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1 Fossil maerl beds as coastal indicators of late Holocene
2 palaeo-environmental evolution in the Bay of Brest
3 (Western France)
4

5 Axel Ehrhold^{a,*}, Gwenaël Jouet^a, Pascal Le Roy^b, Stéphan J.Jorry^a, Jacques Grall^c, Théo Reixach^d, Clément
6 Lambert^e, Gwendoline Gregoire^f, Jérôme Goslin^a, Angélique Roubi^a, Aurélie Penaud^b, Muriel Vidal^b,
7 Raffaele Siano^g

8 * Corresponding author: axel.ehrhold@ifremer.fr
9

10 **Affiliations:**

11 ^a IFREMER, Géosciences Marines LGS, Centre de Brest, B.P.70, 29280 Plouzané, France

12 ^b Université Européenne de Bretagne Occidentale, UMR-6538 Géosciences Océan, IUEM/CNRS, Place Copernic,
13 29280 Plouzané, France

14 ^c Université Européenne de Bretagne Occidentale, UMS3113 Observatoire Marin, OSU-IUEM, Place Copernic, 29280
15 Plouzané, France

16 ^d Université de Perpignan, UMR 7194 Histoire naturelle de l'homme préhistorique, Via Domitia 52 avenue Paul
17 Alduy, 66860 Perpignan, France

18 ^e Université de Bretagne Sud, UMR 6538 Géosciences Océan, F-56000 Vannes, France

19 ^f INTECHMER, LUSAC/CNAM, Boulevard de Collignon, 50110 Turlaville, France

20 ^g IFREMER, DYNECO Pelagos, Centre de Brest, B.P.70, 29280 Plouzané, France
21

22 **E-mail address:**

23 Gwenael.Jouet@ifremer.fr, Pascal.Leroy@univ-brest.fr, stephan.jorry@ifremer.fr, Jacques.Grall@univ-brest.fr,

24 theo.reixach@univ-perp.fr, clement.lambert@univ-ubs.fr, gwendoline.gregoire@lecnam.net,

25 Jerome.Goslin@ifremer.fr, angelique.roubi@ifremer.fr, Aurelie.Penaud@univ-brest.fr, muriel.vidal@univ-brest.fr,

26 Raffaele.Siano@ifremer.fr
27

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Abstract

The Bay of Brest (BB) is a mixed, tide-dominated estuarine system. The shore terraces of this bay are occupied by modern free-living (calcareous) coralline algae locally termed “maerl”, organized in bed-like morphologies (rhodolith deposits). Cores retrieved from around the bay reveal fossilized primitive maerl beds of Holocene age, interbedded in sandy-silt sedimentation. The alternation between biogenic constructions and estuarine sedimentation may provide evidence of varying environmental conditions of the late-Holocene period. This paper mainly focuses on the results of chronostratigraphic and bio-sedimentological interpretations of coring data collected in less than 15 m of water depth in an attempt to decipher the main stages of maerl colonization in the bay. In particular, this study raises several significant points allowing to draw links between centennial to millennial-scale climatic changes in marine estuary sedimentation and episodes within the development of maerl biocenoses. The paleo-bathymetry of the coastal terraces has not changed significantly over the last 5000 years. Yet, the first maerl occurrence only appeared around 2000 cal yr B.P., likely showing that the environmental conditions were not favorable for their emergence prior to that time. Pioneer maerl beds developed on coarse shell deposits inherited from the paleostorms affecting the Atlantic coasts during the colder climatic period of the Iron Age (3100-1950 cal yr B.P.). The accumulations then aggraded at various and discontinuous rates, sometimes reaching up to 2.1 m/kyr. Maerl beds temporarily disappeared in the southern part of the Bay of Brest when sedimentation rates increased throughout the bay during the Dark-Age cold period (1375-1250 cal yr B.P.), suggesting that maerl formations could not keep up with sedimentation rate exceeded a certain threshold. Muddy sedimentation conditions also dramatically changed on two occasions, with the establishment of coarse storm levels, set at the intervals 825-600 cal yr B.P. (MWP) and 113-0 cal yr B.P. But maerl deposits reseed the environment as a result of each new cold period, demonstrating the persistence of such coralline algae against drastic palaeoenvironmental changes in coastal areas.

1. Introduction

Maerl beds are living and dead aggregations of free-living non-geniculate coralline algae that gather to form extensive beds that may accumulate over time to form fossil deposits. In the Bay of Brest, maerl deposits are formed by free living corallines algae of the *Lithothamniaceae* and *Lithophyllaceae* families. In Europe, different maerl-forming species are found in shallow waters of the inner shelves from Norway to the north of Portugal and in the Mediterranean Sea to the south (Kamenos et al., 2017). They are found in particular abundance along the coast of

59 Brittany (Grall, 2002) as well as in the Galician rias (Peña and Bárbara, 2009) and Ireland (Bosence, 1976). They
60 occupy the subtidal zone down to ca. 40 m water depth (Hall-Spencer et al., 2010; Teichert et al., 2012) where the
61 abundance of living maerl reaches up to 9000 thalli/m².

62 Over their long geological history, coralline algae colonized almost all types of marine substrates within the photic
63 zone worldwide as their present-day representatives (Kamenos et al., 2017). They are important ecosystem engineers
64 that produce hard, three-dimensional substrates (Schubert et al., 2020). Calcareous coralline algae are the most
65 common and widely distributed groups of fossilized marine benthic algae since the Late Cretaceous and particularly in
66 the Early Miocene (Aguirre et al., 2000). Fossil coralline algae data are increasingly exploited in palaeoecological
67 studies and reconstruction of palaeoenvironments (Cabioch et al., 1999; Foster, 2001; Burdett et al. 2011; Aguirre et
68 al., 2012; Sarkar, 2017). Recently, Mg/Ca ratios measured in limestone skeletons proved useful for producing
69 environmental reconstructions over the last century (Halfar et al., 2008; Kamenos et al., 2008; Kamenos et al., 2012;
70 Kamenos et al., 2017). Strong relationships have been recorded between Mg/Ca ratios and Sea Surface Temperature
71 (SST) in relation to the North Atlantic Oscillation (NAO) and the Atlantic Multi-decadal Oscillation (AMO) over the
72 past century (Gamboa et al., 2010, Halfar et al., 2007, 2011).

73 Appropriate conditions for maerl bed development were shown to be generally reached during transgressive
74 periods (Friebe, 1993, Bosence et Wilson, 2003; Nalin et al., 2008; Leszczynski et al., 2012) when the sea-level floods
75 coastal environments. The Highstand Systems Tract (HST) and more particularly the maximum flooding period seems
76 to represent the most favorable paleoenvironmental conditions for the settlement and expansion of maerl production
77 areas on internal coastal areas if combined with the absence of massive terrestrial inputs (Aguirre et al., 2012). The
78 Glenan Islands in SW Brittany have the thickest known maerl deposit in the world, with accumulations up to 10 m
79 thick reported by Augris and Berthou (1990). Grall and Hall-Spencer (2003) dated a thallus sampled at the subsurface
80 of the deeper part of the excavation area at 5860 cal yr B.P. At the same depth but tens of kilometers to the south-east
81 on the marine terrace of Belle-île Island, the first occurrence of fossil maerl is dated at 5300 cal yr B.P. (Ehrhold et al.,
82 unpublished data).

83 The main aim of this study is to document the stratigraphic and palaeoenvironmental evolution in the Bay of Brest
84 (BB) over the last 2000 cal yr B.P. by using the evolution of fossil maerl beds as a sensitive geological “proxy” of
85 coastal environment fluctuations under climatic and anthropogenic forcings. Maerl beds are of strong ecological
86 importance and conservation value (Grall and Hall-Spencer, 2003). The Bay of Brest was recently the subject of
87 studies to better constrain the Holocene geological and palaeoenvironmental data (Goslin et al., 2013; Gregoire et al.,
88 2016; 2017; Garcia-Artola et al., 2018; Lambert et al., 2018; 2019; 2020). By integrating new sedimentary records and

89 a new chronostratigraphic framework, the analysis of depositional sequences provides information on the conditions
90 of the development of past maerl beds and the impact of recent climatic events in the context of major landscape
91 changes in the Bay of Brest watersheds.

93 **2. Study area**

95 *2.1 Geological and environmental settings*

96 The Bay of Brest is located in northwestern Brittany (NW France, Fig. 1) and constitutes a shallow, semi-
97 enclosed coastal basin of 180 km² surrounded by a 230 km-long rugged coastline. The bay is sheltered from the Iroise
98 Sea and Atlantic storms by an elongated NE-SW narrow strait (the “Goulet”), one nautical mile wide and 50 m deep
99 (Lowest Astronomical Tide or LAT). Many small coves of a few square kilometres such as those of Roscanvel, Fret,
100 Lanveoc-Poulmic, Daoulas and Auberlac'h in which the water depth does not exceed 10 m, constitute an essential
101 geomorphological feature of the bay, representing 47% of the marine surface (foreshore included). The peninsula of
102 Plougastel-Daoulas separates the bay into two distinct parts, the estuary of the Elorn river to the north and the estuary
103 of the Aulne river to the south. Beyond 10 m water depth, a set of tidal channel networks inherited from the flow of
104 the Elorn and Aulne rivers during the glacial periods plays an important role in the modern hydrodynamical and
105 sedimentological context in each part of the bay. They converge and connect upstream from the Goulet (Gregoire et
106 al., 2016, 2017; Fig. 1).

107 The basement of the bay and surrounding rocky coasts are composed of Brioverian rocks structured by an
108 inherited Hercynian fault system. This N70°E trending fault system separates two regional geological domains
109 composed of the peneplanation of the high Hercynian granitic chain to the north (Leon metamorphic domain) (Chauris
110 and Hallégouët, 1980; Ballèvre et al., 2009; Le Gall et al., 2014) and the main fault and sedimentary rocks to the south
111 (Brioverian and Palaeozoic) which form the whole rocky basement of the bay (Babin et al., 1969; Garreau, 1980;
112 Ballèvre et al., 2014). The study area has subsided since the Eocene and is now considered to experience very limited
113 (0.02 to 0.04 mm/yr; Ziegler, 1992; Bonnet et al., 2000) to no subsidence (Poitevin et al., 2019). The palaeo-fluvial
114 network is established since the Cenozoic (Hallégouët et al., 1994). Palaeo-channels of the two main current rivers,
115 Aulne and Elorn, are respectively about 30 and 15 m deep, and converge to the west in a unique valley of about 60 m
116 deep outside the Goulet (Gregoire et al., 2017). Gregoire et al. (2017) characterized the chrono-stratigraphy of the
117 sediment infilling as corresponding to the late transgressive system track since 10000 cal yr B.P. according to the final
118 stage of deglacial sea-level rise (Camoin et al., 2012). The area switched from a strictly continental domain during late

119 glacial to a ria confined in the main palaeo-fluvial network at early Holocene. Between 10000 and 7000 cal yr B.P.,
120 the still rapid sea level rise (up to 10 cm/yr) caused a fast backstepping of the intertidal area recorded by a first
121 transgressive system tract (TST1) and weathered by a tidal incised surface in response to the development of a strong
122 tidal circulation around 7500 cal yr B.P. Between 7000 and 3000 cal yr B.P., the slow retreat of the shoreline coupled
123 with modest accommodation space allowed the development of a second transgressive interval (TST2) characterized
124 by subtidal deposits associated with the migration of tidal bars in the central part of the bay and the growth of tidal
125 flats in the shallowest embayments.

126 The period of the highstand deposit extends from 3000 cal yr B.P. to the present day. Its lower limit corresponds
127 to the maximum flooding surface (MFS) dated between 3000–2000 cal yr B.P. (Gregoire et al., 2016) when sea-level
128 was almost as high as that of the present day (Goslin et al., 2015). The approximate maximum flooding in such a
129 confined sedimentary system occurred somewhat late compared to the highest sea level imprinted in open-marine bays
130 of the Atlantic (Chaumillon et al., 2010; Tessier et al., 2012) and could be linked to a different organization of the
131 coastal wedges in response to local low sediment supply (Baum and Vail, 1988).

133 ***2.2 Palaeoenvironmental conditions and human activity***

134 Climate variability of the Brittany headland during late Holocene has been well documented (Fernane et al.,
135 2014; Tréguer et al., 2014; Lambert, 2017; Lambert et al., 2018, 2019, 2020; Penaud et al., 2020). The
136 geomorphological (Regnauld et al., 1996; Van Vliet-Lanoë et al., 2014a, 2014b, 2016) and sedimentological (Goslin
137 et al., 2013; Stéphan et al., 2015) responses of the Brittany coasts have been examined on decadal to multi-centennial
138 time scales.

139 During the late Holocene, between 2700 and 2340 yr B.P., the re-activation of dune belts at the tip of the
140 Finistere region reflected a strengthening of storm activity along the French Atlantic coasts (Regnauld et al., 1996;
141 Stéphan, 2008, Van Vliet-Lanoë et al., 2014a, 2014b, 2016; Poirier et al., 2017; Pouzet et al., 2018). The base of the
142 channels of coastal streams was observed to have experienced scouring and subsequent exacerbated infilling (Goslin
143 et al., 2013; Stéphan et al., 2015), likely in response to the major increase in precipitations and terrigenous
144 sedimentation observed at European scale.

145 Between 2400 and 1900 cal yr B.P., Lambert (2017) and Lambert et al.(2020) described the increase in the
146 share of riparian forest and primary production in the BB, simultaneous to the expansion of agropastoralism that began
147 at the end of the Neolithic (4150 yr B.P.) and intensified during the Bronze Age (Marguerie et al., 2001; Gaudin,
148 2004; David, 2014). This agricultural activity also coincides with the extent of land clearing during the Iron Age

149 (2750-2002 yr B.P.) and the decline of mid-latitude forest cover (Dark, 2006; Meurisse, 2007; Roberts et al., 2018).
150 From 1700 cal yr B.P., the establishment of *Corylus*, a pioneer species in plant recovery, could coincide with a
151 collapse of the local agricultural system (Galliou, 1991; Lambert et al., 2020). Lambert et al. (2020) and Fernane et al.
152 (2014) indicate a revival of forest taxa (more than 30% compared with the previous period) up to 1450 yr B.P. This
153 corresponds to a rapid decrease in agro-pastoral activities in the catchment basins with the combination of oceanic and
154 atmospheric configurations with evidence of increased humidity and storms (Lambert et al., 2020).

155 Between 1450 and 1100 cal yr B.P., all palynological records collapsed (Lambert, 2017; Lambert et al., 2020).
156 This period coincides with the onset of a colder and drier climate (Dark Ages Cold Period, Wanner et al., 2008;
157 Helama et al., 2017) and the drying-up of sedimentary inputs, notably from 1200 B.P. (RCC5, Mayewski et al.,
158 2004;). Galliou (1991) estimates that it is likely that the collapse of the agricultural system of Roman Armorica caused
159 the desertification of more than 75% of villages in the middle of the 5th century AD, resulting in a decline in
160 cultivated areas and a return of secondary plant formation (Galliou, 1991; Cassard, 1996). This period is marked in
161 most European regions by a stable forest cover or afforestation (Kaplan et al., 2009; Roberts et al., 2018).

162 From 1100 cal yr B.P., climatic conditions induced arid settings and regular westerly storms over north-western
163 Europe (Van Vliet-Lanoë et al., 2014a, 2014b). Urbanization developed and cereal cultivation increased (Lambert,
164 2017) while forests regressed, representing only 60% of French territory (Mather et al., 1999). Until the 13th century,
165 forests in France were cut back by nearly 15 million hectares (i.e. 30 to 40,000 hectares/year). This major
166 deforestation was followed by the decrease of *Alnus* around 200 years later and anthropization reached its maximum
167 around 750 yr B.P. dominated by a maximum of *Cerealia* and *Cannabaceae* (Fernane et al., 2014). The retreat of
168 Brittany's forests is in line with that on the European-scale (Williams, 2003; Kapland et al., 2009). Three centuries of
169 relative stability ensued, corresponding to the Medieval Warm Period MWP (Hughes and Diaz, 1994; Goosse et al.,
170 2006), during which harvests were more abundant, and the European population tripled. . Simultaneously, monastic
171 communities developed, particularly in the Aulne catchment area (construction of the abbeys of Landevennec with its
172 new 11th-century Romanesque abbey church, Daoulas in 777 yr B.P., and Relecq in 818 yr B.P.). With the support of
173 the local population, these constructions participated in the region's mass deforestation (Dufief, 1998), along with
174 massive use of wood in the form of charcoal for mineral processing and as fuel. From the 11th-century onwards,
175 damming on the rivers developed, limiting sediment supply to the coast (Van Vliet-Lanoë et al., 2016).

176 From 650 years B.P. onwards, plague epidemics (Black Death) drastically reduced populations with more than a
177 third of the European population decimated (Mather et al., 1999). Farms were abandoned and the forests regenerated
178 throughout the territory up to 500 B.P. (Mather et al., 1999). To this episode of decline in human activity

179 corresponded a sharp increase in storminess, responsible for the last major episode of dune formation in Brittany
180 between 600 and 400 cal yr B.P. (Van Vliet-Ianoë et al., 2014a, 2016; Pouzet et al., 2018). The Little Ice Age (LIA)
181 that followed this decline was the most recent and most documented event during which glaciers extended globally
182 (Grove, 2001) and moderately cooler temperatures characterized the Northern Hemisphere from about 500 to 50 B.P.
183 (Mann, 2002; Ilyashuk et al., 2019). Finally, the main episode of forest clearance occurred between the 15th and 17th
184 centuries. With the construction of the Arsenal in Brest (1670), local forests were used for shipbuilding (Le Goff and
185 Meyer, 1971). Since the beginning of the 19th-century, the forest area in France has steadily increased (Cinotti, 1996).
186 The industrial revolution, the substitution of wood for fossil fuels, which became widely available thanks to the
187 increase in transport and trade, and the decline in wooden shipbuilding enhanced to forest restoration. Between 1850
188 and the middle of the 20th-century, the agronomic model in Brittany was based on the parceling of land into wooded
189 embankments (Lambert et al., 2018). The increase in soil erosion and drainage towards rivers is related to the
190 destruction of linear bocage and hedgerows after 1950 (Auzet, 1987).

192 ***2.3 Hydrological, hydrodynamic, and modern sedimentary settings***

193 The Bay of Brest is a macrotidal coastal system characterized by semi-diurnal tidal amplitude ranging from 1.2 to
194 7.3 m (average of 4 m), leading to the presence of extended intertidal flats during low tides (Trodec and Le Goff,
195 1997). Marine waters flow into the BB at each new tidal cycle with current speed reaching 1 m/s, mainly oriented W-
196 E. Near to the Pointe des Espagnols (Fig. 1), coastal geometry and submarine morphology generate a Venturi effect
197 with strong tidal current reaching velocities up to 9 m/s during the spring, limiting swell influence. In the remainder of
198 the Bay, marine hydrodynamics seem to be largely dominated by tidal currents ranging from 0.25 to 2 m/s. However,
199 due to local winds, the sea can be rough and affects the superficial water mass (Petton, 2010). Short-length but steep
200 waves can hence reach the shore with high obliquity (Pommepuy et al., 1979), resulting in localized erosion of barrier
201 beaches (Stéphan et al., 2005).

202 In its easternmost part, the BB receives its main freshwater supplies from the Aulne and Elorn rivers, and the
203 smaller Daoulas River (Fig. 1). The BB watersheds are characterized by 2000 km of waterways and most of their
204 runoff flows into the bay through the Aulne River (114 km long and 36 m³/s of annual flow; Trodec et al., 1997). The
205 Aulne watershed (1842 km²) is about six times the size of the Elorn catchment area. The Aulne and Elorn river
206 outflows contribute up to 85% of total river discharge into the BB (Delmas and Tréguer, 1983). The salinity of the bay
207 is 34.5‰ and shows no evolutionary trend over the last 20 years (Tréguer et al., 2014).

