Long-term dynamics of a *Cladocora caespitosa* bank as recorded by a *Posidonia oceanica* millenary archive

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Abstract :

Along most Mediterranean coasts, the endemic seagrass species Posidonia oceanica builds extensive meadows and complex peat-like bioconstruction known as 'mattes'. These belowground deposits are recognized as a valuable long-term archive allowing the reconstruction and the study of palaeo-climatic and palaeo-ecological changes in the coastal environment over the Holocene period. One of the P. oceanica matte cores sampled during a coring survey along the eastern continental shelf of Corsica Island (France, NW Mediterranean) revealed the unprecedented finding of a dead bank of the scleractinian coral Cladocora caespitosa embedded in the matte. Measurement of the morphological and biometrical features of corallite fragments coupled to biogeosedimentological analysis and radiocarbon dating contributed to provide a basis for the reconstruction of the stratigraphic sequence since the mid-Holocene (last 4750 years). The study of the sediment core enabled identification of three major phases: (i) the settlement of the C. caespitosa colonies (~4750-3930 cal yr BP), (ii) the coexistence of the C. caespitosa bank and the P. oceanica meadow (~3930-1410 cal yr BP), followed by (iii) the death of the coral bank and the development of only the P. oceanica meadow (~1410 cal yr BP-present). The sclerochronological analysis completed on the well-preserved corallite fragments revealed that the mean annual growth rate of the coral ranged between 1.9 and 3.1 mm yr-1 with a mean value estimated at 2.3 ± 0.8 mm yr-1. Trend analysis showed semi-millennial to millennial oscillations in annual growth rates which are probably related to environmental climatic changes since the Cold Phase of the Subatlantic period (2925-2200 cal yr BP). During the Roman Warm Period (2200-1500 cal yr BP), the decline and the death of the bank (~1410 cal yr BP) was probably due to the combined effect of a prolonged increase in summer temperatures and an increase in the competition with the P. oceanica meadow.

Graphical abstract



Highlights

▶ Finding of a *C. caespitosa* coral palaeo-bank embedded in the matte of *P. oceanica*. ▶ Palaeoenvironmental reconstruction of the sequence since the mid-Holocene. ▶ Sclerochronological analysis revealed a coral mean growth rate of 2.3 ± 0.8 mm yr⁻¹. ▶ Growth pattern fluctuations shown to be related to abiotic and climatic conditions. ▶ Bank death was probably due to prolonged SSTs during the Roman Warm Period.

Keywords : Posidonia oceanica, Cladocora caespitosa, Seagrass, Coral bank, Palaeo-ecology, Mediterranean Sea

49 **1. Introduction**

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51 Palaeo-environmental reconstruction studies provide interesting local or regional 52 broad-based information on natural fluctuations and ecosystem successions at millennial to 53 centennial scales (Mateo et al., 2010). The reconstruction of long-term environmental 54 changes requires adequate preservation of palaeo-records and proxies. In terrestrial ecosystems, peatlands and lacustrine sediments represent the best examples of palaeo-55 56 archives (Clymo, 1992, Reille et al., 1999). With a few exceptions (*i.e.* coral reefs, algal reefs, coastal swamps and marine phanerogams; Reille, 1984; Laborel, 1961; Mateo et al., 2002; 57 Peirano et al., 2004; Nalin et al., 2006; Basso et al., 2007; Montagna et al., 2007; Serrano et 58 59 al., 2012; Currás et al., 2017; Bracchi et al., 2016), coastal and marine ecosystems rarely meet the appropriate conditions to ensure reliable palaeo-environmental reconstruction of 60 61 the seabed due to high hydrodynamic energy and bioturbation at the marine-terrestrial 62 interface (Mateo et al., 2002, 2010).

63 In the Mediterranean Sea, the endemic seagrass Posidonia oceanica (Linnaeus) Delile 64 forms extensive and highly productive meadows all along the coast in the infralittoral area 65 (Boudouresque et al., 2012). The development of the meadows results in the formation of a 66 complex peat-like bioconstruction known as 'matte' (Molinier and Picard, 1952). This deposit, mainly composed by biogenic debris from the belowground organs of the plant 67 68 (sheaths, rhizomes and roots), shows has a very low decay rate owing to the highly refractory nature of seagrass remains (Kaal et al., 2016). The accumulation of large 69 70 quantities of *P. oceanica* debris and allochthonous particles associated with the anoxic 71 condition prevailing in the matte results in the formation of structures up to 14 m in 72 thickness (Miković, 1977; Boudouresque et al., 1980; Lo Jacono et al., 2008; Serrano et al., 73 2012). The high chronostratigraphic consistency and preservation of this organic-rich 74 material accumulated over millennia constitutes an interesting biogeochemical sink and a 75 unique palaeo-ecological archive for the study of the historical changes in the 76 Mediterranean coastal environment during the Holocene. In the last decades, several 77 palaeo-ecological applications have proven that *P. oceanica* matte is a valuable archive of 78 environmental information for the reconstruction of vegetation and landscape dynamics, 79 anthropogenic activities and changes in palaeo-climatic and meadow productivity over the last millennia (López-Saéz et al., 2009; Mateo et al., 2010; Serrano et al., 2011, 2012, 2013; 80 81 López-Merino et al., 2015, 2017; El Zrilli et al., 2017; Leiva-Dueñas et al., 2018).

This archive is also recognized for the unusually good preservation conditions of abundant carbonate and siliceous fossil remains from marine organisms inhabiting the

84 microhabitats formed by the leaf canopy, the rhizome layer and the matte of P. oceanica (Harmelin et al., 1964; Russo et al., 1984, 1991a, 1991b; Scipione et al., 1996; Buia et al., 85 86 2000). To our knowledge, Boudouresque et al. (1980), were the first to describe a fossil 87 biogenic reef formation built by calcifying Rhodophyceae embedded in the matte of P. 88 oceanica in the bay of Calvi (France). Although marine bioconstructors and biogenic 89 structures are common in the Mediterranean Sea (Laborel, 1987; Relini, 2009 Ingrosso et al., 90 2018), the discovery and description of the shift from biogenic reef formations from 91 calcareous organisms to marine phanerogam soils are unprecedented and reflect significant 92 environmental and climatic events.

93 One of the most widespread bioengineers is the zooxanthellate and colonial scleractinian coral Cladocora caespitosa (Linnaeus, 1767) (Zibrowius, 1980; Peirano et al., 94 95 2004). This coral can develop in the euphotic zone from a few meters below the sea surface 96 down to 40 m depth on rocky and sandy substratum (Morri et al., 1994; Peirano et al., 1998). 97 This species occurs in a wide range of environmental conditions but exhibits enhanced 98 growth in turbid coastal environments characterized by low irradiance and high availability 99 of nutrients particles as winter conditions (Laborel, 1961; Dodge et al., 1974; Zibrowius, 100 1982; Schiller, 1993a; Peirano et al., 1999, 2005; Kružić and Benković 2008, Kersting and 101 Linares 2012). The seasonal fluctuation of environmental parameters is extremely important 102 to the success of *C. caespitosa* as evidenced by the fossils and living build-ups occurring in 103 the Mediterranean (Peirano et al., 2004, 2005). Like tropical corals, C. caespitosa is sensitive 104 to prolongated temperature increases and irradiance stresses which may cause coral tissue 105 to atrophy extensive mortality events as those reported in the Mediterranean in the last 106 decades (Rodolfo-Metalpa et al., 2000, 2005; Kružić and Požar-Domac, 2002).

107 The C. caespitosa coral forms hemispherical and phaceloid colonies constituted by 108 distinct tubular corallites growing in a continuous rectilinear way. The banding pattern of 109 corallites studied by perfoming sclerochronological analysis, showed an annual growth rate ranging from 1.3 to 6.9 mm yr⁻¹ (Peirano et al., 1999, 2005; Kružić and Požar-Domac, 2002). 110 111 Several studies have reported that the variation in the skeletal growth and calcification 112 processes is related to changes in environmental factors (i.e. temperature, turbidity and 113 irradiance) which proved that C. caespitosa coral represents a valid proxy for past climate 114 fluctuations and an ideal candidate for detailed palaeo-climatic and palaeo-environmental 115 reconstructions (Morri et al., 2001; Ferrier-Pagès et al., 2003; Peirano et al., 2004; Silenzi et 116 al., 2005; Montagna et al., 2007).

117 The colonies of *C. caespitosa* live solitarily but can occur in three distinct formations 118 known as (i) 'beds' (dense populations of several distinct colonies), (ii) 'banks' (formed of 119 several large and connected colonies) rising up to 100 cm above the surrounding seafloor 120 and covering several square meters, and (iii) free-living coral nodules or coralliths of less 10 121 cm in diameter (Kersting et al., 2017, Ingrosso et al., 2018). The development of these 122 morphotypes is related to hydrodynamics (exposure to waves and currents), type of 123 substrata and seafloor morphology (Kružić and Benković 2008, Kersting and Linares 2012; 124 Kersting et al., 2017). In the Mediterranean, the largest living banks or beds have been

125 reported in the Adriatic Sea along the Croatian and Slovenian coasts (Schiller 1993a; Kružić 126 and Požar-Domac, 2002, 2003; Kružić and Benković, 2008), along the coasts of Italy (Morri et 127 al., 1994, 2000; Peirano et al., 2001, 2005; Rodolfo-Metalpa et al., 2008), Spain (Casado-128 Amezúa et al., 2011; 2014; Kersting and Linares 2012; Kersting et al., 2013), France (Laborel 129 and Laborel-Deguen, 1978; Casado-Amezúa et al., 2015), in the Levantine basin along the 130 coasts of Greece (Laborel, 1961, 1987), Turkey (Öztürk, 2004; Özalp and Alparslan, 2011), 131 Cyprus (Jiménez et al., 2014), and in Tunisia (Zibrowius, 1980). The existence of fossil 132 deposits of C. caespitosa from the Holocene and Pleistocene have been mentioned from several localities (Fornós et al., 1996; Kühlmann, 1996; Bernasconi et al., 1997; Peirano et al., 133 134 1998, 2009; Bracchi et al., 2016), but the oldest have been described in Spain (Aguirre and 135 Jiménez, 1998). Throughout the Mediterranean, well-preserved 'subfossil' formations of C. 136 caespitosa covered by thick sediment layers or calcareous algae have been also described 137 (Peirano et al., 1998 and references therein). In Corsica, similar dead banks dated back to 138 600-2400 years BP and reaching several meters diameter were reported by Laborel (1987).

This paper focuses on the description of well-preserved corallite fragments of a *C. caespitosa* deposit found in a *P. oceanica* matte sequence on the eastern coast of Corsica. The analysis of the morphological features of coral fragments coupled to biogeosedimentological characterization and radiocarbon dating provided (i) a first evaluation of the past annual growth rate of *C. caespitosa* in this location, and (ii) the opportunity to describe a colonization event of the substrate by *C. caespitosa* followed by its gradual substitution by a *P. oceanica* meadow.

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147 2. Material and methods

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149 **2.1. Study site**

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151 The shelf of the eastern continental margin of Corsica island (France, NW 152 Mediterranean) is characterized by a 5-25 km width range with a low gradient slope ($^{-1-2^\circ}$) 153 (Gervais et al., 2006; Pluquet, 2006). The widest extension of this continental shelf is notably 154 observed off the Golo fan system (Bellaiche et al., 1994; Mulder and Maneux, 1999; Gervais 155 et al., 2004). The infralittoral zone of the underwater delta of the Golo river presents the 156 largest P. oceanica meadow in Corsica (Pergent-Martini et al., 2015; Valette-Sansevin et al., 157 2019; Fig. 1). The C. caespitosa deposits studied occurs near the upper bathymetric limit of 158 the *P. oceanica* meadows established at 8 m depth. The marine currents on the east margin, 159 represented by coastal drift mainly oriented towards the south (Millot et al., 1987 in 160 Pluquet, 2006), are moderate to strong and have generated several landscape 161 discontinuities ('intermattes'; Abadie et al., 2015). The sea bottom is dominated by sand 162 fractions with interspersed areas with larger grain sizes, from gravels to pebbles (Guennoc et 163 al., 2001). Though the concentrations of suspended matter have been lowering over the last 164 century due to the effects of anthropogenic activities on land (Mulder and Maneux, 1999), 165 the Golo river discharges show a strong seasonal variability linked to the subtropical

Mediterannean climate in Corsica (Molliex et al., 2021). The high variability in precipitation 166 result in a strong variability of the Golo river discharges (mean annual value: 14.8 m³ s⁻¹, 167 maximum value: 734 m³ s⁻¹; Valpajola station 1969-2019; HYDRO French database, 168 www.hydro.eaufrance.fr; Molliex et al., 2021). The sediment deposition by the Golo river has 169 170 been strongly influenced by the Mediterranean climate, extreme events (e.g. flash floods, shelf storms, snow melt) and long-shore drift (Conchon, 1975; Orszag-Sperber and Pilot, 171 172 1976; Conchon and Gauthier, 1985). The mean monthly sea surface temperature (SST) 173 recorded between 2014 and 2019 ranges from 14.21 ± 0.22°C (February) to 26.85 ± 0.96°C 174 (August) (buoy WMO #6100295; http://www.emodnet-physics.eu/map).

