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Environmental factors affecting maerl bed structure in Brittany (France)

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Abstract :

This study used a large spatial scale approach in order to better quantify the relationships between maerl bed structure and a selection of potentially forcing physical factors. Data on maerl bed structure and morpho-sedimentary characteristics were obtained from recent oceanographic surveys using underwater video recording and grab sampling. Considering the difficulties in carrying out real-time monitoring of highly variable hydrodynamic and physicochemical factors, these were generated by three-dimensional numerical models with high spatial and temporal resolution. The BIOENV procedure indicated that variation in the percentage cover of thalli can best be explained (correlation = 0.76) by a combination of annual mean salinity, annual mean nitrate concentration and annual mean current velocity, while the variation in the proportion of living thalli can best be explained (correlation = 0.47) by a combination of depth and mud content. Linear relationships showed that the percentage cover of maerl thalli was positively correlated with nitrate concentration ($R2 = 0.78$, $P < 0.01$) and negatively correlated with salinity ($R2 = 0.81$, $P < 0.01$), suggesting a strong effect of estuarine discharge on maerl bed structure, and also negatively correlated with current velocity ($R2 = 0.81$, $P < 0.01$). When maerl beds were deeper than 10 m, the proportion of living thalli was always below 30% but when they were shallower than 10 m, it varied between 4 and 100%, and was negatively correlated with mud content ($R2 = 0.53$, $P < 0.01$). On the other hand, when mud content was below 10%, the proportion of living thalli showed a negative correlation with depth ($R2 = 0.84$, $P < 0.01$). This large spatial scale explanation of maerl bed heterogeneity provides a realistic physical characterization of these ecologically interesting benthic habitats and usable findings for their conservation and management.

Keywords : Benthic habitats, Brittany, environmental factors, estuary, large spatial scale, maerl

1. Introduction

Maerl beds refer to intricate benthic habitats constituted by accumulations of living and dead unattached thalli of coralline algae which occur in tropical, temperate and polar environments (Bosence, 1983; Freiwald & Henrich, 1994). In European waters, most of them are patchily distributed and found at less than 30 m deep, except in the Mediterranean Sea where they can be found down to 100 m (Jacquotte, 1962; Birkett *et al.*, 1998; Hall-Spencer, 1998; De Grave *et al.*, 2000; Foster, 2001). Although this geographical distribution seems to be mainly constrained by the ecological requirements of the species constituting European maerl beds, such as *Phymatolithon calcareum* (Pallas) W.H. Adey & D.L. McKibbin and *Lithothamniom corallioides* (P.L. Crouan & H.M. Crouan) P.L. Crouan & H.M. Crouan, only a few studies have investigated the relationships between environment and physiological responses in these species, resulting in very variable conclusions about their ecological niches (Adey & McKibbin, 1970; Hall-Spencer & Moore, 2000; Wilson *et al.*, 2004; Martin *et al.*, 2006; 2007*a*; 2007*b*). Furthermore, although the morpho sedimentary environment of maerl beds can be clearly established by field samplings, the effect of the highly-variable hydrodynamics and physico-chemical properties of the water column may be misinterpreted due to the difficulty of carrying

out real-time monitoring, especially in temperate coastal ecosystems subject to a semi-diurnal tidal cycle, freshwater outflows and a seasonal cycle (Barbera *et al.*, 2003; Wilson *et al.*, 2004; Dutertre *et al.*, 2013). The development of three-dimensional environmental models generating continuous data on the variability of a large variety of environmental factors, including hydrodynamic conditions and physico-chemical properties (Cugier & Le Hir, 2002; Ménesguen *et al.*, 2007), can therefore greatly improve the identification of environmental factors responsible for the existence, structure and spatial distribution of benthic habitats such as maerl beds (Warwick & Uncles, 1980; Gogina & Zettler, 2010; Dutertre *et al.*, 2013).

Accumulations of calcified thalli result in a large number of microhabitats (microniches) formed by the space between branched forms together with hard calcareous surfaces. Such complexity is characterized by a high diversity and density of macrofaunal and algal species (Birkett *et al.*, 1998; Barbera *et al.,* 2003; Steller *et al.*, 2003; Grall *et al.*, 2006; Hall-Spencer *et al.*, 2008; Peña & Bárbara, 2008; 2010; Dutertre *et al.*, 2013). Maerl beds also provide nursery grounds of importance for commercial species of fish and shellfish (Hall-Spencer *et al.*, 2003; Steller *et al.*, 2003). Being hot-spots of biodiversity and considered as a non-renewable resource due to the slow growth rate of the thalli (Wilson *et al.*, 2004), maerl beds are a priority of the European conservation policies, in particular when being massively extracted to provide calcareous products for soil conditioning, water filtration systems, cosmetics and also for the oil industry (Barbera *et al.*, 2003). The species richness and density of the associated biodiversity are strongly dependent on the three-dimensional structure of the maerl beds corresponding to the density and morphology of thalli, the heterogeneity of the constituent particles (coexistence of fine particles with large maerl thalli), and on the proportion of living thalli (Steller *et al.*, 2003;

Sciberras *et al.*, 2009; Meihoub Berlandi *et al.*, 2012). In spite of the ecological influence of the structural heterogeneity of maerl beds, few data are available about its determinism and evolution. Thus, although water motion, sedimentation and some human activities have been considered driving factors of the variations in morphology and vitality of maerl (Scoffin *et al.*, 1985; Steller & Foster, 1995; Marrack, 1999; Barbera *et al.*, 2003), no clear quantitative relationships have been established between environmental factors and maerl bed structure. In order to understand better how the structure of maerl beds differs between them and how it may change with time, a clear quantification of the influence of environmental factors forcing maerl bed structure now appears necessary (Barbera *et al.*, 2003; Grall & Hall-Spencer, 2003; Przeslawski *et al.*, 2011). Such quantification, essential for the development of management tools such as habitat modelling, can be accomplished by a large spatial scale approach, enabling the elimination of local misinterpretations by comparing distant sites and, therefore, a more realistic physical characterization of benthic habitats, as well as a discrimination between human and natural effects (Ellis & Schneider, 2008; Dutertre *et al.*, 2013).

The aim of this study was to investigate and quantify relationships between variations in maerl bed structure and a selection of potentially-forcing physical factors in order to provide a consistent baseline for conservation and management purposes. This was performed by integrating local structural data regarding the maerl beds of Brittany, which are some of the most extensive in Europe, into a large spatial scale approach. Maerl bed structure was described from data on the percent cover of maerl thalli and the proportion of living thalli which were recently obtained using a combination of underwater video-recordings and grab samplings. Quantitative relationships between maerl bed structure and environmental factors were

124 determined using hydrodynamic and physico-chemical variables generated by three-
125 dimensional numerical models in order to better integrate their high spatio-temporal
126 variability.
127

128 **Materials and methods**

129

130 *Remote sensing and sampling strategy*

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132 Within the framework of the French program REBENT ("Réseau Benthique")
133 and the European Water Framework Directive, the physical structure of five maerl
134 beds of the Brittany coast was investigated by IFREMER (French Research Institute
135 for Exploration of the Sea) using a combination of remote sensing systems,
136 underwater video-recordings and grab samplings. The maerl beds of Paimpol and
137 Molène were investigated in 2008, while those of Glénan, Trévignon and Belle-Ile
138 were investigated in 2009 (Figure 1). A digital sidescan sonar EDGETECH DF-
139 1000©, towed by the coastal vessel THALIA, was first used to carry out acoustic
140 profiles in order to identify maerl beds amongst the other morpho-sedimentary units,
141 while geographic locations were determined by a differential Global Positioning
142 System THALES AQUARIUS©. Sediment samplings and underwater video-
143 recordings were then performed within the areas where maerl beds had been
144 identified on acoustic profiles (Table 1). Sediment samples were collected with a
145 0.042 m² Shipek grab deployed from the coastal vessel THALIA, put into plastic bags
146 and frozen during their storage. In the laboratory, about 300 g of each sediment
147 sample was first wet-sieved using a 50-µm stainless steel sieve. The fraction above

50 µm was dry-sieved on a sieve shaker, using a range of stainless steel sieves placed at -4 phi intervals, down to 4 phi (63 µm). The retained fractions were weighed in order to give a full particle size distribution and GRADISTAT 4.0 software was used to calculate the mud content of the distribution, which corresponds to the percentage of particles smaller than 63 µm. Living and dead maerl thalli were included in sedimentary analysis. Underwater video-recordings were made using a KONSBERG OE1372A-003 high-resolution colour video camera, equipped with a waterproof projector and mounted on a metallic support in order to have a constant distance between the camera and the surface of the maerl bed. The video camera was towed by the coastal vessel THALIA above the maerl beds and dropped down randomly near sediment sampling sites in order to obtain ten 0.160 m^2 photoquadrats of the bottom.