208 Sediment inputs by the two main rivers represent only 12000 T/yr of suspended sediment matter for the Aulne
209 (Bassoulet, 1979) and 1000 T/yr for the Elorn (Monbet and Bassoulet, 1989). Ehrhold et al. (2016) estimated that
210 terrestrial inputs account for only 10% of the deposition in the bay today, which implies a substantial contribution of
211 detrital input from the outer sea. Also, local reworking of sediments can occur through fishing activities, storm-swells
212 (Hily et al., 1992) or tide currents that may generate higher concentrations of re-suspended muddy sediment in
213 estuaries (Beudin et al., 2013). Most of the sedimentation takes place in the inner zone of estuaries because tidal
214 energy is stronger than river flow (Dyer, 1997; Moskalski et al., 2018). Klouch et al. (2016a) demonstrated that the
215 south-east of the bay is disconnected from the Elorn estuary, which is the area exporting the highest proportion of
216 particles outside the BB.

217 218 **2.4 Ecology and distribution of modern free-living maerl**

219 In the BB, live maerl thalli (at least 30% of the present seabed) occupies 40 km² of the bay's shallow waters
220 (Fig. 2) corresponding to muddy terraces (tidal flat) at less than 10 m depth (Grall, 2002, Gregoire et al., 2016) and
221 where sedimentation rates are between 0.5 and 3 mm/year (Fig. 2; Ehrhold et al., 2016). The distribution of maerl beds
222 coincides with areas characterized by an annual mean tidal current velocity of less than 0.26 m/s and wave agitation of
223 less than 0.09 m/s (Dutertre et al., 2015). Both species of free-living thalli, *Phymatholiton calcareum* and
224 *Lithothamnion corallioides*, are found mainly in the region of Brest (Grall, 2002). However, other types of maerl
225 species also exist in the BB: those formed by species of the genus *Lithophyllum* with apparently a more estuarine
226 affinity, particularly for *Lithophyllum fasciculatum* (Peña et al., 2013). Despite slow growth rates that vary according
227 to species and region (about 0.25 to 0.6 mm/yr for *P. calcareum*; Adey and McKibbin, 1970; Grall, 2002; Bosence
228 and Wilson, 2003; Kamenos et al., 2008; Halfar et al., 2011), rhodolith accumulations can reach several metres thick.
229 Bosence and Wilson (2003) compiled information on accumulation rates of maerl beds from different temperate and
230 tropical areas, which does not include the BB. Their results show accumulation rates ranging from 0.08 to 1.4 m/kyr in
231 temperate conditions. Maerl beds constitute three-dimensional multi-centimetric structures with a high volume of
232 sediment matrix (about up 45 to 50% for *Lithothamnion corallioides* through 5 cm thickness of maerl deposit in the
233 BB). Maerl is an important source of modern-day calcium carbonate production (about 100 to 3000 g/m²/yr) in
234 temperate marine environments (Bosence, 1980; Potin et al., 1990; Freiwald, 1998; Wehrmann, 1998; Martin et al.,
235 2006). The maerl beds of the Brittany coast were found in areas characterized by annual mean water temperatures
236 varying between 12.2 and 13.6°C (Dutertre et al., 2015). In these conditions, the annual biomass growth rate of

237 calcium carbonate in *Lithothamnion corallioides* is estimated to be 43.8% of the initial calcite mass (Potin et al.,
238 1990).

239 The development and distribution of maerl accumulations are conditioned by various environmental factors that
240 remain difficult to prioritize (Jacquotte, 1962; Cabioch, 1968; Bosence, 1976; Wilson et al., 2004; Dutertre et al.,
241 2015). Maerl-forming species require clear and relatively shallow water to develop their photosynthetic capacity. The
242 maximum water depth of maerl occurrence, mainly conditioned by light and therefore water turbidity, is 30 m in
243 Galway Bay (De Grave et al., 2000), 25 metres in Scotland (Moore, 2014) and 20 to 25 m in Brittany (Dutertre et al.,
244 2015). The transport capacity of the fruticose rhodoliths depends wave agitation and may only move occasionally due
245 to bioturbation and severe storms (Marrack, 1999; Pardo et al., 2019). Maerl beds can be shaped by the swell to form
246 megaripples, but wave energy can rapidly limit the vitality of the maerl-forming species in contrast with encrusting
247 corallines that can live in such highly hydrodynamic environments. If coastal hydrodynamic conditions are too low,
248 fine sediment particles settle, stifling algal growth (Steller et al., 2007). Conversely, in the case of strong
249 hydrodynamics, the fine sediments are re-suspended, inhibiting photosynthetic activity and coarser particles such as
250 sand or broken shells are transported, burying the thalli under the sediment. Maerl beds are consequently very
251 sensitive to sediment input and sediment mobility. In the estuarine domain, river inflows contribute to turbid load,
252 limiting light penetration and inhibiting the regular growth of maerls (Adey and MacIntyre, 1973; Steller and Foster,
253 1995; Foster et al., 1997; Wilson et al., 2004). In the BB, the maximum growth rate was recorded in summer (July),
254 while it was close to zero in winter (Potin et al., 1990). Coralline algae are very sensitive to sediment influx (Aguirre
255 et al., 2017). Off the Brazilian coast, rhodoliths form one of the largest known living deposits of coralline algae
256 (Amado-Filho et al., 2012). Vale et al. (2018) showed that the turbid plume of the Amazon River mouth is probably
257 the main driver for rhodolith structure and composition as it determines light penetration, and nutrient and organic
258 matter levels. Deterioration of living rhodoliths occurs after being covered for two weeks by 1 mm of fine sediment
259 (Riul et al. 2008; Villas-Bôas et al., 2014), and even sooner if contains a high concentration of organic matter (Wilson
260 et al. 2004; Hall-Spencer et al. 2006). In the case of *Lithothamnion* sp., death occurs after 41 days of being buried by
261 sediments (Villas-Bôas et al. 2014). The negative influence of terrigenous sedimentation on the development of
262 rhodolith beds has been demonstrated in Pliocene deposits in SE Spain (Aguirre et al., 2012). The species that make
263 up the maerl are sensitive to environmental disturbances such as excessive turbidity and a decrease in light intensity
264 (extraction, fishing, aquaculture, eutrophication, invasive species, Grall and Hall-Spencer, 2003). Sea temperature also
265 strongly influences the specific composition of European maerl beds (Wilson et al., 2004), probably being the main
266 factor affecting their geographical distribution (Adey, 1973).

267

268 **3. Core acquisition and methods**

269

270 **3.1 Core sampling**

271 Fifty-two Kullenberg gravity cores (10 cm in diameter, 2-5 m in length) were retrieved from the BB during the
272 SERABEQ3 (2015) and the PALMIRA (2017) surveys, and 45 interface sediment cores (10 cm in diameter, 1 m
273 maximum in length) were sampled during the AL2013 and SERABEQ1-LEG2 expeditions (respectively in November
274 2013 and May 2014). All Kullenberg core acquisitions were made onboard the Genavir-Ifremer R/V *Thalia* and the
275 short interface cores on the INSU RV *Albert Lucas* (Fig. 3). The cores were retrieved between 2 m and 15 m water
276 depth from the lowest low-tide level. SERABEQ core locations were determined using the stratigraphic framework
277 interpreted by Gregoire et al. (2017) on the basis of an extensive set of seismic data. Lithological description and
278 photographs were performed directly after core opening on sliced half-core surfaces. Gregoire et al. (2017) already
279 described the lithology of five main Kullenberg cores (SRQ3-KS02-KS34-KS39-KS41-KS44) and discussed the
280 sedimentary infilling of this bay starting around 9000 cal yr B.P. In this study, we focused on the most superficial
281 sediment deposits (upper seismic unit) and more particularly in the shallowest areas of this bay, corresponding to the
282 last HST composed of muddy sediments interbedded with coralline deposits.

283

284 **3.2 AMS ¹⁴C dating**

285 AMS radiocarbon dating was conducted on several cores from the AL2013, SERABEQ and PALMIRA
286 expeditions (tab. 1) using either CaCO₃ from fresh juvenile marine shells (bivalve mollusks with still articulated
287 valves when possible and gastropods such as *Turritella*), bulk benthic foraminifera or algal thalli in fossil maerl beds.
288 These carbonate samples were picked from the sediment using X-ray imagery and washed from adhering particles to
289 remove any external source of older (reworked) carbon. For each sample, AMS ¹⁴C dating was performed using a
290 minimum amount of 1.0 mg of pure carbon. Measurements were conducted at the Poznan Radiocarbon Laboratory
291 (Poland) and at Beta Analytics (UK). Absolute dating was corrected for the mean ¹⁴C age difference between the
292 atmosphere and oceanic surface waters by applying a reservoir correction (R) of 325 years (Tisnérat-Laborde et al.,
293 2010) and a regional deviation (DR) for the BB of 46 years. Absolute ages were calibrated using Calib Rev 7.1
294 software (Stuiver and Reimer, 1993) from the “Intcal13” calibration curve (Reimer et al., 2013), with a confidence
295 level of 95% for the standard deviation (2 sigma). Despite the fact that the sampling was systematically carried out on

296 the outer coralline thallial surface which may represent the most recent carbonate concretion, radiocarbon dates from
297 corallines present a ^{14}C age offset up to 200 years for the most recent ages, compared to the age model defined on
298 other marine species datings, and so were not considered when younger than 400 cal yr B.P. (Fig. 4).

300 **3.3 Fossil maerl bed characterization**

301 In this study, we used the Geotek XCT system which provided digital linear images similar to half or full
302 section X-ray images of cores obtained by X-ray tomography. X-ray computed tomography (XCT) was used to locate
303 fossil maerl beds accumulated in BB coastal sediments and to determine their geometric signature (Fig. 5). XCT
304 imagery is a non-destructive imaging technique able to provide 3-D data of the internal structure of objects,
305 determined mainly by variations in density and atomic composition (Ketcham and Carlson, 2001; Yang et al., 2010).
306 The X-rays are emitted by a micro-focal source and are then detected by a sensor after passing through the core. The
307 software associated with the device then produces images with a resolution of 100-150 μm in TIFF format. For each
308 core, one to three analysis angles were acquired at 0° , 45° and 90° . To better determine maerl beds before sampling
309 (Fig. 5), original imagery was enhanced from edge-detection filters using the open-source image-processing program
310 (GIMP software), and more particularly the Neon filter (Sekanina et al., 2011). Image processing is a helpful tool for
311 detecting layer boundaries as a prerequisite for qualitative and quantitative analysis of sediment cores (Bube et al.,
312 2006). The maerl beds described under XCT were numbered from the oldest to the most recent from the base of the
313 cores (Fig. 5). A 2 cm section in the maerl signature recognized by XCT was sampled, dried and weighed. To avoid
314 breaking the maerl thalli mechanically, the sample was then sieved underwater to separate grain size fractions greater
315 than 2 mm, 250 and 50 μm respectively. The sieve refusals were then dried again and the unbroken maerls (fruticose
316 rhodoliths) were separated under stereomicroscope and weighed, together with the broken maerls (fruticose coralline
317 fragments) and associated coarse bulk shells (Fig. 6). Lastly, the sediment matrix below 250 μm was counted. Two
318 classes of fruticose rhodoliths were considered (Fig. 7): (1) a percentage of dead thalli between 5 and 25% of the total
319 weight for the 2 cm section and (2) a percentage exceeding 25%. For the unsampled maerl beds recognized by XCT
320 signature and the lithological description, a third class was defined considering at least 5% of thalli presence. Fossil
321 maerl fragments were sampled within the identified facies for further identification. Morphological as well as cell
322 arrangement analyses showed that all fossil maerl fragments sampled belonged to the species *Lithothamnion*
323 *corallioides*.

325 **4. Results**

327 The succession of mixed siliciclastic-carbonate deposits was examined over the seven coastal zones that cut
328 through the BB from the Roscanvel cove in the west, to the Aulne estuary in the east, and north of Brest commercial
329 harbor at the outlet of the Elorn river. Modern sedimentation is characterized by mixed sediment with a muddy
330 fraction in more or less concentrated (Gregoire et al., 2016). This characteristic is due to estuarine dynamics,
331 influenced by the seabed morphology of the BB and controlled by tidal currents in deep water areas. Based on
332 granulometric analyses and lithological descriptions, three main sedimentary facies have been described in the cores
333 selected for this study. Sandy-silt sediments with a mean percentage of silt and clay of more than 65 % correspond to
334 the original estuarine sedimentation accumulated on tidal flats under low-energy conditions. This facies also
335 constitutes the sediment matrix between the thalli in the maerl beds. Two others classes of sediment are interbedded in
336 the lithology succession and associated with a high energy event: *i*) a thin layer of sand (Ssd for Sand sedimentary
337 deposit), moderately to relatively poorly sorted, composed of medium to coarse sand (more than 70 % of
338 granulometric distribution) mixed with finely crushed bioclasts and, *ii*) a thick layer of coarse shelly debris (Csd for
339 Coarse sedimentary deposit) poorly sorted, for which granulometric classes of sand and gravel constitute more than
340 60% of the weight of the sample. The last represents the maximum flooding surface at the base of the highstand
341 system tract in the BB (Gregoire et al., 2017). The Holocene shallow marine deposits observed in this study reflect
342 these conditions but also show abrupt stratigraphic changes in the muddy deposit sequence at the scale of the BB.
343 They are denominated as major Coarse Sedimentary Events (CSE) associated with basal erosive surfaces. The age of
344 the base of the fossil maerl beds as well as the main erosive surfaces, at the origin of time gaps were fixed for each
345 area on the basis of local radiocarbon datings (Table 1).

346

347 **4.1 The Roscanvel cove (RC)**

348 In the inner zone on the seafloor of Roscanvel cove (less than 10 m water depth), the oldest muddy sediments
349 (older than 4000 cal yr B.P.) present, locally, some horizontal laminae rich in plant debris and are associated with
350 *Turritella* shelly levels and other coastal gastropods typical of a sheltered environment. In the outer zone beyond 10 m
351 depth (towards the open sea), this homogeneous and continuous sandy-silt sedimentation is well observed in core
352 SRQ3-KS39, between 123 and 193 cm below the seafloor (bsf), and after 167 cm (bsf) in core SRQ3-K40, but seems
353 to correspond to older sediments (more than 7000 cal yr B.P.). However, the most recent muddy deposits succession
354 (after 2000 cal yr B.P.) presents some interbedded maerl beds (MB1 to MB5) in the sandy-silt series. The oldest
355 preserved fossil maerl bed or First Maerl Occurrence (FMO-MB1-KS39) is dated between 1850 and 1932 cal yr B.P.

356 and the youngest at about 1365-1418 cal yr B.P. (MB4-KS39). In RC, four high-energy coarse-grain levels of variable
357 thicknesses are also found intercalated between the muddy and carbonate units. The bases of these coarse deposits
358 (CSE) lie on erosional surfaces which lead to variable time gaps. The coarse-shell sediments (CSE1 and CSE2) (Fig.
359 7a, cores SRQ3-KS39 and KS40) are thicker and probably represent the accumulation of several high-energy episodes
360 that have washed out the fines from the sediment. The erosional events associated with CSE1 (core SRQ3-KS39),
361 dated at around 5135 cal yr B.P. at 123 cm (bsf), have reworked and eroded at least 3000 years of deposits until 7800
362 cal yr B.P. The event associated with CSE2 (end dated around 1980 cal yr B.P.) often presents a fining-upward
363 sequence, and is followed by the establishment of a first maerl bed (cores SRQ3-KS39 and KS40). The sedimentary
364 layer corresponding to CSE3 (Fig. 7a) becomes thicker at the edge of the terrace (core SRQ3-VZ29). The
365 hydrodynamic event related to these coarse CSE3 deposits is sealed around 577 cal yr B.P. and erodes down to 1245
366 cal yr B.P. (core SRQ3-KS39). In RC (Fig. 7a), exclusively in the very shallow water zone ($Z < 5$ m), the first coarse-
367 grain level is a well-sorted homogeneous sand associated with the CSE4 event (Fig. 7a, cores SRQ1-IS03 and IS30),
368 with some angular elements at the base. It represents one or more contemporary events centered on 0 B.P. The
369 superficial sediments are characterized by sandy-silt (Fig. 7a) containing the *Crepidula* gastropod and shows low
370 sedimentation rates (1.2 mm/yr, Ehrhold et al., 2016). This muddy sedimentation evolves along the northern edge of
371 the coastal terrace towards coarse sand deposits (core SRQ1-IS30) that become thicker with increasing depth (core
372 SRQ3-VZ29).

373

374 **4.2 The Fret cove (FC)**

375 In the inner zone, between 5 and 10 m water depth (Fig. 7b), below the CSE2 deposit, the sedimentation dated before
376 3100 cal yr B.P. (core SRQ1-IS04) is homogeneous and contains many large bivalves with their two shells adjoined.
377 In the outer zone, basal sandy-silt deposits at 122 cm and 140 cm (bsf) respectively for cores SRQ3-KS28 and SRQ3-
378 KS27, are similar granulometrically and in age to those found in RC. The event associated with CSE1 began before
379 4900 cal yr B.P. (Fig. 7b, cores SRQ3-KS38), reworking and eroding at least 3000 years of deposits. The foot of the
380 terrace, beyond 15 m water depth, was subjected to a more active tidal dynamic between CSE1 and CSE2 events.
381 However, CSE2 is thinner than in RC. Its upper termination with a fining-upward sequence reflects decreasing
382 hydrodynamic settings during this episode of coarse sedimentation. The fine estuarine sedimentation then took place
383 with the development of the first maerl occurrence at around 1873 cal yr B.P. (FMO-MB1-KS38), age is estimated
384 from the age-depth model of RC. This age is concomitant with the one determined in RC. The succession of
385 lithological facies in core SRQ3-KS38 is similar to that found in RC core KS39, located at the same water depth but 3

386 km further west. At this location, up to 9 levels of maerl beds can be distinguished, with the last-extracted bed (MB9)
387 having an extrapolated age of 1271- 1249 cal yr B.P., with only two levels remaining in the deeper core SRQ3-KS27
388 ($Z > 15$ m). Unlike in the neighboring bay, the high hydrodynamic conditions persisted after CSE3 and eroded the
389 littoral mud deposits until the extrapolated date of 1170 cal yr B.P. In the internal area, recent sandy-silt sediments
390 rich in fine shell debris lying on the CSE2 coarse sedimentary deposit do not contain maerl beds.

392 **4.3 The Lanveoc-Poulmic cove (LPC)**

393 At the edge of the littoral terrace (cores SRQ3-KS32 and KS35, Figs. 3, 8) maerl beds and sandy-silty
394 sediments constitute the main deposit succession. It is based on a coarser shell level (CSE2) particularly thick on core
395 KS32 (more than 45 cm). The maerl deposits, on the other hand, are more developed, than those described in RC and
396 FC, and include 10 levels of taphocoenoses between CSE2 and CSE3 (MB1 to MB10 in core SRQ3-KS32), although
397 it is not uncommon to encounter a few isolated fruticose coralline fragments in the muddy-silty sediments. Taking into
398 account the absence of more complete data, it is difficult to precisely locate CSE2 and CSE3 in chronological order.
399 Conversely to the two more western coves, the succession of maerl deposits in the LPC occurs at the top of all
400 interface cores taken from the inner area (depth < 10 m). The proportions of fruticose rhodoliths can reach more than
401 70% in some layers (with an average ranging from 30 to 50%, Fig. 8). The development of these biocenoses, common
402 to all infralittoral samples (cores SRQ1-IS23-IS24-IS25-IS26-IS28) below 7 m water depth, is interrupted by a
403 decimetric and homogeneous fine-grain broken shell sand deposit associated with the CSE4 erosive surface. The
404 regional hydrodynamic event causing the deposition of this sandy level and the erosion of the underlying sediment is
405 dated to the 1940s, considering the sedimentation rates (0.05 cm/yr, Fig. 2) recorded in this part of the BB (Ehrhold et
406 al., 2016). In the more eastern part of the bay, a pluri-centimetre layer of coarser and poorly-sorted broken shells was
407 deposited around 50 cm (bsf) (cores IS23 and IS24), probably resulting from a change in local hydrodynamic
408 conditions along the Lanvevenec coast.