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Figure 1. Location of the study site on the eastern continental shelf of Corsica. (2-column)

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179 2.2. Sampling of sediment

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181 Sediment sampling was performed with a Kullenberg gravity corer during the oceanographic research survey Carbonsink (August 2018) aboard the R/V L'Europe (Ifremer). 182 183 The core barrel consists of a stainless-steel tube 5 m long with a PVC tube (internal diameter 90 mm) inside it and surmounted by a lead weight of ~1 ton. The coring head is constituted 184 185 of a sharp edge to cut the fibrous matte material and minimize the effects of compression 186 during sediment sampling. Among the 12 cores taken in this sector, deposits of C. caespitosa 187 fragments were only observed in one of them (BIG-10M-PO-A). The collection of this vertical 188 core in the *P. oceanica* meadow was carried out at 10 m depth. The corers were cut open longitudinally, the matte sliced at regular intervals (1 cm slice every 5 cm) and the
 subsamples stored in polypropylene vials at 5°C before processing.

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192 **2.3. Laboratory analysis of sediment core**

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194 Sediment bulk density and grain size were measured after drying of each sampled 195 slice at 70°C until constant weight (Howard et al., 2014). The samples were sieved and 196 weighed after drying and then separated into two fractions: the fine (<2 mm) and coarse 197 fraction (>2 mm). The fine fraction is composed of the inorganic and organic matter of the 198 sediment (SOM). The coarse fraction was sorted into different categories: (i) the coarse 199 organic matter (COM, P. oceanica seagrass and macrophytes remains), (ii) the coarse mineral 200 fraction (siliclastic gravel), and (iii) the coarse carbonate fraction (shells and coral remains). 201 After sorting, the COM was integrated into the SOM, homogenized and ground (<0.063 mm). 202 The total organic matter (TOM) and fine calcium carbonate ($CaCO_3 < 2 \text{ mm}$) content were 203 determined by following loss on ignition method (Heiri et al., 2001). TOM represents the 204 total amount of SOM (<2 mm) and COM (>2 mm). The analyses performed on sediment 205 samples provided a basis for defining 6 main biogeosedimentological sections along the core 206 (Fig. 2). The mean organic matter, mineral and carbonate contents was calculated in each of 207 the biogeosedimentological sections using the values found in the corresponding 1 cm 208 sediment slices sampled every 5 cm (Table 1). The main identifiable molluscan shells in the 209 coarse carbonate fraction (CaCO₃ > 2 mm) were identified and subsequently assigned to 210 assemblages according to the Pérès and Picard (1964) and Pérès (1982) classification system. 211 In this last fraction fragments of *C. caespitosa* were isolated from each subsample for further 212 analysis.

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214 **2.4.** Measurements on corallites of *C. caespitosa*

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216 Samples of corallites were cleaned of epibionts and organic matter by immersion in 217 30% hydrogen peroxide (H₂O₂) solution for 24 hours. Corallites were carefully washed in an 218 ultrasonic bath filled with ultrapure MilliQ[™] water for 5 minutes to remove fine sediment 219 particles. After drying at 70°C, all corallites were weighed to determine the concentration of 220 coral fragments for each sample. High-quality images were taken by stereomicroscopy for 221 morphological measurements (Leica EZ4D stereomicroscope with integrated HD numerical 222 camera) with the LAS EZ Leica Application Suite 3.3.0. (Leica Microsystems, Switzerland). In a 223 first approach, the total length and the diameter of corallites were measured on 224 stereomicroscopy images with the ImageJ software (http://imagej.nih.gov/ij/dowbload.html; Schneider et al., 2012). Annual growth rates of C. caespitosa were also computed by 225 226 measuring, on the outer wall of unbored corallites, the distance between two adjacent thick 227 lines indicating where the high-density bands (HD) start (Kružić and Požar-Domac, 2002) 228 during the winter season (low temperature and low light intensity; Peirano et al., 1999, 229 2005; Silenzi et al., 2005). The mean annual growth rates were calculated for each sediment 230 sample by compiling all measures. For each corallites fragments, the total number of well-231 preserved calices and lateral budding branches growing parallely to the parent corallite were 232 recorded (Peirano et al., 1998; Kružić and Požar-Domac, 2002). Statistical analyses were 233 performed using the statistics software package XLSTAT (Addinsoft, 2019). Normality of 234 parameter values was checked using a Shapiro-Wilk test. Inter-relationships between the 235 biometrical and morphological parameters of coral fragments and biogeosedimentological 236 parameters analyzed in the core were investigated by performing Pearson's correlation test. 237 The correlation coefficient was calculated together with p-values to determine the 238 significance and strength of each relationship. Differences between mean growth rates were 239 analyzed through one-way ANOVA and post-hoc Tukey's HSD tests.

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241 2.5. Radiocarbon dating

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243 The chronostratigraphic reconstruction of the soil was performed from radiocarbon (¹⁴C) measurements by Accelerator Mass Spectrometry at the DirectAMS laboratory (Accium 244 BioSciences, Seattle, WA). Samples of P. oceanica (n = 2) and C. caespitosa debris (n = 3) 245 were collected at ~1 m intervals along the core. Before ¹⁴C measurements, seagrass remains 246 247 were first rinsed and placed in an ultrasonic bath of ultrapure MilliQ[™] water for 5 minutes to 248 remove sediment particles. Finally, seagrass samples were inspected under a 249 stereomicroscope for any attached materials and placed successively in baths of 250 hydrochloric acid (HCl 1M, 80°C for 30 minutes) and sodium hydroxyde (NaOH 0.2M, 80°C 251 for 30 minutes) to eliminate the carbonates, the fulvic and humic acids and the atmospheric carbon dioxide, respectively (Brock et al., 2010). Fragments of C. caespitosa were 252 253 mechanically cleaned in HCl solution to remove the superficial carbonate layer, reducing the 254 mass by ~25-35%. The material was rinsed three times in ultrapure MilliQ[™] water and dried 255 at 60°C prior to crushing and further treatment before dating.

256 Radiocarbon data, expressed as years before present (yr BP), were subsequently 257 calibrated for the local marine reservoir effect ($\Delta R = 46$ years, error $\Delta R = 40$ years; Siani et 258 al., 2000) using the CALIB 7.1.0 software (Stuiver and Reimer, 1993) in conjunction with the 259 Marine 13.14C calibration curve (Reimer et al., 2013). After corrections, the calibrated ages 260 before present (cal. yr BP) were used to produce age-depth models using the clam package 261 in R software (Blaauw, 2010). The best-fitted chronostratigraphic model was obtained with 262 the smooth model (default smoothing spline parameter 0.3; 263 http://chrono.qub.ac.uk/blaauw/; Blaauw, 2010). Ages were calculated every 1 cm from the 264 shallowest (0 cm) to the deepest (320 cm) dated depth of the core. The age-depth model has 265 permitted to approximate every 1 cm the respective sediment accumulation rate (SAR; cm yr⁻¹) and resolution time (yr cm⁻¹) (Blaauw, 2010; Serrano et al., 2012). The SAR 266 267 corresponded to the thickness of sediment accumulated over a defined period of time (per 268 year; a high SAR value reflects significant sediment deposition). Inversely, the resolution 269 time corresponded to the years of sedimentary accumulation over a defined thickness (every 270 1 cm; a high resolution time value reflects low sediment deposition) (Blaauw, 2010). The 271 mean SAR and resolution time in a core section was calculated using all the values in the272 depth interval.

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274 Results

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276 **3.1. General stratigraphy of the sequence**

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Based on the biogeosedimentological analyses performed on the sediment samples, 6 main
units and 2 sub-units (Table 1; Fig. 2) were identified along the core and are described as
follows:

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U1 (365-330 cm, before 4750 cal. yr BP) is mainly composed of pebbles with a medium to coarse grey sand matrix. On average, the sediment in this unit is poor in total carbonate ($4.9 \pm 2.7\%$) and organic content ($2.2 \pm 2.5\%$). Macro- and micro-fauna are rare but badly preserved and eroded. *C. caespitosa* fragments were identified together with several shell remains of marine molluscs (*e.g. Bittium reticulatum, Cerithium vulgatum*).

U2 (330-310 cm, 4750-4610 cal. yr BP) consists of coarse sand to gravel grey sediment with the sporadic occurrence of pebbles. The mean TOM and calcium carbonate are higher than in the U1 section, $5.5 \pm 1.1\%$ and $25.5 \pm 7.7\%$, respectively. The marine mollusc assemblage is very well-preserved and largely composed of *B. reticulatum*, *Jujubinus exasperatus*, *Tricolia speciosa* and *Venus verrucosa*, associated with *C. caespitosa* debris, that represent $6.0 \pm 5.2\%$ of the coarse calcium carbonate content.

U3 (310-285 cm, 4610-4210 cal. yr BP) is characterized by sandy sediment with fine pebbles (~4 cm) and some debris of *P. oceanica*. This unit exhibits a higher content of corallite fragments of *C. caespitosa* which increase continuously from the bottom to the top of the unit, from 11.4% to 41.4% (coarse calcium carbonate content). The mean TOM (5.6 \pm 0.8%) and calcium carbonate (30.4 \pm 3.7%) are similar that of the previous unit. In this case, the faunal assemblage was dominated by *Glans trapezia*, *Arca noae* and individuals of *Alvania* sp.

300 U4 (285-270 cm, 4210-3930 cal. yr BP) is mainly constituted by a sandy-muddy matrix 301 (52.4 \pm 2.2%) with a low content in coarse mineral fraction (8.6 \pm 3.6%) corresponding to 302 gravel. The presence of *C. caespitosa* debris in the coarse calcium carbonate fraction was 303 lower than in section U3 (9.0 \pm 5.0%) and mainly ascribed to a mollusc assemblage strongly 304 similar to the U2-U3 sections. Furthermore, the sequence exhibits a constant content in 305 TOM (5.3 \pm 1.0%).

306 U5 (270-170 cm, 3930-1410 cal. yr BP) is composed by a brown to grey muddy 307 sediment with intact rhizomes and root debris characteristic of the matte of *P. oceanica*. This 308 deposit shows a high constant organic and mineral content ($10.0 \pm 2.1\%$ and $61.1 \pm 6.5\%$, 309 respectively) associated with a significant accumulation of well-preserved *C. caespitosa* 310 corallites in living position. These fragments represent an average 34.1 % of the coarse 311 calcium carbonate content and increase continuously from the bottom (15.8%) to the top (100.0%) of the unit. The faunal assemblage of these two sub-units is overall similar that of
 the previous unit but differ by the occurrence of several individuals of *Haliotis tuberculata* and *Loripes lacteus*. The sequence is characterized notably by two sub-units:

Sub-unit U5a (270-225 cm, 3930-2830 cal. yr BP) is characterized by a 13.5 \pm 9.4% content in *C. caespitosa* in the coarse calcium carbonate fraction and by a total carbonate content of 26.9 \pm 8.5%. The mean mineral fraction (63.8 \pm 6.8%) slowly decreased from the bottom to the top of the sub-unit (60.5 to 51.5%) whereas the organic content (9.3 \pm 2.5%) doubled (from 4.2 to 8.5%).

Sub-unit U5b (225-170 cm, 2830-1410 cal. yr BP) recorded the highest content in *C. caespitosa* in the coarse calcium carbonate fraction (51.7 \pm 28.1%) and the highest content in total carbonate (30.4 \pm 6.3%). In comparison with the previous sub-unit, similar content in mineral and organic fraction was observed with 59.1 \pm 5.7% and 10.6 \pm 1.6%, respectively.

324 As for the previous section of the stratigraphic sequence, U6 (170-0 cm, 1410 cal. yr 325 BP-present) is constituted by the matte of *P. oceanica* in which the TOM content increases 326 from the bottom (12.4%) to the top (58.3%). The mineral fraction is almost entirely 327 composed of the finer fraction and represents on average $81.4 \pm 11.1\%$ of the sediment. The 328 total carbonate fraction decreases from the bottom (13.6%) to the top (4.8%). This lower 329 content is notably due to the absence of *C. caespitosa* fragments. The faunal assemblage is 330 rather well-preserved and is mainly characterized by the presence of B. reticulatum, J. 331 exasperatus, T. speciosa, G. trapezia and Alvania spp.

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Table 1. Mean (± S.D.) content in organic matter, mineral and calcium carbonate in the total fraction of each
 biogeosedimentological units identified in the core. N: number of sediment slices analyzed per core section.

335	Total mineral: mineral fractions <2 mm and >2 mm; Total $CaCO_3$: $CaCO_3$ fractions <2 mm and >2 mm. The	
336	values are expressed as percentage (%).	

