant epiphytic carbonate production responsible for autochthonous sediment formation. Epiphytic carbonate producers occupy seagrass leaves (blades), the bundles of persistent basal leaf sheaths (Gaglianone et al. 2014) resembling “shaving brushes” (den Hartog and Kuo 2006) located on rhizomes, and on the rhizomes themselves (Gobert et al. 2006).

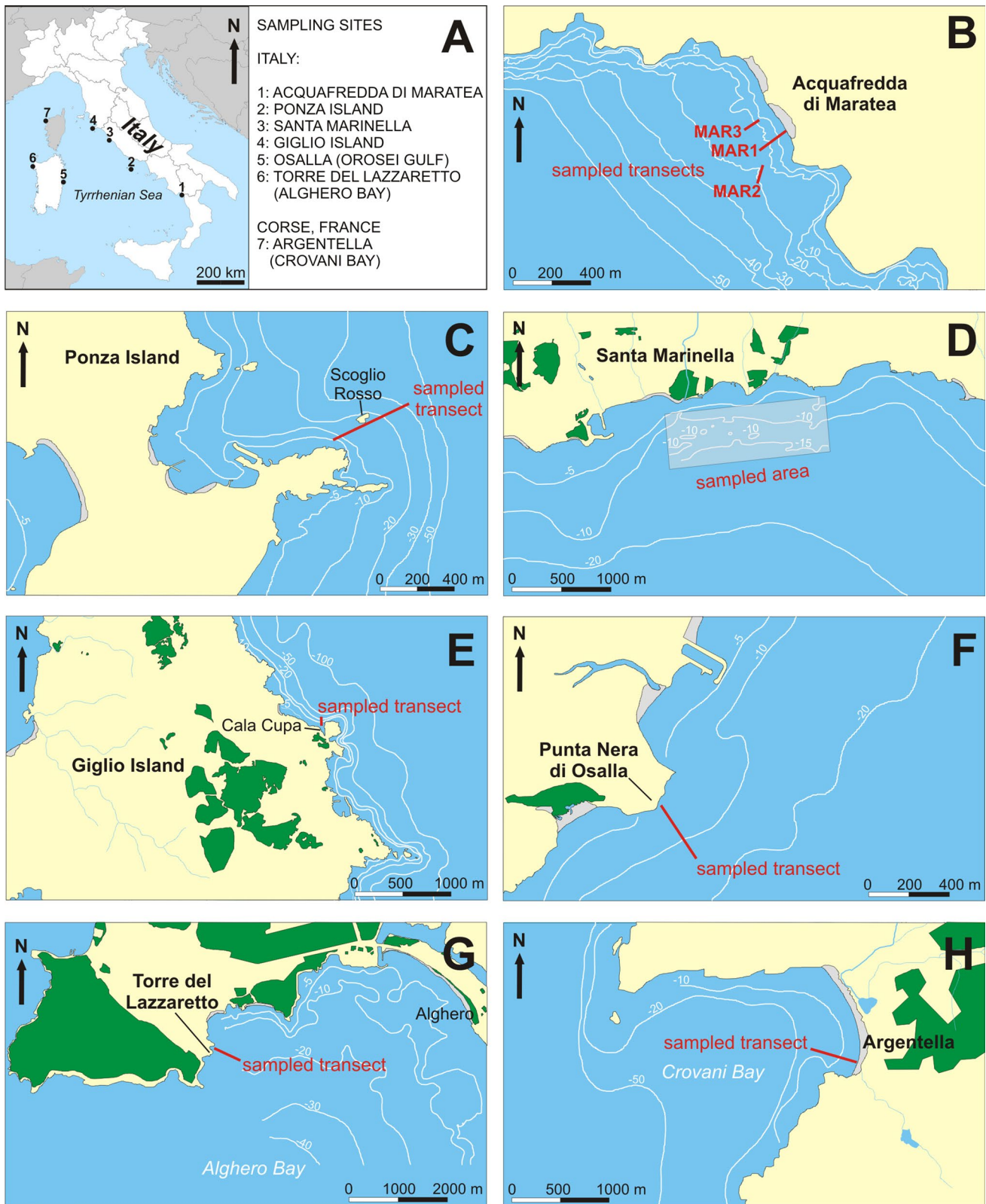
Despite the role of seagrasses in the C cycle since their first occurrence, direct evidence for seagrass occurrence in the fossil record is very scarce due to their low preservation potential and their recognition is usually inferred from indirect indications (e.g., the presence of seagrass dwellers, sedimentological and taphonomic indicators). Thus, a detailed facies characterization of modern counterparts is a key step to improve the ability to recognize the seagrass cover in the fossil record.

The aim of this work is to present the different depositional processes producing the sedimentary facies that constitute the substrate of *P. oceanica* meadows of the central Mediterranean and their influence on the epiphytic carbonate production. Seven *P. oceanica* meadows have been investigated; four meadows (Maratea, Ponza Island, Santa Marinella, and Giglio Island) are located on the eastern Tyrrhenian continental shelf, two meadows on the Sardinian shelf (Osalla in the east, Alghero in the west) and the last one (Argentella), the western Corsica continental shelf (Fig. 1).

In this work, we show the sedimentological characteristics of seagrass substrates along the Tyrrhenian coast and in the western Sardinia and Corsica shelf, encompassing a variety of sedimentary settings located in islands, coasts influenced or not by rivers, and underlying different oceanographic conditions.

## Oceanography and geological setting

The investigated meadow substrates are characterized by a totally different geological context that reflects the complex geological evolution of the Mediterranean area. They are also influenced by their specific oceanographic regime.



**Fig. 1** Location maps of sampled meadows. **a** Overview of sampling sites; **b** Maratea; **c** Ponza Island; **d** Santa Marinella; **e** Giglio Island; **f** Osalla; **g** Alghero; **h** Argentella (images from Google Earth, modified)

## Oceanography

The Mediterranean Sea is a semi-enclosed basin characterized by oligotrophic conditions and, according to most authors, thermohaline circulation (Hopkins 1999; Bricaud et al. 2002). The large-scale circulation structure of the Mediterranean Sea comprises three major zonal vertical circulation belts from shallow to deep in the water column: Atlantic Water (AW), Levantine Intermediate Water (LIW), and Mediterranean deep waters (MDW). The shallow open zone associated with the inflow of AW evolves into the LIW in the Eastern Mediterranean. The Mediterranean outflowing water mass through the Strait of Gibraltar is composed of the LIW with the contribution of the MDW alimanted by Northern Mediterranean areas (Pinardi and Masetti 2000).

The Tyrrhenian Sea is the most isolated and deepest regional sea of the western Mediterranean Sea, whose principal connections with the western sector are the Corsica channel in the north and a broad opening to the southwest between Sardinia and Sicily. The water column of the Tyrrhenian Sea shows a surface layer filled by the modified AW, an intermediate layer containing the LIW from the Eastern Mediterranean through the Sicily Channel, and a bottom layer of resident water called Tyrrhenian Deep Water (TDW). The surface and the intermediate layers enter in the Tyrrhenian basin from the Sardinian channel following a cyclonic route (Astraldi et al. 1994; Vetrano et al. 2010). The cyclonic circulation of Tyrrhenian Sea is strongly influenced by the wind regime, especially in the winter, due to the prevailing winds from SW and from NW (Budillon et al. 2009).

The contiguous Sardinian Sea and the Corsica Sea are interposed between the Algerian basin to the south, the Balearic Sea to the west, and the Ligurian Sea to the north; all of them included in the Liguro-Provençal Basin (Rehault et al. 1985). The circulation of the surface layer of the Sardinian and Corsica Seas is characterized by the AW that, from Alboran Sea, displays an along-slope cyclonic circulation. Just below the AW, the intermediate water mass flows anticlockwise from the northern part and mainly spreads south-westward through the Channel of Ibiza and then eastward across the Algerian Basin (Ribotti et al. 2004).

### Eastern Tyrrhenian shelf

#### *Maratea*

The Maratea locality is placed on the continental platform of the Basilicata region (Southern Tyrrhenian), which is in structural-stratigraphic continuity with the apenninic continental emerged areas. In this region, the Tyrrhenian margin, from bottom to top, is a stratigraphically continuous

sequence of Mesozoic to Cenozoic carbonate and flysch units overlain by the prograding wedge of the last sea-level lowstand. At the Maratea coast, the continental platform extends for only 3 km; the shelf break is located at 80–90 m of water depth (hereinafter mwd), (Colantoni et al. 1997; De Pippo et al. 2004).

#### *Ponza Island*

Ponza Island is the largest island of the Pontine Archipelago it represents a Plio-Pleistocene volcanic structure located on the external margin of the continental shelf in the central Tyrrhenian Sea, about 30 km west off the Gulf of Gaeta (Latium, central Italy) (Chiocci and Orlando 1996).

The shelf break is well defined and occurs between 105 and 160 mwd; in the southwestern part of the shelf, in correspondence with the head of canyons and gullies, erosive processes take place. In this area, the continental slope, connects the shelf to the Vavilov Abyssal Plain (about 3600 mwd).

#### *Santa Marinella*

The Santa Marinella site, placed in the northern Latium coast, represents the southern extension of the Tolfa Mountains and consists of Meso-Cenozoic flysch (Pietraforte and Tolfa Formations), Plio-Pleistocene sedimentary units and Pleistocene volcanic deposits (Abbate and Sagri 1970; Fazzini et al. 1972; Civitelli and Corda 1993). A prograding sedimentary sequence developed during the last glacial maximum in an environment of continental slope (Marani et al. 1986). During the Holocene, sedimentation was influenced by fluvial input and reworking of relict sediments (Tortora 1989).