410 **4.4 The Aulne estuary (AE)**

411 With the exception of core SRQ1-IS16 (Fig. 9), which has characteristics close to those of its neighboring cores
412 in LPC with four successive maerl deposits (MB1 to MB4), the grain size of the upper sedimentary layers of the other
413 cores reflects the intensity of the currents triggered by the channeling of the Aulne River (Fig. 1). Hydrodynamics is
414 responsible for the reworking and mixing of highly eroded coarse-grain shelly sediments that are poorly sorted, and
415 sometimes finer on shallower flats (core SRQ1-IS13). Hypothesizing for a constant sedimentation rate between 2020

cal yr B.P. (92 cm bsf) and 1492 cal yr B.P. (35 cm bsf), the first maerl occurrences are estimated to have appeared around 1950 cal yr B.P. (FMO-MB1-KS20). After the establishment of these first maerl communities, only a few taphocoenoses are preserved, either due to turbidity conditions in the estuarine zone, which were probably not very favorable for the development of coralline algae, or to erosion processes.

4.5 *The Daoulas cove (DC)*

In the open southern zone (Fig. 3), beyond 2 m water depth, fossilized maerl beds are older (up to 500 cal yr B.P.) for MB1-SRQ1-IS21. The very shallow zone (water depth $Z < 2$ m) presents the same succession of sedimentary deposits and maerl beds as in LPC (Figs. 8, 10) south of the Aulne Channel, with fossil maerl beds (four to five successive accumulations; MB1 to MB5) interbedded with sandy-silt layers. Based on a constant sedimentation rate between 15 and 66 cm (bsf) in core SRQ1-IS07, these maerl beds probably developed recently and since approximately 234 cal yr B.P. Core SRQ1-IS20 is distinguished by a coarse-sediment layer composed of fruticose coralline fragments, at 15 cm (bsf), and of a mixture of crushed shells. These layers are probably inherited from the action of fishing dredges on the seafloor at an earlier time, as the extraction of maerl by dredging started only at the beginning of the 20th-century. The proportions of biogenic coarse mixture in the surface layer (more than 40%) reflects the action of dredges of the clam *Venus verrucosa* fishery (Ragueneau et al., 2018; Bernard et al., 2019). Only the most confined sectors of the bay, to the west (core SRQ1-IS11) and to the north (core SRQ1-IS09), show respectively bioturbed and laminated sediments with a high sedimentation rate (4 mm/yr in Klouch et al., 2016b) that hinders the development of maerl beds.

4.6 *The Auberlac'h cove (AC)*

In cores KS34 and KS36 the stratigraphic organization is identical to those described within the same water depth ranges in the other sectors of the bay (Roscanvel, Fret and Lanveoc-Poulmic coves). However, the distribution of maerl deposits is denser, with up to 11 preserved maerl beds to the top of the CSE2 episode (SRQ3-KS34 core) estimated at 1914 cal yr B.P. The first preserved maerl deposit (SRQ3-KS34-MB1) overlies the roof of CSE2 at the origin of the deposition of coarse shelly sediments and the erosion of the underlying sediments. It is therefore dated to 1914 cal yr B.P. based on sedimentation rates extrapolated from the age model (Figs. 11-12). The percentages of maerl in place in the fossil beds show that they are not the densest (5 to 26%) in the whole area, probably due to the location of this core located in the Aulne paleo-channel that guides flux of suspended matter (Gregoire et al., 2017). Sedimentation rates increase very rapidly by a factor of two from 2000 cal yr B.P. (1.02 mm/yr) until the 1400-1300

446 cal yr B.P. (2.07 mm/yr) interval, then decrease sharply after this maximum (1.57 mm/yr around 1000 cal yr B.P.) and
447 collapse after the CSE3 episode (0.41 mm/yr) (Fig. 12). For comparison, modern sedimentation rates in the BB are of
448 the order of 0.45 mm/yr (Ehrhold et al., 2016), i.e. five times less than during the Merovingian era (1474-1199 B.P.).
449 In the inner zone (water depth $Z < 6$ m), as in the LPC, the sedimentary succession is characterized by a multi-
450 centimetre sandy, finely shelly level located 5 cm (bsf), with a base corresponding to the CSE4 event (Fig. 11). In the
451 external zone, the CSE4 event has not been recorded and the maerl accumulations are less numerous (two to three)
452 until the CSE3 episode which ends around 700 cal yr B.P. (Fig. 12). Below, four levels of maerl beds are interspersed
453 at least up to 410 cal yr B.P. age (MB1 to MB5 in core AL2013-IS08).

454 455 **4.7 Brest harbor and the Elorn estuary (BEE)**

456 This is the region of the bay that presents the most complex organization and succession of sedimentary facies
457 (Fig. 13), probably linked to the development of Brest's commercial port since the Second World War and the lateral
458 migration of the Elorn channel in time and space. The sedimentary evolution is therefore even more controlled here
459 than in the other sectors of the bay by the hydrodynamic processes due to river action, Atlantic storm swell penetration
460 and strengthened local winds. The first maerl occurrence is dated to around 1940 cal yr B.P. (SRQ3-KS04-MB1),
461 concomitant with the end of the coarse deposit associated with CSE2. This taphocoenose is preserved on the core
462 PALM-KS05 (216 cm bsf), and was probably almost reached at the base of core SRQ3-KS04. In core SRQ3-VZ33,
463 the resumption of fine sedimentation occurs later than in other regions of the bay (1332 cal yr B.P. at 66 cm bsf),
464 simply because the location of this core is more directly related to the strong tidal dynamic of the channel, as
465 previously shown by Gregoire et al. (2017), who described coarse deposits associated with erosive processes. The
466 erosive base of the CSE3 deposit evolves locally between 1008 cal yr B.P. (core SRQ1-IS32) and 829 cal yr B.P. (core
467 PALM-KS03 in Delebeq et al., 2020) estimated from the local age-depth model (4 mm/yr between 22.5 and 45.5 cm
468 (bsf). The core PALM-KS05 sampled from the artificial sector of the commercial port (Fig. 3) shows a time gap above
469 the CSE3 deposits (Fig. 13) which would have removed about 1 m of sandy-silt deposit and maerl levels, taking into
470 account the 2.35 mm/yr average sedimentation rate calculated over this period. In the internal zone (water depth $Z <$
471 10 m) on the northern (core PALM-KS05) and southern (core SRQ3-KS04) flats on both sides of the channel, the
472 well-conserved sedimentary archives show respectively the intercalation of up to 15 and 11 maerl beds between the
473 FMO and the CSE3 event. On the overall area, the surface layer consists of a mixture of coarse and sandy elements
474 with some fruticose coralline fragments (cores SRQ1-IS17-IS19 in the north and IS03 in the south). The fraction of

475 fruticose rhodoliths never exceeds 4%. In shallow water depths, the sandy deposit associated with the CSE4 event is
476 not present.

478 5. Discussion

479
480 The partitioning of the Bay of Brest, due to its very indented coastline, the inherited submarine topography that
481 strongly guides estuarine and tidal dynamics, and the presence of two estuaries attached to distinct catchment areas
482 implies that the factors controlling the overall sedimentation (i.e. hydrodynamism, climate, sea-level, and anthropism)
483 and the maerl deposits must be examined using all results obtained for at least 3000 years B.P. for the overall study
484 area (Fig. 14). Based on our observations, the successive occurrence of maerl beds and of major regional sedimentary
485 events can be divided into three main phases.

487 *5.1 The CSE2 sedimentary crisis of the Iron Age and the appearance of first maerl occurrence during the Gallo-* 488 *Roman period*

489 Despite a large and well-distributed number of stratigraphic samples (97 cores), we did not find any levels of
490 fossil maerl beds older than 1950 cal yr B.P. in the sedimentary records of the BB (Fig. 14). Considering a relative
491 mean sea-level of 1 m below modern sea-level at 2000 yr B.P. (García-Artola et al., 2018), the maximum depth at this
492 date corresponding to the first maerl occurrence is 15-16 m in front the FC (MB1-SRQ3-KS27-KS38, Fig. 7b) and of
493 the LPC (MB1-SRQ3-KS32, Fig. 8). This implies considering a water depth limit identical to that of maerl beds in
494 front of the Pointe de Pen Ar Vir (Fig. 2). It can be also noted that between 1910 and 1970 cal yr B.P., the seeding of
495 muddy sediments by these pioneer maerl thalli was common along all coastal terraces of the BB. The dominant
496 species was composed of more than 90% of *Lithothamnion corallioides*, as is the case today (Grall, 2002).
497 *Phymatoliton calcareum* and notably the species with webbed strands *Lithophylum fasciculatum* were much rarer.
498 This period of first occurrence is very close to the 1842±320 cal yr B.P. age obtained by Wehrmann (1998) on a maerl
499 level sampled at 160 cm (bsf) and at 15 m water depth near the Bay of Morlaix (northern coast of Brittany; Fig. 1).

500 A major question surrounds the absence of maerl beds older than 2000 cal yr B.P., at least for 5000 years
501 corresponding to the end of the CSE1 episode. Indeed, several regional records of relative sea-level (Stéphan, 2008;
502 Goslin, 2015; García-Artola et al., 2018) indicate that the relative local sea-level at the early Bronze Age was around -
503 5 m below present sea-level, i.e. just below the level of present-day lowest low tides. Correspondingly, the
504 morphological terraces (T3 in Gregoire et al., 2017) suitable for autochthonous accumulations of maerl-forming

505 species were already partly submerged. Even considering the effect of the tidal range (± 5 m), the physiognomy of the
506 seafloor at water depths less than 15 m and the light irradiance necessary for photosynthesis of coralline plants were
507 likely already similar to modern environmental conditions. Maerl beds could have developed to a water depth of 15 m
508 as they did after 2000 yr B.P., and still today in the vicinity of the Pointe de Pen Ar Vir (Fig. 2).

509 Several studies have shown that thick rhodolith deposits imply long time spans (Bosence et Wilson, 2003), and
510 are preferentially established during setting of transgressive contexts (Nalin et al., 2008; Leszczynski et al., 2012) and
511 highstand systems tracts (Aguirre et al., 2012), under conditions of terrigenous starvation and moderate
512 hydrodynamics (Aguirre et al., 2017). Gregoire et al. (2017) and Stéphan (2008) showed a rapid stratigraphic
513 backstepping of the BB coastline from 5500 to 3000-2000 cal yr B.P., accompanied by the establishment of mature
514 salt marshes and a first generation of gravel and pebble barriers. Sedimentary archives along the coasts of Brittany and
515 notably those to the south (Glenan archipelago, Fig. 1) record that massive maerl accumulations appeared as soon as
516 5862 ± 57 cal yr B.P. (Grall & Spencer, 2003). The maximum flooding surface, which represents the point of maximum
517 shoreline transgression when the Holocene relative sea level rise slowed down (Tessier et al., 2012), was reached in
518 the BB around 3000 cal yr B.P. and persisted until 2000 cal yr B.P. (Gregoire et al., 2017). This implies that a rather
519 low sediment input allowed maximum retrograding of the bay line to have occurred before the transition to tidal
520 hydrodynamics and the emplacement of prograding deposits (Baum and Vail, 1988, Tessier et al., 2012). Despite this
521 conjunction of favorable conditions from at least 3000 cal yr B.P. (and likely even from around 5000 cal yr B.P.), no
522 trace of fossil maerl of this age is found in the BB sedimentary records, suggesting that, either some environmental
523 factors did not allow the establishment and preservation of maerl beds, or, to a lesser extent the latter were not
524 preserved due to the erosive potential of CSE1 and CSE2.

525 The first maerl occurrences (Fig. 14) were established in the BB above a succession of coarse multi-decimetre
526 thick shell deposits (CSE2_B, Fig. 12) marked at its base by an erosive surface. The thickness of these coarse deposits
527 records the intensity of the reworking undergone by the underlying sandy-silt sediment they rest on. This sedimentary
528 episode is recorded across the BB, except in the very shallow depths ($Z < 5$ m) with the exception of the commercial
529 port. Between 5 and 10 m water depths, the thickness of the coarse deposits is decimetric, and pluri-decimetric beds
530 occurred below 10 m water depth. At shallow water depths ($Z < 5$ m), the erosive events and associated time gaps are
531 not very well recorded. On the slope break of the coastal terrace (between 6-15 m depth), erosion may be consequent
532 and merge with the similar but older CSE1 episode (5500-6000 cal yr B.P.), even reaching the coarse-grained deposits
533 interpreted as the glacial lag deposit (LST, Gregoire et al., 2017) and the bedrock for cores SRQ3-KS35-KS36 on
534 either side of the Aulne paleo-channel. The hydrodynamic event(s) at the origin of this Csd sequence can be dated

535 between 3100 and 1950 cal yr B.P. This morphogenic episode ends earlier in front of the Aulne estuary (2100 cal yr
536 B.P.). This time lag is probably an expression of the geographical situation of the mouth of the Aulne estuary, which is
537 more protected from the agitation by the waves. Several ^{14}C dates have been made across this coarse deposit, and
538 yielded ages quite evenly spread between 3000 and 2000 cal yr B.P. (3005, 2836, 2250, 2192, 2025, cal yr B.P.).
539 Although due to the reworking nature of this deposit, they can only be integrated except for provide a temporal
540 framework for the processes responsible for this interruption in fine sedimentation. The normal graded bedding at the
541 end of the succession provides information on the progressive decrease in energy in the environment.

542 This coarse interbedded deposit common to all the sedimentary sequences described in the BB evokes similar
543 coarse-grained layers (coarse grain sedimentation pulse CSP) described on the Atlantic coasts (Regnauld et al., 1996;
544 Stéphan, 2008,; Poirier et al., 2017; Pouzet et al., 2018) and northern Europe (Van Geel et al., 1996; Sorrel et al.,
545 2012) all dating back to 3300 to 2000 cal yr B.P., i.e. during the Iron Age period at the Subboreal–Subatlantic
546 transition (Fig. 15d-h). This could be assimilated to a condensed toplap deposit described by Kondo et al. (1998) in the
547 upper unit of HSTs representing events of storm sedimentation in exposed shallow-marine fossiliferous deposits on
548 the Sea of Japan coast. This interval is associated with significant climatic cooling of North Atlantic surface waters
549 and continental temperatures in Western Europe (RCC4 between 2500-3500 B.P. in Mayewski et al., 2004), likely
550 controlled by a 1450-year-old North Atlantic climate cycle (Poirier et al., 2017). Van Vliet-Lanoë et al. (2014a)
551 recorded significant morphogenic episodes at 2350 and 2060 yr B.P. in the dune belts of the Bay of Audierne to the
552 south of the BB (Fig. 1 and Fig. 15f). Even the southwestern sector of the BB, which is sheltered from stormy waves,
553 was affected by the energy of the sea and winds that can occur during successive winters and are sufficient to
554 remobilize biogenic debris down to 15 m water depth. This sediment reworking is concentrated under the effect of
555 tidal currents, leading to an exacerbated flattening of estuaries and erosion of dune barriers (Stéphan, 2008; Goslin,
556 2014; Van Vliet-Lanoë et al., 2014a, 2016). Pouzet et al. (2018) describe the same high energy facies at 100 cm bsf
557 near Anno Domini within very sheltered marsh deposits of the protected north-northwestern coast of the island of Yeu
558 (Fig. 15d).

560 ***5.2 The maerl expansion phase up to CSE3 sedimentary events during the Medieval Warm Period (MWP)***

561 The maerl deposits developed in the BB (all sub-regions combined, Fig. 14b1-b2-b3) almost continuously
562 during the 1970-840 cal yr B.P. period. Even though the seabeds of the southeastern part of the BB with the LPB, AE,
563 DB and AB are the best represented in terms of analyzed data, the three sub-regions of the bay (Fig. 14b1-b2-b3)
564 present a similar disturbance at 1375 cal yr B.P. up to 1250 cal yr B.P. This interruption in the almost continuous

565 evolution of the fossil maerl beds at the regional scale reflects a major environmental change with enhancement of
566 discontinuous development of maerl accumulations until 840 cal yr B.P., corresponding to the beginning of a new
567 major sedimentary episode (CSE3). For the sediment cores in which the alternation of maerl beds and sandy-silt levels
568 is well dated (tab. 2, SRQ3-KS34 and SRQ1-IS28), mean accumulation rates of maerl beds in the BB derived from
569 local sedimentation rate curves (Figs. 12 and 16), are within the range of the measurements compiled by Bosence and
570 Wilson (2003) for temperate waters, and even slightly higher, with rates varying from 1 m/kyr to 2.1 m/kyr. However,
571 these results show that the construction periods of the maerl beds are not linked systematically to a reduction in
572 sedimentary flows and the resulting deposition of suspended particles. Sedimentation rates do not necessary fall
573 during periods of maerl accumulation (for example considering a reduction of 50%), and this would be reflected by a
574 drift in the age model (Fig. 16). So it is challenging to define the evolution of sedimentation rate at the time of the
575 maerl beds formation. It is also likely that for the same period, the sedimentation of estuarine suspended sediment
576 matter above maerl beds was slightly lower than that of the local sedimentation rate outside the maerl bed. Green et al.
577 (1998) and Beudin et al. (2013) showed that dense concentrations of benthic mollusks on the seabed as in the case of
578 *Crepidula* gastropods or horse mussel bivalves, increase seabed roughness parameters and the frictional forces above
579 the dense assemblages, and reduced sedimentation processes and could even initiate resuspension. This may be one of
580 the factors responsible for the development of maerl beds under current estuarine sedimentation conditions ranging
581 from to 0.5-3 mm/yr in the BB (Dutertre et al., 2015; Ehrhold et al., 2016), whilst the annual growth rate of this
582 coralline algae is very slow (about 0.25 mm/year in BB, Potin et al., 1990; Grall, 2002). Consequently, below a certain
583 maximum threshold of sedimentation (about 2.5 mm/yr) and turbidity in the water, other environmental factors are
584 probably responsible for the rapid variations in fossil maerl deposits over time. However the thickness of the maerl
585 beds and their formation time seems to react to the evolution of the sedimentary environment with a common rule
586 whatever the period considered (Fig. 17). The definitive thickness of the fossilized maerl bed is the result of the
587 agglomeration of maerl thalli. The ratio between the ages of the maerl beds calculated on the basis of age-depth model
588 compared to the theoretical ages normalized by the average annual growth (tab. 2) shows that the thickness of the
589 maerl deposits increases twice as fast during periods of high sedimentation rates. This may be a physiological
590 response of the maerl bed to maintain a level of vitality in response to the stress imposed by excess sedimentation in
591 the BB, somehow similar to the keep-up strategies adopted by coral reefs in response to relative sea level rise. For
592 other organisms, such as corals, high-turbidity conditions on reefs do not always impact negatively on their
593 physiology (Perry, 2005; Anthony, 2006). Anthony and Fabricius (2000) found that corallite growth rates in *Porites*
594 species nearly doubled under turbidity loads.

595 In the historical post-RWP (Roman Warm Period) period of the first maerl occurrence, a multi-decadal
596 succession of maerl accumulations is observed in our sedimentary records, but cannot be explained by the first results
597 we obtained. Understanding the origin of this high-frequency variability will require to resort to new, higher-
598 resolution approaches, by tightening the age models and using other environmental proxies. Several physical-chemical
599 factors play a role in the growth and reproduction of coralline algae such as the variation in the calcium concentration
600 in seawater (Martin et al, 2006), the nitrate concentration (Martin et al, 2007), macroalgal epiphyte abundance (Qui-
601 Minet et al., 2018) or temperature variations (Dutertre et al, 2015). All these factors can be modulated by the
602 combined influences of atmospheric and oceanic configurations and the pressure of man on the environment over very
603 short periods of time.