Core section	Ν	SOM	СОМ	том	Mineral	Mineral	Total	CaCO₃ <2	CaCO ₃	Total
					<2 mm	>2 mm	mineral	mm	>2 mm	CaCO ₃
U6 (0-170 cm)	34	7.1 ± 3.1	4.1 ± 9.9	11.2 ± 8.5	81.4 ± 11.1	0.1 ± 0.2	81.5 ± 11.1	7.1 ± 3.0	0.3 ± 0.4	7.4 ± 3.3
U5b (170-225 cm)	12	9.0 ± 1.3	1.6 ± 1.0	10.6 ± 1.6	58.1 ± 6.2	1.0 ± 0.7	59.1 ± 5.7	18.3 ± 2.3	12.1 ± 5.2	30.4 ± 6.3
U5a (225-270 cm)	9	8.6 ± 2.3	0.7 ± 0.6	9.3 ± 2.5	59.0 ± 6.3	4.8 ± 1.6	63.8 ± 6.8	20.6 ± 5.1	6.2 ± 4.3	26.9 ± 8.5
U4 (270-285 cm)	3	5.0 ± 0.7	0.4 ± 0.4	5.3 ± 1.0	52.4 ± 2.2	8.6 ± 3.6	61.0 ± 4.0	22.1 ± 3.4	11.5 ± 6.6	33.6 ± 5.0
U3 (285-310 cm)	5	5.4 ± 0.7	0.2 ± 0.2	5.6 ± 0.8	44.6 ± 6.1	19.4 ± 8.4	64.0 ± 4.0	21.8 ± 2.0	8.6 ± 3.5	30.4 ± 3.7
U2 (310-330 cm)	4	4.3 ± 1.3	1.2 ± 0.7	5.5 ± 1.1	47.0 ± 5.5	22.0 ± 13.3	69.0 ± 7.8	16.5 ± 3.4	9.1 ± 4.5	25.5 ± 7.7
U1 (330-365 cm)	7	2.0 ± 2.2	0.2 ± 0.4	2.2 ± 2.5	22.1 ± 9.9	70.8 ± 14.2	92.9 ± 4.5	4.2 ± 2.2	0.7 ± 0.5	4.9 ± 2.7



Figure 2. Lithology, calibrated radiocarbon dates, content in organic matter, mineral and calcium carbonate in
 the total fraction, content in *Cladocora caespitosa* in the coarse calcium carbonate fraction and
 biogeosedimentological units identified in the core. (2-column)

343 3.2. Age-depth model and accumulation rates

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The radiocarbon dating performed along the core showed that the stratigraphic sequence encompassed the 4750 cal. yr BP (Table 2). The ages corrected for the marine reservoir effect (excluding one inconsistent dating; Table 2), coupled to one hypothetical date at the top of the sequence (present; *i.e.* AD 2018), were used to construct the agedepth model of the core (Fig. 3a). According to this model, the accumulation rates ranging from 0.4 to 4.0 mm yr⁻¹ (mean: 1.2 ± 1.1 mm yr⁻¹; Fig. 3b; Table 3) decreased linearly from the top to the bottom of the core (4.0 to 0.6 mm yr⁻¹; r = -0.808; p<0.05).

The vertical trends showed that the resolution ranged from 2.5 to 27.5 yr cm⁻¹ (mean: 15.1 \pm 8.5 yr cm⁻¹; Fig. 3b; Table 3) and followed an inverse pattern increasing from the bottom to the top of the core (r = 0.774; p<0.05). The 0-170 cm section (~1400 cal. yr BPpresent) showed higher mean accumulation rates ($1.8 \pm 1.1 \text{ mm yr}^{-1}$) than the 170-270 cm section (~2100-1400 cal. yr BP) with a mean SAR of 0.4 ± 1.1 mm yr⁻¹ and the 270-320 cm section (~4600-2100 cal. yr BP) was defined by a mean accumulation rate of 0.6 ± 0.1 mm yr⁻¹.

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Table 2. Radiocarbon dating of the *Posidonia oceanica* debris and *Cladocora caespitosa* fragments collected along the core. *Sample not considered for the age-depth model.

LahiD	Matarial	Depth	Radiocarbon	Calibrated age	Mean calibrated age	
	Wateria	(cm)	age (yr BP)	(cal. yr BP - 2σ)	(cal. yr BP - 2σ)	
D-AMS 030654	P. oceanica	151	1476 ± 33	876-1126	1001 ± 125	
D-AMS 037834	C. caespitosa	170	1894 ± 22	1295-1507	1401 ± 106	
D-AMS 030655	P. oceanica	263	3917 ± 35	3673-3986	3860 ± 157	
D-AMS 037835	C. caespitosa	265	2460 ± 25	1904-2187	2046 ± 142*	
D-AMS 037836	C. caespitosa	320	4599 ± 27	4593-4860	4727 ± 134	

362

363 Table 3. Sediment accumulation rates (SAR) and resolution values calculated for the different
 364 biogeosedimentological sections of the core. No available data for U1 section (330-365 cm; age depth-model
 365 performed between 0 and 320 cm).

		Accumu	lation rate (m	m yr⁻¹)	Resolution (yr cm ⁻¹)				
		Mean ± S.D.	Minimum	Maximum	Mean ± S.D.	Minimum	Maximum		
Core section	U6 (0-170 cm)	1.8 ± 1.1	0.5	4.0	8.3 ± 5.3	2.5	20.1		
	U5b (170-225 cm)	0.4 ± 0.0	0.4	0.5	25.4 ± 2.2	20.4	27.5		
	U5a (225-270 cm)	0.4 ± 0.0	0.4	0.5	24.6 ± 2.2	20.3	27.3		
	U4 (270-285 cm)	0.5 ± 0.0	0.5	0.6	18.7 ± 0.8	17.5	20.1		
	U3 (285-310 cm)	0.6 ± 0.0	0.6	0.7	15.9 ± 0.7	15.0	17.3		
	U2 (310-320 cm)	0.7 ± 0.0	0.7	0.7	14.8 ± 0.1	14.7	14.9		
Total section	U2-U6 (0-320 cm)	1.2 ± 1.1	0.4	4.0	15.1 ± 8.5	2.5	27.5		

366





371 each depth, respectively. The grey areas include 2o confidence range (95% CI) of calibrated dates. (B) SAR and 372 resolution curves. (2-column)

373

374 3.3. Morphology and biometrical values of corallites

375

376 A total of 390 coral fragments were found in the coarse carbonate fraction of the 377 sediment samples. These coral fragments were constituted exclusively of C. caespitosa 378 corallites and were collected in all sediment samples of the core between 169 cm and 325 379 cm (Fig. 4a) except for the 174-175 cm, 239-240 cm and 254-255 cm samples (Fig. 5a). The 380 well-preserved and abundant layer of fragments (Fig. 4c; Fig. 4d) was found in the upper part 381 of section U5a (224-230 cm) and in the whole of section U5b (170-225 cm), both 382 characterized by the presence of P. oceanica matte (Fig. 2). Inversely, a lower content in C. 383 caespitosa and the most degraded fragments were observed in the lower part of the core 384 (230-325 cm) defined by a higher content in coarse mineral fraction (Fig. 2; Table 1; Table 4). 385 Indeed, the coral fragments collected from the lower part of U5a to U2 section were 386 characterized by traces of boring activity, often associated with coral dwellers, and by a high 387 erosion of their external walls (Fig. 4b; Fig. 4e; Fig. 4f). The number of corallite fragments 388 and their content in the sediment revealed to be significantly related to biogeosedimentological parameters as COM (r = 0.442; p-value<0.05 and r = 0.531; p-389 390 value<0.01; Table 3). Inversely, significant negative correlations were evidenced between 391 the number and content of corallite fragments with coarse mineral content (r = -0.424; p-392 value<0.05 and r = -0.500; p-value<0.01; Table 3).

393



394

395 Figure 4. (A) Cladocora caespitosa fragments visible after the core opening, (B) well-preserved (up) and bored 396 coral fragments (down), (C) calice showing septal arrangement and columella, (D) coral fragments with 397 branches, (E, F) eroded corallite fragments characterized by traces of growth pattern on the external wall. Scale 398 bars: 5 mm. (2-column)

399

400 The individual length of coral fragments ranged between 1.0 and 55.0 mm (mean \pm 401 S.D., 11.4 ± 8.1 mm; n = 390; Fig. 5b). The lowest and highest mean values were recorded at 402 314-315 cm (2.5 ± 0.7 mm) and at 184-185 cm (15.5 ± 7.7 mm), respectively. The length of 403 coral fragments was two-fold more important in the 170-230 cm section (12.8 \pm 8.5 mm)

404 than in the 230-325 cm section (6.7 \pm 4.0 mm; Fig. 5b). The minimum and maximum 405 individual diameter of C. caespitosa debris ranged between 1.0 and 6.0 mm with a mean value of 3.0 ± 0.8 mm (± S.D.; n = 390; Fig. 5c). The lowest average value was recorded at 406 407 314-315 cm (2.5 ± 0.7 mm) and the highest at 244-245 cm (4.0 ± 0.5 mm) and 259-260 cm 408 $(4.0 \pm 0.4 \text{ mm}; \text{ Fig. 5c})$. As the number of corallites fragments and their content in the 409 sediment, the length of coral fragments decreased significantly with higher coarse mineral 410 content (r = -0.557; p-value<0.01; Table 3). Nevertheless, the fragments length increased 411 with COM (r = 0.410; p-value<0.05) and SOM contents (r = 0.437; p-value<0.05; Table 3).

412



414 **Figure 5.** (A) Number of *Cladocora caespitosa* fragments, box plots representing (B) the length and (C) the 415 diameter of coral fragments collected along the core. **(1.5-column)**

416

413

417 The colonies of *C. caespitosa* are generally phaceloid but in some cases the corallites 418 build irregular coral branches. The total number of additional ramifications observed with 419 the main corallites found was 104 branches. The highest cumulated number of branches was 420 recorded at 189-190 cm (n = 16 branches) and the highest number of branches for a coral 421 fragment was recorded at 224-225 cm (n = 3 branches on a coral fragment). The mean 422 cumulated number of branches decreased from the top to the bottom of the core with ~6.3 423 \pm 1.2 branches per sample (170-230 cm section) to 1.2 \pm 0.2 branches per sample (230-325 424 cm section). Considering the accumulated number of branches and the number of coral fragments found in each sample, the highest branching rate was detected at 314-315 cm (1.0
± 1.0 branches per fragment), with a mean value estimated at 0.3 ± 0.1 branches per coral
fragment (Fig. 6a).

428 A total of 36 calices were found among the 390 coral fragments of *C. caespitosa*. The 429 highest accumulated number of calices was measured at 219-220 cm (n = 8) where the 430 highest number of calices for a coral fragment was recorded (n = 2 calices on a coral 431 fragment; Fig. 4d; Fig. 4e). Similarly to the branching pattern, the mean accumulated number 432 of calices decreased from the top to the bottom of the core with $\sim 2.2 \pm 0.8$ to 0.4 ± 0.2 (at 433 169-230 and 230-325 cm, respectively). Considering the accumulated number of calices and 434 the number of coral fragments found in each sample, the highest number of calices per 435 fragment and sample were recorded at 219-220 cm (0.3 ± 0.1) and 299-300 cm (0.3 ± 0.2), 436 with a mean value estimated at 0.1 ± 0.0 (Fig. 6b). Contrary to the number and the content 437 in coral fragments, the mean diameter, the number of branches and calices per fragment

438 showed no correlation with biogeosedimentological parameters (Table 3).

439

440**Table 4.** Pearson's correlation matrix between the morphological and biometrical parameters measured on441*Cladocora caespitosa* fragments and biogeosedimentological parameters analyzed in the core. Fragments:442number of fragments; Content: *C. caespitosa* content measured in dry weight percentage of total sample dry443weight (%); Length: mean length (mm); Diameter: mean diameter (mm); Branches: number of branches per444fragment; Calices: number of calices per fragment; Depth: depth in soil; Min.>2 and Min.<2: mineral fraction >2445mm and <2 mm; CaCO₃>2 and CaCO₃<2: CaCO₃ fraction >2 mm and <2 mm. Level of significance: *P≤0.05,</td>446**P≤0.01; NS, P≥0.05. Significant correlations in bold (r value).

Variables	Fragments	Content	Length	Diameter	Branches	Calices	Depth	СОМ	SOM	Min.>2	Min.<2	CaCO ₃ >2	CaCO ₃ <2
Fragments		0.929	0.677	-0.386	-0.101	0.193	-0.697	0.442	0.338	-0.424	0.101	0.456	-0.203
Content	***		0.756	-0.398	-0.029	0.117	-0.665	0.531	0.294	-0.500	0.166	0.531	-0.259
Length	***	***		0.033	0.005	0.089	-0.698	0.410	0.437	-0.557	0.299	0.297	-0.170
Diameter	*	*	NS	5	-0.204	0.279	0.012	-0.265	0.246	-0.023	0.051	-0.371	0.326
Branches	NS	NS	NS	NS		-0.016	0.144	-0.050	-0.154	0.104	-0.131	0.108	0.014
Calices	NS	NS	NS	NS	NS		0.005	-0.213	0.060	0.064	-0.124	-0.007	0.132
Depth	***	***	***	NS	NS	NS		-0.455	-0.744	0.785	-0.592	-0.154	0.296
сом	*	**	*	NS	NS	NS	*		0.416	-0.413	0.222	0.307	-0.453
SOM	NS	NS	*	NS	NS	NS	***	*		-0.681	0.702	-0.238	-0.392
Min.>2	*	**	**	NS	NS	NS	***	*	***		-0.732	-0.177	0.099
Min.<2	NS	NS	NS	NS	NS	NS	***	NS	***	***		-0.411	-0.428
CaCO ₃ >2	*	**	NS	NS	NS	NS	NS	NS	NS	NS	*		0.004
CaCO ₃ <2	NS	NS	NS	NS	NS	NS	NS	*	*	NS	*	NS	



447

Figure 6. Mean values (± S.D.) observed along the core of (A) branches per coral fragment and (B) calices per
 coral fragment of *Cladocora caespitosa*. (1.5-column)

450

451 3.4. Growth rates of C. caespitosa

452

453 The annual growth rates were determined by measuring the distance between two adjacent thick lines which occur on the outer wall of corallites (Fig. 4a; Fig. 4e). However, 454 455 these thick lines deposited annually were not always clearly noticeable on external walls of 456 coral fragments due to high bio-erosion and boring features associated with organisms 457 inhabiting the coral (Fig. 4a; Fig. 4e). Consequently, a high number of corallites had to be 458 discarded for coral growth rate measurements. Thus, the image analysis for growth patterns 459 was performed on the corallite fragments occurring between 169 and 230 cm depth (Fig. 7). 460 In total, 427 measurements were made on 83 coral skeleton images representing ~4.6 ± 1.2 461 measurements per corallite and 38.8 ± 12.0 measurements per sediment sample. The 462 number of measurements ranged between 6 and 114 (at samples 214-215 and 204-205 cm, 463 respectively).