The continental platform at Santa Marinella reaches up to 20 km wide, with the shelf break situated at 120–150 mwd. The continental sediment supply is relatively low, increasing towards the north due to the presence of the Mignone and Fiora Rivers. The nearshore substrate is rather irregular and is composed of sand to gravel-sized sediments with sparse clumps and *matte* of *P. oceanica*.

#### *Giglio Island*

The Giglio Island is the second major island of Tuscan Archipelago in the Northern Tyrrhenian Sea consisting of upper Miocene monzonitic granitic intrusions (Rossetti et al. 1998, 1999). Mesozoic metamorphic and sedimentary rocks are limited to the NW part of the island, (Aringoli et al. 2009) and they are locally overlaid by quaternary cross-bedded deposits.

## The Sardinia continental shelf

### *Osalla (eastern continental shelf)*

The Osalla coast is located off the small headland of Punta Nera (Orosei Gulf), just south to the Marina di Orosei location and the Cedrino River mouth where Plio-Pleistocene volcanic rocks crop out (Lustrino et al. 2002). The eastern continental shelf of Sardinia has a maximum extension of few miles and contains active canyons, with their edge placed above 100 mwd, and down to 1400 mwd forming a considerable slope gradient (Giresse et al. 2014).

### *Alghero (western continental shelf)*

The second sampling site of Sardinia is located in the Alghero Bay, where marine to continental Pleistocene, cross-bedded deposits crop out continuously for 2 km along the coast. The continental shelf of the northwestern portion of Sardinia, compared with that of the eastern side, appears wider, more gently sloping down to the shelf break, without canyons. Canyons occur in the central sector of the western platform (canyons “Il Catalano” and the canyon of Oristano) and in the northern (canyons of Posada, Gonone and Orosei) and central (canyon Arbatax) sectors of the eastern platform. The platform is connected to the abyssal plain of the Sardo-Balearic Basin, through the continental slope of the Nurra region. In Alghero Bay, the seafloor substrate shows a great lithological variability, from Permian–Triassic sandstones and continental conglomerates to Jurassic carbonates and Pliocene–Quaternary volcanic deposits (Andreucci et al. 2010).

## Western Corsica shelf

### *Argentella*

The Argentella site is located in the Crovani Bay where the Paleozoic metamorphic and volcanic rocks crop out (Zarki-Jakni et al. 2004).

The western continental shelf of Corsica is generally a few kilometers wide but very steep; passing along the continental slope, to the deep bathyal plain of the Corso-Ligurian Basin.

## Materials and methods

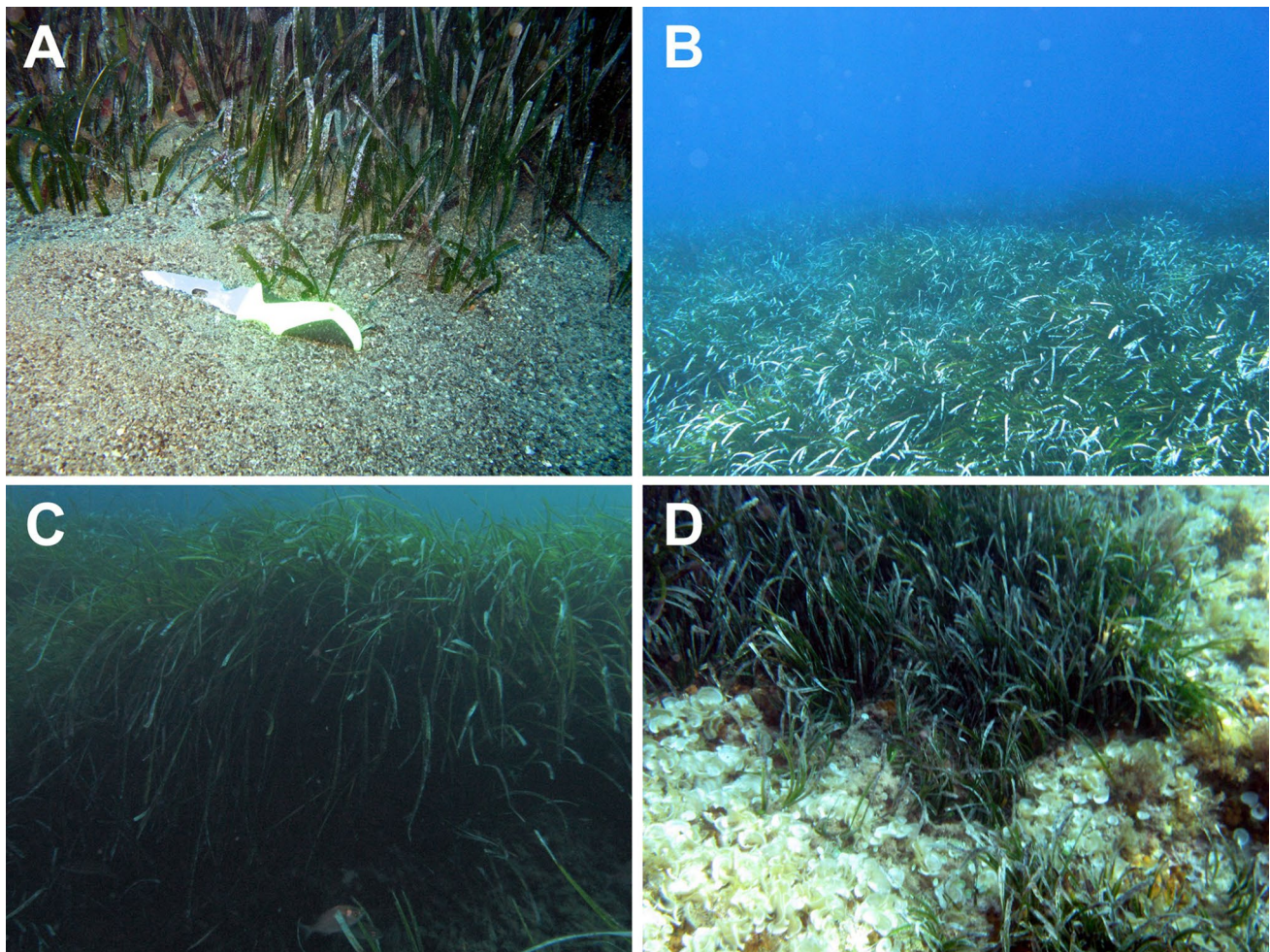
A total of 111 samples were collected by scuba diving along downdip transects, covering the whole bathymetric range of seagrass meadows in Ponza, Santa Marinella, Giglio, Osalla, while in Maratea, Alghero and in Argentella the downdip transects cover only partially the bathymetric extension of the meadows (Table 1). During sampling, qualitative observations of shoot density in the meadow (low: 100 shoots m<sup>-2</sup>; medium: 100–500 shoots m<sup>-2</sup>, high: 500 shoots m<sup>-2</sup>) and the type of substrate were noted (sandy, gravelly or rocky substrate) (Fig. 2).

Samples were washed with hydrogen peroxide and distilled water, dried at 40 °C and subsequently split into four parts. One part was preserved at the archive of the Earth Science Department of Sapienza University of Rome. The second part was used to perform the granulometric analysis by sieving 100 g of each sample. The resulting fractions (mud <63 mm; sand 63–2 mm; gravel >2 mm) were weighed to obtain a quantitative distribution of the different grain sizes.

**Table 1** Number of samples, bathymetric range, and upper and lower limits of sampled meadows

Sampling site	Transect acronym	No. of samples	Sampled bathymetric range (mwd)	Meadow upper limit (mwd)	Meadow lower limit (mwd)
Maratea (Acquafredda di Maratea Bay, Maratea, Basilicata, Italy)	MAR	27	0–21	5–6	Not reached 30–35 (IAMC-CNR 2008)
Ponza (P.ta Madonna—Scoglio Rosso, Ponza Island, Lazio, Italy)	PONZ	20	5–35	3–4	35 (diffusive limit)
Santa Marinella (Santa Marinella coast, Lazio, Italy)	SM	13	7–13	5	~13 (regressive limit)
Giglio (Cala Cupa, Giglio Island, Tuscany, Italy)	GIGL	10	4–28	2–3	26 (diffusive limit)
Osalla (Punta Nera di Osalla, Gulf of Orosei, Sardinia Island, Italy)	OSA	10	3–12	3	11 (erosive boundary)
Alghero (Torre del Lazzaretto, Alghero Bay, Sardinia Island, Italy)	ALGH	14	5–17	3	Not reached 35 (Pala et al. 2009)
Argentella (Argentella, Crovani Bay, Corse Island, France)	ARG	17	2–16	2	Not reached (at least 35 mwd, personal observation)

mwd meters of water depth



**Fig. 2** Types of substrate of the investigated *P. oceanica* seagrass meadows. **a** Maratea, 15 mwd, gravelly sand substrate, high shoot-density seagrass; **b** Giglio Island, 20 mwd, meadow on sand, high