604 Our study shows that maerl beds in the Bay of Brest flourished after the high-intensity marine weather episodes
605 of the Iron Age and an increase in the share of riparian forest (Lambert, 2017; Lambert et al., 2020). This period gave
606 way to an improvement of climatic conditions during the climatic optimum of the Upper Roman Empire (between
607 2060 and 1900 cal yr B.P.), favorable to human colonization of coastal sites (Meurisse, 2007) and to agro-pastoralism.
608 At the end of this period, during which a short, colder and a drier climate persisted (Fernane et al., 2014; Fig. 15j) and
609 lead to reduced terrigenous sediment influx into the Bay of Brest, (Fig. 12) the development of maerl beds affected
610 the entire seabed of the region. Two centuries of prolonged drought reduced agricultural productivity in the
611 catchments (Galliou, 1991) and restored tree vegetation (Fernane et al., 2014; Lambert, 2017; Fig. 15c), probably
612 beneficial to maerl biocenoses. However, sedimentation rates gradually increased from 1800 cal yr B.P. and then
613 accelerated in the BB from 1600 cal yr B.P. to reach a maximum between 1450 and 1250 cal yr B.P (Figs. 12, 16).
614 Since 1800 cal yr B.P. this rate then doubled in the southern part of bay over a few centuries, and almost tripled in the
615 northern BB, with values five times higher locally than those measured today in front of the AC (Ehrhold et al., 2016).
616 This gradual increase in sedimentation rate of the bay, coincides with the increase in terrigenous inputs observed on
617 other environmental proxies (Fig. 15c), particularly palynological (*Corylus*) by Lambert et al. (2020) and with the
618 synchronous disappearance of maerl beds around 1375 cal yr B.P. throughout the southern BB. It can be assumed that
619 the amounts of suspended solids and associated deposition exceeded the capacity of biocenoses to remain in place
620 during this short period. This signal of terrigenous input was observed by Durand et al. (2018) in the estuary of the
621 Loire (Fig. 15a), and Lambert et al. (2020) based on arboreal taxa pollen characterization (increase in *Corylus*, Fig.
622 15c). Pears et al. (2020) note that from 1600 to 1400 yr B.P., the accumulation rates increased in the Severn River
623 (south-west UK), with evidence of large flood events associated with the climatic deterioration of the Dark Age Cold
624 Period (Fig. 15m). From 1250 cal yr B.P. when a new, colder and drier climate period occurred (Fig.15l), combined

625 with the drying-up of sedimentary input (RCC5, Mayewski et al., 2004), maerl biocenoses developed again. In most
626 regions of Europe, this period is marked by moister conditions (Fig. 15k-l), stable forest cover (Fig. 15b) or small
627 forest recovery (Kaplan et al., 2009; Corella et al., 2013; Helama et al., 2017).

628 From about 850 cal yr B.P., the bio-sedimentary record of the BB seafloor, in areas deeper than 15 m water-
629 depth, is truncated by a new erosive event that left a decimetric deposit of sediments that were more sandy than a
630 shell-bed (Ssd, CSE3 in Fig. 12). Even if dating is missing to better specify the end of the event(s) at the origin of this
631 temporal *hiatus*, we suppose that it would have ended around 600 cal yr B.P. as observed at Roscanvel and Auberlac'h
632 coves (Fig. 7). Nevertheless, two datings performed on material sampled within this interval allow to situate the
633 erosive event responsible for this deposit between 834 and 614 cal yr B.P. The erosive impact is more pronounced in
634 Fret and Roscanvel coves than anywhere else on the bay's coast (erosion respectively up to 1245 to 1167 cal yr B.P.).
635 The related sandy deposit is not found in the shallows waters of the south-eastern area of the BB due to a lack of long
636 cores. This sand deposition in the Elorn estuary erodes the underlying sediment at least until 825 cal yr B.P.
637 Differential erosion as a function of geography and the nature of the seafloor can be an indicator of the preferential
638 wind direction that drives sediment remobilization processes, with a strengthening of northerly winds and
639 consequently an increase in fetch distance and in the height of wind-waves towards the south shore of the bay. This
640 period of enhanced paleo-storminess was also found to be responsible for the disturbance of Yeu's environment at the
641 beginning of the LIA (Pouzet et al., 2018, Fig. 15d). Van Vliet-Lanoë et al. (2014b, 2016) and Poirier et al. (2017)
642 show that the MWP was originally responsible for considerably modifying the coastal morphology of Brittany under
643 the action of regular stormy winds. A succession of eleven major paleostorms was recorded in the Brittany dune belts
644 (Fig. 15f) between the 10th and 12th centuries (Van Vliet-Lanoë et al., 2016). At the same time and from 1100 cal yr
645 B.P., Brittany forests retreated (Fig. 15c), as did European forests (Fig. 15b) (Mather et al., 1999; Williams, 2003;
646 Kaplan et al., 2009) in conjunction with the development of monastic communities in the region, contributing to a
647 profound modification of watersheds (Dufief, 1998). It seems that the sedimentation conditions in the BB controlled
648 by anthropic and climatic effects throughout the MWP and until the beginning of the LIA, were not conducive to the
649 development of maerl deposits.

651 **5.3 The maerl of modern times**

652 From 600 cal yr B.P. and onwards, the evolution of maerl in the sediment is only continuous until today in the
653 south-eastern region of the BB east of the Auberlac'h-Lanveoc limit (Fig. 14b3). This is also probably the case in the
654 northern parts of the bay, but the extent of maerl beds is limited to the outlet of the Elorn estuary. In the Roscanvel and

655 Fret coves (Fig. 14b1), as in the commercial harbor of Brest (Fig. 14b2), other factors are responsible for its temporary
656 or more permanent disappearance. Consistent with the first major post-RWP maerl occurrence period, maerl deposits
657 re-established in the BB during a new cold event (RCC6, Fig. 15 k-l, in Mayewski et al., 2004): The climatological
658 event of the Little Ice Age typically associated with negative NAO modes, solar lows, and usually reduced
659 precipitation (Van Vliet-Lanoë et al., 2016). In the BB, sedimentation rates collapse during this period and are
660 between three to five times lower than those of the period preceding stage 1900-1100 cal yr B.P. (Fig. 12). The maerl
661 deposit is interrupted by sandy deposition (CSE4 event) which intersperses a temporal *hiatus* of lower intensity and is
662 more localized than in previous climatic events (CSE2 and CSE3). This multi-centimetre deposit is difficult to identify
663 because it is very close to the top of the cores. Moreover, it is not found everywhere in the BB and is limited to very
664 shallow depths (less than 7 m). This sandy level is associated with a limited erosive effect on the silty sediments and
665 the underlying maerl beds. On the south coast in the Roscanvel and Auberlac'h coves, where it is best expressed, it is
666 present since 1830s. The origin of this late and contemporary event is poorly constrained in the BB. Several major
667 well-recorded winter storms impacted the Brittany coasts after the 1800s (Van Vliet-Lanoë et al., 2014b), notably the
668 storm in 74 cal yr B.P. (Tabeaud et al., 2009). It is difficult to know which event would be responsible for this
669 sedimentary remobilization and contribution. The sedimentary record of this episode in the shallow waters between
670 RC and FC may suggest a preponderant action of northerly winds (from northwest to northeast), occurring dominantly
671 during the spring. In the area of Brest's commercial port, this sand deposit is absent from the cores for depths of less
672 than 2m. At depths of up to 7 m, it does not appear clearly, because it is confused with the recent sedimentary
673 dynamics of the Elorn estuary (SRQ1-IS19). Major works were involved in this area during the development and
674 expansion of the commercial port in the 1970s and 1980s. This invisible truncation surface on the lithology of core
675 PALM-KS05 had been described by Delebecq et al. (2020) and on other nearby cores for the study of ancient
676 dinoflagellate communities over time.

677 The early 20th century should have marked the end of favorable sedimentary conditions for maerl biocenoses
678 with the acceleration of global warming and storm intensity as in previous episodes (3100-1950 cal yr B.P.; 825-600
679 cal yr B.P.). It is probably too early to say, but several factors may be responsible for slowing down the degradation of
680 sedimentary conditions (increased turbidity and sediment reworking) in the bay. The lack of terrigenous input from
681 watersheds (Ehrhold et al, 2016) is partly the result of the development of watercourses, particularly the Aulne River
682 with the construction of the Nantes to Brest canal between 1805 and 1842 (Cucarull, 1991). Other factors have indeed
683 limited soil leaching and drainage of watercourses: *i*) the implementation of reforestation and forest management
684 policy throughout Brittany (Gautier, 1938), and *ii*) the break-up of agricultural lands from 1850 to 1950 into many

685 small cultivated plots delimited by slopes and hedges composed of bushes and shrubs (Lambert et al., 2018).
686 However, the changes in maerl occurrence since the Roman period raises questions about the fate of this community
687 in the BB and in a context of rapid climate change (warming waters, heavy rainfall) the introduction of new species to
688 this region (Lejart and Hily, 2011) or the decline of others (Travers et al, 2009). The most recent period, after the
689 Second World War, shows a trend towards a progressive increase in storms on the Atlantic coasts with significant
690 impact on coastal erosion (Wasa, 1998; Dreveton, 2002, Lozano et al., 2004; Charles et al., 2012). This period also
691 corresponds to the implementation of a new agricultural policy which led to the reunification of agricultural holdings
692 (Flatrès, 1963). Runoff from the watersheds of the BB is currently increasing, contributing to changes in the trophic
693 conditions of marine waters (Lambert et al., 2018; Ragueneau et al., 2018). Finally, the current maerl biocenoses are
694 locally replaced by a coarse deposit composed of fruticose coralline fragments and shell debris, as shown on several
695 cores in front of Auberlac'h and Daoulas bays, and in the commercial port, under the action of clam fishing dredges.
696 The muddy sediments reworking upwards through the use of fishing gear will also eventually weaken the habitat of
697 maerl increasing ecological stress due to turbidity (Bernard et al., 2019).

699 **6. Conclusions**

700
701 Our results allowed to characterize the evolution of maerl beds interbedded in coastal fine sediments deposits
702 over the last 3000 cal yr B.P. in the Bay of Brest (western Brittany NW France). This study highlights the fact that
703 maerl beds record the main evolution of coastal systems in a context of rapid climate change and anthropogenic
704 pressure.

705 - The fossil maerl deposits (mainly *Lithothmanion corallioides*) develop from 1950 cal yr B.P. above the all
706 muddy marine terraces and down to 15 m water depth, from the northern part of the BB to the southern region with a
707 short time shift. The autochthonous and discontinuous accumulations of maerl beds in coastal areas could have
708 developed above this terrace once the sea reached the highest levels during the late Holocene. Three main periods of
709 maerl bed development have been recorded in the last Highstand System Track: between 1950 and 1350 cal yr B.P.,
710 between 1250 and 850 cal yr B.P., and since 600 cal yr B.P. These periods coincide with the establishment of cold-
711 climate periods in Europe (RCC in Mayewski et al., 2004) typically associated with negative NAO modes and low
712 solar activity. The cold-climate periods combined with favorable marine morphological factors (shallowest flat
713 terraces, moderate currents) enable maerl aggregations to prosper in the BB environment. The rates of maerl bed
714 accumulation varied from 1 m/kyr to 2.1 m/kyr and seem positively correlated with sedimentation rates.

715 - Several main periods of climate deterioration have prevented or profoundly disrupted the development of
716 these maerl beds over the last 2000 years. They are associated with increased paleo-storm activity. Their intensity has
717 reworked all the seafloors of the BB and has resulted in the deposition of high-energy sedimentary layers with varying
718 thickness depending on the exposure of the bottom to swells and currents. The CSE2 episode recorded in the form of a
719 poorly sorted and broken shell bed occurred during the 3100-1950 cal yr B.P. period (Iron Age) and coincided in the
720 BB with the MFS (Gregoire et al., 2017). Erosion of underlying sandy-silt sediments can be significant in places.
721 Despite its geographical situation, relatively sheltered by the Goulet strait, the seabed of the BB recorded equivalent
722 morphogenic responses to the increase in storminess to the ones found elsewhere in various environments along the
723 Atlantic and Northern European coasts. The CSE3 episode, dated to 825 to 600 cal yr B.P. (during MWP), was
724 responsible for the deposition of thick sandy layers and the remobilization of coastal marine terraces of the BB down
725 to a depth of 15 m. Sediment erosion associated with major storms is more significant in front of the RC and FC sites,
726 likely indicating a more northerly orientation of the wind sectors during this period. The CSE4 deposits are more
727 limited in time and space. This event or series of events occurred between 113 and 0 cal yr B.P. and mainly affected
728 the very shallow areas (< 7m) of the southern region of the BB.

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731
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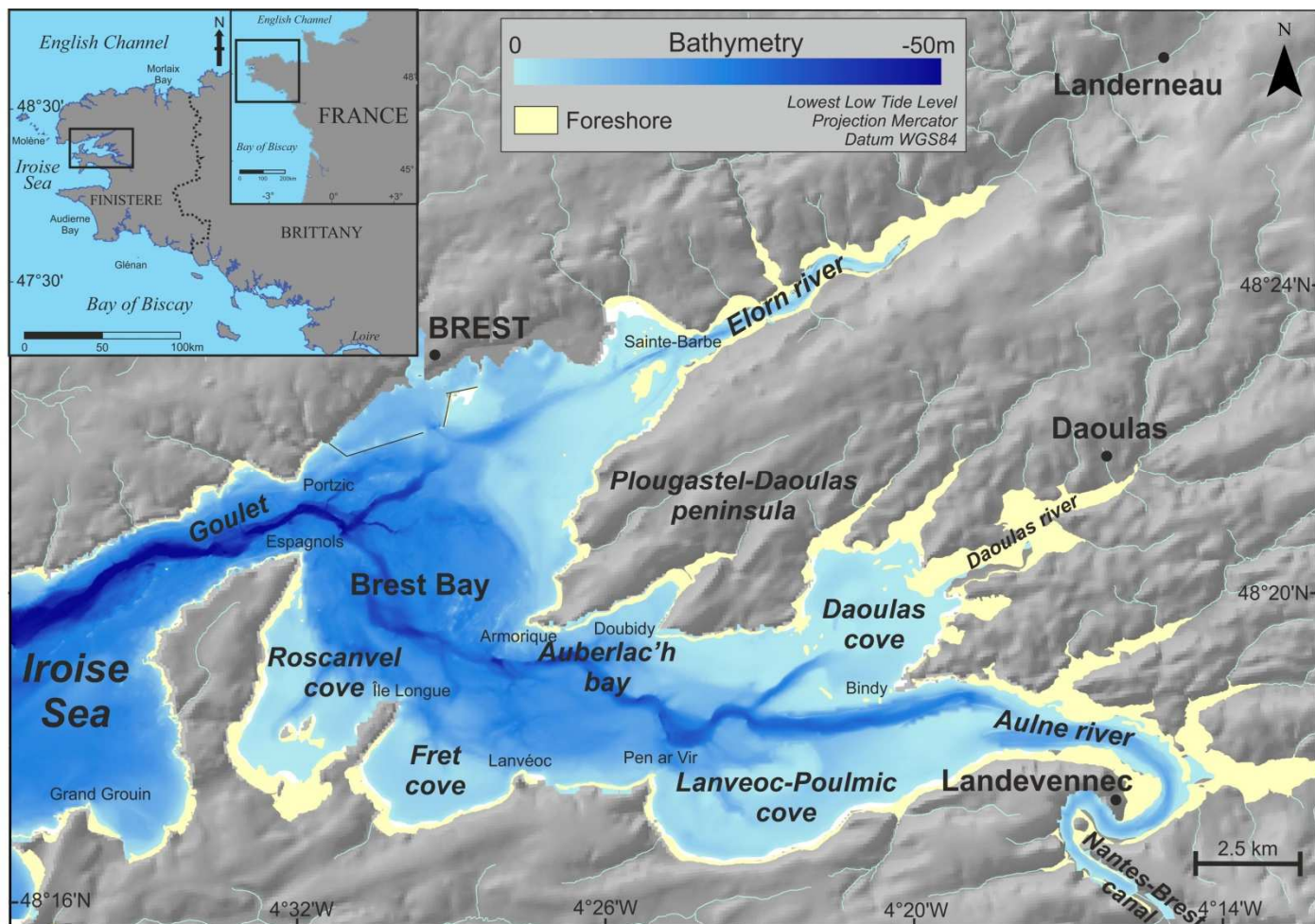


Figure 1: Geographical (© BDalti) and bathymetrical (Gregoire et al., 2016) settings of the Bay of Brest (BB).

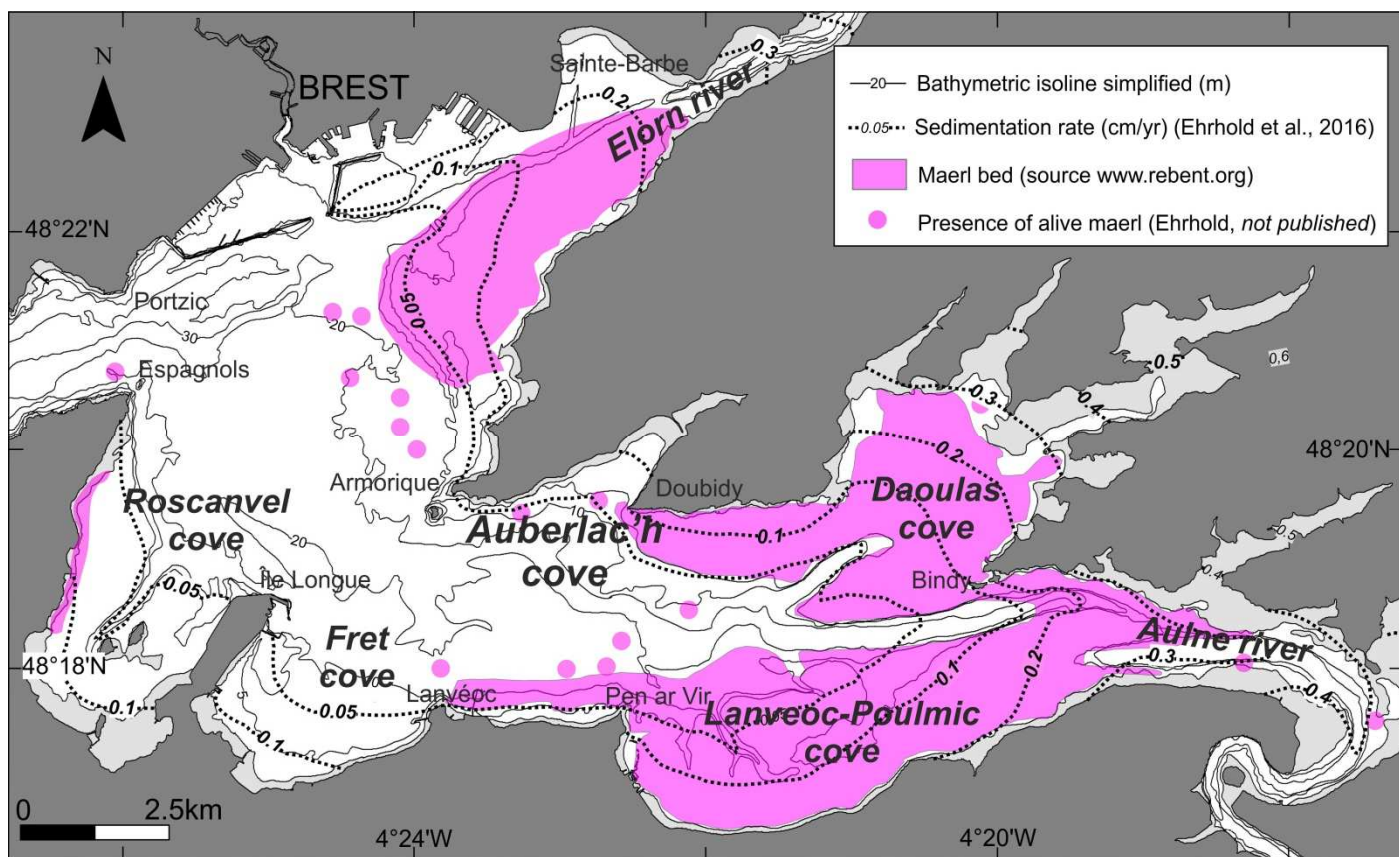


Figure 2: Modern sedimentation rates (modified from Ehrhold et al., 2016) and maerl bed deposits in the Bay of Brest.

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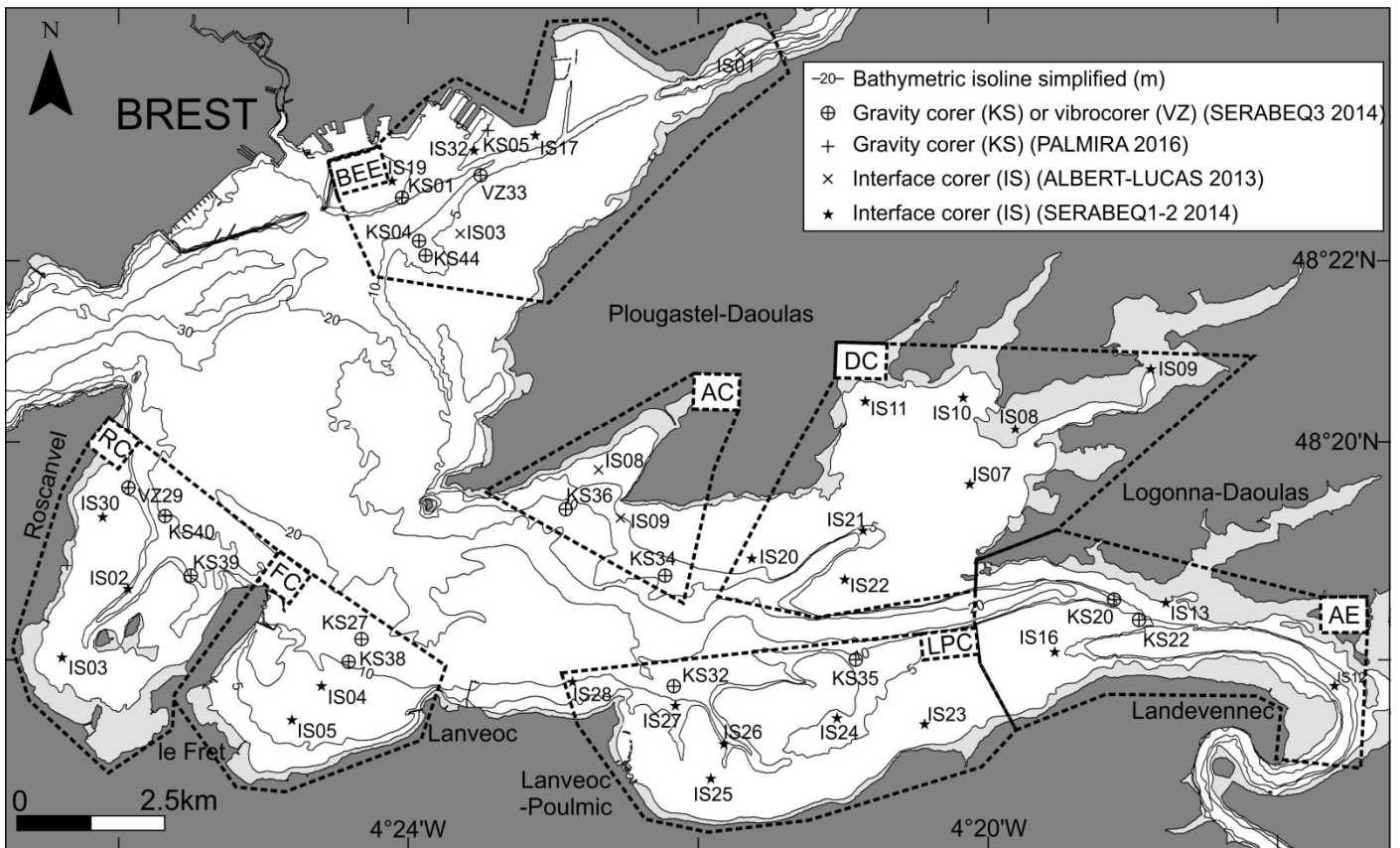


Figure 3: Location of sediment cores (KS) and interface cores (IS) used in this study (RC: Roscanvel cove; FC: Fret cove; LPC: Lanvéoc-Poulmic cove; AE: Aulne estuary; DC: Daoulas cove; AC: Auberlac'h cove; BEE: Brest-Elorn estuary).

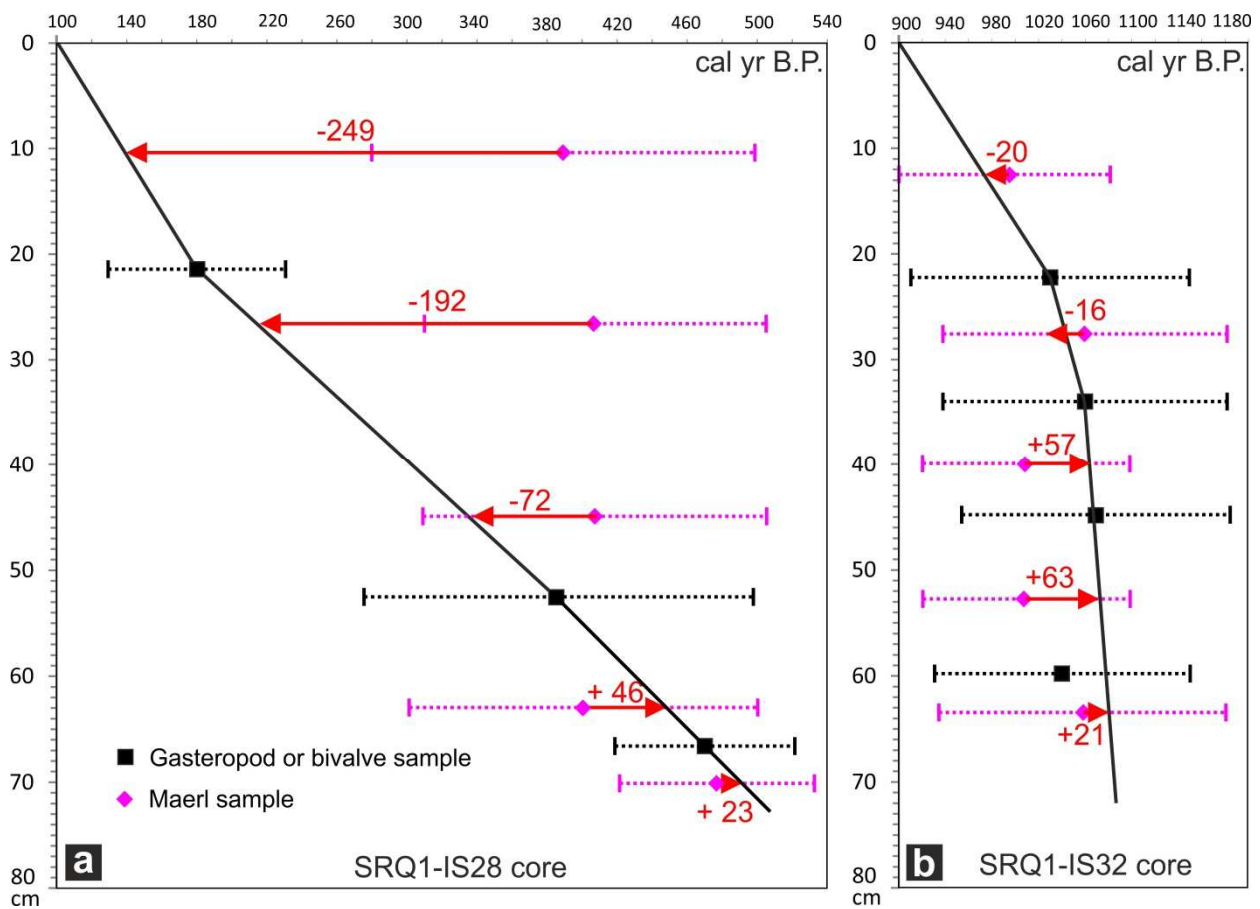


Figure 4: Drift (red arrow) and uncertainties (dashed point) on the ¹⁴C ages obtained on maerl thalli and compared with mollusk samples in two age-depth models (a: SRQ1-IS28; b: SRQ1-IS32).

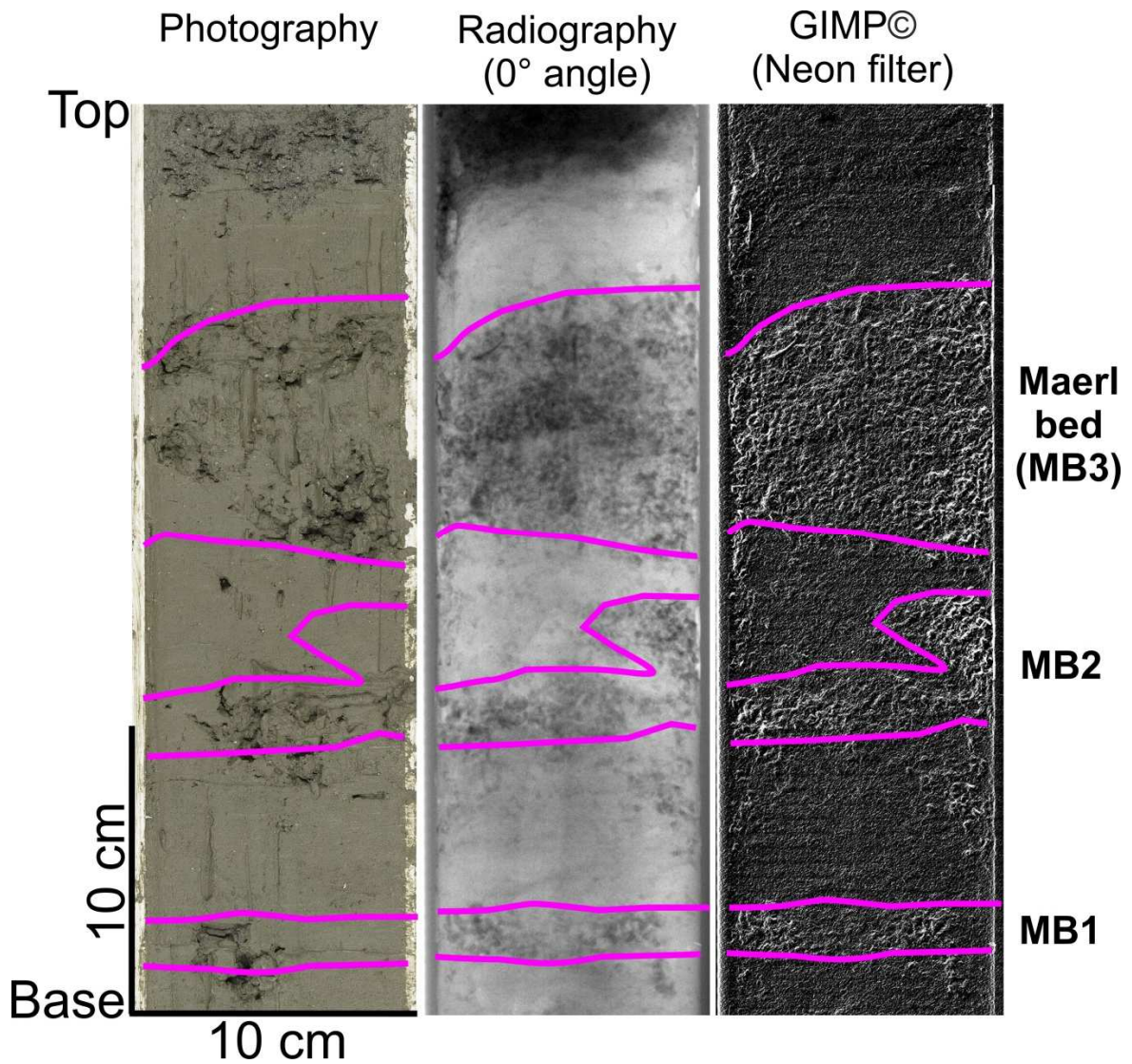


Figure 5: Methodology used within the study to detect fossil maerl beds (example of core SRQ3-KS34-38-68cm).

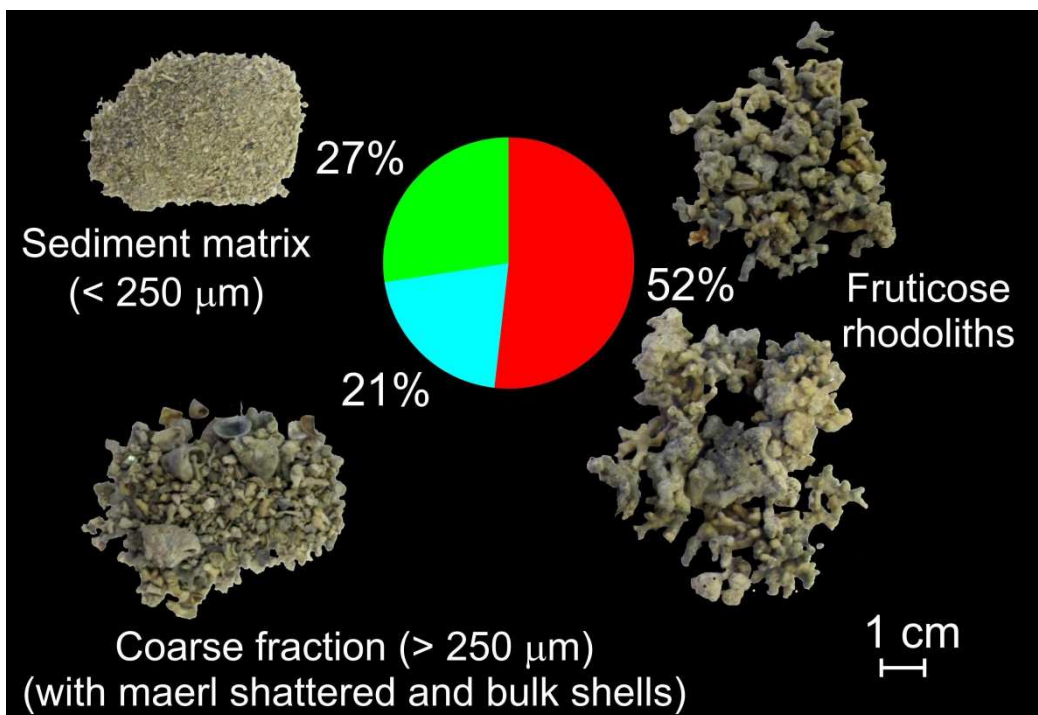


Figure 6: Example of the extraction of different granulometric fractions to define percentage of unaltered maerl bed and associated sedimentary fractions.

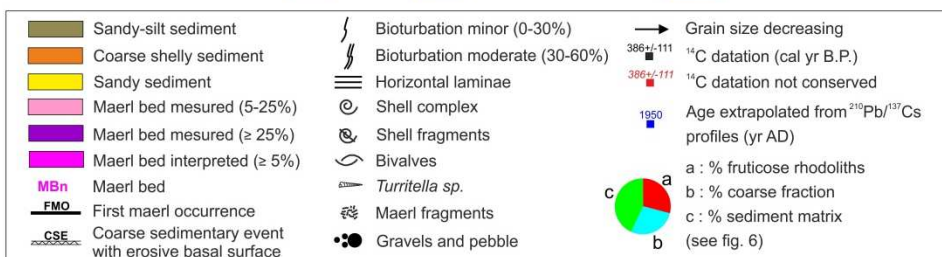
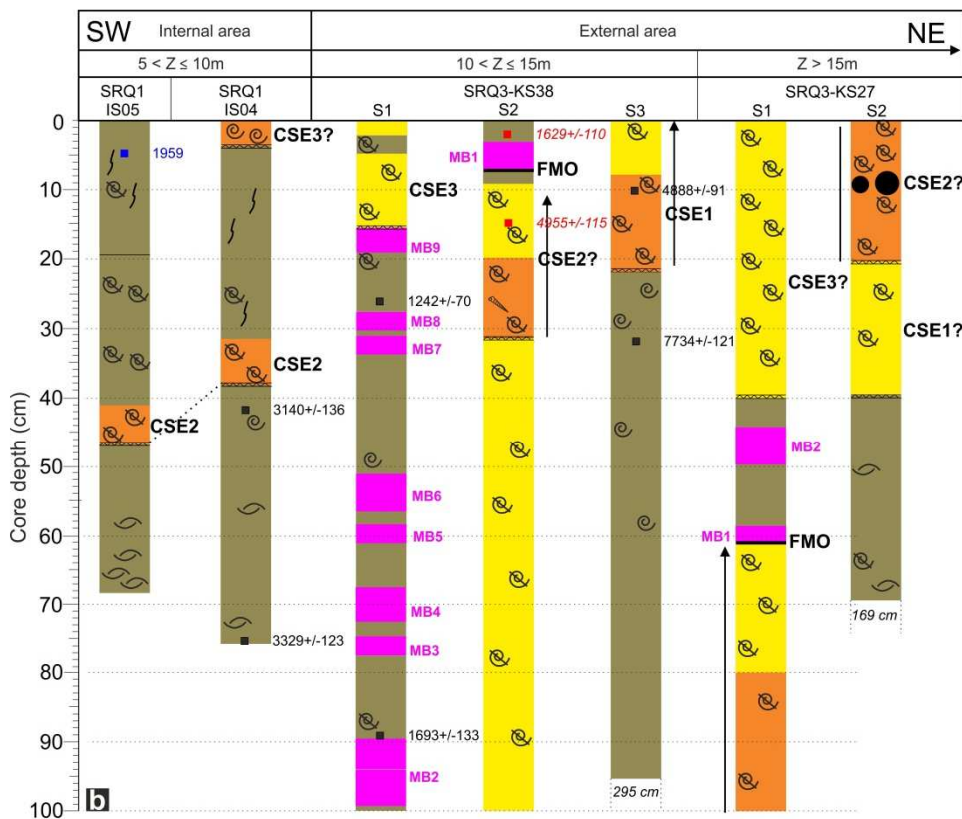
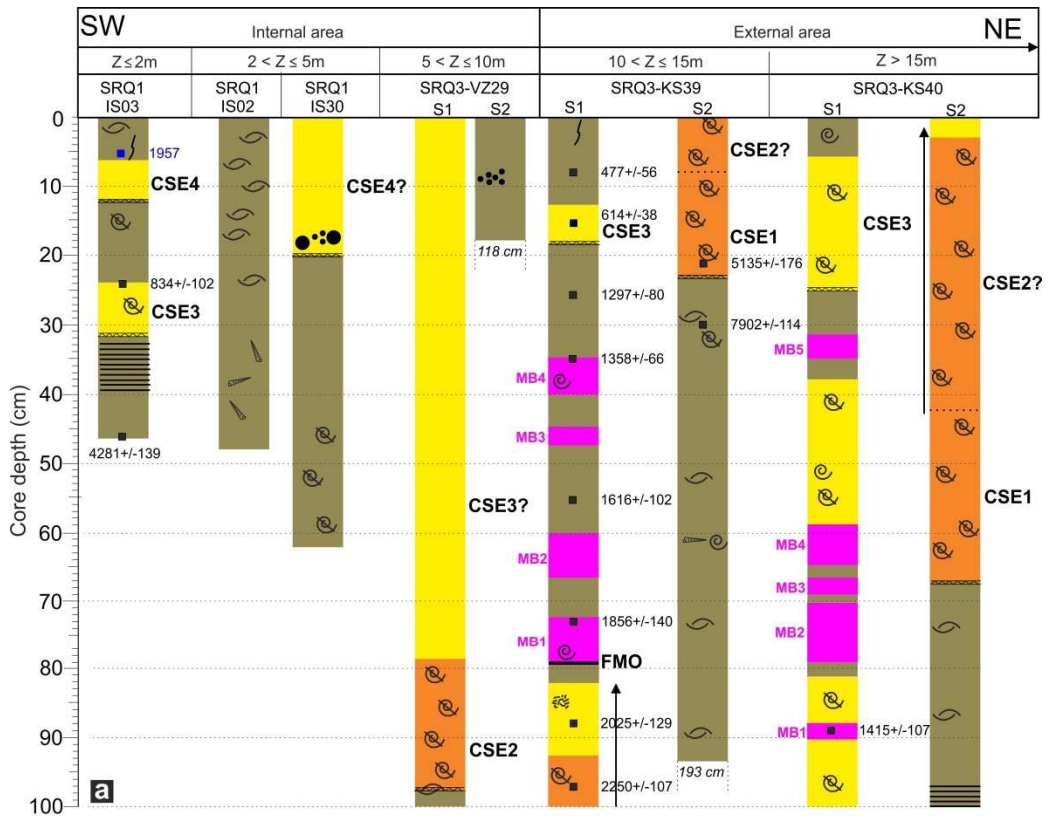


Figure 7: Synthetic lithological descriptions of selected gravity cores in Roscanvel cove (a) and Le Fret cove (b) (see figure 3 for geographical location of cores).

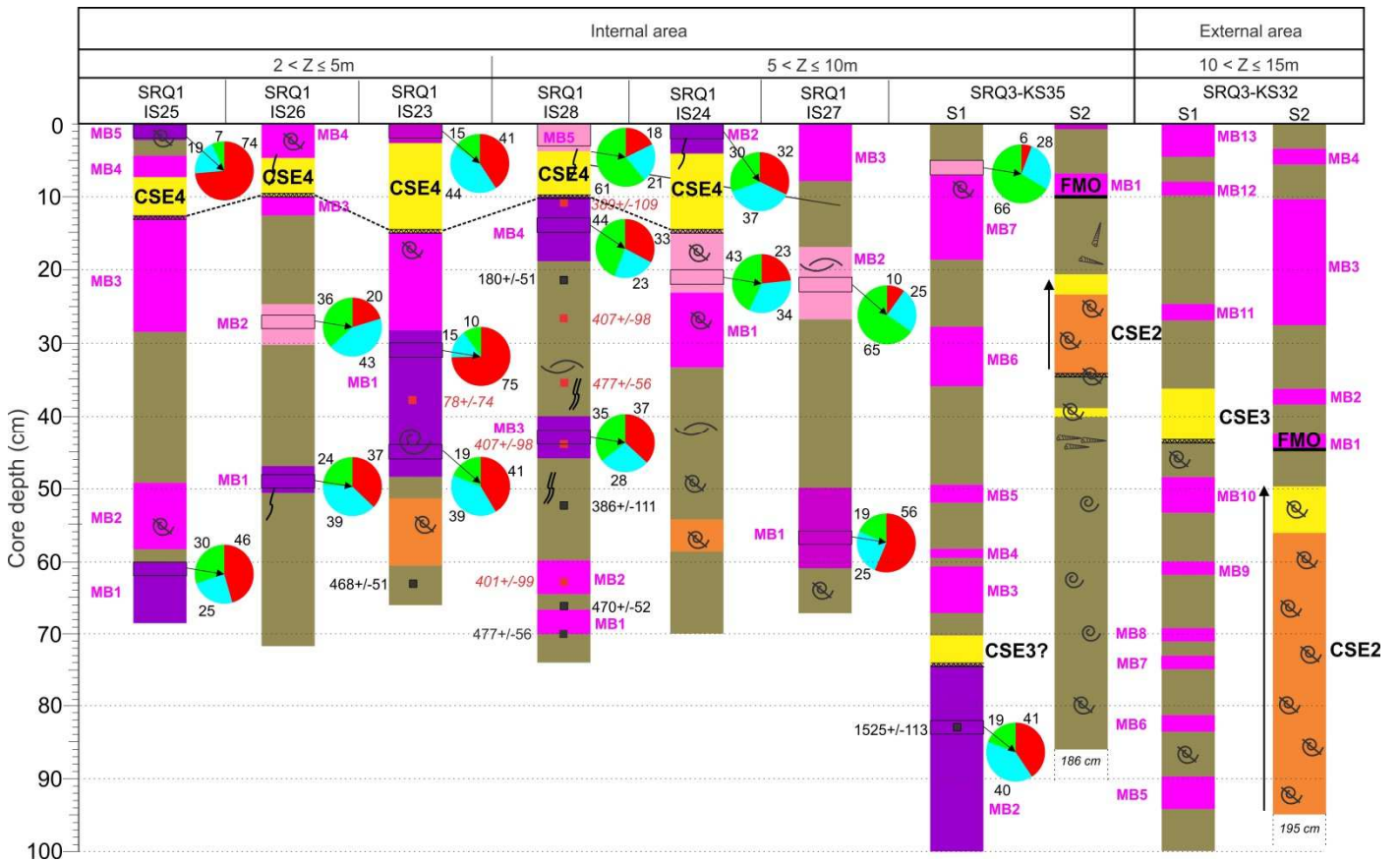


Figure 8: Synthetic lithological descriptions of selected gravity cores in Lanveoc-Poulmic cove (see figure 7 for the legend and figure 3 for geographical location of cores).

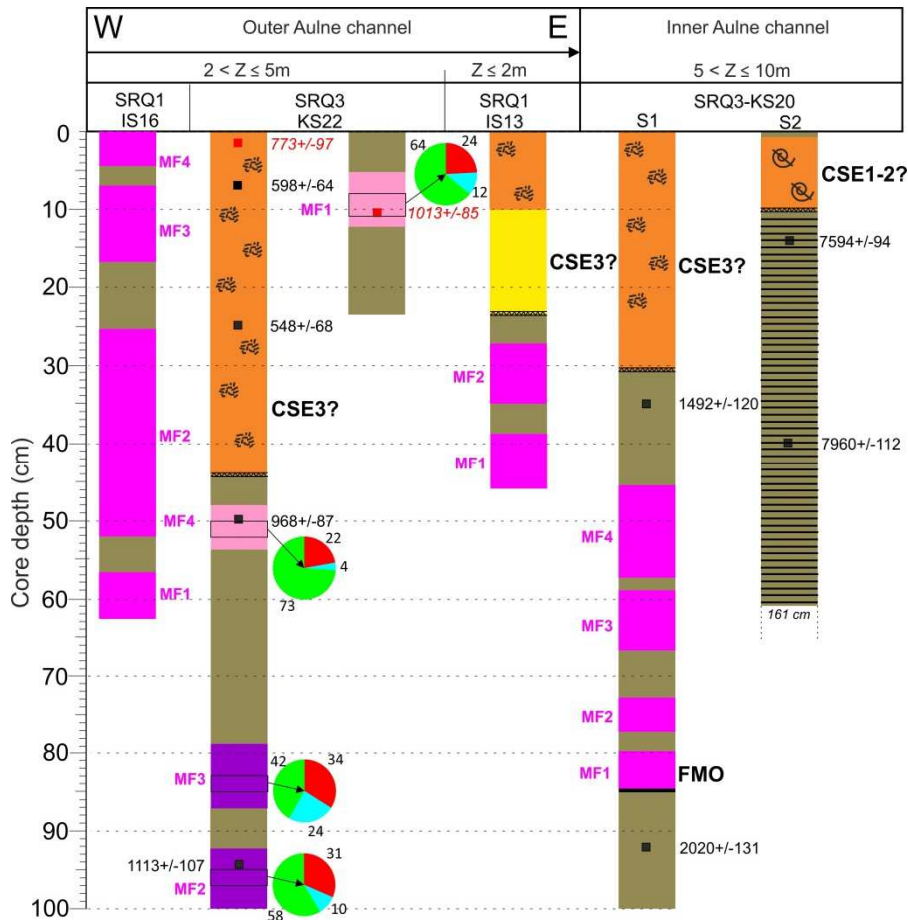


Figure 9: Synthetic lithological descriptions of selected gravity cores in Aulne estuary (see figure 7 for the legend and figure 3 for geographical location of cores).

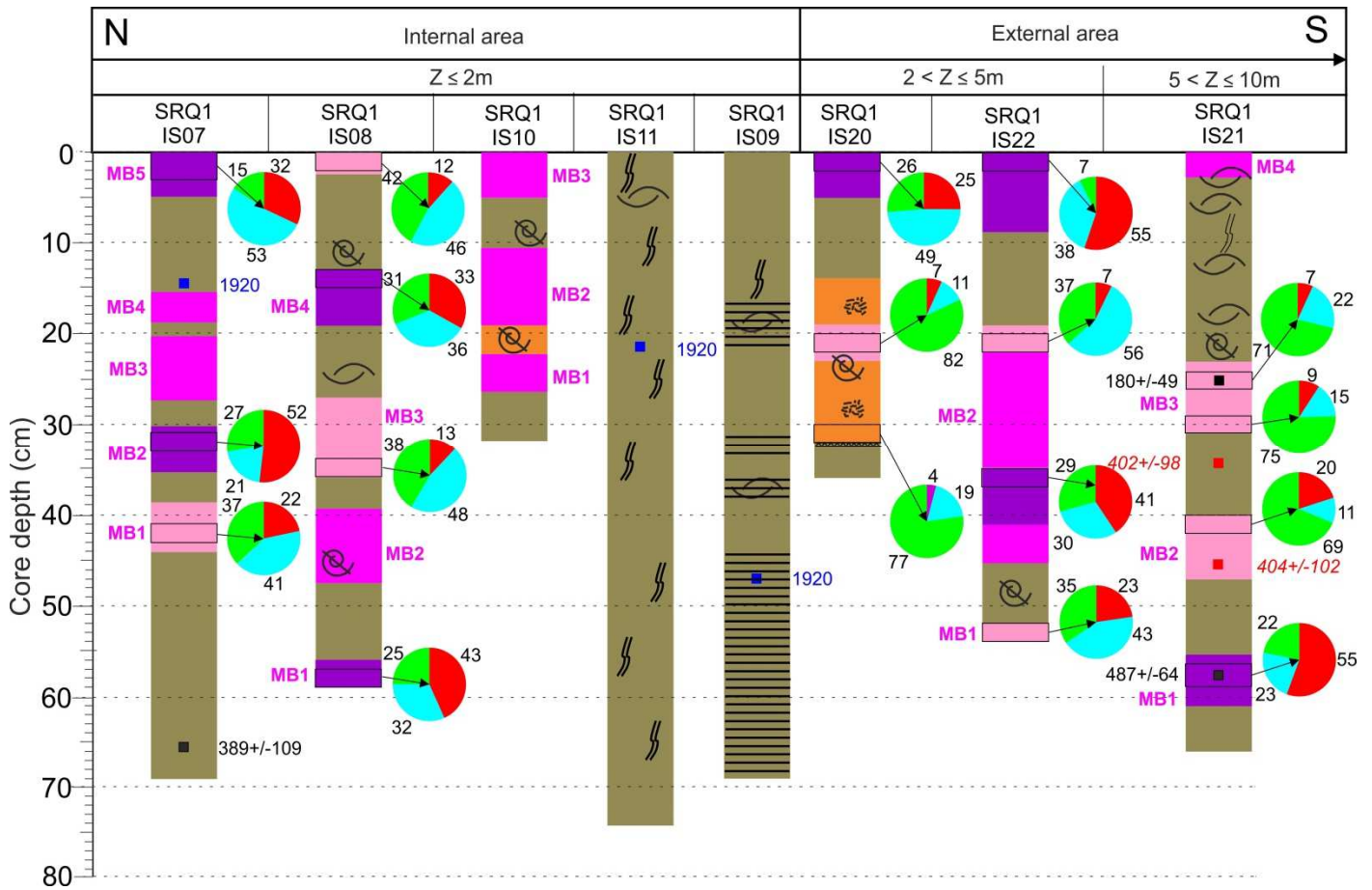


Figure 10: Synthetic lithological descriptions of selected gravity cores in Daoulas cove (see figure 7 for the legend and figure 3 for geographical location of cores).

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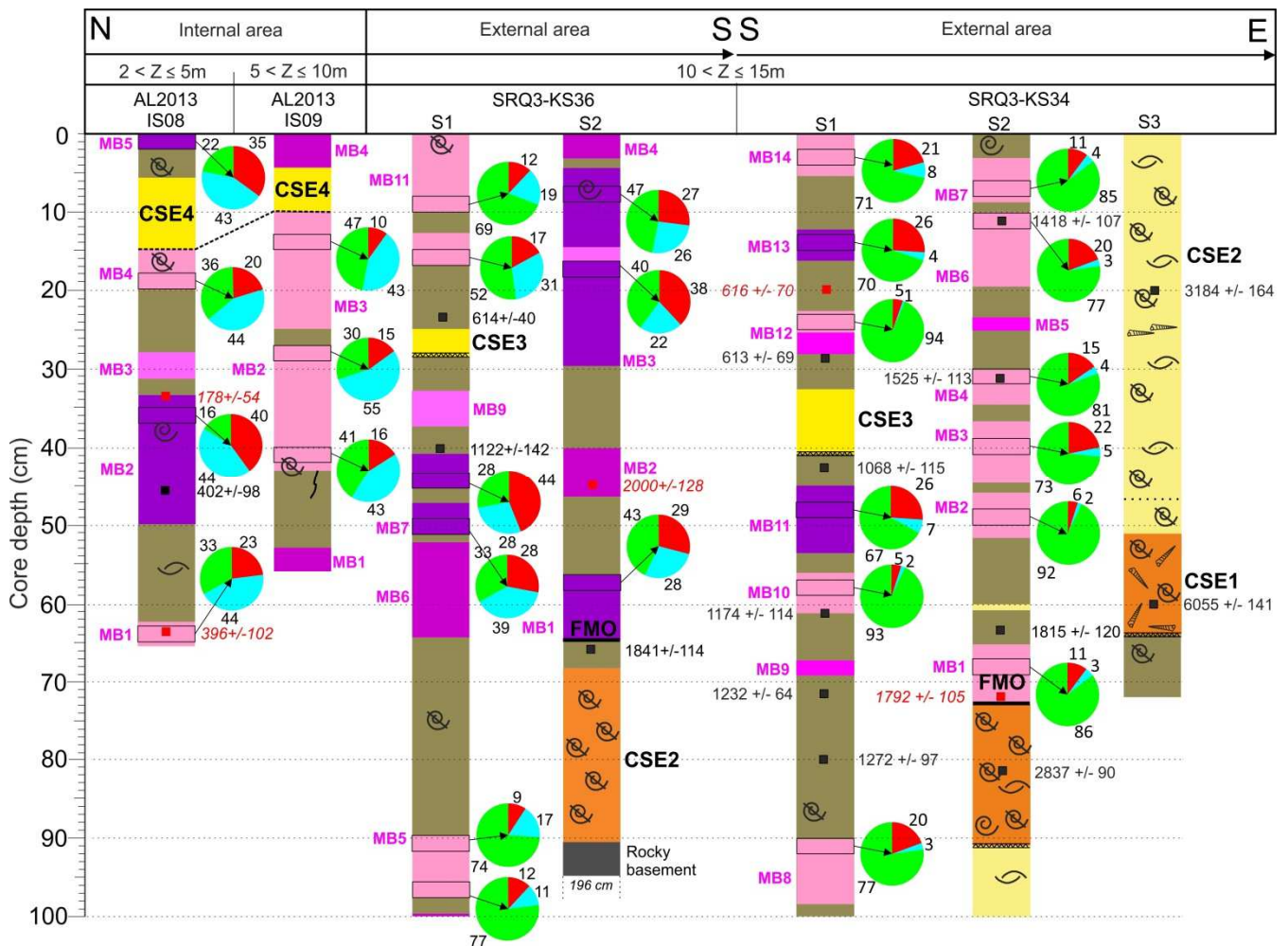


Figure 11: Synthetic lithological descriptions of selected gravity cores in Auberlac'h cove (see figure 7 for the legend and figure 3 for geographical location of cores).

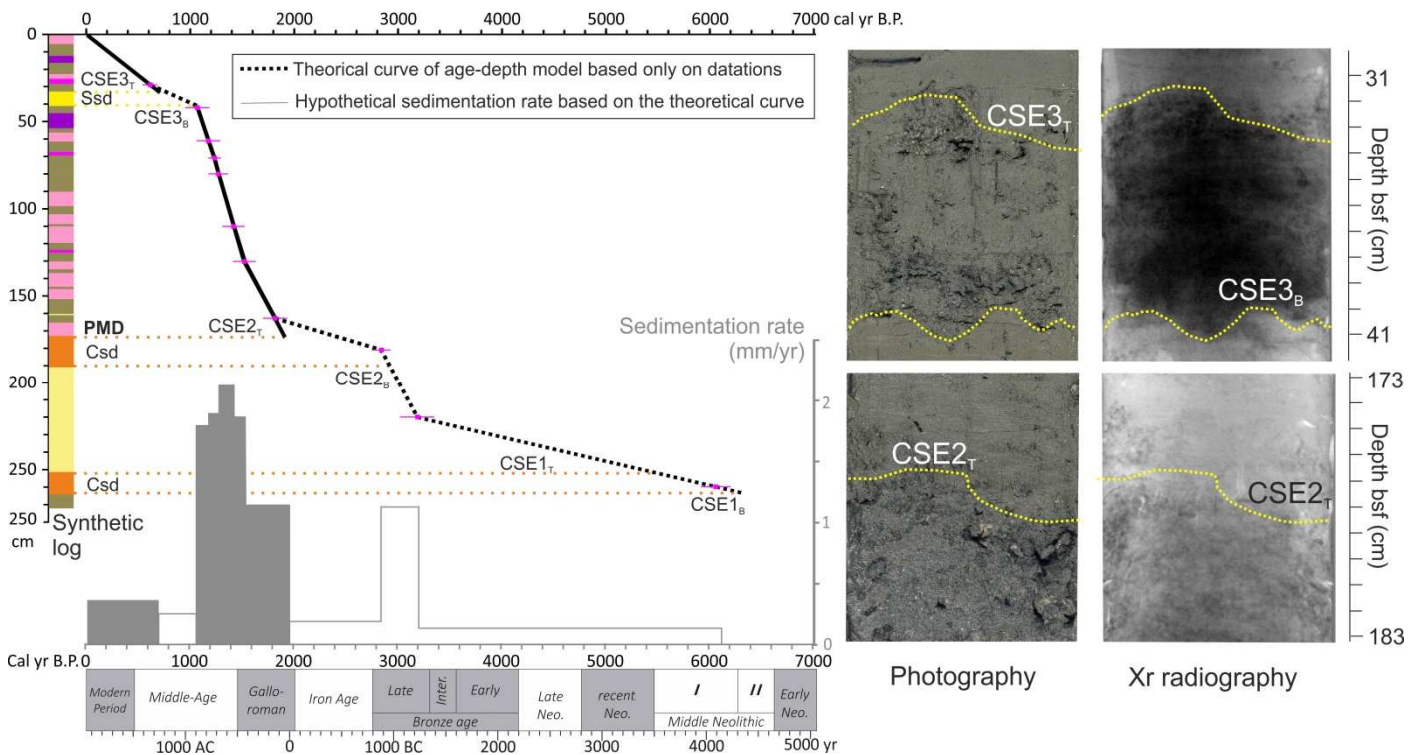


Figure 12: Age-depth model for external part of Auberlac'h bay (SRQ3-KS34 core) and imagery evidence of major hiatus limits (CSE1, 2 and 3). FMO: First maerl occurrence; Ssd: Sand sedimentary deposit; Csd: Coarse sedimentary deposit. Synthetic log of core SRQ3-KS34 (Fig. 11).

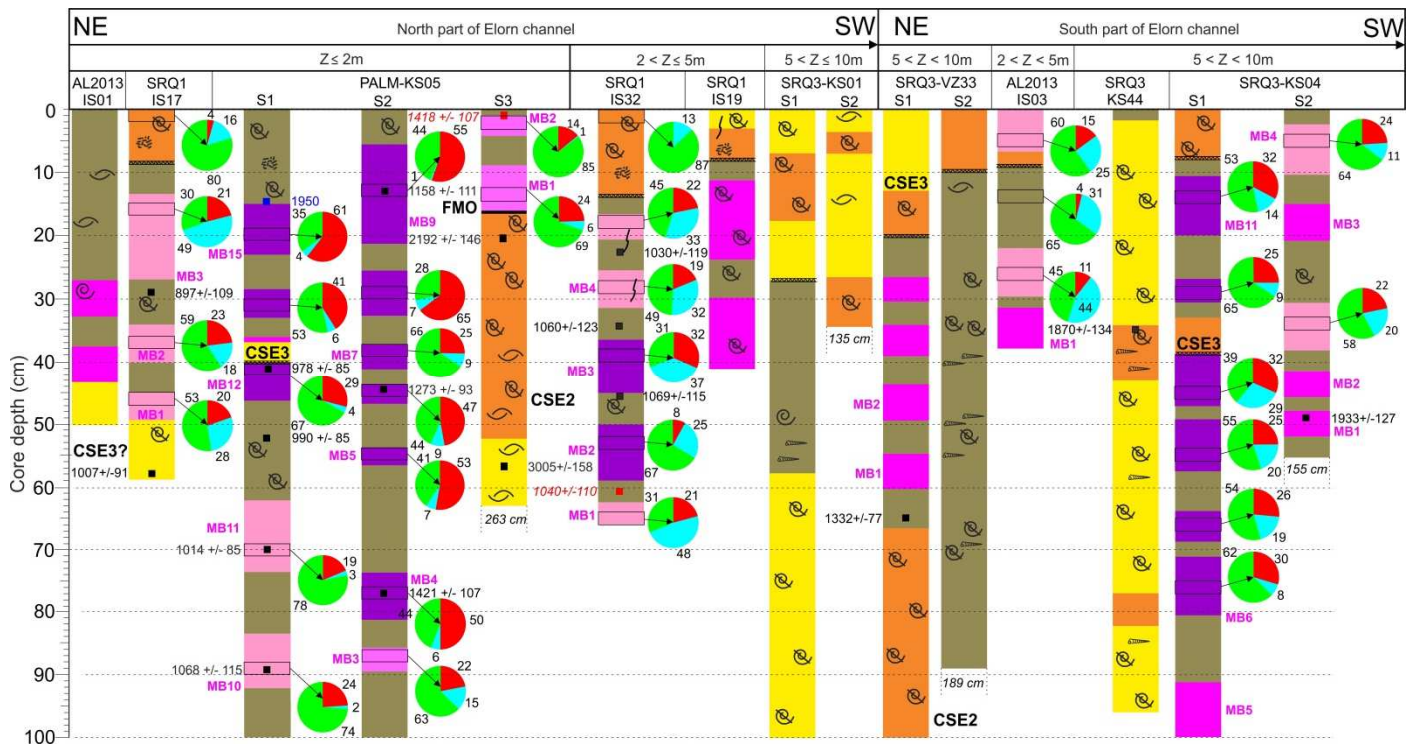


Figure 13: Synthetic lithological descriptions of selected gravity cores in Brest-Elorn estuary (see figure 7 for the legend and figure 3 for geographical location of cores).

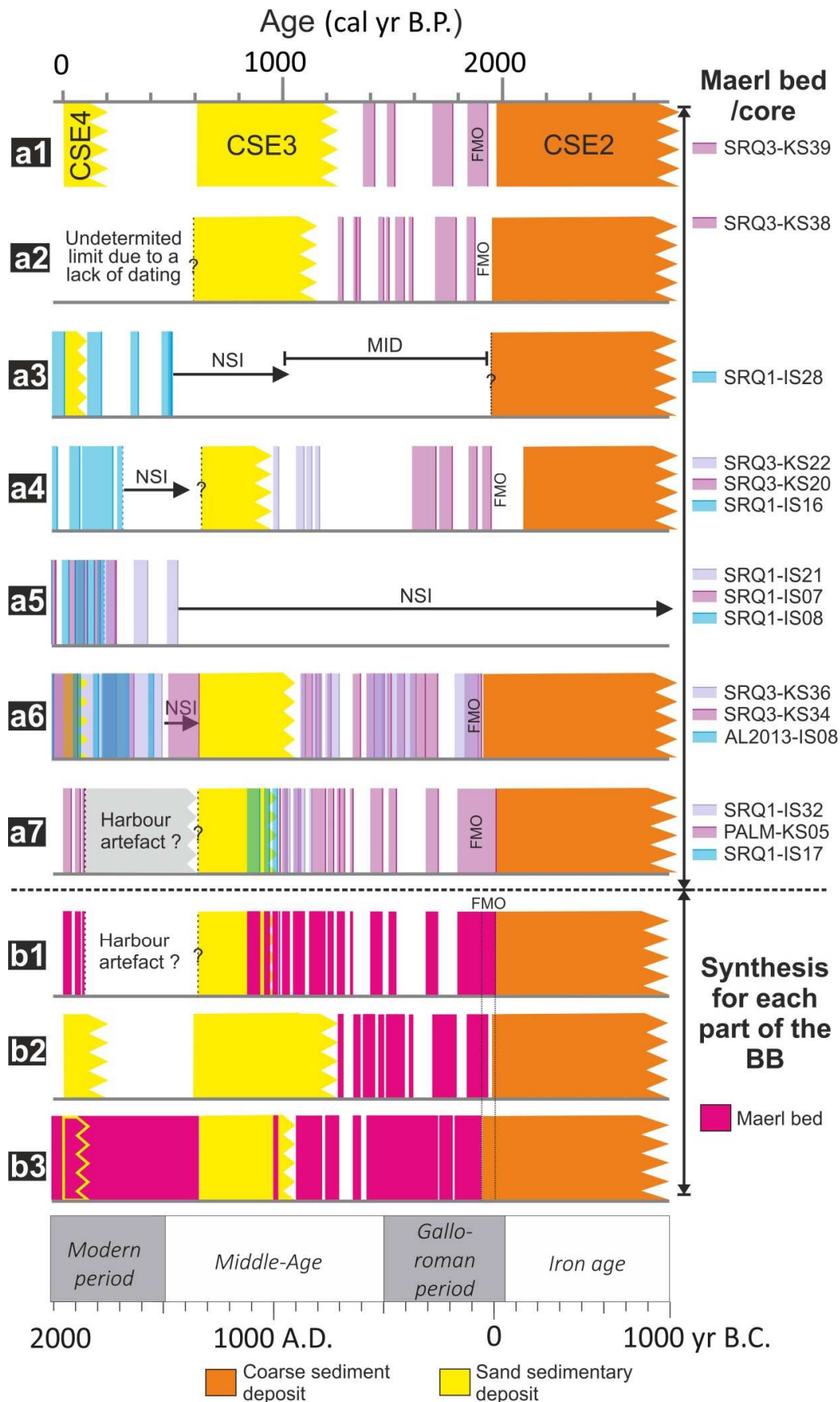
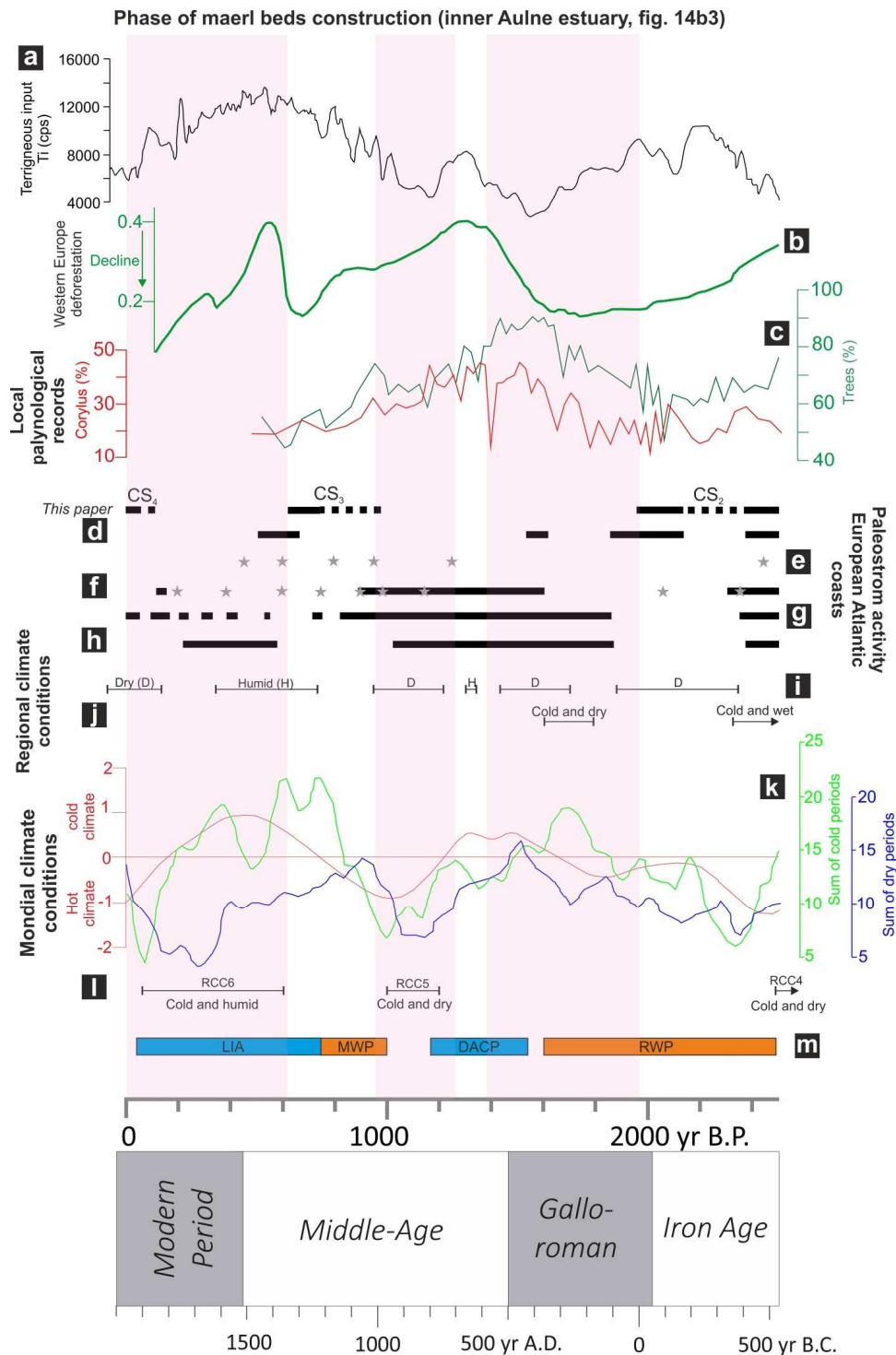
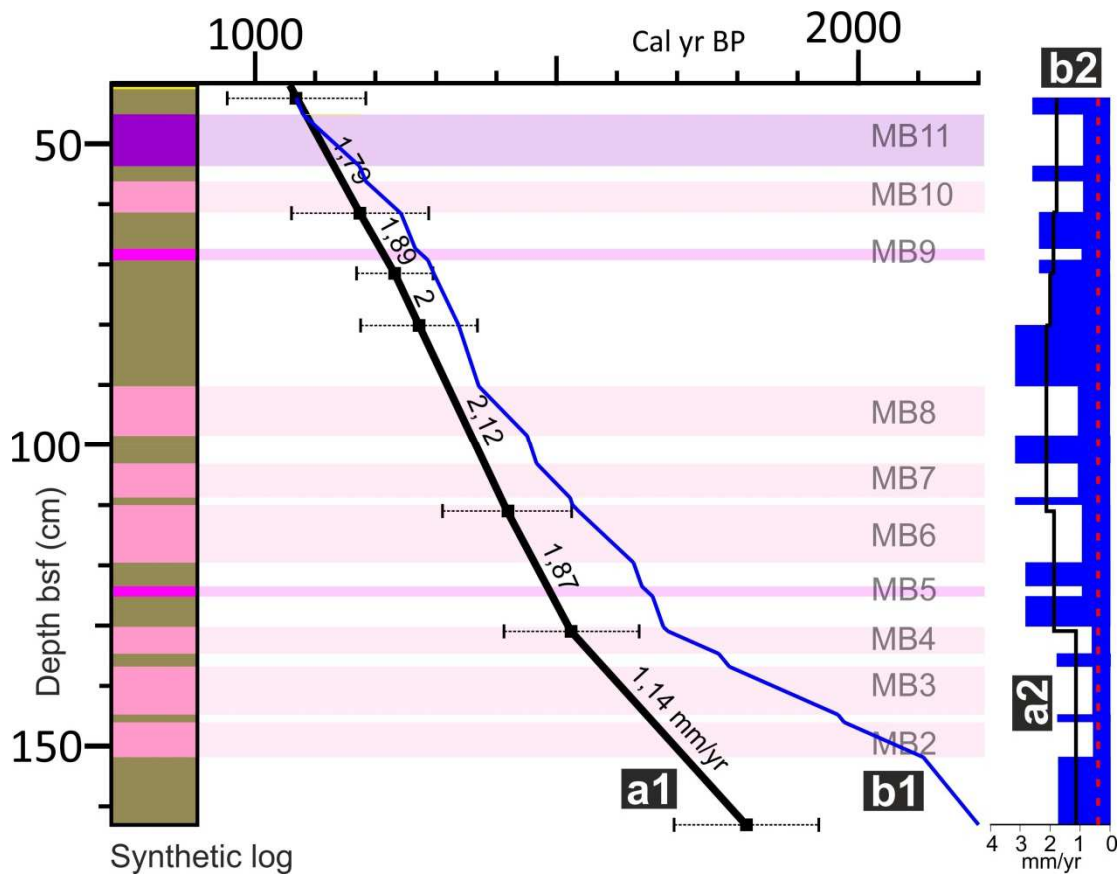


Figure 14: Position of fossil maerl beds and sedimentary crises over the last 3000 years for (a) each sector of the Bay of Brest (1: RC; 2: FC; 3: LPC; 4: AE; 5: DC; 6: AC; 7: BEE) and (b) synthesis of all fossil maerl beds for each main domain of the BB (1: inner Elorn estuary (northern BB); 2: outer Aulne estuary (southern BB); 3: inner Aulne estuary (southern BB)). MID: Presence of maerl bed but insufficient Dating; NSI: No Sedimentary Information in shallow water depth $Z < 5$ m; FMO: First maerl occurrence; CSE: Coarse Sedimentary Events).



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 177 Figure 15: The main phases of maerl bed construction (illustrated by pink bands) compared with a selection of global
 178 and regional proxies, and displayed in cal. yr B.P. (upper scale) and AD/BC (lower scale): a - Terrigenous input for
 179 Loire estuary (Durand et al., 2018). b - Western Europe deforestation (Kaplan et al., 2009). c – Local palynological
 180 records (Lambert et al., 2020). d.h – Paleostorm activity (grey star for event and solid line for period) on European
 181 Atlantic coasts (d, Pouzet et al., 2018; e, Poirier et al., 2017; f, Van Vliet-Lanoë et al., 2014 and 2016; g, Durand et al.,
 182 2018; h, Sorrel et al., 2012). i-j – Regional climate conditions (i, Durand et al., 2018; j, Fernane et al., 2014; Goslin,
 183 2014). k-l – Global climate conditions (k, Wanner et al., 2011; l, Rapid Climate Change (RCC) for Mayewski et al.,
 184 2004). m – Climatic periods (LIA, Ilyashuk et al., 2019; MWP, Helama et al., 2009; DACP, Helama et al., 2017; RWP,
 185 Wang et al., 2012).



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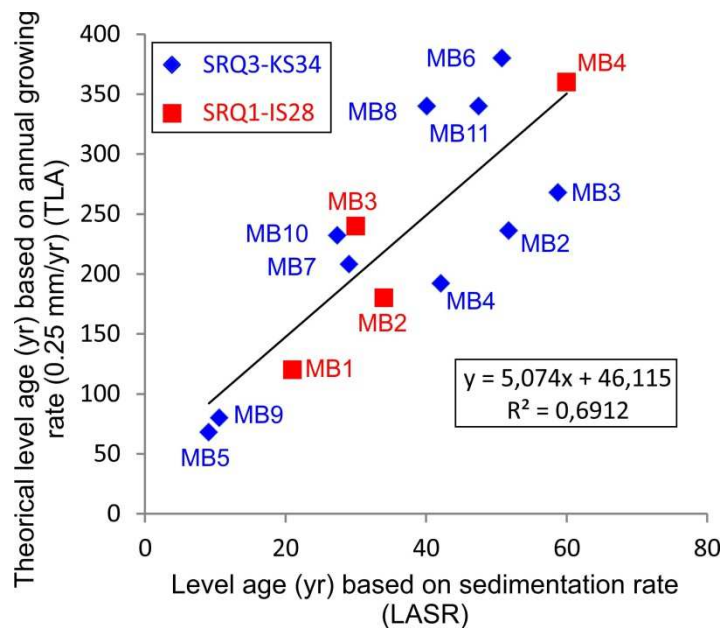
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Figure 16: a1: Sedimentation rates and maerl bed development (a1: age-depth model (black line) for the SRQ3-KS34 core section limited between 40 to 160 cm bsf (extracted from Fig. 12); b1: Theoretical age-depth model (blue line) for 50% reduction of local sedimentation rate during maerl bed development; a2: Sedimentation rates based on a1; b2: sedimentation rates based on b1). Red dashed line: modern sedimentation rate (Ehrhold et al., 2016, Fig. 2). MB: maerl bed facies.



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Figure 17: Comparison of maerl bed ages based on sedimentation rates and annual growth for SRQ3-KS34 (40-160 cm bsf, see Fig. 16) and SRQ1-IS28 cores (10-70 cm bsf).

Sites in the Bay of Brest	Sample and lab. no.	Core depth (cm)	Altitude LTL (m)	AMS ¹⁴ C ages (radiocarbon yr B.P.)	Calibrated aged cal yr B.P. (mean) ΔR = 46	Age cal (A.D./B.C.)	Dated material	References
Roscanvel	SRQ1-IS03 (Beta-397592)	24	-1.8	1260 ± 30	937 - 732 (835)	1013 - 1218 (A.D.)	Molluscs	
Roscanvel	SRQ1-IS03 (Poz-65763)	46-47	-1.8	4175 ± 35	4420 - 4141 (4282)	2471 - 2192 (B.C.)	Molluscs	
Roscanvel	SRQ3-KS39 (Poz-76861)	8	-11.5	740 ± 30	533 - 421 (477)	1417 - 1529 (A.D.)	Molluscs	Gregoire et al. (2017)
Roscanvel	SRQ3-KS39 (Beta-468466)	15-16	-11.5	880 ± 30	653 - 576 (615)	1297 - 1374 (A.D.)	Molluscs	
Roscanvel	SRQ3-KS39 (Beta-468467)	25-26	-11.5	1690 ± 30	1378 - 1217 (1298)	572 - 733 (A.D.)	Molluscs	
Roscanvel	SRQ3-KS39 (Poz-76862)	35	-11.5		1425 - 1292 (1359)	252 - 658 (A.D.)	Molluscs	Gregoire et al. (2017)
Roscanvel	SRQ3-KS39 (Beta-468468)	55-56	-11.5	2010 ± 30	1718 - 1514 (1616)	232 - 436 (A.D.)	Molluscs	
Roscanvel	SRQ3-KS39 (Poz-76863)	73	-11.5	2250 ± 30	1996 - 1716 (1856)	46 (B.C.) - 234 (A.D.)	Molluscs	Gregoire et al. (2017)
Roscanvel	SRQ3-KS39 (Poz-76864)	87-88	-11.5	2395 ± 30	2154 - 1896 (2025)	204 (B.C.) - 54 (A.D.)	Molluscs	Gregoire et al. (2017)
Roscanvel	SRQ3-KS39 (Poz-76837)	97	-11.5	2590 ± 30	2357 - 2143 (2250)	407 - 193 (B.C.)	Molluscs	Gregoire et al. (2017)
Roscanvel	SRQ3-KS39 (Poz-76838)	121	-11.5	4810 ± 30	5311 - 4959 (5135)	3361 - 3009 (B.C.)	Molluscs	Gregoire et al. (2017)
Roscanvel	SRQ3-KS39 (Poz-76840)	130	-11.5	7410 ± 40	8016 - 7788 (7902)	6066 - 5838 (B.C.)	Molluscs	Gregoire et al. (2017)
Roscanvel	SRQ3-KS40 (Beta-462612)	88-90	-19.6	1830 ± 30	1522 - 1308 (1415)	425 - 642 (A.D.)	Molluscs	
Fret	SRQ1-IS04 (Poz-68933)	41-42	-7.1	3320 ± 30	3277 - 3004 (3141)	1327 - 1054 (B.C.)	Benthic foram.	
Fret	SRQ1-IS04 (Poz-68934)	75-76	-7.1	3445 ± 35	3453 - 3206 (3330)	1503 - 1256 (B.C.)	Benthic foram.	
Fret	SRQ3-KS38 (Poz-76850)	26	-13.7	1635 ± 30	1312 - 1171 (1242)	638 - 779 (A.D.)	Molluscs	
Fret	SRQ3-KS38 (Poz-76851)	89	-13.7	2105 ± 35	1826 - 1560 (1693)	124 - 390 (A.D.)	Molluscs	
Fret	SRQ3-KS38 (Poz-85263)	101-103	-13.7	2030 ± 30	1740 - 1519 (1630)	210 - 431 (A.D.)	Maerl	
Fret	SRQ3-KS38 (Poz-76852)	115	-13.7	4700 ± 40	5071 - 4840 (4956)	3121 - 2890 (B.C.)	Molluscs	
Fret	SRQ3-KS38 (Poz-76853)	210	-13.7	4605 ± 35	4979 - 4797 (4888)	3029 - 2847 (B.C.)	Molluscs	
Fret	SRQ3-KS38 (Poz-76855)	232	-13.7	7220 ± 40	7855 - 7613 (7734)	5905 - 5663 (B.C.)	Molluscs	
Fret	SRQ3-KS38 (Poz-76856)	304	-13.7	7330 ± 50	7954 - 7695 (7825)	6004 - 5745 (B.C.)	Molluscs	
Fret	SRQ3-KS38 (Poz-76857)	320	-13.7	7360 ± 50	7973 - 7707 (7840)	6023 - 5757 (B.C.)	Molluscs	
Lanveoc-Poulmic	SRQ1-IS23 (Beta-397594)	38	-4.0	450 ± 30	152 - 4 (78)	1798 - 1946 (A.D.)	Maerl	
Lanveoc-Poulmic	SRQ1-IS23 (Poz-65762)	63	-4.0	720 ± 30	519 - 417 (468)	1431 - 1533 (A.D.)	Maerl	
Lanveoc-Poulmic	SRQ1-IS28 (Poz-85162)	10-11	-9.7	620 ± 30	498 - 280 (389)	1452 - 1670 (A.D.)	Maerl	
Lanveoc-Poulmic	SRQ1-IS28 (Poz-89695)	21-22	-9.7	550 ± 30	231 - 130 (181)	1719 - 1820 (A.D.)	Molluscs	
Lanveoc-Poulmic	SRQ1-IS28 (Poz-85163)	26-27	-9.7	690 ± 30	505 - 309 (407)	1445 - 1641 (A.D.)	Maerl	
Lanveoc-Poulmic	SRQ1-IS28 (Poz-89696)	35-36	-9.7	740 ± 30	533 - 421 (477)	1417 - 1529 (A.D.)	Molluscs	
Lanveoc-Poulmic	SRQ1-IS28 (Poz-85164)	45	-9.7	690 ± 30	505 - 309 (407)	1445 - 1641 (A.D.)	Maerl	
Lanveoc-Poulmic	SRQ1-IS28 (Poz-89697)	52-53	-9.7	615 ± 30	497 - 275 (386)	1453 - 1675 (A.D.)	Molluscs	
Lanveoc-Poulmic	SRQ1-IS28 (Poz-85167)	63	-9.7	665 ± 30	501 - 302 (402)	1449 - 1648 (A.D.)	Maerl	
Lanveoc-Poulmic	SRQ1-IS28 (Poz-89698)	66-67	-9.7	725 ± 30	522 - 418 (470)	1428 - 1532 (A.D.)	Molluscs	
Lanveoc-Poulmic	SRQ1-IS28 (Poz-85168)	70	34	740 ± 30	533 - 421 (477)	1417 - 1529 (A.D.)	Maerl	
Lanveoc-Poulmic	SRQ3-KS35 (Beta-462615)	82-84	-9.8	1980 ± 30	1638 - 1412 (1525)	312 - 538 (A.D.)	Molluscs	
Aulne	SRQ3-KS20 (Poz-76810)	35	-8.2	1925 ± 30	1612 - 1371 (1492)	338 - 579 (A.D.)	Molluscs	
Aulne	SRQ3-KS20 (Poz-76811)	92	-8.2	2380 ± 30	2151 - 1888 (2020)	201 (B.C.) - 62 (A.D.)	Molluscs	
Aulne	SRQ3-KS20 (Poz-76812)	114	-8.2	7070 ± 40	7688 - 7499 (7594)	5738 - 5549 (B.C.)	Molluscs	
Aulne	SRQ3-KS20 (Poz-76813)	140	-8.2	7480 ± 50	8072 - 7847 (7960)	6122 - 5897 (B.C.)	Molluscs	
Aulne	SRQ3-KS22 (Poz-78271)	2-3	25	1180 ± 30	870 - 676 (773)	1080 - 1274 (A.D.)	Molluscs	Lambert (2017)
Aulne	SRQ3-KS22 (SacA49421)	7	25	990 ± 30	662 - 533 (598)	1288 - 1417 (A.D.)	Molluscs	Lambert (2017)
Aulne	SRQ3-KS22 (SacA47758)	25	25	890 ± 30	616 - 480 (548)	1334 - 1470 (A.D.)	Molluscs	Lambert (2017)
Aulne	SRQ3-KS22 (SacA49422)	50	25	1370 ± 30	1055 - 880 (968)	895 - 1070 (A.D.)	Molluscs	Lambert (2017)
Aulne	SRQ3-KS22 (Poz-78273)	94-95	25	1515 ± 30	1220 - 1005 (1113)	730 - 945 (A.D.)	Molluscs	Lambert (2017)
Aulne	SRQ3-KS22 (Poz-85262)	110-112	25	1425 ± 30	1099 - 928 (1014)	851 - 1022 (A.D.)	Maerl	
Daoulas	SRQ1-IS07 (Poz-68936)	65-67	-1.4	620 ± 30	498 - 280 (389)	1452 - 1670 (A.D.)	Molluscs	
Daoulas	SRQ1-IS21 (Poz-85169)	25-26	-8.4	560 ± 40	230 - 131 (181)	1720 - 1819 (A.D.)	Molluscs	
Daoulas	SRQ1-IS21 (Poz-85171)	34-35	-8.4	670 ± 30	501 - 304 (403)	1449 - 1646 (A.D.)	Maerl	
Daoulas	SRQ1-IS21 (Poz-85170)	45-46	-8.4	675 ± 30	502 - 306 (404)	1448 - 1644 (A.D.)	Maerl	
Daoulas	SRQ1-IS21 (Poz-85173)	57-58	-8.4	770 ± 30	552 - 423 (488)	1398 - 1527 (A.D.)	Maerl	
Auberlac'h	Al2013_IS08 (Poz-85175)	33-34	-3.9	545 ± 30	232 - 124 (178)	1718 - 1826 (A.D.)	Maerl	
Auberlac'h	Al2013_IS08 (Poz-85265)	45-46	-3.9	670 ± 30	501 - 304 (403)	1449 - 1646 (A.D.)	Maerl	
Auberlac'h	Al2013_IS08 (Poz-85255)	63-64	-3.9	650 ± 30	499 - 294 (397)	1451 - 1656 (A.D.)	Maerl	
Auberlac'h	ESCALICO-KS02 (Poz-85159)	2	-3.2	690 ± 30	456 - 289 (373)	1494 - 1661 (A.D.)	Molluscs	Lambert et al. (2020)
Auberlac'h	ESCALICO-KS02 (SacA49423)	20	-3.2	1430 ± 30	1125 - 924 (1025)	825 - 1026 (A.D.)	Molluscs	Lambert et al. (2020)
Auberlac'h	ESCALICO-KS02 (SacA47761)	42	-3.2	1740 ± 40	1438 - 1238 (1338)	512 - 712 (A.D.)	Molluscs	Lambert et al. (2020)
Auberlac'h	ESCALICO-KS02 (Poz-78153)	85-86	-3.2	1850 ± 30	1530 - 1338 (1434)	420 - 612 (A.D.)	Molluscs	Lambert et al. (2020)
Auberlac'h	ESCALICO-KS02 (Poz-8545632)	140-141	-3.2	2040 ± 30	1769 - 1546 (1658)	181 - 404 (A.D.)	Molluscs	Lambert et al. (2020)
Auberlac'h	ESCALICO-KS02 (Poz-78154)	180-181	-3.2	2075 ± 35	1814 - 1575 (1695)	136 - 375 (A.D.)	Molluscs	Lambert et al. (2020)
Auberlac'h	ESCALICO-KS02 (SacA45633)	249-250	-3.2	2515 ± 30	2320 - 2124 (2222)	370 - 174 (B.C.)	Molluscs	Lambert et al. (2020)
Auberlac'h	SRQ3-KS34 (Poz-76814)	20	-10.0	990 ± 30	686 - 546 (616)	1264 - 1404 (A.D.)	Molluscs	Gregoire et al. (2017)
Auberlac'h	SRQ3-KS34 (Poz-94708)	29-30	-10.0	980 ± 30	681 - 544 (613)	1269 - 1406 (A.D.)	Molluscs	
Auberlac'h	SRQ3-KS34 (Poz-94709)	42-43	-10.0	1475 ± 30	1183 - 953 (1068)	767 - 997 (A.D.)	Molluscs	
Auberlac'h	SRQ3-KS34 (Poz-94710)	61-62	-10.0	1575 ± 30	1288 - 1060 (1174)	662 - 890 (A.D.)	Molluscs	
Auberlac'h	SRQ3-KS34 (Poz-94711)	71-72	-10.0	1605 ± 30	1296 - 1168 (1232)	654 - 782 (A.D.)	Molluscs	
Auberlac'h	SRQ3-KS34 (Poz-76816)	80	-10.0	1670 ± 30	1368 - 1175 (1272)	582 - 775 (A.D.)	Molluscs	Gregoire et al. (2017)
Auberlac'h	SRQ3-KS34 (Beta-462613)	110-112	-10.0	1840 ± 30	1525 - 1311 (1418)	425 - 639 (A.D.)	Molluscs	
Auberlac'h	SRQ3-KS34 (Beta-462614)	130-132	-10.0	1980 ± 30	1637 - 1412 (1525)	313 - 538 (A.D.)	Molluscs	
Auberlac'h	SRQ3-KS34 (Poz-76817)	163	-10.0	2200 ± 30	1935 - 1695 (1815)	15 - 255 (A.D.)	Molluscs	Gregoire et al. (2017)
Auberlac'h	SRQ3-KS34 (Poz-85261)	171-172	-10.0	2170 ± 30	1896 - 1687 (1792)	54 - 263 (A.D.)	Maerl	
Auberlac'h	SRQ3-KS34 (Poz-76818)	181	-10.0	3035 ± 30	2927 - 2747 (2837)	977 - 797 (B.C.)	Molluscs	
Auberlac'h	SRQ3-KS34 (Poz-76820)	220	-10.0	3325 ± 30	3347 - 3020 (3184)	1397 - 1070 (B.C.)	Molluscs	Gregoire et al. (2017)
Auberlac'h	SRQ3-KS34 (Poz-76821)	260	-10.0	5590 ± 40	6195 - 5914 (6055)	4245 - 3964 (B.C.)	Molluscs	Gregoire et al. (2017)
Auberlac'h	SRQ3-KS36 (Beta-468469)	23-24	-13.1	880 ± 30	653 - 576 (615)	1297 - 1374 (A.D.)	Molluscs	
Auberlac'h	SRQ3-KS36 (Poz-76823)	40	-13.1	1520 ± 40	1264 - 980 (1122)	686 - 970 (A.D.)	Molluscs	
Auberlac'h	SRQ3-KS36 (Poz-76824)	145	-13.1	2350 ± 30	2128 - 1871 (2000)	178 (B.C.) - 79 (A.D.)	Molluscs	
Auberlac'h	SRQ3-KS36 (Poz-76825)	164	-13.1	2245 ± 30	1955 - 1727 (1841)	5 (B.C.) - 223 (A.D.)	Molluscs	
Brest - Elorn	SRQ1-IS17 (Beta-397593)	29	-2.0	1330 ± 30	1006 - 789 (898)	944 - 1161 (A.D.)	Maerl	
Brest - Elorn	SRQ1-IS17 (Poz-65761)	58	-2.0	1405 ± 30	1099 - 916 (1008)	851 - 1034 (A.D.)	Maerl	
Brest - Elorn	SRQ1-IS32 (Poz-85256)	12-13	-2.5	1385 ± 30	1087 - 901 (994)	863 - 1049 (A.D.)	Maerl	
Brest - Elorn	SRQ1-IS32 (Poz-89699)	22-23	-2.5	1400 ± 30	1149 - 911 (1030)	801 - 1039 (A.D.)	Molluscs	
Brest - Elorn	SRQ1-IS32 (Poz-85257)	27-29	-2.5	1470 ± 30	1182 - 937 (1060)	768 - 1013 (A.D.)	Maerl	
Brest - Elorn	SRQ1-IS32 (Poz-89692)	34-35	-2.5	1470 ± 30	1182 - 937 (1060)	768 - 1013 (A.D.)	Molluscs	
Brest - Elorn	SRQ1-IS32 (Poz-85258)	40-41	-2.5	1410 ± 30	1097 - 920 (1009)	853 - 1030 (A.D.)	Maerl	
Brest - Elorn	SRQ1-IS32 (Poz-89693)	45-46	-2.5	1480 ± 30	1184 - 954 (1069)	766 - 996 (A.D.)	Molluscs	
Brest - Elorn	SRQ1-IS32 (Poz-85259)	53-54	-2.5	1410 ± 30	1097 - 920 (1009)	853 - 1030 (A.D.)	Maerl	
Brest - Elorn	SRQ1-IS32 (Poz-89694)	60-61	-2.5	1435 ± 30	1150 - 931 (1041)	800 - 1019 (A.D.)	Molluscs	
Brest - Elorn	SRQ1-IS32 (Poz-85260)	64-65	-2.5	1465 ± 30	1181 - 935 (1058)	769 - 1015 (A.D.)	Maerl	
Brest - Elorn	SRQ3-KS44 (Poz-76826)	35	-6.2	2275 ± 30	2004 - 1736 (1870)	54 (B.C.) - 214 (A.D.)	Molluscs	
Brest - Elorn	SRQ3-VZ33 (Poz-122703)	65	-9.8	1730 ± 30	1408 - 1255 (1332)	542 - 695 (A.D.)	Molluscs	
Brest - Elorn	SRQ3-KS04 (Poz-122702)	149	-7	2290 ± 30	2060 - 1806 (1933)	110 (B.C.) - 144 (A.D.)	Molluscs	
Brest - Elorn	PAL-KS05 (Poz-102087)	40-42	-3.1	1360 ± 30	1063 - 892 (978)	887 - 1058 (A.D.)	Molluscs	
Brest - Elorn	PAL-KS05 (Poz-102088)	53-53	-3.1	1380 ± 30	1082 - 898 (990)	868 - 1052 (A.D.)	Molluscs	
Brest - Elorn	PAL-KS05 (Poz-102089)	69-71	-3.1	1425 ± 30	1099 - 928 (1014)	851 - 1022 (A.D.)	Molluscs	
Brest - Elorn	PAL-KS05 (Poz-102090)	88-90	-3.1	1475 ± 30	1183 - 953 (1068)	767 - 997 (A.D.)	Molluscs	
Brest - Elorn	PAL-KS05 (Poz-102091)	112-114	-3.1	1530 ± 30	1269 - 1047 (1158)	681 - 903 (A.D.)	Molluscs	
Brest - Elorn	PAL-KS05 (Poz-102092)	143,5-145,5	-3.1	1685 ± 30				

Subregions of Brest Bay	Core name	Levels (name) in Figs. 8-11	Level bsf (cm) in Fig. 8-11	Maerl bed thickness (cm)	Sedimentation rate (mm/yr) (Fig. 16)	Level age (yr) based on sedimentation rate (LASR)	Accumulation rate (cm/yr - m/kyr)	Theoretical level age (yr) based on annual growing rate (0,25mm/yr) (TLA)	TLA/LASR	Maerl species
Lanveoc Poulmic cove	SRQ1-IS28	MB4	10 - 19	9,00	1,5	60	0,15 - 1,5	360	6,00	<i>Lithothamnion corallioides</i>
Lanveoc Poulmic cove	SRQ1-IS28	MB3	40 - 46	6,00	1,50	30	0,2 - 2	240	8,00	<i>Lithothamnion corallioides</i>
Lanveoc Poulmic cove	SRQ1-IS28	MB2	60 - 64,5	4,5	1,67	34	0,13 - 1,3	180	5,29	<i>Lithothamnion corallioides</i>
Lanveoc Poulmic cove	SRQ1-IS28	MB1	67 - 70	3,00	1,67	21	0,14 - 1,4	120	5,71	<i>Lithothamnion corallioides</i>
Auberlac'h cove	SRQ3-KS34	MB11	45 - 53,5	8,5	1,79	47	0,16 - 1,6	340	7,23	<i>Lithothamnion corallioides</i>
Auberlac'h cove	SRQ3-KS34	MB10	56,1 - 61,3	5,2	1,79	29	0,19 - 1,9	208	7,17	<i>Lithothamnion corallioides</i>
Auberlac'h cove	SRQ3-KS34	MB9	67 - 69	2,00	1,89	11	0,22 - 2,2	80	7,27	<i>Lithothamnion corallioides</i>
Auberlac'h cove	SRQ3-KS34	MB8	90 - 98,5	8,5	2,12	40	0,22 - 2,2	340	8,50	<i>Lithothamnion corallioides</i>
Auberlac'h cove	SRQ3-KS34	MB7	103 - 108,8	5,8	2,12	27	0,22 - 2,2	232	8,59	<i>Lithothamnion corallioides</i>
Auberlac'h cove	SRQ3-KS34	MB6	110 - 119,5	9,5	1,87	51	0,19 - 1,9	380	7,45	<i>Lithothamnion corallioides</i>
Auberlac'h cove	SRQ3-KS34	MB5	123,3 - 125	1,7	1,87	9	0,17 - 1,7	68	7,56	<i>Lithothamnion corallioides</i>
Auberlac'h cove	SRQ3-KS34	MB4	130 - 134,8	4,8	1,14	42	0,15 - 1,5	192	4,57	<i>Lithothamnion corallioides</i>
Auberlac'h cove	SRQ3-KS34	MB3	137,8 - 144,5	6,7	1,14	59	0,16 - 1,6	268	4,54	<i>Lithothamnion corallioides</i>
Auberlac'h cove	SRQ3-KS34	MB2	145,9 - 151,8	5,9	1,14	52	0,11 - 1,1	236	4,54	<i>Lithothamnion corallioides</i>

Table 2: Accumulation rates of rhodolith beds calculated for two cores in the Bay of Brest (SRQ1-IS28 and SRQ3-

KS34). The age of each maerl bed was extrapolated from local age-depth model.