The minimum and maximum growth rates recorded on a corallite were 0.67 and 5.02 mm yr⁻¹, respectively. The average growth rate calculated on corallites was 2.32 \pm 0.79 mm yr⁻¹ (Fig. 8). The lowest and highest mean annual growth rates were 1.85 \pm 0.78 and 3.09 \pm 0.81 mm yr⁻¹ (at 224-225 and 184-185 cm, respectively). Significant differences were found between growth rates in investigated sediments samples of the 169-230 cm core section (ANOVA p<0.001). Tukey HSD *post hoc* test contributed to identify three groups with high (A; 3.09 mm yr⁻¹), intermediate (AB; 2.26 to 2.62 mm yr⁻¹) and low growth rate (B; 1.85 to 2.15

471 mm yr⁻¹; Fig. 7). Over the 169-230 cm section, the mean annual growth rate followed a cyclic 472 pattern and exhibited two distinct semi-millennial to millennial oscillation (Fig. 7; Fig. 8). The 473 first oscillation ranged between the minimum growth rates observed at 224-225 cm (2830 474 cal. yr BP) and at 194-195 cm (2010 cal. yr BP) with a maximum at 204-205 cm (2280 cal. yr 475 BP). The second oscillation occurred between 194-195 cm (2010 cal. yr BP) and 169-170 cm 476 (1410 cal. yr BP) with a peak at 184-185 cm (1750 cal. yr BP).

477 Overall, the mean annual growth rate between the 169-170 cm and 229-230 cm 478 samples appeared to decrease with depth in the soil (Fig. 7; Fig. 8) but no significant 479 correlation was found (r = -0.386; p>0.05; Table 4). Similarly, although the mean annual 480 growth rate of corallites and the SAR followed the same pattern with depth in the soil (Fig. 481 8), no significant correlation was highlighted between these two parameters (r = 0.055; p>0.05; Table 4). For the same core section, the mean annual growth was higher than the 482 mean accumulation rate of the sediment (0.39 \pm 0.03 mm yr⁻¹; Fig. 8) highlighting no burial 483 484 of coral colonies at this period.







Figure 7. Box plot of growth rates measured on well-preserved *Cladocora caespitosa* corallites from the core.
 Dissimilar letters (A, AB, B) denote significant differences between groups (p<0.05). For major climatic periods,
 see Fig. 2. (1-column)



491

492 Figure 8. Relationship between the mean growth rate measured on *C. caespitosa* corallites and SAR from the
 493 core. (1-column)

494

495 4. Discussion

496

497 The sedimentary sequence collected on the north-eastern continental margin of 498 Corsica enabled us to provide a first palaeo-environmental reconstruction of the area over 499 the last 5000 years. The biogeosedimentological and the chronostratigraphic analyses have 500 shown that the sequence was characterized by a succession of marine ecosystems since 501 ~4750 cal. yr BP. *Cladocora caespitosa* corallites revealed that the mean annual growth rate 502 is similar to other values recorded in the Mediterranean. The occurrence of this coral deposit 503 and its growth pattern appeared to be closely related to the environmental conditions and 504 climatic periods since the mid-Holocene.

505

4.1. The settlement phase: establishment of the *C. caespitosa* colonies following a major sediment alluvial input (~4750-3930 cal. yr BP)

508

509 The lower part of the core from U1 (365-330 cm, up to 4750 cal. yr BP) to U4 sections 510 (285-270 cm, 3930 cal. yr BP) was defined by a graded bedding of sedimentary layers which 511 evidenced the variation in the marine depositional environment during the End of the Holocene Climate Optimum (~5000-4500 cal. yr BP) and the 4.2 kyr climatic event (~4500-512 513 3900 cal. yr BP). The analysis of the mollusc assemblages performed at the base of the core (U1 section) revealed the presence of macro- and micro-shell debris assigned to the marine 514 515 environment (mainly B. reticulatum, J. exasperatus and T. speciosa; Pérès and Picard, 1964; 516 Pérès, 1982). However, these shell fragments may not have been produced locally but may 517 have been imported from adjacent marine areas by hydrodynamic forces during high energy 518 events as evidenced by their state of conservation (i.e. calcareous fragments). Additionally, 519 the coarse sedimentary deposit found at the bottom end of the core and characterized by 520 well-rounded pebbles embedded in a sandy grey matrix may have resulted from littoral drift, 521 shelf storms or high alluvial sediment input after major river floods (Orszag-Sperber and 522 Pilot, 1976; Gauthier, 1981; Conchon and Gauthier, 1985; Gervais et al., 2004). In the east 523 coast of Corsica, the Golo river is the largest drainage basin and has developed both a wide 524 underwater delta (Ottman, 1958) and a large deltaic plain (Marana Plain; Fig. 1). This deltaic 525 plain was mainly constituted of recent alluvial terraces with grey soil (Fy3; Orofino et al., 526 2010) exhibiting similar geological properties than the sedimentary layer observed at the 527 base of the studied core. The high sediment input identified here may perhaps be linked to 528 the maximum of precipitation observed during the mid-Holocene period in the western parts 529 of the Mediterranean (Roberts et al., 2011a, 2011b; Peyron et al., 2013). Thus, the exact 530 origin of this pebble layer is difficult to determine but could be related to (i) massive alluvial 531 deposits from the Golo river (Conchon and Gauthier, 1985; Mulder and Maneux, 1999) 532 associated with (ii) a redistribution of sediments on the shelf by littoral drift generally oriented from south to north (Gauthier, 1981; Gaillot and Chavarot, 2001). 533

534 The setting up of pebble beds in this sector has most likely favored the formation of 535 coral colonies of C. caespitosa. Similar fossil build ups settled on basal conglomerate with 536 pebbles or boulders have been already found by D'Alessandro and Bromley (1994) and 537 Schiller (1993a). This coral species preferentially grows on rocky substrates (Peirano et al., 538 1998; Kersting et al., 2012) even if it can also be found free on sedimentary or organic 539 substrates (Laborel, 1987; Kružić and Benković, 2008). Though some coral debris of C. 540 caespitosa was found in the 344-345 cm sample (Fig. 2), the most probable settlement of the 541 C. caespitosa colonies at this site was situated at the basal part of the U2 section (320 cm) 542 and dated back to ~4750 cal. yr BP. Cladocora caespitosa can colonize areas with a wide 543 range of marine currents and turbid conditions (Laborel, 1961; Zibrowius, 1980; Peirano et 544 al., 1998). In the Mediterranean, the occurrence of the widest C. caespitosa banks were 545 recorded in the vicinity of river mouths exposed to abundant sedimentary and alluvial inputs 546 (Fornós et al., 1996; Aguirre, 1998, Drinia et al., 2010; Tremblay et al., 2011). Such a turbid 547 environment is consistent with the observation of coral fragments in this study. 548 Nevertheless, the development of this coral species in shallow waters remains strongly 549 influenced by other parameters such as temperature, food supply and irradiance (Schiller, 550 1993a, 1993b; Peirano et al., 1998, 2005; Kružić and Benković, 2008; Chefaoui et al., 2017). 551 Considering the reconstruction of the Relative Sea Level (RSL) changes in Corsica performed 552 by Vacchi et al. (2017), the RSL at this period was placed ~2.7 m below the present mean sea 553 level (MSL), allowing us to estimate the beginning of the *C. caespitosa* colonization at around 554 7.3 m below the MSL. At this depth, the light intensity was enough for the symbiotic 555 zooxanthellae to perform photosynthesis efficiently, hence allowing coral calcification even 556 if the growth process is linked to a combination of autotrophy and heterotrophy (Schiller, 557 1993b; Peirano et al., 1999; Rodolfo-Metalpa et al., 2008). This capability gives C. caespitosa

an advantage for undertaking the colonization of deeper areas or locations with higher 558 559 sedimentation rates (Peirano et al., 1998; Morri et al., 2001). The particulate organic matter 560 from turbid waters have proved to play directly or indirectly a role in coral metabolism 561 (Schiller and Herndl, 1989; Rodolfo-Metalpa et al., 2008) to build large coral beds or banks 562 (Laborel, 1961; Tur and Pere Godall, 1982; Peirano et al., 1998; Kružić and Benković 2008). 563 Here, the increase in the TOM content, and notably SOM content (Table 1), between U2 to 564 U4 sections could have been advantageous for the growth of C. caespitosa. Overall, the 565 increase of coral fragment content observed from U2 to U4 sections probably could be 566 related to a development of *C. caespitosa* colonies which probably benefited from favorable 567 environmental conditions (i.e. high hydrodynamic conditions and high turbidity of coastal 568 waters associated to high sediment alluvial inputs).

569

570

4.2. The transitional phase: coexistence between the C. caespitosa colonies and the P. 571 oceanica meadow (~3930-1410 cal. yr BP)

572

573 At the end of the 4.2 kyr event (4500-3900 cal. yr BP), a major environmental change 574 occurred with the settlement of the *P. oceanica* meadow, as suggested by a major increase 575 in the SOM content (~5% to 10%) and also by the presence of COM remains from the 576 seagrass species (root and rhizome debris). The colonization of the studied site was probably related to the progressive RSL rise rate of ~2 mm yr⁻¹, observed during the End of the 577 578 Holocene Climate Optimum and the 4.2 kyr event (~5450-3950 cal. yr BP; Vacchi et al., 579 2017). According to Vacchi et al. (2016, 2017), the MSL has increased from ~7.3 m (4750 cal. 580 yr BP) to ~8.5 m (3930 cal. yr BP) between the C. caespitosa settlement and the P. oceanica 581 meadow colonization. Thus, the progression of the upper limit of the P. oceanica meadow 582 towards the coast could be related to the MSL rise and coincides with the 4.2 kyr event (Fig. 583 2) characterized by a global climatic shift and major drought through the Mediterranean 584 region (Desprat et al., 2003; Roberts et al., 2011b; Magny et al., 2013). Furthermore, the 585 occurrence of C. caespitosa may have also influenced the settlement of the P. oceanica in 586 this area. As the topography of sea bottom which has proved to play a major role in the 587 establishment patterns of seagrass meadows, the substratum type can strongly influence in 588 the root anchoring and consequently the seedling survival. Consequently, the presence of 589 consolidated substrate with higher roughness, like C. caespitosa colonies studied here, may 590 have strongly favored the anchorage to the bottom of young plants of *P. oceanica* in shallow 591 waters experiencing hydrodynamic exposure (Alagna et al., 2015, 2019; Balestri et al., 2015; 592 Montefalcone et al., 2016; Zenone et al., 2020).

593 Sub-section U5a, ranging between the 269-270 cm (3930 cal. yr BP) and 224-225 cm 594 samples (2830 cal. yr BP), is notably defined by a transitional phase characterized by the 595 coexistence of P. oceanica meadow and the coral colonies of C. caespitosa. During this 596 phase, a decrease in the coral fragments content (Fig. 2) and in the accumulation rate (Table 597 3) was observed. The radiocarbon dating performed on P. oceanica remains and C. 598 caespitosa fragments at the basal part of sub-section U5a has contributed to highlighting a 599 significant disruption in the SAR. The anomalous age of *C. caespitosa* of 2046 cal. yr BP found 600 beneath the 3860 cal. yr BP date measured on the P. oceanica remains could be related to the collection and the processing of the sedimentary sequence with the Kullenberg corer. 601 Contrary to P. oceanica fragments which have been directly collected after core splitting in 602 603 the inner part of the core in order to avoid any contamination, the coral fragments to date 604 were selected after sieving process. The coral fragment selected for radiocarbon dating 605 could have been displaced during the sampling of the core in the lower part of the core. The 606 occurrence of such reworked material has been also identified during the chrono-607 stratigraphic reconstruction of a *P. oceanica* matte sequence obtained by performing 608 successive coring operations (Serrano et al., 2012).

609 In the subsequent core sub-section U5b, delimited between the 224-225 cm (2830 610 cal. yr BP) and the 164-165 cm (1300 cal. yr BP) samples, the *P. oceanica* meadow is already 611 well-established and the matte is very dense. During this period, an increase in the C. 612 caespitosa content was observed and appeared to be significantly and positively correlated 613 with the content in organic matter (r = 0.531; p<0.01; Table 4). Similarly, the length of coral 614 fragments was revealed to be negatively correlated to depth in the soil (r = -0.698; p < 0.001; 615 Table 4). The occurrence of lengthier corallites fragments in the upper part of the sequence 616 (Fig. 2; Fig. 5b) could suggest a good coexistence of coral colonies with the seagrass 617 meadows and reflect enhanced preservation of coral fragments within the P. oceanica 618 matte. These results confirm that the formation of such recalcitrant organic deposits favor 619 the preservation of carbonate fossil over millennia and constitute valuable palaeo-620 environmental archive in the Mediterranean (Romero et al., 1994; Mateo et al., 1997, 2002; 621 Serrano et al., 2012). Though, the actual preservation of corallites debris within the matte 622 appears to be enhanced, caution must be taken during biogeosedimentological 623 interpretation. The current abundance of corallites does not necessarily reflect the palaeo-624 abundance of the coral in the past and can be affected by a major environmental events 625 (e.g. major flooding, shelf storms).