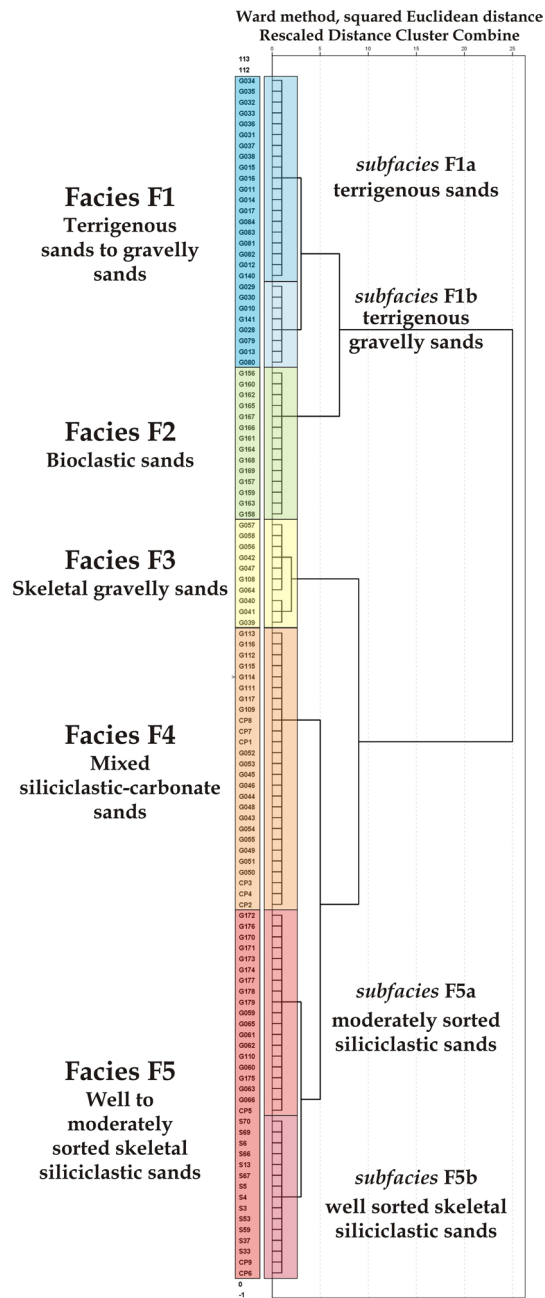
shoot-density; **c** Argentella, 10 mwd, high shoot-density meadow forming a “matte”; **d** Maratea, 6 mwd, rocky substrate, meadow with high shoot-density patches, upper limit

The third part was used for the chemical and mineralogical analyses. One gram of the sediment bulk was used to determine the carbonate content by means of gasometric measurements (Siesser and Rogers 1971). X-ray diffraction (XRD) was performed on gravel, sand and mud fractions. Finally, the fourth part was used for the component analysis that consisted of counting at least 300 granules with a stereomicroscope. The sediment constituents were categorized into: red algae fragments (non-geniculate red algae), red algae branches (geniculate red algae), bryozoans, echinoids, molluscs (bivalves, gastropods, pteropods and scaphopods), serpulids, sponges, crustaceans (ostracods, decapods and barnacles), hydrozoans, foraminifera and terrigenous components (Table 1S).

The components percentages, sediment textures (gravel, sand, and mud percentages, mean size and sorting) and carbonate content ( $\text{CaCO}_3$ -content weighted

average) (Table 2S) were statistically analyzed by means of a Q-mode hierarchical cluster analysis (HCA) with the Ward method and squared Euclidean distance (Parker and Arnold 1999), using the IBM SPSS 19 for Windows program. Only components showing frequencies greater than 5% are used for the cluster analysis, because rarely represented components have low effects on the cluster composition (Kovach 1987, 1989). For the same reason, the terrigenous fraction was not used because of its high frequency. Finally, facies analysis was compared with the results of HCA (Fig. 3).

Lastly, at the Maratea and Ponza sites, the epiphytic carbonate annual production of the seagrass meadows was evaluated analyzing separately the canopy (leaves) and the basal parts (rhizomes). Calcium carbonate content was obtained from calcimetric analysis (Siesser and Rogers 1971; ASTM D4373-14 2014) performed on ashes of leaves and rhizomes, previously dried at 105 °C for



**Fig. 3** Dendrogram from hierarchical cluster analysis showing five distinct sedimentary facies. Facies 1 and facies 5 split into two different subfacies each according to slight differences on grain size and sediment sorting

24 h and weighed and burned in an oven at 550 °C for 4 h (LOI<sub>550</sub> method) (Santisteban et al. 2004). Calcium carbonate content has been calculated for leaves and rhizomes separately and has been converted into annual average values in accordance with Canals and Ballesteros (1997) by multiplying by 1.88.

## Results

### Grain size, carbonate content, and sediment composition

#### Maratea

The sediments of the seagrass substrate in the Maratea area were sampled along three downdip transects, MAR 1, MAR 2, and MAR 3, along 170 m (0–16 mwd interval), 90 m (15–21 mwd interval), and 80 m (8–13 mwd interval), respectively. Generally, the sediments are sand-dominated, with percentages ranging between 56.8 and 97.9% in MAR1 (median 83.5%), between 57.3 and 97.6% in MAR2 (median 86.9%) and between 32.5 and 99.4% in MAR3 (median 88.4%). The gravel size fraction is quite variable (MAR1 range, 0.2–42.9%, median 15.5%; MAR2 range, 0.5–39.5%, median 10.8%; MAR3 range, 0.0–67.1%, median 11.2%) and the mud fraction is scarce in MAR1 (0.0–2.6%, median 0.8%) and in MAR3 (0.2–1.4%, median 0.4%). However, mud is more abundant in MAR2 (0.8–4.2%, median 2.6%). In all of the investigated transects, seagrass meadows display high shoot density and bioclastic content is low; the MAR1 transect shows major bioclastic abundances (0.7–40.7%, median 23.0%), being red algae (up to 18.0%, median 9.7%), echinoids (median 4.7%) and bivalves (median 3.7%) the most common bioclastic grains, followed by less abundant bryozoans, gastropods, and foraminifera. In the MAR2 transect (3.7–31.0%, median 17.5%), foraminifera (up to 13.3%, median 6.0%) and red algae (up to 6.3%, median 2.8%) dominate the bioclastic assemblages. The MAR3 transect presents the lowest bioclastic abundances (2.7–12.8, median 5.7%) and none of the counted bioclastic groups prevails (Table 2S).

Despite the low the bioclastic fraction, the carbonate content is high in all transects due to the composition of the lithoclasts of, both in the sand (median: MAR1 93.9%, MAR2 95.6%, and MAR3 97.6%) and gravel fractions, (median: MAR1 95.5%, MAR2 98.6%, and MAR3 99.0%). In contrast, carbonate content is much lower in the mud (median: MAR1 51.9%, MAR2 70.7%, and MAR3 51.0%).

The mineralogical composition of gravel-sized and sand-sized lithoclasts is mostly calcite and dolomite, with quartz subordinated. Only in the mud fraction do other minerals occur. These are, in order of abundance, alkali feldspar, biotite, aragonite, kaolinite, and augite.

#### Ponza

In Ponza Island, samples were obtained along a downdip, 500-m-long, transect between 5 and 35 mwd. The seagrass meadows are characterized by high shoot densities. Sediments are poorly sorted ( $\sigma = 1.79$ ) and sand-dominated

(42.3–98.0%; median 83.2%). The gravel fraction is quite variable (0.4–55.3%, median 9.6%) and the mud fraction is generally low (1.4–12.3%, median 3.8%).

Bioclasts are conspicuous sedimentary components, ranging between 26.3 and 78% (median 40.2%). The benthic foraminifera (up to 29.0%, median 12.2%) and red algae (up to 23.3%, median 11.2%) are the most common skeletal grains, followed by less abundant bryozoans, bivalves, gastropods, echinoids, serpulids, sponges, and ostracods. Pteropods and scaphopods are accessory (Table 2S).

Carbonate content is quite variable and higher in the gravel-size fraction (14.3–87.2%, median 69.0%) than in the sand-size (7.9–61.7%, median 15.5%) and in the mud-size (16.3–43.5%, median 27.1%) fractions.

X-ray diffraction reveals a dominance of silica (in the pumice and in the volcanic glass) and biogenic aragonite (due to bioclastic skeletal remains) on the gravel-size fraction, whereas the sand-size fraction consists of siliciclastic minerals (feldspar, biotite, clinopyroxene, and quartz). The mud-size fraction shows a dominance of quartz and calcite, whereas feldspar, clinopyroxene, and clay minerals (illite, kaolinite, montmorillonite) are subordinate.

#### *Santa Marinella*

The Santa Marinella meadows were sampled in a water depth interval between 7.5 and 13.5 mwd. Seagrass shoot densities are low. The sediments are well sorted ( $\sigma = 0.47$ ) and sand-dominated 85.9–98.8% (median 96.8%), whereas the gravel (0.3–10.0%, median 2.4%) and mud fractions (0.3–4.6%, median 4.9%) are generally scarce.

At this location, the bioclastic fraction is subordinate (14.0–35.0%, median 22.3%), foraminifera (up to 18.0%, median 8.7%) being the most abundant components (Table 2S).

At this location, carbonate content is higher in the gravel-size fraction, because it consists of limestone pebbles and skeletal remains (44.8–89.1%, median 62.4%), while it decreases in the sand-size (34.7–67.8%, median 56.3%) and in the mud-size (6.3–18.9%, median 10.9%) fractions. The mineralogical composition of Santa Marinella sediments shows a predominance of quartz, followed by calcite and subordinated biotite, kaolinite, alkali feldspar, pyroxene (essentially diopside and enstatite) and chlorite.