In 2010, the European Institute for Marine Studies (IUEM) investigated the physical structure of the maerl beds of Rade de Brest and Camaret (Figure 1). Within each maerl bed, random sediment samplings were performed with a 0.100 m^2 Smith McIntyre grab and then processed using the method described above (Table 1). However, these investigations did not include underwater video-recordings.

Analysis of the physical structure of the maerl beds

The physical structure of the maerl beds was characterized by the percent cover of maerl thalli (live + dead) determined *in situ* and the proportion of living thalli determined in the laboratory. The percent cover of maerl thalli (live + dead) was estimated by superimposing a 20×20 cm square grid on drop-down still images of the

maerl beds in order to determine the percentage of the seabed covered by maerl. Due to the difficulty of distinguishing between living and dead thalli in the field, the proportion of living thalli was estimated in the laboratory from the grab samples used for the sedimentary analysis. According to their marked coloration, varying from reddish-pink to reddish-purple, all the living thalli sampled in grab were separated from the rest of the sediment (including dead thalli) and deposited on a 10×10 square grid corresponding to the area of seabed sampled by the grab (0.042 m^2 and 0.100 m^2 for the Shipek and Smith McIntyre grab samples, respectively) in order to determine the proportion of living thalli (i.e. the number of the sub-squares filled by living thalli on the grid) on the seabed. Except for the subarea R16 of the maerl bed of Rade de Brest where the seabed was 100 % covered by maerl stacks, the amount of living thalli has never exceeded the size of the grid used to determine the proportion of living thalli. While the proportion of living thalli was determined for each sampling station of the seven maerl beds (Belle-Ile, Trévignon, Glénan, Camaret, Rade de Brest, Molène and Paimpol), the percent cover of maerl thalli was not determined for the maerl beds of Rade de Brest and Camaret due to the lack of drop-down still images. *P. calcareum* and *L. corallioides* have been reported as the dominant maerl-forming species in Brittany (Grall & Hall-Spencer, 2003), however, as visual inspection of the thalli cannot enable a reliable taxonomic identification of the maerl species, thalli were considered as if they belonged to the same maerl species. Nevertheless, visual inspection enables a qualitative description of the relative thallus morphology taking into account the shape and the branching pattern.

Three-dimensional environmental models

The MARS 3D (Three Dimensional Model for Applications at Regional Scale) model has been developed by IFREMER to provide realistic descriptions of spatial and temporal variations in coastal hydrodynamics (Ménesguen *et al.*, 2007; 2014; Lazure & Dumas, 2008). It uses regular orthogonal grids with square meshes, aligned with geographic axes, in the horizontal plane. For each mesh, the water column is divided into ten horizontal layers for which thickness is proportional to the local water depth (σ-coordinates). Mechanical forcing of the MARS 3D hydrodynamical model is made by barotropic sea-level oscillation at the oceanic boundaries, and wind and atmospheric pressure at the sea surface (Arpege Model, Météo-France). The salinity and temperature are calculated with a classic time integration scheme. Flow rates of rivers such as Loire and Vilaine derive from measured daily discharges. The ECOMARS 3D model, resulting from the coupling of the MARS 3D model and a biochemical model, enables the description of spatial and temporal variations in nutrient (nitrate, phosphate and silicate) concentrations and oxygen saturation. River nutrient concentrations are computed from empirical statistical relationships involving flow rate and time fitted. Suspended particulate matter derives from satellite data and the suspended matter brought by the rivers, which is simply simulated as a particulate conservative tracer. Oxygen saturation derives from oxygen concentration measured in surface and bottom waters by buoys. Environmental simulations generated by MARS 3D and ECOMARS 3D models have been validated by numerous data from monitoring networks for the French coastal zone (e.g. REPHY, MAREL, SOMLIT) and oceanographic cruises. Following the recent development of the models in the framework of the PREVIMER project and the possibility of having good validations by means of satellite observations and seawater measurements, the year 2009 was chosen as the “reference” year to

222 generate hydrological variations because of the absence of exceptional climatic
223 events. For the maerl beds of Paimpol, Molène, Glénan, Trévignon and Belle-Ile,
224 temperature (°C), salinity, oxygen saturation (%), suspended particulate matter
225 (SPM, $mg.L^{-1}$) and nutrients concentrations (nitrate and phosphate, µM) were
226 derived from the ECOMARS 3D-BRETAGNE model (resolution grid = 3 km, period =
227 12 h), while current velocity ($m.s^{-1}$) was obtained from the MARS 3D-MANGA
228 (MANche-GAscogne) model (resolution grid = 3 km, period = 1 h). For the maerl
229 beds of Rade de Brest and Camaret, the physico-chemical properties of the water
230 column were derived from the ECOMARS 3D-BRETAGNE zoom FINIS model
231 (resolution grid = 500 m, period = 12 h), while current velocity ($m.s^{-1}$) was obtained
232 from the MARS 3D-MANGA model zoom IROISE (resolution grid = 150 m, period = 1
233 h).

234 In its operational configuration, the WAVEWATCH III model is a wind-wave
235 model using unstructured grids with adaptive time stepping, which has been adapted
236 to be interfaced with ocean and atmospheric circulation models (Tolman, 2002;
237 Ardhuin *et al.*, 2014). Wave simulations have been extracted on regular grids for the
238 year 2009 and validated by numerous data from buoys, satellite observations and
239 oceanographic cruises. For all the maerl beds, significant wave agitation ($m.s^{-1}$) was
240 derived from the WAVEWATCH III ® NORGAS-UG (Nord-Gascogne-Unstructured
241 Grid) model (resolution grid = 200 m, period = 3 h).

242 Temporal and spatial variations in hydrological factors (temperature, salinity,
243 oxygen saturation, SPM concentration, nitrate concentration, current velocity and
244 significant wave agitation) were generated over all the year 2009 using the MARS 3D
245 and WAVEWATCH III environmental models in their operational configurations
246 implemented within the framework of the PREVIMER project (Dumas *et al.*, 2014).

247 For each hydrological factor, annual descriptive statistics (mean, standard deviation,
248 maximum and minimum) were calculated from the continuous temporal data
249 generated at the horizontal bottom layer of the water column, representing 1/10th of
250 the local water depth, in each mesh of the resolution grid covering a part of the maerl
251 beds. Annual standard deviation was used as an indicator of environmental
252 variability.
253
254 *Statistical analysis*
255
256 Seabed areas covered by the maerl beds of Paimpol, Molène, Glénan,
257 Trévignon and Belle-Ile, were virtually subdivided into geographical subareas
258 according to the 3×3 km meshes of the resolution grid of the MARS 3D model (Table
259 1). For these maerl beds, the percent cover of maerl thalli, proportion of living thalli,
260 depth, mud content and wave agitation were therefore averaged within each subarea
261 corresponding to a MARS 3D model's mesh. For the maerl beds of Rade de Brest
262 and Camaret, each subarea corresponded to a single sampling station and to a
263 single 0.5×0.5 MARS 3D model's mesh (Table 1).
264 The BIOENV procedure, implemented in the PRIMER© V6 software package,
265 was used to identify which combination of the tested environmental variables (mud
266 content, depth and the annual descriptive statistics of the hydrological factors
267 generated by the numerical models) best explained variations in maerl bed structure
268 (Clarke & Ainsworth, 1993). The results of the BIOENV procedure were illustrated by
269 a parallel display of nonmetric multidimensional scaling (NMDS) ordinations of the
270 subareas based on each structural component (percent cover of maerl thalli and
271 proportion of living thalli) of the maerl beds (Bray-Curtis dissimilarities) and the

associated best subset of explanatory environmental variables (Euclidean dissimilarities). Non-parametric Spearman tests, implemented in Sigmastat 3.1 software, were also used to determine correlations between environmental predictors. Finally, after checking the normality and homoscedasticity of the distributions, linear regressions were used to describe the relationships between maerl bed structure and selected environmental variables.