626 In this sub-section, the mean annual growth rate measurements were determined by 627 performing direct measurements on the external walls of corallites and were highly 628 dependent on the coral fragments. This method was efficiently and easily implemented with 629 minimal manipulation of the corallite fragments. However, further analyses should be 630 performed by combining different methods (X-ray method, Alizarin method; Table A.1.) in 631 order to assess the accuracy of the measurements, and also to estimate the annual growth 632 rate on eroded or bored corallite fragments (Peirano et al., 1999, 2004). The mean annual growth rates obtained for *C. caespitosa* in this study are within the 1.3 to 6.9 mm yr⁻¹ range 633 634 obtained by different authors using either Alizarin staining or X-ray analysis on living or fossil 635 colonies (Table A.1.).

The analysis of the mean annual growth rate in the U5b sub-section highlighted a steady increase and the occurrence of oscillations (Fig. 7; Fig. 8). Considering the chronostratigraphic model and the SAR curve (Fig. 3a; Fig. 3b), the wide oscillations on the growth pattern of *C. caespitosa* corallites can be related to major climatic periods (Fig. 7). 640 While decadal growth rate oscillation has been already described in the Late Pleistocene 641 bank of Santa Teresiola by Peirano et al., (2009), in this study, the growth pattern appears to 642 follow semi-millennial to millennial oscillations.

643 The first oscillation coincides with the Cold Phase of the Subatlantic period (2925-644 2200 cal. yr BP) and the beginning of the Roman Warm Period - RWP (2200-1500 cal. yr BP; Desprat et al., 2003; Klimenko and Klimanov, 2003). Over the first oscillation, the annual 645 mean growth rate was 2.2 \pm 0.3 mm yr⁻¹ and was characterized by intermediate and low 646 mean growth rate (Fig. 7). Peirano et al. (1999) suggests that the coral growth rate of 647 648 corallites cannot be interpreted just as SSTs effect alone, but also as a result of the light 649 intensity that affects the photosynthetic efficiency of zooxanthellae. Kružić and Benković 650 (2008) propose that the biometrical values are affected by sea currents, temperature and 651 sedimentation. According to Vella et al. (2016), from 2650-2450 cal. yr BP, the mouth of the 652 Golo river was located 1-2 km northwards of its modern position (Tanghiccia mouth; Fig. 1). 653 Consequently, the influence of the alluvial inputs of fine sediments was probably higher due 654 to the shift in the location of the mouth of the Golo river coupled to the Cold Phase of the 655 Subatlantic period contributing to low light intensity and SSTs. The stratigraphic sequence 656 mainly constituted by the matte of *P. oceanica* exhibited a lower SAR (0.4 \pm 0.0 mm yr⁻¹) 657 than other meadows in the Mediterranean (Serrano et al., 2012 and references therein). A 658 decline in irradiance has been shown to have a significant impact on the physiology, 659 morphology and structure of the meadow and also on its productivity (Serrano et al., 2011; 660 Leiva-Dueñas et al., 2018). However, Peirano et al. (2005) showed that C. caespitosa exhibits 661 enhanced growth in low light intensities and turbid waters during the winter when the 662 energy and nutrient supply is high. Thus, low irradiance could have led both to a decrease in 663 the productivity of the *P. oceanica* meadow and in its regression helping indirectly the 664 growth of C. caespitosa. Similar phenomena have been observed along the Ligurian coast 665 after heavy anthropogenic siltation causing the regression of the P. oceanica meadows 666 (Bianchi and Peirano, 1990) which could have enhanced the development of the C. 667 caespitosa bank (Peirano et al., 1998).

668 The second oscillation coincides with the climatic RWP in Corsica (Desprat et al., 669 2003; Currás et al., 2017) and the Dark Ages Cold Period - DACP (1500-1000 cal. yr BP; 670 Ljungqvist, 2010). This oscillation is characterized by a slightly higher mean growth rate of 671 corallites and SAR than during the first oscillation, with 2.4 \pm 0.4 mm yr⁻¹ and 0.4 \pm 0.0 mm 672 yr⁻¹, respectively. Similarly, the content and the mean total length of coral fragments were 673 the highest recorded in the core (Fig. 2; Fig. 5a; Fig. 5b). The warmer and dryer climatic 674 epoch of the RWP was probably advantageous for the development of C. caespitosa colonies 675 and the P. oceanica meadow. Although studies confirmed the good adaptation of this 676 temperate coral to cold and turbid environmental conditions (Peirano et al., 2005, 2009; 677 Kružić and Benković, 2008), the largest bank of C. caespitosa occurred in coastal 678 environments characterized by alluvial inputs and warmer temperatures. Several analyses of 679 growth patterns of corallites showed a sinusoidal trend in accordance with the air 680 temperature (Peirano et al., 1999, 2004, 2005) and the SSTs (Morri et al., 2001; Kružić and Požar-Domac, 2002; Silenzi et al., 2005; Peirano et al., 2005). However, after the mean annual growth rate of 3.1 ± 0.4 mm yr⁻¹ peaked at 184-185 cm, the growth pattern steadily decreased down to the 169-170 cm sample where the *C. caespitosa* colonies abruptly disappeared (Fig. 2; Fig. 7).

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4.3. The decline phase: death of the *C. caespitosa* colonies and development of the *P. oceanica* meadow (~1410 cal. yr BP-present) 688

689 The disappearance of the *C. caespitosa* colonies seems to be linked to a major event. 690 The analysis of the biogeosedimentological features of this period has revealed no major 691 environmental phenomena. Nevertheless, another possible cause of the death of the 692 colonies was linked to the high sensitivity of C. caespitosa to elevated and prolonged SSTs 693 (Peirano et al., 2005). While warmer climate has proved to enhance corallite growth (Peirano 694 et al., 2004, 2009), the increase of SSTs up to 26-28°C during more than one month coupled 695 to high irradiance may have caused extensive mortality events, as observed in the Ligurian 696 Sea by Rodolfo-Metalpa et al. (2000, 2005, 2006) and in the Adriatic Sea by Kružić and Požar-697 Domac (2002). The death of these colonies would probably be linked to thermal and 698 irradiance stresses causing a major mortality event during the RWP (1750 cal. yr BP). This 699 hypothesis seems to be confirmed by the estimations of decadal mean temperature 700 variations over the two last millennia in the northern Hemisphere (Ljungqvist, 2010).

701 Nevertheless, the presence of C. caespitosa and the continuous decrease in the 702 growth pattern between 1700-1410 cal. yr BP suggest rather a progressive decline of the C. 703 caespitosa colonies resulting from the combination of phenomena. Firstly, the dryer and 704 warmer climate observed during the RWP could have resulted in enhanced development 705 and productivity of the P. oceanica meadow. Peirano et al. (1998) suggest that the 706 distribution, occurrence, and abundance of the C. caespitosa in the La Spezia region is mainly 707 controlled by competition with soft and frondose algae. Here, the presence of a well-708 developed seagrass meadow could have competed with C. caespitosa already weakened by 709 the mortality events. Secondly, an increase in meadow coverage and leaf canopy could have 710 favored a trapping of silt and mud deposition, and also an increase in bioclastic sediments 711 linked to epiphyte and invertebrate production (De Falco et al., 2000). Although C. 712 caespitosa polyps are well-adapted to high sedimentation, this excessive siltation could have 713 contributed to definitively limited the development of C. caespitosa colonies as reported by 714 Tins (1978).

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716 **5. Conclusion**

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The analysis of a stratigraphic sequence has revealed the presence of a massive *C. caespitosa* coral deposit surrounded by the matte of the *P. oceanica* meadow. The well-preserved corallite fragments found in the matte added on the known role of this bioconstruction as

paleoarchive in the Mediterranean coastal areas. The sedimentological analysis coupled to

the biological measurements performed on the C. caespitosa corallites provided the 722 723 opportunity to perform a paleoenvironmental reconstruction of the conditions of the site 724 during the last 4750 years. Given the results, the features of this C. caespitosa build up meet 725 all the requirements to be recognized as a fossil bank. The presence and the abundance of 726 the colonial coral C. caespitosa but also the fluctuations observed in its growth pattern 727 showed to be likely related to the abiotic parameters (i.e. marine currents, sedimentation, 728 competition) and to past climate conditions (major events and climatic periods) since the 729 Mid-Holocene. The progressive decline of this coral bank appeared to be related to a mass 730 mortality events resulting from prolongated increase in SSTs during RWP associated with 731 higher intraspecific competition with P. oceanica meadow. The study of the skeletal growth 732 pattern confirms that C. caespitosa coral represents a valid proxy for past climate 733 fluctuations and an ideal candidate for detailed palaeo-climatic and palaeo-environmental 734 reconstructions in the Mediterranean Sea.

735

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754 Appendix

Table A.1. Annual mean growth rates of living or fossil *Cladocora caespitosa* and their standard deviations
 obtained in this study and as reported in the literature. Table modified from Kersting and Linares (2012).

Site	Annual growth rate (mm yr ⁻¹)	Method	Authors
Mallorca (NW Med., Aquarium)	5	Direct measurement	Oliver Valls (1989)
Bay of Piran (Adriatic)	4.4 ± 0.6	Alizarin	Schiller (1993a)
La Spezia (NW Med.)	$1.3 \pm 0.6 - 4.3 \pm 1.4$	X-ray	Peirano et al. (1999)
La Spezia (NW Med.)	4.8 ± 1.7	Alizarin	Rodolfo-Metalpa et al. (1999)
Mljet (Adriatic)	4.7 ± 0.6 / 4.7 ± 0.6	Alizarin / X-ray	Kružić and Požar-Domac (2002)
Tuscany	6.3 ± 3.0	X-ray	Peirano et al. (2004)

Calabria	2.6 ± 0.8	X-ray	Peirano et al. (2004)
Sardinia	$2.1 \pm 0.7 - 4.1 \pm 1.3$	X-ray	Peirano et al. (2004)
Apulia	2.1 ± 0.9 – 6.9 ± 2.1	X-ray	Peirano et al. (2004)
La Spezia (NW Med.)	3.01	X-ray	Peirano et al. (2005)
Prvić (Adriatic)	3.2 ± 0.1	X-ray	Kružić and Benković (2008)
Pag (Adriatic)	3.1 ± 0.1	X-ray	Kružić and Benković (2008)
Mljet (Adriatic)	3.7 ± 1.3	X-ray	Kružić and Benković (2008)
N to S Adriatic	$2.6 \pm 0.2 - 4.1 \pm 0.6$	X-ray	Peirano et al. (2009)
Ligurian Sea	$3.7 \pm 0.5 - 3.3 \pm 0.4$	X-ray	Peirano et al. (2009)
South Italy	$3.1 \pm 0.3 - 3.2 \pm 0.3$	X-ray	Peirano et al. (2009)
Tunisia	2.3 ± 0.2	X-ray	Peirano et al. (2009)
Illa Grossa (NW Med.)	2.5 ± 0.8 / 2.5 ± 0.8	Alizarin / X-ray	Kersting and Linares (2012)
Corsica (NW Med.)	$1.9 \pm 0.8 - 3.1 \pm 0.8$	Direct measurement	This study

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759 **References**

760

Abadie, A., Gobert, S., Bonacorsi, M., Lejeune, P., Pergent, G., Pergent-Martini, C., 2015. Marine
space ecology and seagrasses. Does patch type matter in *Posidonia oceanica* seascapes? Ecological
Indicators 57, 435-446. http://dx.doi.org/10.1016/j.ecolind.2015.05.020.

Addinsoft, 2019. XLSTAT statistical and data analysis solution. Long Island, NY, USA.
 https://www.xlstat.com.

767

764

Aguirre, J., 1998. Bioconstrucciones de Saccostrea cuccullata Born, 1778 en el Plioceno superior de
Cádiz (SW de España) : implicaciones paleoambientales y paleoclimáticas. Revista Española de
Paleontología 13, 27-36.

771

Aguirre, J., Jiménez, A.P., 1998. Fossil analogues of the present day ahermatypic *Cladocora caespitosa*coral banks: sedimentary setting, dwelling community, and taphonomy (Late Pliocene, W
Mediterranean). Coral Reefs 17, 203-213. https://doi.org/10.1007/s003380050119.

Alagna, A., Vega Fernaandez, T., D'Anna, G., Magliola, C., Mazzola, S., Badalamenti, F., 2015.
Assessing Posidonia oceanica seedling substrate preference: an experimental determination of
seedling anchorage success in rocky vs. sandy substrates. PloS One 10 (4), e0125321.
https://doi.org/10.1371/journal.pone.0125321Alagna.

780

Balestri, E., de Battisti, D., Vallerini, F., Lardicci, C., 2015. First evidence of root morphological and
architectural variations in young *Posidonia oceanica* plants colonizing different substrate typologies
Estuarine, Coastal and Shelf Science 154, 205-2013.