#### *Giglio Island*

The sediments of Giglio Island were collected in high-shoot-density meadows, along a 150-m transect from 4 to 28 mwd. The sediments are moderately sorted ( $\sigma = 1.18$ ) and sand-dominated (54.3% and 94.5%; median 91.1%). The gravel size fraction is quite variable (1.6–45.1%, median 6.7%) and the mud fraction content is generally low (0.3–5.1%,

median 2.8%). The bioclastic content is high (34.4–62.3%, median 56.8%), and mostly corresponds to red algae (up to 13.4%, median 12.4%) and foraminifera (up to 13.7%, median 8.3%); other frequent components are bivalves, gastropods, bryozoans and echinoids. Serpulids, ostracods and scaphopods are accessory.

Carbonate content of Giglio Island sediments is low in all granulometric fractions (weighted average 15.8%), with moderate values in the mud-size fraction (25.3–50.8%, median 45.1%), low to moderate in the gravel-size fraction (6.0–48.5%, median 32.1%) and generally low in the sand-size fraction (6.9–20.6%, median 14.3%). Indeed the mineralogical composition of these sediments mostly consists of quartz, microcline and calcite followed by albite (plagioclase feldspar), augite, biotite, and aragonite. Kaolinite and calcite show very low abundances and are limited to the mud-size fraction.

#### *Osalla*

Sampling was performed between 3 and 12 mwd, in a 350-m-long transect in meadows with medium to high shoot densities. The sediments are moderately sorted ( $\sigma = 1.17$ ) and sand dominated (86.3–98.0%, median 96.1%), with low content of gravel (0.9–12.9%, median 2.9%) and mud (0.2–2.5%, median 1.2%). The bioclastic fraction is relatively abundant (16.0–28.0%, median 23.0%) and dominated by foraminifera (up to 12.0%, median 8.2%) and red algae (up to 6.7%, median 5.0%). Carbonate content is generally moderate in all grain-size fractions, (mud: 15.3–24.7%, median 19.8%; sand: 9.2–17.2%, median 11.8%; gravel: 13.2–70.3%, median 27.8%), with the exception of one isolated sample where the gravel-size fraction can reach high values. X-ray diffraction of sediments of Osalla reveals a dominance of quartz, followed by albite, muscovite and chlorite and calcite.

#### *Alghero*

In Alghero Bay, the sediment was collected between 5 and 17 mwd along a 300-m transect, in seagrass meadows with low shoot densities. The sediments are moderately sorted ( $\sigma = 1.21$ ) and dominated by sand-size fraction ranging from 50.3 to 98.6% (median 90.9%). Gravel is generally scarce with some exceptionally high values (0.0–41.8%, median 1.7%) and mud is low to moderate (1.4–12.2%, median 6.0%).

The bioclastic content is high (49.2–87.1%, median 72.4%) and dominated by red algae (up to 30.4%, median 20.3%) and foraminifera (up to 25.7%, median 20.9%),



while other less frequent components are bryozoans, gastropods, bivalves, and echinoids. The carbonate content is generally high in all sedimentary fractions (sand: 87.7–96.9%, median 92.7%; gravel: 90.9–100.0%, median 98.1%; mud: 66.8–86.3%, median 75.3%) and the mineralogical composition is dominated by calcite, magnesium calcite, aragonite, and dolomite, while muscovite and chlorite are subordinate.

### Argentella

Sediment samples were collected along a 300-m transect in the water-depth interval between 2 and 16 mwd in seagrass meadows with generally high shoot densities. The sediment at Argentella is moderately sorted ( $\sigma = 1.20$ ) and sand-dominated (0.2–98.8%, median 77.6%), except for the shallowest samples where the gravel-size fraction may be more abundant (0.9–99.9%, median 22.2%). The mud fraction is very low (0.0–0.6%, median 0.2%). Bioclasts can be abundant (0.9–69.4%, median 64.5%), mostly represented by red algae (up to 18.6%, median 15.9%), bivalves (up to 14.9%, median 13.3%), foraminifera (up to 15.3%, median 10.4%), gastropods (up to 14.3%, median 10.4%) and echinoids (up to 12.4%, median 8.1%). Bryozoans are subordinate (up to 7.5%, median 5.2%), serpulids, ostracods, and scaphopods are very rare.

Carbonate content is generally low to moderate (pondered average 3.7–37.9%, median 30.8%). In the gravel-size fraction, carbonate content is quite variable but generally low (3.7–55.8%, median 13.7%), while in the mud-size fraction (0.0–60.1%, median 45.8%) and in the sand-size fraction (0.0–39.6%, median 34.7%) it is slightly more abundant. The mineralogical composition of all the granulometric fractions of Argentella sediments includes quartz, albite, augite and aragonite and secondarily microcline, biotite, kaolinite and calcite.

### Sedimentary facies

On the basis of component abundance, carbonate content, and sedimentological characters (grain size, sorting, and textural maturity of sediments), five seagrass-associated facies have been recognized (Table 2; Figs. 4a–h, 5a–e): terrigenous sands to gravelly sands (F1), bioclastic sands (F2), skeletal gravelly sands (F3), mixed siliciclastic–carbonate sands (F4), and well- to moderately sorted skeletal siliciclastic sands (F5). Samples with analogous compositional characteristics but with some differences in grain size percentages allowed, in some cases, the splitting of the facies into subfacies (F1a, b; F5a, b). The facies delimitation was subsequently tested by means of hierarchical cluster analysis (Fig. 3), using components presented in Table 2S.

### Epiphytic carbonate production

In the investigated sites, the most abundant calcareous epiphytic production occurs at ~10 mwd, corresponding to geniculate (articulated) and non-geniculate (encrusting) coralline algae that together comprise up to 50% of the epiphytic carbonate. Other significant epiphytes are bryozoans and benthic foraminifers, which contribute equally (~25% each) to the carbonate production.

Considering leaves and basal parts altogether, the epiphytic carbonate annual production in the studied sites *P. oceanica* meadows is estimated to be around  $400 \text{ g m}^{-2} \text{ year}^{-1}$ .

### Discussion

#### Grain size

Grain-size analysis reflects that, in general, sedimentary deposits from seagrass meadows are sand-dominated. However, local environmental conditions play an important role in determining the abundance of other fractions (Fig. 6). Thus, gravel-sized particles can be exceptionally abundant, reaching up to 99% as occurs in samples from Argentella. In contrast, the mud fraction is generally low (<12%). These results are consistent with observations from other sites of the Mediterranean (Boudouresque and Jeudy De Grissac 1983; Fornós and Ahr 1997; De Falco et al. 2008; Mateu-Vicens et al. 2010) as well as from Indo-Pacific areas such as Shark Bay (Australia, Read 1974), and Inhaca Island (Mozambique, Perry and Beavington-Penney 2005).

Comparing the investigated sites on the basis of grain-size and sorting of seagrass sediment, four main domains can be recognized. One domain is characterized by well-sorted sediment constituted only by sand, as occurs in the Santa Marinella site. According to Tortora (1989, 1996), the sediment of this site and, in general, of the Tyrrhenian coast between northern Latium and southern Tuscany mainly derives from different local fluvial systems that sort the sediment during transport. A minor percentage of this sediment has intrabasinal origin from relict sediment of last transgression unit. In consequence, the mature textural character of the sediment is strictly related to its ancestral origin and to the low contribution of the bioclastic fraction.

The second domain comprises sand-dominated, moderately sorted, bioclast-rich sediments. Sorting can be related to meteorological conditions and their effect on the marine environment. The seagrass meadows from Osalla, Giglio Island, and Alghero sites are located in small bays protected from the strong winds and sea storms coming from NW (Mistral) and SW (Libeccio), favoring the accumulation of poorly sorted deposits with abundant skeletal grains

**Table 2** Facies and subfacies summary table

Facies	Subfacies	Main components	Other components	Carbonate content (%)	Sorting and texture	Depth (mwd)	Type of substrate	Meadow density
F1	F1a	Red algae (0–18%, median 5.3%) Foraminifers (0–13%, median 2.0%) Bivalves (0–6%, median 2.0%) Bryozoans (0–4%, median 2.0%)	Gastropods, echinoids, ostracods, and serpulids	89–100	Moderately sorted sand G: 0–23%, median 3.0% S: 77–99%, median 94.7% M: 0–4%, median 0.9%	0–21	Sandy, <i>matte</i>	From medium–high to high
	F1b	Red algae (1–8%, median 3.2%) Foraminifers (0–9%, median 1.5%)	Bryozoans, bivalves, gastropods, and echinoids	91–99	Poorly sorted gravelly sand G: 29–67%, median 37.0% S: 33–71%, median 62.6% M: 0–3%, median 0.6%	4–17	Rocky	High
F2		Foraminifers (12–26%, median 20.9%) Red algae (7–30%, median 20.3%) Bryozoans (3–12%, median 10.2%) Gastropods (4–16%, median 8.1%) Bivalves (1–9%, median 4.6%) Echinoids (1–7%, median 4.0%)	Ostracods, serpulids and sponge spicules	85–96	Poorly sorted sand G: 0–42%, median 1.7% S: 50–99%, median 90.9% M: 1–12%, median 6.0%	5–17	<i>Matte</i> on rocks	High
F3		Red algae (0–19%, median 15.2%) Bivalves (0–13%, median 8.0%) Foraminifers (0–11%, median 6.9%) Bryozoans (0–11%, median 5.9%) Echinoids (0–12%, median 5.1%) Gastropods (0–11%, median 4.4%)	Ostracods, serpulids and scaphopods	4–25	Poorly- to very poorly sorted skeletal sand to gravelly sand G: 28–100%, median 46.8% S: 0–70%, median 52.7% M: 0–4%, median 0.4%	2–13	Rocky	Low

**Table 2** (continued)

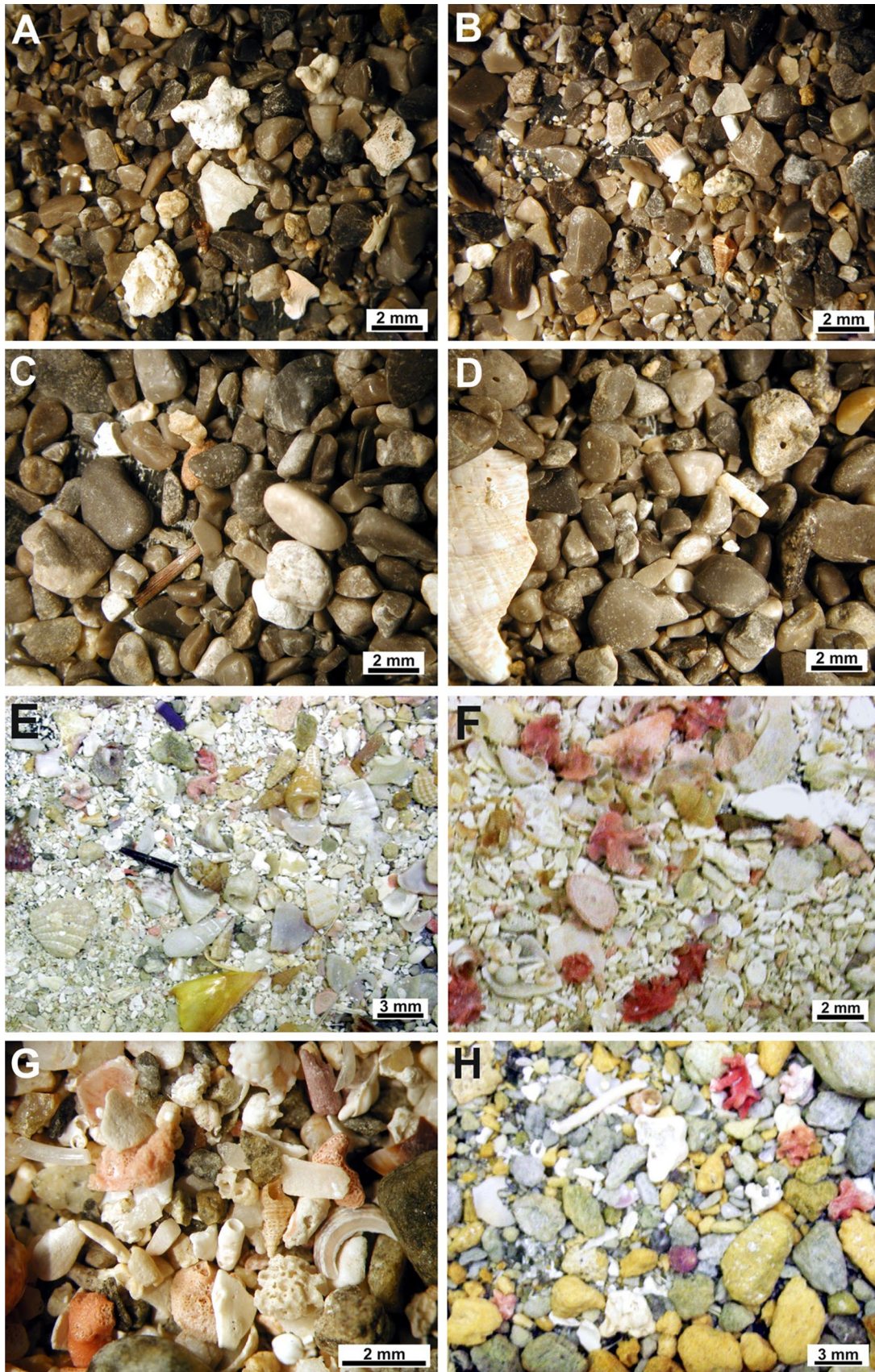
Facies	Subfacies	Main components	Other components	Carbonate content (%)	Sorting and texture	Depth (mwd)	Type of substrate	Meadow density
F4		Red algae (3–23%, median 13.8%) Foraminifers (3–29%, median 11.2%) Bivalves (3–15%, median 10.9%) Gastropods (3–14%, median 9.4%) Bryozoans (4–15%, median 6.3%) Echinoids (1–12%, median 6.2%)	Serpulids, ostracods, and scaphopods	8–62	Poorly sorted mixed siliciclastic–carbonate sand G: 1–27%, median 8.7% S: 73–99%, median 87.7% M: 0–11%, median 1.4%	5–29	<i>Matte</i> on sand	High
F5	F5a	Foraminifers (1–19%, median 9.7%) Red algae (0–13%, median 5.7%) Bryozoans (1–7%, median 3.0%)	Bivalves, gastropods, ostracods, echinoids, serpulids, and sponge spicules	7–2	Moderately sorted siliciclastic sand G: 0–16%, median 5.2% S: 82–98%, median 93.0% M: 0–5%, median 1.4%	3–21	<i>Matte</i> on rocks and sand	From medium to high
	F5b	Foraminifers (3–18%, median 9.3%) Bivalves (0–9%, median 2.3%) Red algae (0–11%, median 2.0%) Echinoids (0–5%, median 2.0%)	Bryozoans, gastropods, ostracods sponge spicules, and serpulids	34–67	Well-sorted sand G: 0–10%, median 2.6% S: 79–99%, median 96.4% M: 0–12%, median 0.9%	7–35	<i>Matte</i>	Low

from the autochthonous carbonate-producing biota (Fig. 7). On the contrary, the third domain includes sites exposed to high-intensity sea storms that eventually winnow away the medium- to fine-grained sediments. This is reflected in sediments of seagrass from Argentella and Maratea sites, which are characterized by the highest abundances of the gravel-size fraction (up to 99% in the Argentella). Both sites are characterized by subaerial cliffs fringed by beaches of coarse to fine gravels, dipping seawards, and fed by torrential and alluvial, coarse-grained systems. Seagrass meadows start to develop on the gravelly to coarse sand substrates of the shoreface and pass basinward into the sandy lower shoreface.

The fourth domain, represented by Ponza Island, corresponds to poorly sorted sediments with variable percentages of the gravel-size fraction, which may be conspicuous in the deep samples. Gravel grains consist of coarse bioclastic remains of molluscs, echinoderms, and coralline algae,

representing a prolific production and accumulation of the seagrass meadows close to the storm wave base.

Seagrass-deposits from Central Mediterranean are scarce in mud content, which is related to re-suspension and transport processes that winnow away the fines. These processes are typical of the sedimentary dynamics within the meadow (Koch 1999), regardless of the ability of seagrasses to attenuate the near-bottom turbulence and produce a baffling effect (Gacia and Duarte 2001). This is the result of the structural organization of the meadows. The upper part of the canopy, where the exposed leaf area is greater, absorbs part of the kinetic energy and reduces the current velocity. In contrast, at the plant stems, the plant surface decreases, offering a lower resistance to the flow and, in consequence, velocity is slightly higher than in the leaf canopy. Local increase of mud percentage (12%) in the deepest site (Ponza) and in the protected bay (Alghero) may be associated to the calm conditions of the depositional environment rather than to the



**Fig. 4** Sediment samples of facies F1, F2 and F3. **a** Facies F1a, sample G035 (Maratea, 13 mwd); **b** facies F1a, sample G036 (Maratea, 14 mwd); **c** facies F1b, sample G028 (Maratea, 6 mwd); **d** facies F1b, sample G030 (Maratea, 8 mwd); **e** facies F2, sample G160 (Alghero, 9 mwd); **f** facies F2, sample G161 (Alghero, 10 mwd); **g** facies F3, sample G042 (Argentella, 4 mwd); **h** facies F3, sample G064 (Ponza, 13 mwd)

trapping capacity of seagrasses. In Ponza, the sample with higher mud percentage was collected just below the SWB (storm wave base), where hydrodynamic energy is lower.

On the other hand, the low mud content can also be related to the absence of biogenic micrite production. Most of the micritic production in modern shallow-water systems is operated by aragonitic factory that corresponds to the calcareous green algae such as *Penicillus* and *Udotea* (Bosence 1995; Schlager 2003), which is known to calcify at lower latitudes, in tropical environments (Johnson 1961; Wray 1977). In contrast, in subtropical (e.g., Perry and Beavington-Penney 2005) and temperate seas, the carbonate autochthonous mud-production is limited to the thin, monostromatic, encrusting coralline algae that live attached to the seagrass blades.

### Facies interpretation and distribution

The recognized facies and subfacies display a heterogeneous distribution in the investigated seagrass meadows of the Mediterranean. Two of them, F1 and F2, formed only in two of the sampling sites, respectively in Maratea and in Alghero. Facies F3, F4, and F5 are displayed in the other sites forming a facies mosaic (sensu Wright and Burgess 2005), rather than occupying well-defined belts along a bathymetric gradient.

The origin of F1 sediment can be related with sporadic terrigenous inputs from the subaerial cliff erosion, and from torrential and aluvional systems. This sediment is successively reworked by wave action. The low percentage of bioclastic and mud fractions may be interpreted as the product of wave action that favors the breaking and mechanical abrasion of less-resistant bioclasts. Resuspension of smaller bioclastic particles and mud causes their removal and bypassing seaward of the meadow.

Facies F1 is divided into two subfacies (Fig. 4a–d). F1a is sandier, better sorted, and with a slightly higher bioclastic content than F1b. F1a represents the substrate of meadows forming *matte* with medium–high to high shoot densities. In contrast, the F1b subfacies corresponds to the sediment of meadows occupying rocky substrate without forming *matte* in distal areas, still with high shoot densities.