Results

Structural description of the maerl beds

The total areas of the Brittany maerl beds, which were then virtually subdivided into subareas according to the resolution grids of the MARS 3D model, varied between 1.9 and 23.0 km² (Table 1).

The maerl bed of Belle-Ile corresponded to a single subarea (B) where the seabed was 92.5 ± 14.5 % covered by maerl thalli, while the proportion of living thalli was 23.4 ± 15.5 %. Most of the thalli were characterized by short branches, while few of them exhibited spherical shapes (Figure 2). Underwater video-recordings showed that living thalli were mainly concentrated in hollows of megaripples generated by wave action.

The maerl bed of Trévignon was subdivided into two subareas (T1 and T2). Within T1, the percent cover of maerl thalli was 73.8 ± 11.3 %, while the proportion of living thalli was 38.3 ± 13.0 %. Within T2, the seabed was 96.9 ± 18.3 % covered by maerl thalli, while the proportion of living thalli was 83.0 ± 16.4 %. Thalli were

296 characterized by short branches within T1 (Figure 3), while they exhibited more
297 ramified morphotypes with longer branches within T2 (Figure 4).

298 The maerl bed of Glénan was subdivided into two subareas (G1 and G2). The
299 percent cover of maerl thalli was 78.5 ± 10.6 % within G1 and 68.5 ± 23.3 % within
300 G2. Grab samplings showed 10.0 ± 8.4 % of living thalli within G1 and 16.5 ± 10.6 %
301 of living thalli within G2. Within G1 and G2, thalli were relatively small and poorly
302 ramified (Figures 5-6).

303 The maerl bed of Molène was subdivided into two subareas (M1 and M2).
304 Within M1, the seabed was 71.0 ± 34.4 % covered by maerl thalli, while the
305 proportion of living thalli was 80.5 ± 27.5 %. Within M2, the seabed was 66.8 ± 7.2 %
306 covered by thalli, while the proportion of living thalli was 21.6 ± 16.9 %. Ramified
307 thalli were observed within each subarea of the maerl bed of Molène; however, within
308 M2, they were associated with sub-discoidal morphotypes with warty protuberances
309 (Figures 7-8).

310 The maerl bed of Paimpol was subdivided into three subareas (P1, P2 and P3).
311 The covering of the seabed by thalli within P1, P2 and P3 was 39.3 ± 15.7 %, 42.2 ±
312 28.6 % and 59.1 ± 29.6 %, respectively. The proportion of living thalli within P1, P2
313 and P3 was 28.6 ± 9.5 %, 24.4 ± 18.4 % and 37.5 ± 26.2 %, respectively. Highly
314 abraded sub-spheroidal thalli with warty protuberances were the dominant
315 morphotype within P1 (Figure 9), while they were mixed with nodulus and branched
316 ones within P2 (Figure 10). Within P3, branched thalli were clearly dominant (Figure
317 11).

318 For the maerl beds of Rade de Brest and Camaret, each sampling station
319 corresponded to a single subarea. On the whole, the proportion of living thalli varied
320 between 16.0 ± 12.4 and 100.0 ± 0 % within the maerl beds of Rade de Brest, while it

varied between 0.8 ± 0.2 and 28.3 ± 17.4 % within that of Camaret. Within Rade de Brest and Camaret, thalli exhibited branched forms (Figures 12-13).

Environmental setting of the maerl beds

Within the maerl beds of the Brittany coast mud content varied between 0 and 46.6 % (Table 2). The highest mud content was found within the maerl beds of Rade de Brest (average mud content = 28.6 ± 12.5 %) and Camaret (average mud content = 7.9 ± 7.4 %), while other maerl beds developed on sediment with less than 2 % of mud. The maerl beds of the Brittany coast were found between 0.7 and 25.9 m deep. The shallowest maerl beds developed within the Rade de Brest, between 0.7 and 6.8 m, while the deepest developed at Paimpol, between 10.8 and 25.9 m (Table 2).

The Brittany maerl beds were found in areas characterized by an annual mean current velocity varying between 0.02 and 0.73 $m.s^{-1}$ (Table 2). The lowest values were found at Trévignon (T2) and the highest at Paimpol (P1), where the maximum reached 1.71 $m.s^{-1}$. On the other hand, the annual mean wave agitation was lowest at Paimpol (P3 = 0.19 ± 0.15 $m.s^{-1}$) and highest at Belle-Ile (B = 0.62 ± 0.49 $m.s^{-1}$), where the maximum was 3.56 $m.s^{-1}$.

The maerl beds of the Brittany coast were found in areas characterized by annual mean water temperatures varying between 12.2 and 13.6°C, calculated for Rade de Brest and Belle-Ile, respectively, while the lowest winter value was 3.9°C, calculated for Rade de Brest (Table 3). Annual mean salinity was highest at Paimpol (35.3) and lowest at Rade de Brest (31.9) which showed the lowest annual value (24.5) (Table 3). Annual mean suspended particulate matter (SPM) concentration varied between 0.5 and 2.2 $mg.L^{-1}$, while annual mean nitrate concentration varied

between 3.3 and 41.0 µM (Table 3). Rade de Brest showed the highest nitrate concentrations which could reach 148.2 µM (Table 3). Annual mean oxygen saturation, varying between 92 and 100 %, appeared elevated for all the maerl beds (Table 3). The lowest oxygen saturation was calculated for Trévignon, where the summer value fell to 59 %.

Relationships between maerl bed structure and environmental factors

The BIOENV procedure indicated that the variations in the percent cover of thalli can best be explained by a combination of three environmental variables (correlation = 0.76). These corresponded to annual mean salinity, annual mean nitrate concentration and annual mean current velocity, showing individually a relatively high correlation with the percent cover of maerl thalli (correlation = 0.70, 0.64 and 0.62, respectively) compared to other environmental variables (correlation < 0.30). The NMDS ordinations based on the percent cover of maerl thalli and the best subset of explanatory environmental variables (annual mean salinity, annual mean nitrate concentration and annual mean current velocity), showed a relatively similar arrangement of the subareas along a horizontal axis (especially for B, P1 and P2) tending to respect their geographic distribution along the Brittany coast (Figures 14-15). However, the subareas were separated into four distinct clusters in the NMDS ordination based on the percent cover of maerl thalli (Figure 14), while only the subareas corresponding to the maerl bed of Paimpol (P1, P2 and P3) were distinctly separated from the others in the NMDS ordination based on the best subset of explanatory environmental variables (Figure 15). The significance of these relationships was revealed by linear relationships between the percent cover of maerl

thalli and annual mean salinity (log (percent cover) = - 0.26 × annual mean salinity + 10.84, n = 10, R^2 = 0.81, p < 0.01), annual mean nitrate concentration (log (percent cover) = 0.06 × annual mean nitrate concentration + 1.47, n = 10, R^2 = 0.78, p < 0.01), and annual mean current velocity (log (percent cover) = - 0.46 × annual mean current velocity + 1.97, n = 10, R^2 = 0.81, p < 0.01) (Figures 18-20). Spatial variations in annual mean salinity and annual mean nitrate concentration appeared to be negatively correlated (Spearman correlation = - 0.84, p < 0.01). Annual mean current velocity also showed some degree of correlation with annual mean salinity (Spearman correlation = 0.61, p < 0.01) and annual mean nitrate concentration (Spearman correlation = - 0.68, p < 0.01). For the maerl beds of Belle-Ile, Trévignon, Glénan, Molène and Paimpol, there was no significant relationship between the percent cover of maerl thalli and the proportion of living thalli (Spearman correlation = 0.13, p = 0.68).