784

Bellaiche, G., Droz, L., Gaullier, V., Pautot, G., 1994. Small submarine fans on the eastern margin of
Corsica: Sedimentary significance and tectonic implications. Marine Geology 117(1-4), 177-185.
https://doi.org/10.1016/0025-3227(94)90013-2.

788

Basso, D., Nalin, R., Massari, F., 2007. Genesis and composition of the Pleistocene Coralligène de
plateau of the Cutro Terrace (Calabria, southern Italy). Neues Jahrbuch für Geologie und
Paläontologie - Abhandlungen 244(2), 173-182. https://doi.org/10.1127/0077-7749/2007/02440173.

- Bernasconi, M.P., Corselli, C., Carobene, L., 1997. A bank of the scleractinian coral *Cladocora caespitosa* in the Pleistocene of the Crati valley (Calabria, Southern Italy): growth versus
 environmental conditions. Bolletino della Società Paleontologica Italiana 36(1-2), 53-61.
- Bianchi, C.N., Peirano, A., 1990. Mappatura delle praterie di *Posidonia oceanica* in Mar Ligure. ENEACRAM S. Teresa, Rapporto tecnico interno, 372 pp.
- Blaauw, M., 2010. Methods and code for 'classical' age-modelling of radiocarbon sequences.
 Quaternary Geochronology 5, 512-518. https://doi.org/10.1016/j.quageo.2010.01.002.
- Boudouresque, C.F., Bernard, G., Bonhomme, P., Charbonnel, E., Diviacco, G., Meinesz, A., Pergent,
 G., Pergent-Martini, C., Ruitton, S., Tunesi, L., 2006. Préservation et conservation des herbiers à *Posidonia oceanica*. RAMOGE Publication, 202 pp.
- Boudouresque, C.F., Giraud, G., Thommeret, J., Thommeret, Y., 1980. First attempt at dating by ¹⁴C
 the undersea beds of dead *Posidonia oceanica* in the bay of Port-Man (Port-Cros, Var, France).
 Travaux scientifiques du Parc national de Port-Cros 6, 239-242.
- 811
 812 Bracchi, V.A., Nalin, R., Basso, D., 2016. Morpho-structural heterogeneity of shallow-water
 813 coralligenous in a Pleistocene marine Terrace (Le Castella, Italy). Palaeogeography,
 814 Palaeoclimatology, Palaeoecology 454, 101-112. http://dx.doi.org/10.1016/j.palaeo.2016.04.014.
- Bradley, R.S., Hughes, M.K., Diaz, H.F., 2003. Climate in Medieval Time. Science 302, 404-405.
 https://doi.org/10.1126/science.1090372.
- Brock F., Higham, T., Ditchfield, P., Ramsey C.B., 2010. Current pretreatment methods for AMS
 radiocarbon dating at the Oxford Radiocarbon Accelerator Unit (ORAU). Radiocarbon, 52(1), 103-112.
- Buia, M.C., Gambi, M.C., Zupo, V., 2000. Structure and functioning of Mediterranean seagrass
 ecosystems: an overview. Proceedings 4th International Seagrass Biology Workshop, Biologia Marina
 Mediterranea, Balagne, Corsica, France, pp. 167-190.
- 825

800

803

807

815

818

- Casado-Amezúa, P., García-Jiménez, R., Kersting, D.K., Templado, J., Coffroth, M.A., Acevedo, I.,
 Machordom, A., 2011. Development of microsatellite markers as a molecular tool for conservation
 studies of the Mediterranean reef builder coral *Cladocora caespitosa* (Anthozoa, Scleractinia).
 Journal of Heredity 102(5), 622-626. https://doi.org/10.1093/jhered/esr070.
- Casado-Amezúa, P., Kersting, D., Linares, C.L., Bo, M., Caroselli, E., Garrabou, J., Cerrano, C., Ozalp, B.,
 Terrón-Sigler, A., Betti, F., 2015. *Cladocora caespitosa*. The IUCN Red List of Threatened Species 2015:
 e.T133142A75872554.
- 834

838

842

- Casado-Amezúa, P., Kersting, D.K., Templado, J., Machordom, A., 2014. Regional genetic
 differentiation among populations of *Cladocora caespitosa* in the Western Mediterranean. Coral
 Reefs 33, 1031-1040. https://doi.org/10.1007/s00338-014-1195-5.
- Chefaoui, R.M., Casado-Amezúa, P., Templado J., 2017. Environmental drivers of distribution and reef
 development of the Mediterranean coral *Cladocora caespitosa*. Coral Reefs 36, 1195-1209.
 https://doi.org/10.1007/s00338-017-1611-8.
- 843 Clymo, R.S. 1992 Productivity and decomposition of peaetland ecosystems. Peatland Ecosystems and
 844 Man: An Impact Assessment. Department of Biological Sciences, Dundee, U.K., pp. 3-16.
- 845

846 Conchon, O., 1975. Les formations quaternaires de type continental en Corse orientale. Thèse de847 doctorat, Université de Paris VI, pp. 1-514.

848

849 Conchon, O., Gauthier A., 1985. Phénomènes naturels exceptionnels en Corse : intérêt pour l'étude
850 géologique de la période Quaternaire. Bulletin de la Société des Sciences Historiques et Naturelles
851 Corse 648, 141-165.

852

858

865

869

872

877

853 Currás, A., Ghilardi, M., Peche-Quilichini, K., Fagel, N., Vacchi, M., Delanghe, D., Contreras, D., Vella, 854 C., Ottaviani, J.C., 2017. Reconstructing past landscapes of the eastern plain of Corsica (NW 855 Mediterranean) during the last 6000 years based on molluscan, sedimentological and palynological 856 analyses. Journal Archaeological Science : Reports 755-769. of 12, 857 https://doi.org/10.1016/j.jasrep.2016.09.016.

D'Alessandro, A., Bromley, R., 1995. A new ichnospecies of Spongeliomorpha from the Pleistocene of
Sicily. Journal of Paleontology 69(2), 393-398. https://doi.org/10.1017/S0022336000034727.

862De Falco, G., Ferrari, S., Cancemi, G., Baroli, M., 2000 Relationship between sediment distribution863and Posidonia oceanica seagrass.Geo-Marine Letters 20, 50-57.864https://doi.org/10.1007/s003670000030.

- Desprat, S., Sánchez Goñi, M.F., Loutre M.F., 2003. Revealing climatic variability of the last three
 millennia in northwestern Iberia using pollen influx data. Earth and Planetary Science Letters 213, 6778. https://doi.org/10.1016/S0012-821X(03)00292-9.
- B70 Dodge, R.E., Aller, R.C., Thomson, J., 1974. Coral growth related to resuspension of bottom
 B71 sediments. Nature 247, 574-576. https://doi.org/10.1038/247574a0.
- Drinia, H., Koskeridou, E., Antonarakou, A., Tzortzaki, E., 2010. Benthic foraminifera associated with
 the zooxanthellate coral *Cladocora* in the Pleistocene of the Kos Island (Aegean Sea, Greece): Sea
 level changes and palaeoenvironmental conditions. Bulletin of the Geological Society of Greece
 43(2), 613-619. https://doi.org/10.12681/bgsg.11223.
- 878 El Zrelli, R., Courjault-Radé, P., Rabaoui, L., Daghbouj, N., Mansour, L., Balti, R., Castet, S., Faouzi, A., 879 Michel, S., Bejaoui, N., 2017. Biomonitoring of coastal pollution in the Gulf of Gabes (SE, Tunisia): use 880 of Posidonia oceanica seagrass as a bioindicator and its mat as an archive of coastal metallic 881 contamination. Environmental Science Pollution and Research, 24(28), 22214-22225. 882 https://doi.org/10.1007/s11356-017-9856-x.
- Ferrier-Pagès, C., Witting, J., Tambutté, E., Sebens, K., 2003. Effect of natural zooplankton feeding on
 the tissue and skeletal growth of the scleractinian coral *Stylophora pistillata*. Coral Reefs 22, 229-240.
 https://doi.org/10.1007/s00338-003-0312-7.
- 887

883

- Fornós, J.J., Baron, A., Pons G.X., 1996. Arrecifes de corales hermatípicos (*Cladocora caespitosa*) en el
 relleno holoceno de la zona de Es Grau (Menorca, Mediterraneo Occidental). Geogaceta 20(2), 303306.
- 891

- Gaillot, S., Chavarot S., 2001. Méthode d'étude des littoraux à faible évolution. Cas du delta du Golo
 (Corse) et du littoral du Touquet (Pas-de-Calais) en France. Géomorphologie : relief, processus,
 environnement 1, 47-54. https://doi.org/10.3406/morfo.2001.1086.
- Gauthier, A., 1981. Contribution à l'étude du débit solide et genèse des sédiments au cours de celuici : Exemple du Fium'Orbo, fleuve de la Corse Orientale. Rapport BRGM 30, pp. 163-172.

898	
899	Gervais, A., Mulder, T., Savove, B., Gonthier, E., 2006. Sediment distribution and evolution of
900	sedimentary processes in a small sandy turbidite system (Golo system, Mediterranean Sea):
901	implications for various geometries based on core framework. Geo-Marine Letters 26(6), 373-395.
902	https://doi.org/10.1007/s00367-006-0045-z.
903	
904	Gervais & Savove B. Piner D.I.W. Mulder T. Cremer M. Pichevin I. 2004 Present mornhology
905	and denositional architecture of a sandy confined submarine system: the Golo turbidite system
906	(eastern margin of Corsica) Geological Society London Special Publications 222(1) 59-89
907	$\frac{1}{1000}$ https://doi.org/10.1144/GSL SP 2004 222.01.05
908	http://doi.org/10.1144/052.51.2004.222.01.05.
900	Guennoc P. Palvadeau F. Pluquet F. Morando A. Vairon J. 2001 LIMA cartographie des plates-
909 Q10	formes sous-marines de la Corse entre 0 et 100m de profondeur. Rapport BRGM, RD-51523-ER, pp. 1-
011	52
012	55.
91Z 012	Harmalia I.C. 1064 Etuda da l'andofauna das "mattas" d'harbiars da Pacidania assanica Dalila
915	Ramelin, J.G., 1964. Elude de l'endoladire des mattes d'herbiers de <i>Posidomid ocednica</i> Deme.
914	Recueil des Travaux de la Station Marine d'Endoume 35, 43-105.
915	Usiri O Lattar A.F. Lanaka C. 2001 Loss on ignition as a method for actimating argonic and
910	Heiri, O., Lotter, A.F., Lemcke, G., 2001. Loss on ignition as a method for estimating organic and
917	Carbonate content in sediments: Reproducibility and comparability of results. Journal of
918	Paleolimnology 25, 101-110. https://doi.org/10.1023/A:1008119611481.
919	University & University & Telephonetic M. Bideser, F. 2014. Constal Blue Carbon. Matheda for
920	Howard, J., Hoyt, S., Isensee, K., Teiszewski, M., Pidgeon, E., 2014. Coastal Blue Carbon: Methods for
921	assessing carbon stocks and emissions factors in mangroves, tidal salt marsnes, and seagrasses. CIOC-
922	UNESCO, IUCN, Arlington, Virginia, USA., pp. 1-180.
923	Januara C. Alekisti M. Dadalamanti F. Davatralla C. Dalmanta C. Cannas D. Davadatti Cashi
924	Ingrosso, G., Abbiati, M., Badalamenti, F., Bavestrello, G., Belmonte, G., Cannas, R., Benedetti-Cecchi,
925	L., Bertolino, M., Bevilacqua, S., Blanchi, C.N., Bo, M., Boscari, E., Cardone, F., Cattaneo-Vietti, R., Cau,
926	A., Cerrano, C., Chemello, R., Chimienti, G., Congiu, L., Corriero, G., Costantini, F., De Leo, F.,
927	Donnarumma, L., Falace, A., Fraschetti, S., Glangrande, A., Gravina, M.F., Guarnieri, G., Mastrototaro,
928	F., Milazzo, M., Morri, C., Musco, L., Pezzolesi, L., Piraino, S., Prada, F., Ponti, M., Rindi, F., Russo, G.F.,
929	Sandulli, R., Villamor, A., Zane, L., Boero F., 2018. Mediterranean bioconstructions along the Italian
930	coast. Advances in Marine Biology, 79, 61-136. https://doi.org/10.1016/bs.amb.2018.05.001.
931	
932	Jimenez, C., Hadjioannou, L., Petrou, A., Nikolaidis, A., Evriviadou, M., Lange M.A., 2014. Mortality of
933	the scieractinian coral <i>Cladocora caespitosa</i> during a warming event in the Levantine Sea (Cyprus).
934	Regional Environmental Change 16, 1963-1973. https://doi.org/10.1007/s10113-014-0729-2.
935	
936	Kaal, J., Serrano, O., Nierop, K., Schellekens, J., Martinez Cortizas, A. Mateo, M.A., 2016. Molecular
937	composition of plant parts and sediment organic matter in a Mediterranean seagrass (<i>Posidonia</i>
938	oceanica) mat. Aquatic Botany 133, 50-61. https://doi.org/10.1016/j.aquabot.2016.05.009.
939	
940	Kersting, D.K., Bensoussan, N., Linares, C., 2013. Long-term responses of the endemic reef-builder
941	<i>Cladocora caespitosa</i> to Mediterranean warming. PLoS One 8, e70820.
942	https://doi.org/10.13/1/journal.pone.0070820.
943	
944	Kersting, D.K., Cebrián, E., Verdura, J., Ballesteros, E., 2017. A new <i>Cladocora caespitosa</i> population
945	with unique ecological traits. Mediterranean Marine Science 18(1), 38-42.
946	https://doi.org/10.12681/mms.1955.
947	