The F2 facies, only recognized in the Alghero site, represents a conspicuous carbonate production and accumulation in the *matte* of dense seagrass meadows in a protected embayment (Fig. 1). The low percentage of terrigenous

clasts, the highest content of mud with respect the other sites are in agreement with deposition in meadows of sheltered areas, little affected by action of storm waves and by river inputs. The most abundant sediment-producing biota are encrusting and articulated coralline algae, foraminifera, molluscs, bryozoans, and echinids (Figs. 7, 8a–h). Similar facies are reported in the seagrass meadows of the Mallorca shelf (western Mediterranean) (Fornós and Ahr 2006).

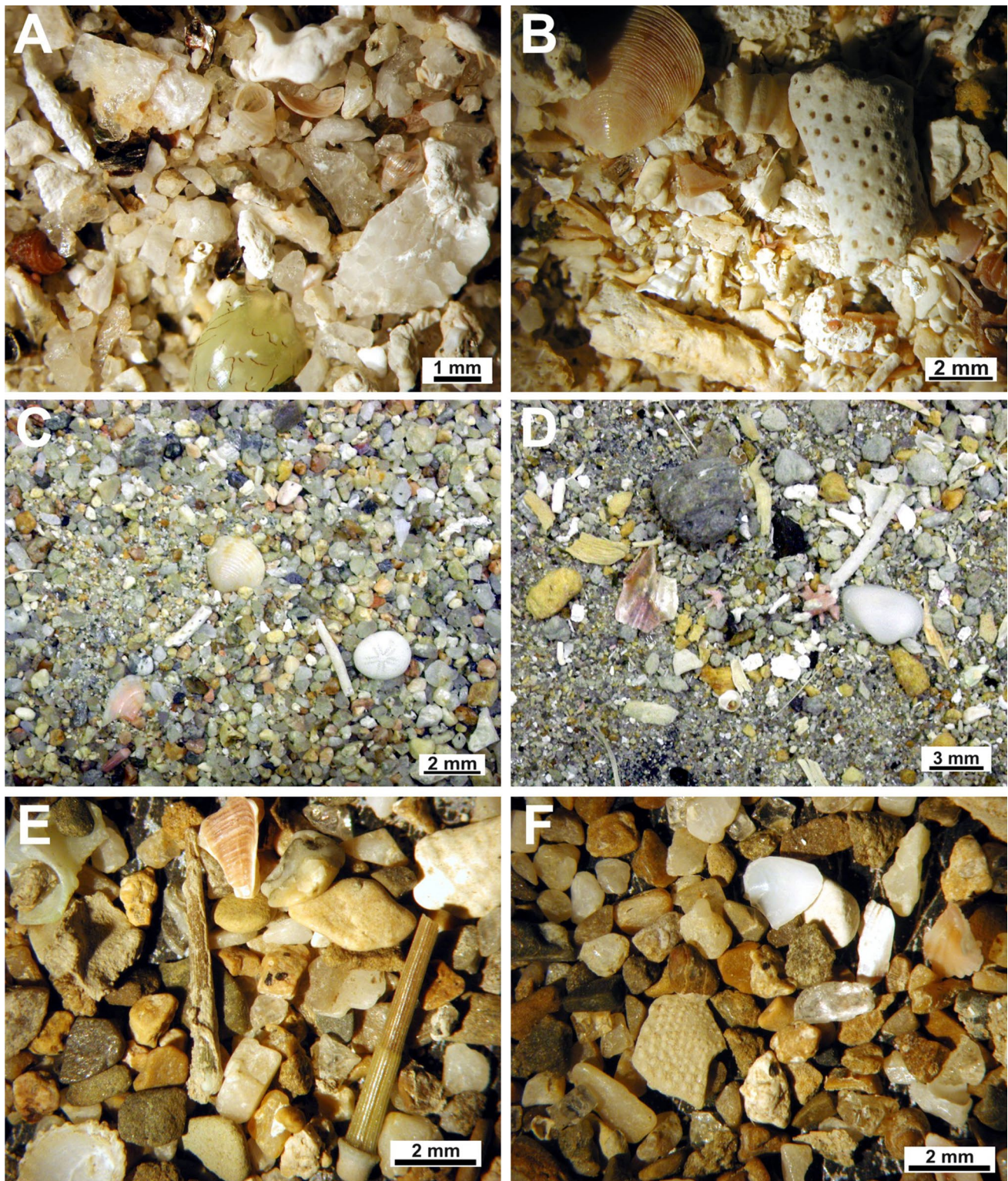
Facies F3 represents accumulation in meadows developed on rocky substrates colonized by sparse *P. oceanica* assemblages at Argentella, the Giglio Island and Ponza in a shallow water depth interval (4–13 mwd) under the influence of wave action. In this environment, high hydrodynamic energy favored the winnowing of fines and the concentration of gravel grains. However, despite the very shallow depths, carbonate production is dominated by coralline algae and symbiont-bearing foraminifera. The first group is adapted to low-light conditions produced by the blade canopy and the holes and fissures in the rocky substrate. The foraminiferal assemblage corresponds to epiphytic forms strictly dependent on light (soritids and peneroplids; see Frezza et al. 2011), and associated with the *P. oceanica* meadow. Bryozoans are also an important part of the carbonate content.

Facies F4 characterizes the sediment of shallow-water meadows in Argentella (5–16 mwd) and an intermediate to deep-water meadow in Giglio and Ponza Island (6–29 mwd).

This facies develops in dense meadows that attenuate the waves and promote the trapping and accumulation of both autochthonous carbonate production and allochthonous siliciclastic input. However, a variable amount of the gravel size fraction occurs and it can be interpreted as an in the proportion increase of coarser skeletal components such as red algae, bryozoans, and molluscs.

Facies F5 is characterized by sand-sized sediments, mostly dominated by the terrigenous fraction. The moderately sorted subfacies F5a represents meadows developed on more than one type of substrate (rocky and forming *matte*) with shoot densities from medium to high, in shallow water depths of Osalla (3–12 mwd), and Ponza Island (8–15 mwd and one from 21 mwd). This facies is present also in one sample of Giglio Island (8 mwd). This subfacies corresponds to the littoral zone, above storm wave-base colonized by seagrass where the skeletal components fail to accumulate because of the strong hydrodynamic conditions.

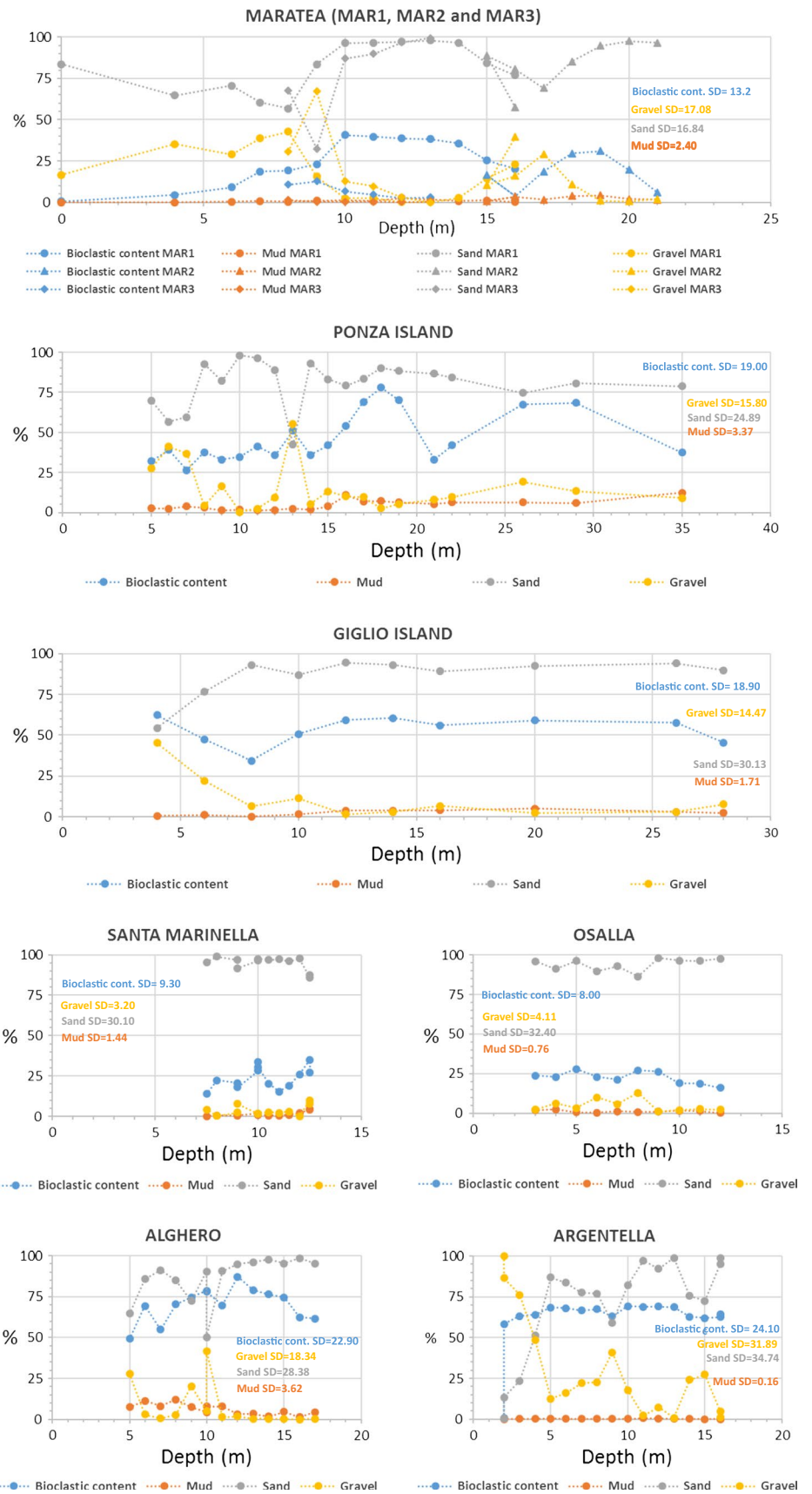
The well-sorted subfacies F5b is found in meadows forming *matte*, with abundant sediment and low shoot densities. This subfacies corresponds to shallow meadows of Santa Marinella, and two deep-water samples of Ponza Island (22 and 35 mwd). It is dominated by the terrigenous input and can be considered as the product of local environmental