As revealed by the BIOENV procedure, the variations in the proportion of living thalli can best be explained by the combination of depth and mud content (correlation = 0.47). These two environmental variables showed individually higher correlations (correlation = 0.36 and 0.23 for depth and mud content, respectively) with the proportion of living thalli than the others (correlation < 0.18). The NMDS ordinations based on the proportion of living thalli and the best subset of explanatory environmental variables (depth and mud content) tended to separate the subareas of the shallow maerl bed of Rade de Brest (R1 - R18, depth < 6.8 m) from those of the the deeper maerl bed of Camaret (C1 - C10, depth > 13.6 m) (Figures 16-17). Similarly, the shallow subarea (T2, depth = 6.1 m) of the maerl bed of Trévignon was separated from the deeper subarea (T1, depth = 14.1 m) in the NMDS ordinations. For the maerl bed of Rade de Brest, where the range of mud content was the largest

(2.7 - 46.6 %), NMDS ordinations separated also the subareas showing the lowest mud content (R1, R15 and R16, mud content < 10 %) from those showing the highest mud content (R4, R5, R6, R7 and R13, mud content > 40 %), independently from the depth. For the maerl bed of Camaret, NMDS ordinations based on the proportion of living thalli and the best subset of explanatory environmental variables also showed a relatively good match for the muddiest subareas (C1, C6, C9 and C10, mud content > 10 %), independently from the depth. Although mud content showed an overall correlation with depth (Spearman correlation = - 0.65, $p < 0.01$), these two environmental variables were not significantly correlated for a depth less than 10 m (Spearman correlation = - 0.15, $p = 0.52$). For subareas deeper than 10 m, proportion of living thalli was always lower than 30 % while for subareas at less than 10 m, it varied between 4 and 100 % and showed a significant linear relationship with mud content (Figure 21, log (proportion of living thalli) = - 0.01 × mud content + 2.03, $n = 20$, $R^2 = 0.53$, $p < 0.01$). In this case, the proportion of living thalli progressively decreased when mud content increased from 0 to 46.6 %. On the other hand, for mud content lower than 10 %, the proportion of living thalli showed a significant linear relationship with depth (Figure 22, log (proportion of living thalli) = - 0.05 × depth + 2.11, $n = 15$, $R^2 = 0.84$, $p < 0.01$). Being strongly affected by human exploitation (see below), the proportions of living thalli within the maerl bed of Glénan (subareas G1 and G2) were not used to establish the linear relationships.

Discussion

Influence of estuarine outputs on the percent cover of maerl thalli

Within the maerl beds of the Brittany coast, the percent cover of maerl thalli appeared to be strongly related to spatial variations in both salinity and nitrate concentration. In fact, from the eastern part of Southern Brittany to the eastern part of Northern Brittany, the percent cover of maerl thalli decreased simultaneously with the increase in annual mean salinity and the decrease in annual mean nitrate concentration. Spatial variations in these two environmental variables are strongly driven by regular estuarine outputs from the Vilaine and Loire estuaries, situated in the eastern part of Southern Brittany, which generate a marked east-west gradient between riverine-influenced waters and oceanic-influenced waters (Dutertre *et al.*, 2013). Simulations from the three-dimensional environmental models, as well as remote sensing observations, showed that the attenuated effects of plumes from both these rivers can also be detected as far as the Molène Archipelago during winter (December-February) floods. On the other hand, small rivers situated along the Brittany coast generate slightly decreasing gradients of estuarine conditions with distance from the shore. In Northern Brittany, the maerl bed of Paimpol was not affected by the estuarine outputs and was therefore subject to the lowest annual mean nitrate concentration and the highest annual mean salinity. The influence of estuarine outputs was clearly visible along the coastal fringe of Southern Brittany where the highest percent cover - more than 92 % of the seabed covered - was found at Belle-Ile, directly exposed to releases from the Loire and Vilaine Rivers, and at Trévignon, situated near the mouths of small rivers of Concarneau Bay. In areas adjacent to these maerl beds, the influence of estuarine outputs on benthic ecosystems was confirmed by the presence of particular macrofaunal communities (Glémarec, 1969; Dutertre *et al.*, 2013). Although these results demonstrate an influence of estuarine outputs on the percent cover of maerl thalli, the individual

446 effect of riverine-influenced factors is difficult to distinguish because they co-vary.
447 The occurrence of European maerl beds near estuaries was formerly attributed to a
448 drop in salinity measured in surface waters (Joubin, 1910). However, experimental
449 studies appear necessary to understand how the spatial variations of the bottom
450 salinity observed in this study influence the percent cover of maerl thalli. On the other
451 hand, the data available about the nutrient fluxes in maerl communities found on
452 Rade de Brest (Martin *et al.* 2007*b*) suggest that nitrate concentration could be the
453 main riverine-influenced factor responsible for the variations in the percent cover of
454 maerl thalli along the Brittany coast. In the same way, in the sublittoral zone of south-
455 western Hokkaido, a positive relationship was experimentally demonstrated between
456 thallus growth of the coralline alga *Lithophyllum yessoense* and nitrate concentration
457 ranging from 0 to 10 µM (Ichiki *et al.*, 2000) while, in the present study, annual mean
458 nitrate concentration ranged from 3.32 to 8.16 µM. Taking into account the gradual
459 increase in the amount of nitrates released by rivers since the 1970's, especially in
460 relation to farming activities, their potential effect on maerl bed structure should be
461 considered for conservation and management purposes. Another potential influence
462 of estuarine outputs on the growth and reproduction of coralline algae constituting
463 maerl beds could be variations in calcium concentration (Martin *et al.*, 2006; 2007a).
464 In fact, available data suggest that calcium carbonates accumulated in the Loire
465 River are dissolved at the level of the estuary (Grosbois *et al.*, 2001), involving a
466 massive release of dissolved calcium which is probably spread by the river's plume.
467
468 *Influence of current velocity on the percent cover of maerl thalli*
469

The Brittany maerl beds are found in seabed areas where the current velocity showed an annual mean varying from 0.02 to 0.73 $m.s^{-1}$, and a maximum reaching 1.71 $m.s^{-1}$. In these areas, the percent cover of maerl thalli appeared related to the annual mean current velocity. The lowest percent cover - less than 59 % of the seabed covered - was found within the Paimpol maerl bed, where the annual mean current velocity is higher than 0.50 $m.s^{-1}$ whereas, within the other maerl beds, where the annual mean current velocity is lower than 0.30 $m.s^{-1}$, the percent cover of maerl thalli was higher than 66 %. Moreover, within the Paimpol maerl bed, the percent cover of maerl thalli was higher in the more sheltered subareas (P2 and P3). The strong relationship established between bottom current velocity and the percent cover of maerl thalli is probably due to their transport by water current as demonstrated in tropical reefs, where Scoffin *et al.* (1985) showed that individual branched thalli moved when the tidal current velocity reached 0.30 - 0.40 $m.s^{-1}$. The dispersion of thalli occurring above this threshold of hydrodynamics is consistent with the lowest densities of maerl found within the maerl bed of Paimpol. Thus, the dominance of abraded sub-spheroidal thalli with warty protuberances in this maerl bed (Figures 9-11), as well as their presence in the maerl bed of Molène (Figures 7-8), can be associated with abrasion generated by the movements of thalli during their transport (Marrack, 1999).

Variations in both the percent cover and morphology of thalli can affect the associated biodiversity of maerl beds (Steller *et al.*, 2003; Sciberras *et al.*, 2009; Meihoub Berlandi *et al.*, 2012). For example, when thalli are sparse or non-branched, maerl beds exhibit a less heterogeneous structure and contain less interstitial fauna. However, variations in thallus morphology due to the diversity of coralline algal species should also be considered. Although *P. calcareum* and *L. corallioides* are not

495 characterized by sub-spheroidal thalli and have been reported to be dominant in
496 Brittany maerl beds (Grall & Hall-Spencer, 2003), this dominance must be confirmed
497 by genetic studies.
498
499 *Environmental factors affecting the proportion of living thalli*
500
501 The proportion of living thalli in the maerl beds of the Brittany coast appeared
502 significantly linked to depth and mud content. The relationship with depth was clearly
503 highlighted by the fact that the proportion of living thalli was always lower than 30 %
504 in areas deeper than 10 m, while the highest proportions of living thalli were only
505 found at less than 10 m. On the other hand, at less than 10 m, the proportion of living
506 thalli was also affected by the amount of mud contained in the sediment. For this
507 depth range, the proportion of living thalli, which varied between 84 and 100 % when
508 sediment contained less than 10 % of mud, decreased simultaneously with the
509 increase in mud content. The effect of these two environmental variables on the
510 proportion of living thalli can be related to the diminution of light intensity, even
511 though the irradiance requirements of maerl species are not known and they are
512 generally considered as low-light adapted organisms (Birkett *et al.*, 1998; Wilson *et*
513 *al.*, 2004; Teichert *et al.*, 2012). The proportion of penetrating light is known to
514 decrease with depth, while silt deposition on thalli involves a smothering effect,
515 limiting their access to light and/or gaseous exchange (Steller & Foster, 1995; Hall-
516 Spencer, 1998; Hall-Spencer & Moore, 2000; Riul *et al.*, 2008). For example, the
517 burial of thalli resulting from the re-suspension of sediment by scallop dredging is
518 known to involve a reduction in living thalli of more than 70 %, with no sign of
519 recovery after four years (Wilson *et al.*, 2004). Thus, the disappearance between

1969 and 2009 of the maerl bed situated at the south of Quiberon Bay, where residual macrofaunal communities characterizing maerl habitat still subsist (Dutertre *et al.*, 2013), probably results from the silting of thalli due to increased shellfish dredging activities and oyster farming. Although turbidity can also affect the penetration depth of light, the simulations of three-dimensional environmental models and remote sensing observations revealed that the concentration of suspended particle matter was relatively low (annual mean SPM concentration < 2.2 $mg.L^{-1}$) above the maerl beds. While Lemoine (1910) reported between 50 and 100 % of living thalli within the maerl bed of Glénan, the lower proportions of living thalli (< 20 %) observed now probably result from the huge exploitation which occurred during the second part of the twentieth century (Grall & Hall-Spencer, 2003; Hall-Spencer *et al.*, 2008). Indeed, the wash of extracted maerl involves a release of fine particles which deposit on the sea bottom and kill living maerl. The dominance of small poorly-branched thalli observed within the maerl bed of Glénan (Figures 5-6) can be also associated to fragmentation by dredging and extraction (Hall-Spencer & Moore, 2000).

Implications for the conservation and management of the maerl beds

The large spatial scale ecological approach implemented in this study provides findings having significant implications for the conservation and management of the ecologically interesting benthic habitats constituted by maerl beds. This approach enables the detection of the influence of some important factors, such as estuarine outputs, occurring at a wider spatial scale than that considered by local surveys generally performed in marine benthic ecology. Moreover, while local environmental

545 conditions can lead to misinterpretations of benthic habitat characteristics at a small
546 spatial scale (Ellis & Schneider, 2008), site-to-site comparisons of the physical
547 environment reduce site-related artefacts and enable a more realistic environmental
548 setting of the maerl beds, including anthropogenic effects. More specifically, the
549 quantitative results provided by this study enable the determination of environmental
550 thresholds explaining the structural heterogeneity of maerl beds on which depends
551 the biological diversity associated with this habitat (Steller *et al.*, 2003; Sciberras *et*
552 *al.*, 2009; Meihoub Berlandi *et al.*, 2012). The non-explained part of this structural
553 heterogeneity can be therefore related to non-tested factors, including the impacts of
554 human activities such as fishing, aquaculture or extraction, which are often difficult to
555 quantify and distinguish from naturally-induced effects (Barbera *et al.*, 2003). Within
556 the framework of the implementation of conservation and management strategies of
557 the maerl beds, and of the improvement of benthic habitat modeling, such
558 quantifications are usable to understand better how the structure of maerl beds
559 differs between them and how it may change with time (Barbera *et al.*, 2003; Méléder
560 *et al.*, 2010).

561 The output from mathematical models may not fully represent the complex
562 functioning of the coastal environment and their use is dependent on the spatial and
563 time resolutions. Nevertheless, the significant relationships established between
564 maerl bed structure and physical factors suggest that, after validations by field data,
565 three-dimensional environmental models can be useful tools to support ecosystem
566 management in particular by enabling the generation of summary statistics to
567 quantify the effect of highly variable hydrological factors. In fact, numerical models
568 can generate continuous variations in a large variety of environmental factors, even
569 in marine areas where monitoring is not easy such as the sea bottom. Considering

570 the diversity of the environmental factors used and the reliability of the 3D models at
571 a large spatial scale (Ménesguen *et al.*, 2007), our results provide a good estimation
572 of the part of the structural heterogeneity of the maerl beds which can be explained
573 by the abiotic factors tested. However, as maerl beds are persistent in time and
574 constituted by long-lived maerl thalli (Barbera *et al.*, 2003), their structural
575 heterogeneity can also result from environmental changes (e.g. climate warming and
576 nutrient enrichment) and/or exceptional climatic events (e.g. storms) which occurred
577 over past years but cannot be correctly estimated with the models used in this study
578 due to the lack of consistent and reliable field validations for years prior to 2009.
579 Another important point to take into account when determining the
580 environmental influence on maerl beds is the taxonomic diversity of the maerl thalli.
581 For example, as it is difficult to distinguish dominant “maerl” species clearly without
582 histological observations or genetic analyses, maerl beds may be constituted by a
583 mix of different coralline algal species. Thus, although the ecological requirements of
584 each “maerl” species are still not clearly known, the relative proportion of these
585 species within a maerl bed could influence variations in the environmental setting of
586 maerl beds.
587

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589

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598

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600

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742

743 Table 1. Subareas and associated number of sampling stations for the Brittany maerl
744 beds. For each maerl bed, the total area and the materials used for the determination
745 of maerl bed structure are indicated.

Maerl bed	Total area (km^2)	Subareas (number of sampling stations)	Materials
Belle-Ile	16.8	B(12)	Shipek grab samples Underwater video recordings
Trévignon	23.0	T1(2), T2(4)	Shipek grab samples Underwater video recordings
Glénan	5.2	G1(5), G2(2)	Shipek grab samples Underwater video recordings
Camaret	1.9	C1 – C10 (1 sampling station / subarea)	Smith-McIntyre grab samples
Rade de Brest	10.7	R1 – R18 (1 sampling station / subarea)	Smith-McIntyre grab samples
Molène	2.8	M1(11), M2(2)	Shipek grab samples Underwater video recordings
Paimpol	22.2	P1(5), P2(12), P3(5)	Shipek grab samples Underwater video recordings

746

747

748 Table 2. Morpho-sedimentary and hydrodynamic characteristics of the maerl beds of
749 the Brittany coast. Mud content was measured in grab samples, while current velocity
750 and wave agitation were generated near the bottom by three-dimensional numerical
751 models. For current velocity and wave agitation, annual mean (bold characters) and
752 annual maximum values are given, while annual minimum values are equal to 0 in all
753 cases.