- Kersting, D.K., Linares, C., 2012. *Cladocora caespitosa* bioconstructions in the Columbretes Islands
 Marine Reserve (Spain, NW Mediterranean): distribution, size structure and growth. Marine Ecology
 33, 427-436. https://doi.org/10.1111/j.1439-0485.2011.00508.x.
- Klimenko, V.V., Klimanov, V.A., 2003. Cold Climate of the Early Subatlantic Age in the NorthernHemisphere. Doklady Earth Sciences 391(6), 845-849.
- Kružić, P., Benković, L., 2008. Bioconstructional features of the coral *Cladocora caespitosa* (Anthozoa,
 Scleractinia) in the Adriatic Sea (Croatia). Marine Ecology 29, 125-139.
 https://doi.org/10.1111/j.1439-0485.2008.00220.x.
- Kružić, P., Požar-Domac, A., 2002. Skeleton growth rates of coral bank of *Cladocora caespitosa*(Anthozoa, Scleractinia) in lake Veliko jezero (Mljet National Park). Periodicum Biologorum 104(2),
 123-129.
- Kružić, P., Požar-Domac, A., 2003. Banks of the coral *Cladocora caespitosa* (Anthozoa, Scleractinia) in
 the Adriatic Sea. Coral Reefs 22(4), 536. https://doi.org/10.1007/s00338-003-0345-y.
- Kühlmann, D.H.H., 1996. Preliminary report on Holocene submarine accumulations of *Cladocora caespitosa* (L., 1767) in the Mediterranean. Göttinger Arbeit Geologie Paläontologie 2, 65-69.
- Laborel, J., 1961. Sur un cas particulier de concrétionnement animal. Concrétionnement à *Cladocora caespitosa* (L.) dans le Golfe de Talante. Rapports et Procès-verbaux du Conseil Internationale pour
 l'Exploration de la Mer 16(2), 429-432.
- Laborel, J., 1987. Marine biogenic constructions in the Mediterranean: a review. Scientific Reports ofthe Port-Cros National Park, 13, 97-126.
- Laborel, J., Laborel-Deguen, F., 1978. Abondance du madréporaire *Cladocora caespitosa* (Linné 1767)
 dans les herbiers de posidonies de la baie de Port-Cros. Travaux scientifiques du Parc national de
 Port-Cros 4, 273-274.
- Lamb, H.H., 1965. The early Medieval Warm Epoch and its sequel. Palaeogeography,
 Palaeoclimatology, Palaeoecology 1, 13-37. https://doi.org/10.1016/0031-0182(65)90004-0.
- Leiva-Dueñas, C., López-Merino, L., Serrano, O., Martínez Cortizas, A., Mateo, M.A., 2018. Millennialscale trends and controls in *Posidonia oceanica* (L. Delile) ecosystem productivity. Global and
 Planetary Change 169, 92-104. https://doi.org/10.1016/j.gloplacha.2018.07.011.
- 986
 987 Ljungqvist, F.C., 2010. A new reconstruction of temperature variability in the extra-tropical Northern
 988 Hemisphere during the last two millennia. Geografiska Annaler: Series A, Physical Geography 92(3),
 989 339-351.
- 990 001 Lo Jaco

954

958

962

965

972

975

- Lo Iacono, C., Mateo, M.A., Gràcia, E., Guasch, L., Carbonell, R., Serrano, L., Serrano, O., Danõbeitia,
 J., 2008. Very high-resolution seismo-acoustic imaging of seagrass meadows (Mediterranean Sea):
 Implications for carbon sink estimates. Geophysical Research Letters 35(18), 1-5.
 https://doi.org/10.1029/2008GL034773.
- López-Merino, L., Colás-Ruiz, N.R., Adame, M.F., Serrano, O., Martínez Cortizas, A., Mateo, M.A.,
 2017. A six thousand-year record of climate and land-use change from Mediterranean seagrass mats.
 Journal of Ecology 105(5), 1267-1278. https://doi.org/10.1111/1365-2745.12741.
- 999

López-Merino, L., Serrano, O., Adame, M., Mateo M., Martínez Cortizas, A., 2015. Glomalin
accumulated in seagrass sediments reveals past alterations in soil quality due to land-use change.
Global and Planetary Change 133, 87-95. https://doi.org/10.1016/j.gloplacha.2015.08.004.

López-Sáez, J.A., López-Merino, L., Mateo, M.A., Serrano, O., Pérez-Díaz, S., Serrano, L., 2009.
Palaeoecological potential of the marine organic deposits of *Posidonia oceanica*: A case study in the
NE Iberian Peninsula. Palaeogeography, Palaeoclimatology, Palaeoecology 271(3-4), 215-224.
https://doi.org/10.1016/j.palaeo.2008.10.020.

Magny, M., Combourieu-Nebout, N., de Beaulieu, J.L., Bout-Roumazeilles, V., Colombaroli, D.,
Desprat, S., Francke, A., Joannin, D., Ortu, E., Peyron, O., Revel, M., Sadori, L., Siani, G., Sicre, M.A.,
Sanmartin, S., Simonneau, A., Tinner, W., Vannière, B., Wagner, B., Zanchetta, G., Anselmetti, F.,
Brugiapaglia, E., Chapron, E., Debret, M., Didier, J., Essallami, L., Galop, D., Gilli, A., Haas, J.N., Kallel,
N., Millet, L., Stock, A., Turon, J.L., Wirth, S., 2013. North-south palaohydrological contrasts in the
central Mediterranean during the Holocene: tentative synthesis and working hypothesis. Climate of
the Past 9, 2043-2071. https://doi.org/10.5194/cpd-9-1901-2013.

Mateo, M.A., Julia, R., Romero, J., Michener, R., 2002. An unexplored sedimentary record for the
study of environmental change in Mediterranean coastal environments: *Posidonia oceanica* (L.) Delile
peats. International Atomic Energy Agency, January, 163-173.

Mateo, M.A., Renom, P. Michener, R.H., 2010. Long-term stability in the production of a NW
Mediterranean *Posidonia oceanica* (L.) Delile meadow. Palaeogeography, Palaeoclimatology,
Palaeoecology 291(3-4): 286-296. https://doi.org/10.1016/j.palaeo.2010.03.001.

Mateo, M.A., Romero, J., Pérez, M., Littler, M.M., Littler, D.S., 1997. Dynamics of Millenary Organic
Deposits Resulting from the Growth of the Mediterranean Seagrass *Posidonia oceanica*. Estuarine,
Coastal and Shelf Science 44(1), 103-110. https://doi.org/10.1006/ecss.1996.0116.

1029 Miković, M., 1977. Istražni radovi u moru. Bagerovanje u zavisnosti od bioloških uslova. Izgradnja. 9.

1031 Millot, C., 1987. Circulation in the western Mediterranean Sea. Oceanologica Acta 10(2), 143-149.

1033 Molinier, R., Picard, J., 1952. Recherches sur les herbiers de Phanérogames marines du littoral 1034 méditerranéen français. Annales de l'Institut Océanographique (Paris) 27(3), 157-234.

Molliex, S., Jouet, G., Blard, P.H., Moreau, J., Demartini, J., Storms J.E.A., Vella, C., Team, A., 2021.
Quaternary evolution of the Golo river alluvial plain (NE Corsica, France). Quaternary Geochronology
61, 101115. https://doi.org/10.1016/j.quageo.2020.101115.

1040 Montagna, P., McCulloch, M., Mazzoli, C., Silenzi, S., Odorico, R., 2007. The non-tropical coral 1041 *Cladocora caespitosa* as the new climate archive for the Mediterranean: high-resolution (~weekly) 1042 trace element systematics. Quaternary Science Reviews 26, 441-462. 1043 https://doi.org/10.1016/j.quascirev.2006.09.008.

1044

1003

1008

1016

1028

1030

1032

1035

1039

Morri, C., Peirano, A., Bianchi, C.N., Rodolfo-Metalpa, R., 2000. *Cladocora caespitosa*: a colonial
zooxanthellate Mediterranean coral showing constructional ability. Reef Encounter 27, 22-25.

1048 Morri, C., Peirano, A., Bianchi, C.N., 2001. Is the Mediterranean coral *Cladocora caespitosa* an 1049 indicator of climatic change? Archivio di Oceanografia e Limnologia 22, 139-144.

Morri, C., Peirano, A., Bianchi, C.N., Sassarini, M., 1994. Present-day bioconstructions of the hard
coral, *Cladocora caespitosa* (L.) (Anthozoa, Scleractinia), in the Eastern Ligurian Sea (NW
Mediterranean). Biologia Marina Mediterranea 1(1), 371-372.

Mulder, T., Maneux, E., 1999. Flux et bilan sédimentaires. Impact des apports fluviatiles sur la
construction des éventails sous-marins profonds de la marge Est-Corse, Université de Bordeaux I,
Rapport, pp. 1-20.

Nalin, R., Basso, D., Massari, F., 2006. Pleistocene coralline algal build–ups (coralligéne de plateau)
and associated bioclastic deposits in the sedimentary cover of Cutro marine terrace (Calabria,
Southern Italy). *In:* Pedley, H.M., Carannante, G. (Eds.). Cool–Water Carbonates: Depositional
Systems and Palaeoenvironmental Controls, The Geological Society of London 2006, pp. 11-22.
https://doi.org/10.1144/GSL.SP.2006.255.01.02.

1065 Oliver Valls, J.A., 1989. Développement de *Cladocora caespitosa* (Linné, 1767) en aquarium. Bulletin 1066 de l'Institut Océanographique de Monaco, 5, 205-209.

1068 Orofino, S., Baltassat, J.M., Frissant, N., Lanini, S., Prognon, C., Winckel, A., 2010. Etude des
1069 interactions entre les eaux souterraines, les eaux de surface et l'étang de Biguglia. Rapport BRGM,
1070 RP59068-FR, pp. 1-150.

1072 Orszag-Sperber, F., Pilot, M.D., 1976. Grands traits Néogène de Corse. Bulletin de la Société
1073 Géologique de France 7(5), 1183-1187.

1075 Ottman, F., 1958. Les formations pliocènes et quaternaires sur le littoral corse. Mémoires de la
1076 Société Géologique de France 37(84), 176-181.

1078 Özalp, H.B., Alparslan, M., 2011. The first record of *Cladocora caespitosa* (Linnaeus, 1767) (Anthozoa,
1079 Scleractinia) from the Marmara Sea. Turkish Journal of Zoology 35(5), 701-705.
1080 https://doi.org/10.3906/zoo-0907-80.

1082 Öztürk, B., 2004. Marine Life of Turkey in the Aegean & Mediterranean Sea. *In:* Phylum Cnidaria,
1083 Turkish Marine Research Foundation, Turkey, pp. 1-48.

Peirano, A., Morri, C., Bianchi, C. N., Aguirre, J., Antonioli, F., Calzetta, G., Carobene, L., Mastronuzzi,
G., Orrù, P., 2004. The Mediterranean coral Cladocora caespitosa: a proxy for past climate
fluctuations? Global and Planetary Change 40(1-2), 195-200. https://doi.org/10.1016/S09218181(03)00110-3.

Peirano, A., Abbate, M., Cerrati, G., Difesca, V., Peroni, C., Rodolfo-Metalpa, R., 2005. Monthly
variations in calyx growth, polyp tissue and density banding of the Mediterranean scleractinian *Cladocora caespitosa* (L.). Coral Reefs 24, 404-409. https://doi.org/10.1007/s00338-005-0020-6.

1093
1094 Peirano, A., Kružić, P., Mastronuzzi, G., 2009. Growth of Mediterranean reef of *Cladocora caespitosa*1095 (L.) in the Late Quaternary and climate inferences. Facies 55(3), 325-333. https://doi.org/
1096 10.1007/s10347-008-0177-x

Peirano, A., Morri, C., Bianchi, C.N., 1999. Skeleton growth and density pattern of the temperate,
zooxanthellate scleractinian *Cladocora caespitosa* from the Ligurian Sea (NW Mediterranean).
Marine Ecology Progress Series 185, 195-201. https://doi.org/10.3354/meps185195.

1101

1097

1054

1058

1064

1067

1071

1074

1077

1081

1084

Peirano, A., Morri, C., Bianchi, C.N., Rodolfo-Metalpa, R., 2001. Biomass, carbonate standing stock
and production of the Mediterranean coral *Cladocora caespitosa* (L.). Facies 44, 75-80.
https://doi.org/ https://doi.org/10.1007/BF02668168.

Peirano, A., Morri, C., Mastronuzzi, G., Bianchi, C.N., 1998. The coral *Cladocora caespitosa* (Anthozoa,
Scleractinia) as a bioherm builder in the Mediterranean Sea. Memorie Descrittive Carta Geologica
d'Italia, 52(1994), 59-74.

- Pérès, J.M., 1982. Major benthic assemblages. *In:* Kinne, O. (Ed.). Marine Ecology 5, Part 1. Wiley,
 Chichester, pp. 373-522.
- Pérès, J.M., Picard, J., 1964. Nouveau manuel de bionomie benthique de la mer Méditerranée.
 Recueil des Travaux de la Station Marine d'Endoume 31(47), 5-138.
- Pergent-Martini, C., Pergent, G., Alami, S., Bonacorsi, M., Clabaut, P., Mezière, A., Valette-Sansevin,
 A., 2015. Identification des impacts anthropiques sur le Grand Herbier de la Plaine Orientale. Rapport
 Université de Corse, Equipe Ecosystèmes Littoraux, pp. 1-39.