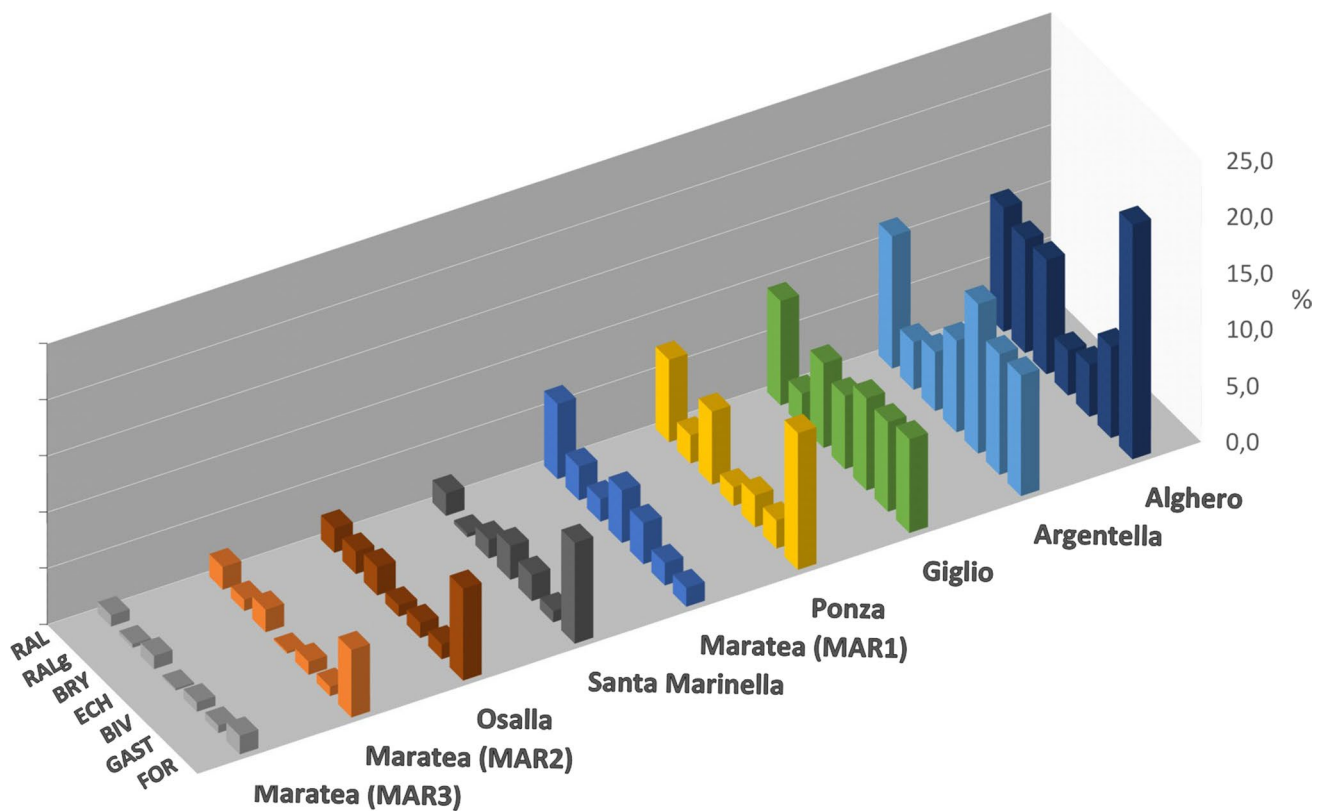


**Fig. 5** Sediment samples of facies F4 and F5. **a** Facies F4, sample G114 (Giglio, 16 mwd); **b** facies F4, sample CP7 (Ponza, 29 mwd); **c** facies F5a, sample G173 (Osalla, 6 mwd); **d** facies F5a, sample

G066 (Ponza, 15 mwd); **e** facies F5b, sample S4 (Santa Marinella, 10 mwd); **f** facies F5b, sample S67 (Santa Marinella, 10 mwd)

**Fig. 6** Grain size and total bioclastic content percentages in the sampled meadows. *SD* standard deviation





**Fig. 7** Main composition of the skeletal assemblages percentage along the investigated sites

conditions that prevent the accumulation of bioclastic fraction. Low shoot densities, associated with little light penetration due to the fluvial influence (Santa Marinella), and the increasing depth (deep samples from Ponza) reduce the epiphytic carbonate production. Furthermore, the good sorting of Santa Marinella samples is coherent with the conspicuous fluvial continental source as reported by previous works in the Latium coasts (Tortora 1989, 1996). In this case, the terrigenous input may overtake and hide the carbonate production and accumulation.

#### **Epiphytic carbonate production and mixing process (carbonate vs. terrigenous)**

The rate of epiphytic carbonate production in the Tyrrhenian Sea averages  $400 \text{ g m}^{-2} \text{ year}^{-1}$ . This value is higher than the one obtained by Canals and Ballesteros (1997) in the Balearic Islands, while they are in agreement with data obtained for other sites of western Mediterranean (Sardinia, De Falco et al. 2008). Data from leaf carbonate production are available from both tropical and temperate environments (Bosence 1989; Nelsen and Ginsburg 1986; James et al. 2009), showing that the total epiphytic production for seagrass fits within the range of the Tyrrhenian seagrass meadows. This carbonate production contributes to

the formation of mixed terrigenous–carbonate sediments in shallow-marine environments. It is worth noting that most of the carbonate production is performed by heterotrophic organisms, except for the red algae and symbiont-bearing foraminifera, which are entirely and partially autotrophic (mixotrophic), respectively (Fig. 7). Although this skeletal assemblage belongs to the heterozoan group, it is inseparably related to the euphotic zone because of the vital linking with the seagrass meadows. This is a key point that needs to be taken into account for a correct paleoenvironmental reconstruction of fossil sedimentary records, where deposits can originate in the euphotic zone even if they are characterized by the absence or very reduced presence of photozoan components.

In the Tyrrhenian shelf, mixed terrigenous–carbonate sedimentation occurs from the nearshore to the offshore environments (Brandano and Civitelli 2007; Mateu-Vicens et al. 2012). As a general context, the shallower substrate is characterized by terrigenous input deriving from coastal erosion and/or from fluvial input reworked by wave current and coastal processes. The terrigenous input is generally dominant over the carbonate production in shallow-water settings. In deep waters, the limiting factor for the carbonate production is the light penetration. In the Tyrrhenian and in western Mediterranean areas, pure carbonate sediment



accumulation occurs in the circalittoral zone, where prolific production by red algae forms unmixed carbonate sediments (Carannante et al. 1988; Canals and Ballesteros 1997; Fornós and Ahr 1997; Brandano and Civitelli 2007). Notwithstanding, some exceptions may occur in particular geographical settings (e.g., the island of Mallorca, Balearic Islands, Spain) where almost purely carbonate sediments are produced and accumulated in seagrass meadows. Two main reasons are invoked for the absence or the large reduction in the amount of mixed deposits. Firstly, the lithology of the geological substrate is limestone and therefore the terrestrial input is also carbonate-dominated. In consequence, carbonate content does not allow the distinction between the in situ, bioclastic, production from the imported, terrestrial, input. Another issue to consider is the absence of rivers or permanent streams that provide a volumetrically important terrestrial input, which instead is associated with seasonally active but eventually strong currents (torrents).

The transition between siliciclastic and carbonate environments generally occurs in near-shore and inner-shelf environments where seagrass meadows develop and where the in situ mixing (*sensu* Mount 1984) processes take place (Mateu-Vicens et al. 2012). We propose to name this type of mixing operated by seagrass as seagrass in situ mixing. In fact, *P. oceanica* meadows and, in general, any seagrass species have an important role in the mixing that, in turn, depends on many factors. A crucial factor is the ability of seagrass for colonizing and growing on pure siliciclastic substrates. Another fundamental factor is the capacity of the epiphytes for producing, which depends on light penetration, temperature, pCO<sub>2</sub> in seawater, shoot density, etc. Another key aspect is the efficiency in retaining and trapping the carbonate sediment produced by the epiphytes and by the biota colonizing the substrate. The result of this study evidences that the trapping efficiency increases with decreasing hydrodynamic conditions along the bathymetric gradient or, like in the Alghero site, in relation to the geomorphological characters that form protected bay. The terrigenous input also plays an important role. Thus, high rates of terrigenous supply can dilute the carbonate production until it decreases to disappear.

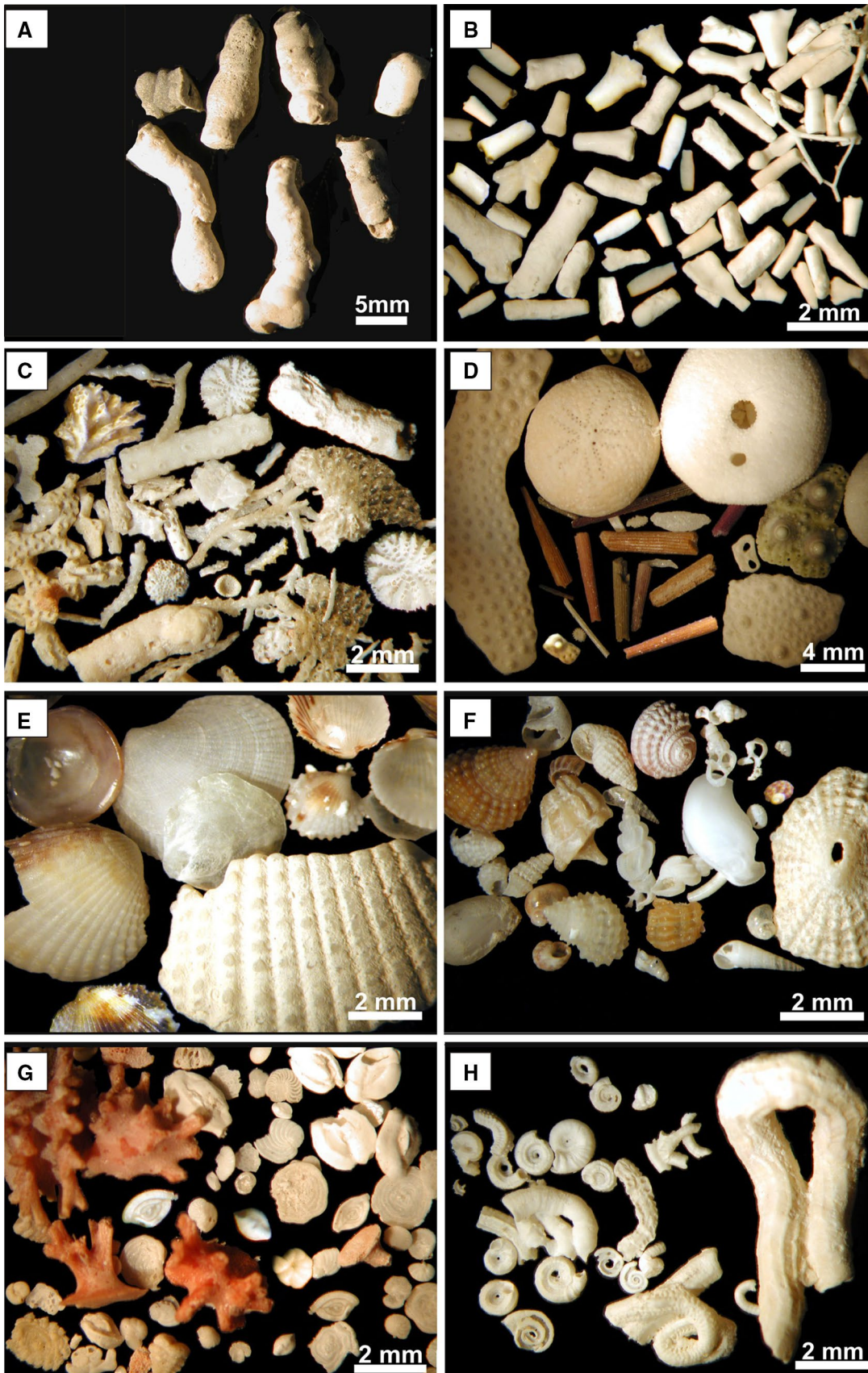
The scarcity of biogenic components, despite the exceptionally high meadow densities in some localities such as Maratea and in the shallower samples of Ponza, Giglio and Argentella can be related with the strong control of waves on sediments, which cause resuspension, breaking, and removal. In contrast, in meadows developed in a protected area, such as Alghero Bay, bioclasts are also abundant in shallow-water settings, resulting from low-to-moderate terrigenous contributions. Finally, continuous terrigenous river input, mostly of fine suspended sediments, negatively affect Santa Marinella meadow, promoting low shoot densities

and the subsequent decrease of biogenic content in the sediments.

### Implication for fossil record

In the fossil record, sedimentary successions containing remains of seagrasses are quite rare due to the low preservation potential of seagrass. Thus, the occurrence of seagrasses is generally reported from indirect evidence such as sediment composition and textures (e.g., Pomar et al. 2002; James and Bone 2007; Mateu-Vicens et al. 2008a, b; Brandano 2003; Brandano et al. 2009; Mateu-Vicens et al. 2012; Tomassetti et al. 2016; Tomás et al. 2006).

Seagrasses are strictly linked to the photic zone where both heterozoan and photozoan types of production can occur, being more or less abundant depending on seawater temperature (Mateu-Vicens et al. 2012). The mean seawater temperature in the Mediterranean is 13 °C (Betzler et al. 1997), which favors the typically photoindependent carbonate factory (heterozoan assemblages) over the photic carbonate production (photozoan assemblage). Nevertheless, most seagrass-related heterotrophic organisms that form the carbonate factory (e.g., molluscs, echinoids, epiphytic foraminifers) are strongly linked to the presence of *P. oceanica* since they require the meadows as a shelter, a source of food, or a substrate to grow (Mateu-Vicens et al. 2012). Consequently, the close relationship between the carbonate-producing biota and the seagrass meadow limits this facies to the euphotic zone, where the plant fully satisfies its photosynthetic requirements. Therefore, in order to identify a fossil seagrass environment, it is fundamental to recognize the seagrass-associated components, unrelatedly of whether they are photosynthetic or not. A key element is the growth form of biota dwelling among the seagrasses. Functional morphology and life style of foraminifera (e.g., morphotype of Langer 1993; Mateu-Vicens et al. 2014) are key factors for paleoenvironmental and paleoecological reconstruction. It is not important to identify the species or the genus of foraminifers or coralline algae; in contrast, it is fundamental to recognize their growth form and structural adaptations to the seagrass substrate. For example, the presence of hooked forms, both in gypsinids and coralline algae, is indicative of vegetated environments when they are identified in the fossil record (Ungaro 1996; Beavington-Penney et al. 2004; Tomassetti et al. 2016; Tomás et al. 2006); this morphology with a flat attachment surface and a hooked termination at one side deriving from their growing on the modern seagrass leaf margins. The result of the investigated sites along the Mediterranean coast evidences that temperate seagrass deposits are generally grainy, sand-size dominated sediments with mud-producing biota such as green algae that are not present or are not calcifying (Mateu-Vicens et al. 2012).



**Fig. 8** Main skeletal categories of seagrass sediment: **a** non-geniculate coralline algae; **b** geniculate coralline algae; **c** bryozoan colonies; **d** echinoid specimens and fragments; **e** bivalves; **f** gastropods; **g** encrusting, hyaline and porcelaneous foraminifers; **h** serpulids

Skeletal assemblages are dominated by molluscs, larger and small benthic foraminifers, red algae (Betzler et al. 1997; Mateu-Vicens et al. 2012). The absence of mud-size particles together the trapping action of rhizomes and roots, will result in a poorly sorted grainstone rather than a packstone without sedimentary structures.

Lastly, the preservation potential of seagrass sediments may be strongly influenced by their skeletal mineral composition (Wright and Cherns 2008). In all of the investigated transects, calcite is the dominant carbonate species, which is consistent with the notion that calcite is dominant in temperate heterozoan carbonates and, in turn, strengthens the preservation potential of the biotic association considerably (Wright and Cherns 2008). Calcite-dominated biota are represented by foraminifers, red algae, barnacles, epifaunal bivalves, echinoids, and bryozoans, whereas aragonite contributors are limited to gastropods, scaphopods, and serpulids.

## Conclusions

*Posidonia oceanica* meadows develop on sand-dominated substrates. The gravelly fraction is generally subordinated and variable, whereas the muddy fraction is generally low, which is attributable to re-suspension processes and to the absence of biogenic micrite production.

In the Tyrrhenian shelf, five main sedimentary facies form the substrate of seagrass meadows: terrigenous sand to gravelly sand, bioclastic sands, skeletal gravelly sands, mixed siliciclastic–carbonate sands, and well- to moderately sorted skeletal siliciclastic sands.

The rate of epiphytic carbonate production in the Tyrrhenian Sea averages  $400 \text{ g m}^{-2} \text{ year}^{-1}$ , fitting within the range of tropical and subtropical seagrass carbonate factories. This type of carbonate-production mostly corresponds to heterozoan skeletal assemblages, indirectly linked to well-illuminated conditions that ensure the development of extensive seagrass meadows.

Seagrass meadows play a key role in the production of mixed siliciclastic–carbonate sediments, through the process of seagrass in situ mixing. This process works through retaining and trapping the sediment produced by epiphytes and calcareous biota living in the substrate.

A fundamental implication for the fossil record is represented by the type of carbonate production. This is dominated by elements of heterozoan skeletal assemblages

represented by heterotrophic organisms such as molluscs, echinoids, epiphytic foraminifers, forming carbonate sediments. The only photosynthetic calcifying biota are represented by coralline algae and, at a lesser extent, large benthic foraminifers. Therefore, the recognition of seagrass-dominated environments in the fossil record is hardly effectuated by direct evidence but more likely by seagrass-associated components, structurally adapted to grow on the plant, regardless of whether they are photosynthetic or not.

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