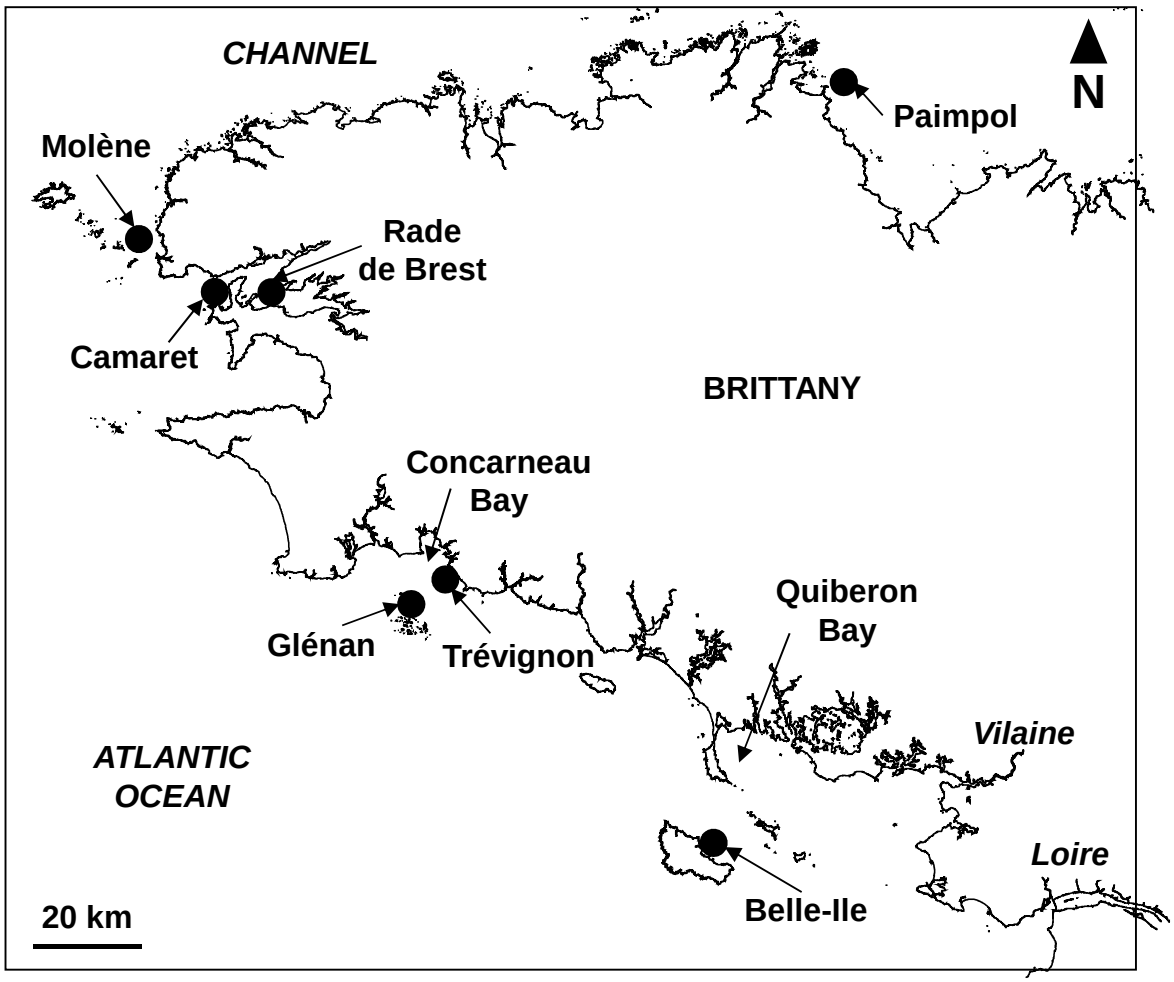
Maerl bed	Mud content (%)	Depth (m)	Current velocity ($m.s^{-1}$)	Wave agitation ($m.s^{-1}$)
Belle-Ile	0	10.0 - 17.9	**0.20** max. = 0.34	**0.62** max. = 3.56
Trévignon	1.0 - 2.0	1.9 - 15.8	**0.02 - 0.06** max. = 0.18	**0.36 - 0.37** max. = 2.86
Glénan	0	4.8 - 19.5	**0.14 - 0.23** max. = 0.49	**0.35 - 0.39** max. = 3.10
Camaret	0.4 - 21.2	13.6 - 20.8	**0.07 - 0.31** max. = 0.44	**0.14 - 0.36** max. = 5.50
Rade de Brest	2.7 - 46.6	0.7 - 6.8	**0.08 - 0.26** max. = 0.43	**0.01 - 0.09** max. = 3.57
Molène	0	7.0 - 12.6	**0.26** max. = 1.52	**0.22 - 0.39** max. = 2.57
Paimpol	0	10.8 - 25.9	**0.59 - 0.73** max. = 1.71	**0.19 - 0.27** max. = 1.87

754

755

Table 3. Physico-chemical properties of the water column generated near the bottom by three-dimensional numerical models for the maerl beds of the Brittany coast. For each environmental variable, annual mean value (bold characters) and annual range of variations are given.

Maerl bed	Temperature (°C)	Salinity	SPM concentration ($mg.L^{-1}$)	Nitrate concentration (µM)	Oxygen saturation (%)
Belle-Ile	**13.6**	**34.2**	**2.2**	**7.3**	**95**
	min. = 7.7	min. = 32.8	min. = 0.6	min. = 2.2	min. = 81
	max. = 18.5	max. = 34.8	max. = 6.9	max. = 19.2	max. = 100
Trévignon	**12.8 - 12.9**	**34.3 - 34.4**	**1.6 - 1.7**	**7.8 - 8.1**	**90 - 92**
	min. = 7.4	min. = 32.5	min. = 0.5	min. = 3.0	min. = 59
	max. = 17.9	max. = 34.9	max. = 5.2	max. = 23.3	max. = 100
Glénan	**13.3**	**34.5**	**1.7 - 1.8**	**6.7 - 6.8**	**94**
	min. = 7.7	min. = 33.0	min. = 0.6	min. = 2.9	min. = 74
	max. = 17.6	max. = 35.1	max. = 5.4	max. = 19.5	max. = 100
Camaret	**13.2**	**35.1**	**0.5**	**6.5 - 7.3**	**94 - 95**
	min. = 9.1	min. = 34.4	min. = 0.4	min. = 0.5	min. = 69
	max. = 16.5	max. = 35.4	max. = 0.8	max. = 21.2	max. = 100
Rade de Brest	**12.2 - 13.1**	**31.9 - 34.5**	**0.7 - 1.6**	**12.0 - 41.0**	**98 - 100**
	min. = 3.9	min. = 24.5	min. = 0.5	min. = 0.1	min. = 78
	max. = 17.9	max. = 35.3	max. = 6.5	max. = 148.2	max. = 100
Molène	**13.2 - 13.3**	**34.8**	**1.2**	**5.5 - 6.1**	**98**
	min. = 8.7	min. = 34.1	min. = 0.5	min. = 3.0	min. = 91
	max. = 17.4	max. = 35.2	max. = 3.1	max. = 18.0	max. = 100
Paimpol	**13.1 - 13.2**	**35.3**	**0.9 - 1.2**	**3.3**	**99**
	min. = 7.8	min. = 35.2	min. = 0.5	min. = 0.2	min. = 97
	max. = 17.9	max. = 35.4	max. = 2.4	max. = 8.1	max. = 100

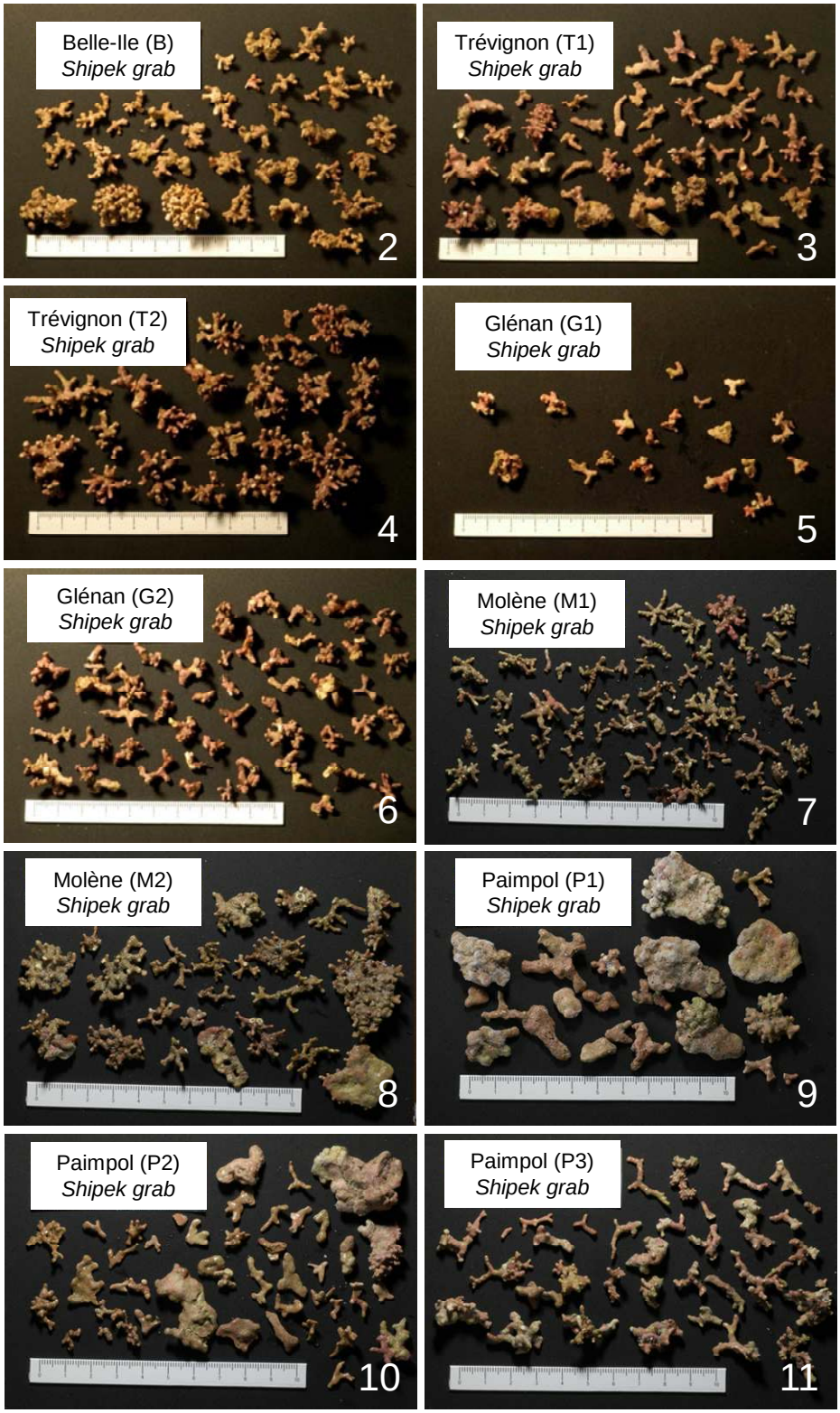


761

762 Figure 1. Location of the seven Brittany maerl beds studied by IFREMER (Paimpol,

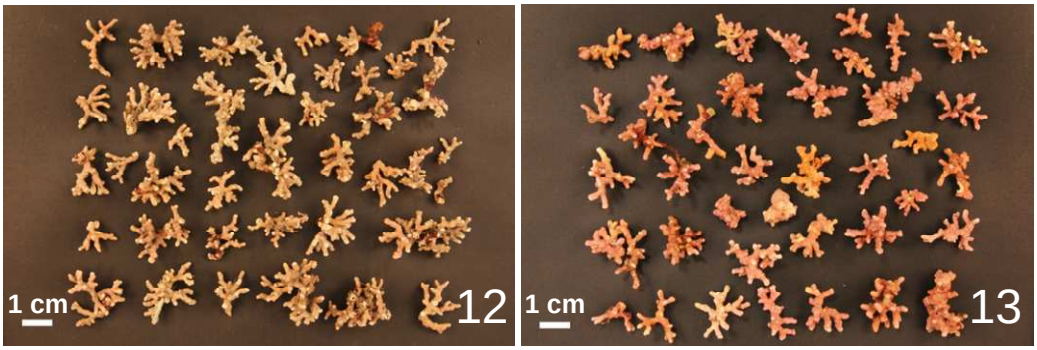
763 Molène, Glénan, Trévignon and Belle-Ile) and IUEM (Rade de Brest and Camaret).

764



765

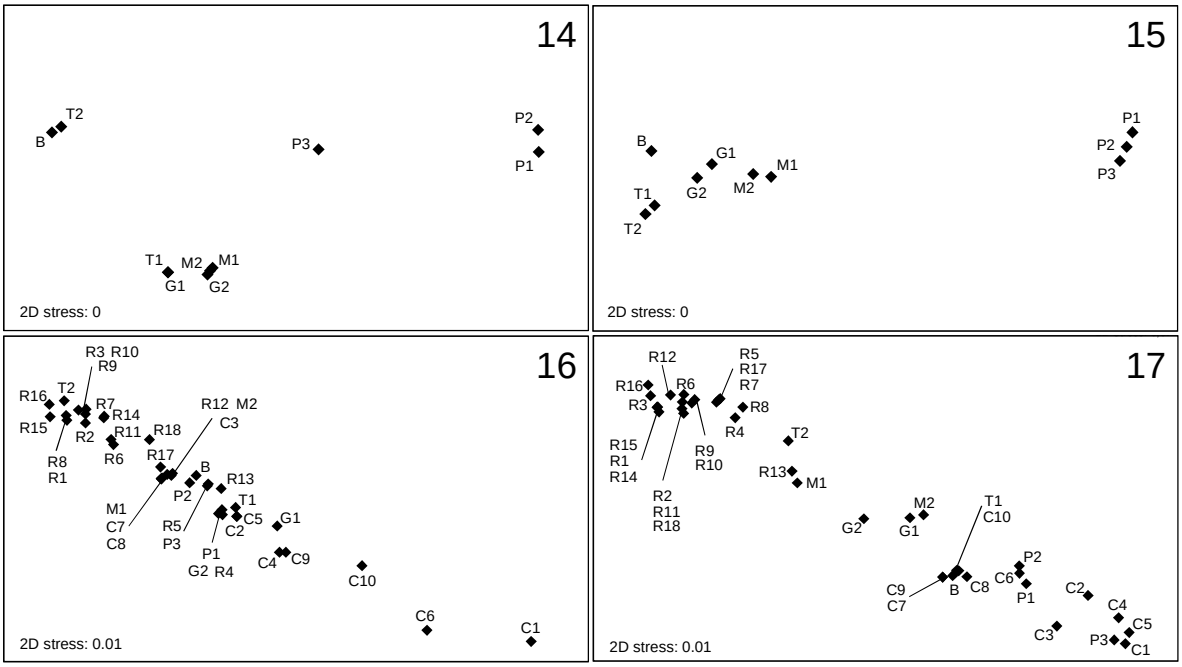
766 Figures 2-11. Examples of thallus morphology found within the subareas of the maerl
767 beds of Belle-Ile (B), Trévignon (T1 and T2), Glénan (G1 and G2), Molène (M1 and
768 M2) and Paimpol (P1, P2 and P3).



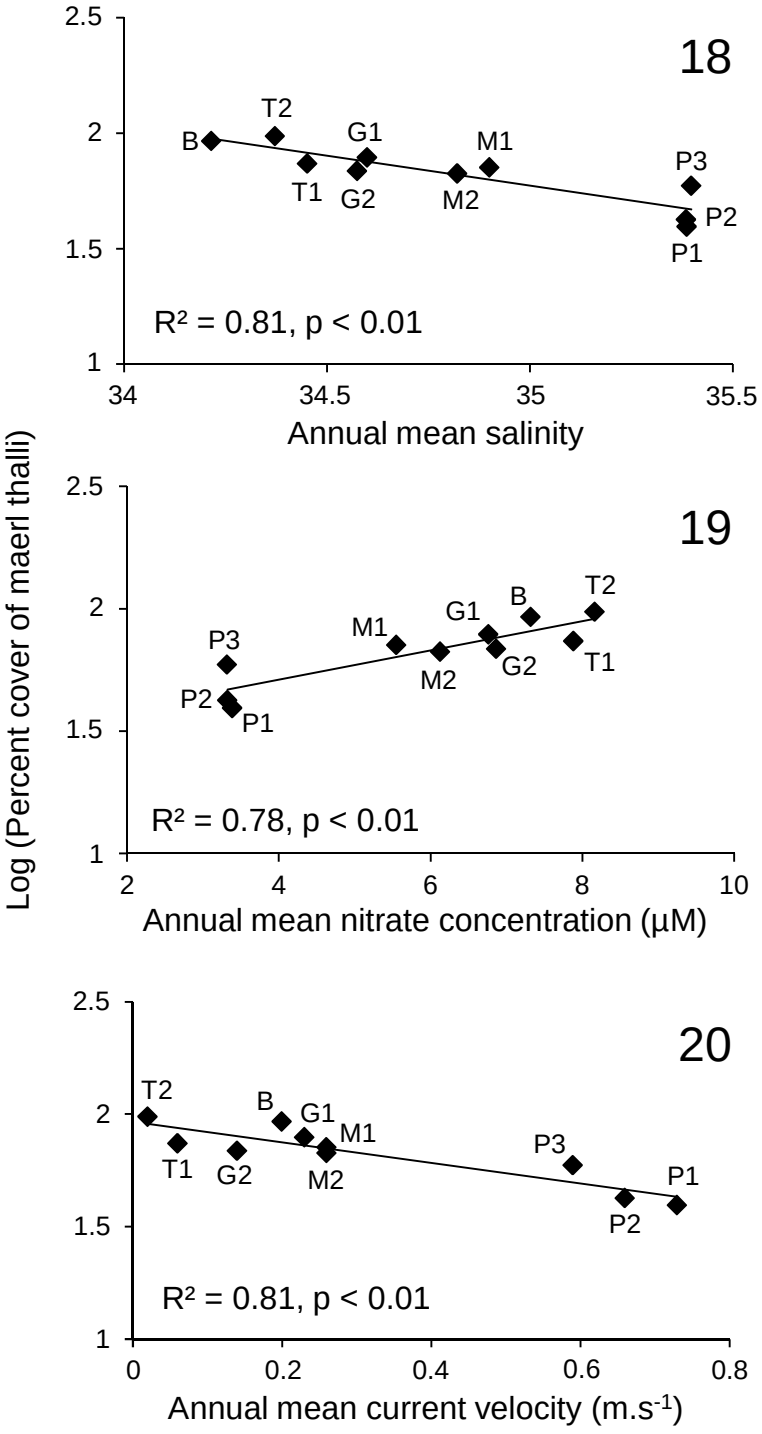
769

770 Figures 12-13. Examples of thallus morphology found within the Smith-McIntyre grab
771 samples collected within the maerl beds of Rade de Brest (subarea R15, Figure 12)
772 and Camaret (subarea C2, Figure 13).

773

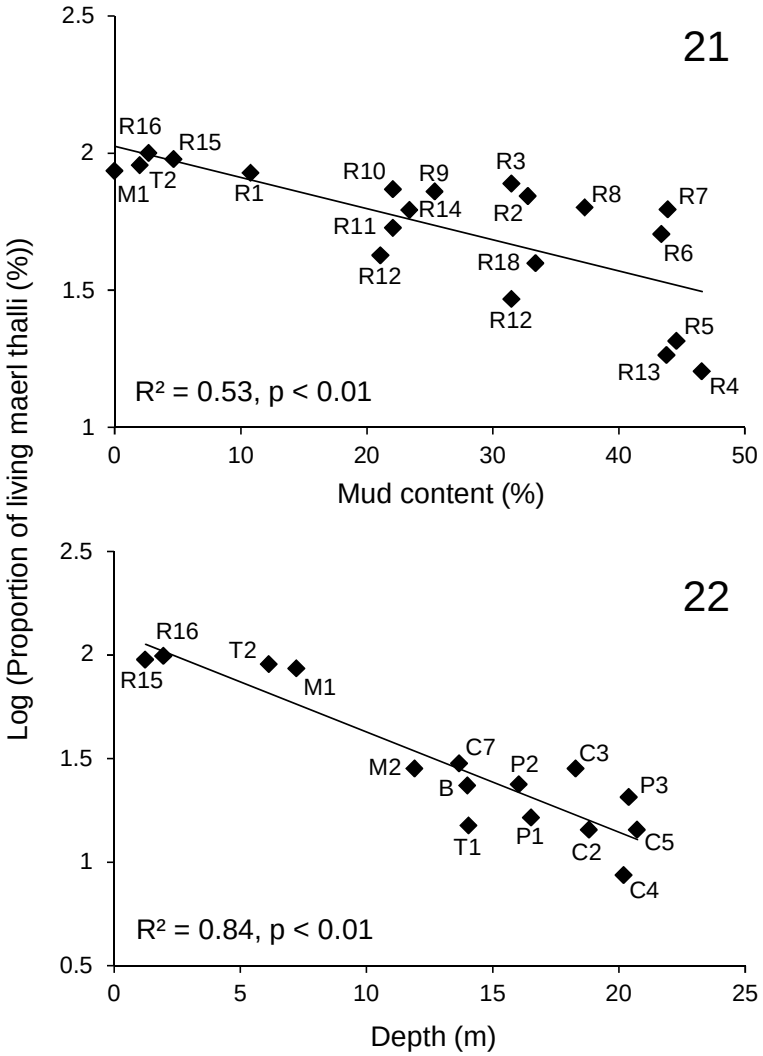


Figures 14-17. Nonmetric multidimensional scaling (NMDS) ordinations of the subareas of the Brittany maerl beds (Belle-Ile (B), Trévignon (T1 - T2), Glénan (G1 - G2), Camaret (C1 - C10), Rade de Brest (R1 - R18), Molène (M1 - M2), and Paimpol (P1 - P3)). NMDS ordinations are based on the percent cover of maerl thalli (Figure 14) and the associated best subset of explanatory environmental variables (annual means of salinity, nitrate concentration and current velocity, Figure 15), and on the proportion of living thalli (Figure 16) and the associated best subset of explanatory environmental variables (depth and mud content, Figure 17).



784

785 Figures 18-20. Significant linear relationships ($p < 0.01$) between the percent cover of
786 maerl thalli observed in the subareas of the Brittany maerl beds (Belle-Ile (B),
787 Trévignon (T1 - T2), Glénan (G1 - G2), Molène (M1 - M2), and Paimpol (P1 - P3))
788 and environmental variables (annual means of salinity, nitrate concentration and
789 current velocity).



790

791 Figures 21-22. Significant linear relationships ($p < 0.01$) between the proportions of
792 living thalli observed in the subareas of the Brittany maerl beds (Belle-Ile (B),
793 Trévignon (T1 - T2), Camaret (C1 - C10), Rade de Brest (R1 - R18), Molène (M1 -
794 M2), and Paimpol (P1 - P3)) and environmental variables (depth and mud content).
795 The relationship with mud content was established for subareas situated at less than
796 10 m of depth (Figure 21), while the relationship with depth was established for
797 subareas showing less than 10 % of mud (Figure 22).

798

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