Peyron, O., Magny, M., Goring, S., Joannin, S., de Baulieu J.L., Brugiapaglia, E., Sadori, L., Garfi, G., K.
Kouli, K., Ioakim, C., Combourieu-Nebout, N., 2013. Contrasting patterns of climatic changes during
the Holocene across the Italian Peninsula reconstructed from pollen data. Climate of the Past 9,
1233-1252. https:// 10.5194/cp-9-1233-2013.

- Pluquet, F., 2006. Évolution récente et sédimentation des plates-formes continentales de la Corse.
 Thèse de doctorat, Université de Corse, France, pp. 1-300.
- 1128 Reille, M., 1984. Origine de la végétation actuelle de la Corse sud-orientale ; analyse pollinique de 1129 cinq marais côtiers. Pollen et Spores 26(1), 43-60.
- 1131 Reille, M.J., Gamisans, V., Andrieu-Ponel, V., De Balieu, J.L., 1999. The Holocene at Lac de Creno,
 1132 Corsica, France: a key site for the whole island. The New Phytologist 141, 291-307.
 1133 https://doi.org/10.1046/j.1469-8137.1999.00343.x.
- Reimer, P., Bard, E., Bayliss, A., Beck, J.W., Blackwel, P.G., Bronk Ramsey, C., Buck, C.E., Cheng, H.,
 Edwards, R.L., Friedrich, M., Grootes, P.M., Guilderson, T.P., Haflidason, H., Hajdas, I., Hatte, C.,
 Heaton, T.J., Hoffmann, D.L., Hogg, A.G., Hughen, K.A., Kaiser, K.F., Kromer,B., Manning, S.W., Niu,
 M., Reimer, R.W., Richards, D.A., Scott, E.M., Southon, J.R., Staff, R.A., Turney, C.S.M., van der Plicht,
 J., 2013. Intcal13 and Marine13 radiocarbon age calibration curves 0-50,000 years cal BP.
 Radiocarbon 55(4), 1869-1887. https://doi.org/10.2458/azu_js_rc.55.16947.
- Relini, G., 2009. Italian Habitats. Marine Bioconstructions. Nature's Architectural Seascapes. Italian
 Ministry of the Environment and Territorial Protection. Friuli Museum of Natural History, Udine, pp.
 1144 1-159.
- Roberts, N., Brayshaw, D., Kuzucuoğlu, C., Pérez, R., Sadori, L., 2011a. The mid-Holocene climatic
 transition in the Mediterranean: causes and consequences. The Holocene 21(1), 3-13.
 https://doi.org/10.1177/0959683610388058.
- Roberts, N., Eastwood, W.J., Kuzucuoğlu, C., Fiorentino, G., Caracuta, V., 2011b. Climatic, vegetation
 and cultural change in the eastern Mediterranean during the mid-Holocene transition. The Holocene
 21(1), 147-162. https://doi.org/10.1177/0959683610386819.
- 1153

1105

1109

1112

1115

1119

1124

1127

1130

1134

1141

1145

1154 Rodolfo-Metalpa, R., Bianchi, C.N., Peirano, A., 2000. Coral mortality in NM Mediterranean. Coral 1155 Reefs 19, 24. 1156 1157 Rodolfo-Metalpa, R., Bianchi, C.N., Peirano, A., Morri, C., 2005. Tissue necrosis and mortality of the 1158 temperate coral Cladocora caespitosa. Italian Journal of Zoology 72, 271-276. 1159 https://doi.org/10.1080/11250000509356685. 1160 1161 Rodolfo-Metalpa, R., Peirano, A., Houlbrèque, F, Abbate, M, Ferrier-Pagès, C., 2008. Effects of 1162 temperature, light and heterotrophy on the growth rate and budding of the temperate coral 1163 Cladocora caespitosa. Coral Reefs 27, 17-25. https://doi.org/10.1007/s00338-007-0283-1. 1164 1165 Rodolfo-Metalpa, R., Peirano, A., Morri, C., Bianchi, C.N., 1999. Coral calcification rates in the 1166 Mediterranean Scleractinian coral Cladocora caespitosa (L., 1767). Atti Associazione Italiana 1167 Oceanologia Limnologia 13(1), 291-299. 1168 1169 Rodolfo-Metalpa, R., Richard, C., Allemand, D., Ferrier-Pagès, C., 2006. Growth and photosynthesis of 1170 two Mediterranean corals, Cladocora caespitosa and Oculina patagonica, under normal and elevated 1171 temperatures. The Journal of Experimental Biology 209, 4546-4556. 1172 https://doi.org/10.1242/jeb.02550. 1173 1174 Romero, J., Pérez, M., Mateo, M.A., Sala, E., 1994. The belowground organs of the Mediterranean 1175 seagrass Posidonia oceanica as a biogeochemical sink. Aquatic Botany 47(1), 13-19. 1176 https://doi.org/10.1016/0304-3770(94)90044-2. 1177 1178 Russo, G.F., Chessa, L.A., Vinci, D., Fresi, E., 1991a. Molluscs of Posidonia oceanica beds in the bay of 1179 Porto Conte (North-Western Sardinia): Zonation pattern, seasonal variability and geographical 1180 comparison. Posidonia Newsletter 4(1), 5-14. 1181 1182 Russo, G.F., Fresi, E., Vinci, D., Chessa, L.A., 1984. Mollusk syntaxon of foliar stratum along a depth 1183 gradient in Posidonia oceanica (L.) Delile meadows: seasonal variability. In: Boudouresque, C.F., 1184 Jeudy de Grissac, A., Olivier, J. (Eds.), First International Workshop on Posidonia oceanica Beds, 1, GIS 1185 Posidonie Publication, 311-318. 1186 1187 Russo, G.F., Vinci, D., Scadri, M., Fresi, E., 1991b. Mollusc syntaxon of foliar stratum along a depth 1188 gradient in a Posidonia oceanica bed: 3 a year's cycle at Ischia Island. Posidonia Newsletter 4, 15-25. 1189 1190 Schiller, C., 1993a. Ecology of the symbiotic coral *Cladocora caespitosa* (L.) (Faviidae, Scleractinia) in 1191 the Bay of Piran (Adriatic Sea): I Distribution and biometry. P.S.Z.N.: Marine Ecology 14(3), 205-219. 1192 https://doi.org/ 10.1111/j.1439-0485.1993.tb00480.x. 1193 1194 Schiller, C., 1993b. Ecology of the symbiotic coral Cladocora caespitosa (L.) (Faviidae, Scleractinia) in 1195 the Bay of Piran (Adriatic Sea): II. Energy budget. P.S.Z.N.: Marine Ecology 14(3), 221-238. 1196 https://doi.org/10.1111/j.1439-0485.1993.tb00481.x. 1197 1198 Schiller, C., Herndl, G.J., 1989. Evidence of enhanced microbial activity in the interstitial space of 1199 branched corals: possible implications for coral metabolism. Coral Reefs 7, 179-184. 1200 https://doi.org/10.1007/BF00301596. 1201 1202 Schneider, C.A., Rasband, W.S., Eliceiri, K.W., 2012. NIH Image to ImageJ: 25 years of image analysis. 1203 Nature Methods 9, 671-675. https://doi.org/10.1038/nmeth.2089. 1204

Scipione, M.B., Gambi, M.C., Lorenti, M., Russo, G.F., Zupo, V., 1996. Vagile fauna of the leaf stratum
of *Posidonia oceanica* and *Cymodocea nodosa* in the Mediterranean Sea. Seagrass Biology:
Proceeding of an International Workshop, Rottnest Island, Australia, pp. 249-260.

1208

1213

1216

1220

1224

1228

1231

1234

1238

1241

1245

1250

1255

Serrano, O., Mateo, M.A., Dueñas-Bohórquez, A., Renom, P., López-Sáez, J.A., Martínez Cortizas, A.,
2011. The *Posidonia oceanica* marine sedimentary record: A Holocene archive of heavy metal
pollution. Science of The Total Environment 409(22), 4831-4840.
https://doi.org/10.1016/j.scitotenv.2011.08.001.

Serrano, O., Mateo, M.A., Renom, P., Julià, R., 2012. Characterization of soils beneath a *Posidonia oceanica* meadow. Geoderma 185, 26-36. https://doi.org/10.1016/j.geoderma.2012.03.020.

Serrano, O., Martínez-Cortizas, A., Mateo, M.A., Biester, H. Bindler, R., 2013. Millennial scale impact
on the marine biogeochemical cycle of mercury from early mining on the Iberian Peninsula. Global
Biogeochemical Cycles 27(1), 21-30. https://doi.org/10.1029/2012GB004296.

Siani, G., Paterne, M., Arnold, M., Bard, E., Métivier, B., Tisnerat, N. Bassinot, F., 2000. Radiocarbon
reservoir ages in the Mediterranean Sea and Black Sea. Radiocarbon 42, 271-280.
https://doi.org/10.1017/S0033822200059075.

Silenzi, S., Bard, E., Montagna, P., Antonioli, F., 2005. Isotopic records in a non-tropical coral
(*Cladocora caespitosa*) from the Mediterranean Sea: evidence of a new high-resolution climate
archive. Global and Planetary Change 49, 94-120. https://doi.org/10.1016/j.gloplacha.2005.05.005.

Stuiver, M., Reimer, P.J., 1993. Extended 14C database and revised CALIB radiocarbon calibration
program. Radiocarbon 35, 215-230. https://doi.org/10.1017/S0033822200013904.

1232 Tins, W., 1978. Biotische und abiotische Limitierung bei der Koralle *Cladocora caespitosa* 1233 (Madreporaria). Verhandlung der Gesellschaft für Ökologie 7(1977), 79-87.

Tremblay, P., Peirano, A., Ferrier-Pagès, C., 2011. Heterotrophy in the Mediterranean symbiotic coral
 Cladocora caespitosa: comparison with two other scleractinian species. Marine Ecology Progress
 Series 422, 165-177. https://doi.org/10.3354/meps08902.

1239 Tur, J.M., Pere Godall, 1982. Consideraciones preliminaries sobre la ecología de los antozoos del1240 litoral sur de la Costa Brava. Oecologia aquatica 6, 175-183.

Vacchi, M., Ghilardi, M., Spada, G., Currás, A., Robresco, S., 2017. New insights into the sea-level
evolution in Corsica (NW Mediterranean) since the late Neolithic. Journal of Archaeological Science:
Reports 12, 782-793. https://doi.org/10.1016/j.jasrep.2016.07.006.

Vacchi, M., Marriner, N., Morhange, C., Spada, G., Fontana, A. Rovere, A., 2016. Multiproxy
assessment of Holocene relative sea-level changes in the western Mediterranean: Sea-level
variability and improvements in the definition of the isostatic signal. Earth-Science Reviews 155, 172197. https://doi.org/10.1016/j.earscirev.2016.02.002.

Valette-Sansevin, A., Pergent, G., Buron, K., Pergent-Martini, C., Damier, E., 2019. Continuous
mapping of benthic habitats along the coast of Corsica: A tool for the inventory and monitoring of
blue carbon ecosystems. Mediterranean Marine Science 0, 585-593.
https://doi.org/10.12681/mms.19772.

1256 Varda, D., 2015. Some historical records of *Posidonia oceanica* matte in surrounding of Bar,

- Montenegro. 4th Mediterranean Seagrass Workshop Sardinia 2015, 18-22 May 2015, Oristano, pp.
 1258
 125.
- 1259

Vella, C., Costa, K., Istria, D., Dussouillez, P., Ghilardi,M., Fleury, J., Delanghe, D., Demory, F.,
Cibecchini, F., Moreau, J., Jouët, G., 2016. Evolution du fleuve Golo autour des sites antique et
médiéval de Mariana (Corse, France). La géoarchéologie des îles de Méditerranée, Actes du colloque
GEOMEDISLANDS (30 juin-2 juillet 2015, Cargèse). CNRS éditions, pp. 229-244.

1264

Zenone, A., Alagna, A., D'Anna, G., Kovalev, A., Kreitschitz, A., Badalamenti, F., Gorb, S.N., 2020.
Biological adhesion in seagrasses: The role of substrate roughness in *Posidonia oceanica* (L.) Delile
seedling anchorage via adhesive root hairs. Marine Environmental Research 160, 105012.

1268

1269 Zibrowius, H., 1980. Les Scléractiniaires de la Méditerranée et de l'Atlantique nord-oriental.
1270 Mémoires de l'Institut Océanographique 11, 1-284.

1271

1272 Zibrowius, H., 1982. Taxonomy in a hermatypic scleractinian corals. Paleontographica Americana 54,1273 80-85.

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- Finding of a *C. caespitosa* coral palaeo-bank embedded in the matte of *P. oceanica*
- Palaeoenvironmental reconstruction of the sequence since the mid-Holocene
- Sclerochronological analysis revealed a coral mean growth rate of 2.3 ± 0.8 mm yr⁻¹
- Growth pattern fluctuations shown to be related to abiotic and climatic conditions
- Bank death was probably due to prolonged SSTs during the Roman Warm Period

Declaration of interests

 \boxtimes 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.

□The authors declare the following financial interests/personal relationships which may be considered as potential competing interests: