Quantifying maerl (rhodolith) habitat complexity along an environmental gradient at regional scale in the Northeast Atlantic

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ABSTRACT

Maerl beds are ecologically important marine biogenic habitats founded on a few species of free-living coralline algae that aggregate and form highly complex rhodoliths. The high biodiversity found in these habitats have been mainly justified by the structural complexity that they provide. However, few attempts to quantify this complexity have been made. Maerl species distribution, density, rhodolith growth forms, and shapes vary with environmental conditions. Hydrodynamics and depth have been shown to drive morphology. Using species-specific metrics such as sphericity and branching density, as well as diameter and fractal dimension at the rhodolith level, and maerl density at the habitat level, we quantified the habitat complexity within ten maerl beds at a regional scale (along ~400 km of the coastline of Brittany in Western France). Using both long-term monitoring data and environmental models, we investigated how maerl habitat complexity varies among beds and which environmental conditions drive those differences. The effects of currents, exposure to wind-generated waves, temperature and sediment granulometry were evaluated. We confirmed variations in complexity in maerl beds at the habitat and rhodolith levels at local and regional scales, which might have ecological and conservational implications for their associated biodiversity. The analysed environmental conditions drive around a third of the variance in habitat complexity. Sediment granulometry is the main driver of maerl habitat complexity in Brittany, while the isolated effects of depth and hydrodynamics accounted for less than 5% of the variability each. Our results have important implications for paleoecology, and we suggest that maerl facies should be interpreted carefully. Our study provides a first attempt at explicitly quantifying maerl habitat complexity, and further contributes to the understanding of this fundamental ecological question.

1. Introduction

Crustose or non-geniculate coralline algae (Corallinophycidae, Rhodophyta) are important bioengineers that can aggregate and form free-living or unattached complex nodules called maerl or rhodoliths (Foster, 2001). Although the term maerl has sometimes been related to fruticose rhodoliths only, both terms have been historically used interchangeably (Foster, 2001; Wilson et al., 2004; Aguirre et al., 2017), mainly in Europe, and more so in Brittany, as maerl is originally a Breton word used both to describe the habitats such coralline nodules formed and the soil treatment based on nodules of any growth form (Grall and Hall-Spencer, 2003). For clarity, we use both terms as synonyms and refer to individual nodules of any growth form as rhodoliths and to the habitats dominated by them as maerl beds. Living and/or dead rhodoliths can accumulate forming maerl beds, which are ecologically

important habitats distributed worldwide that can be found from coastal areas to depths over 200 m (Riosmena-Rodríguez et al., 2017). Maerl beds occur on soft bottoms of variable sediment compositions, from mud to coarse sand (Grall et al., 2006; Wilson et al., 2004; Schubert et al., 2020).

Maerl-forming coralline algae are usually long-lived (up to over 100 years) and have extremely low growth rates, with estimates ranging from <0.01 to 0.48 mm.y^{-1}, and a widely accepted average of 0.4 mm. y^{-1} (Bosellini and Ginsburg, 1971; Foster, 2001). Species distributions are mostly limited by light availability, temperature, and salinity (Carvalho et al., 2020; Wilson et al., 2004), which affect growth rates and reproduction. Additionally, rhodolith growth patterns and shape have long been thought to depend on environmental conditions, namely on hydrodynamics and depth (Bahia et al., 2010; Bosellini and Ginsburg, 1971; Peña and Criado, 2008; Riosmena-Rodríguez et al., 2017),

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although others argued that growth forms could be independent of water motion (Adey and Macintyre, 1973). Maerl species such as *Phymatolithon calcareum* and *Lithothamnion corallioides* are considered resistant to different environmental pressures since they can recover from and reproduce through moderate fragmentation, and have abundant starch reserves that allow them to survive in poor light conditions (Foster, 2001; Wilson et al., 2004). However, they are considered low-resilient due to their slow growth rate and the fact that they face several anthropogenic threats globally (Barbera et al., 2003; Grall and Hall-Spencer, 2003; Wilson et al., 2004; Ragueneau et al., 2018).

A cornerstone of ecology is that structurally complex habitats promote species richness by providing more niches and, therefore, more ways of resource exploitation (MacArthur and MacArthur, 1961; Tews et al., 2004). The high diversity harboured by maerl beds is historically attributed to the three-dimensional complexity created by the rhodoliths and the high local productivity found in these habitats (Hinojosa-Arango and Riosmena-Rodríguez, 2004; Wilson et al., 2004; Nelson, 2009; Riosmena-Rodríguez et al., 2017; Schubert et al., 2020). Recently, the high community stability and functional redundancy in Breton maerl beds (France) have also been linked to their biogenic structure (Boyé et al., 2019). Nevertheless, only a few projects have explicitly investigated the role of maerl structural complexity on biodiversity (Hinojosa-Arango and Riosmena-Rodríguez, 2004; Harvey and Bird, 2008; Berlandi et al., 2012; Gabara et al., 2018).

Although it has been extensively explored, generalization of the topic has been hindered by several reasons, terminology being one of them (Bell et al., 1991). Terms such as habitat or spatial structure (Warfe et al., 2008), habitat or spatial heterogeneity (Vroom et al., 2005), architectural complexity (Dibble et al., 1996; Lawton, 1983), structural complexity (Commito and Rusignuolo, 2000) among others, have been used interchangeably with habitat complexity in the literature, which has limited the understanding of its role (Bell et al., 1991; Kovalenko et al., 2012; Tokeshi and Arakaki, 2012). In their book, Bell et al. (1991) define habitat complexity as one aspect of habitat structure: "that provided by the arrangement of objects in space", specifically the abundance of structural elements. Tokeshi and Arakaki (2012) further expanded the concept, arguing five facets of complexity should be taken into account when assessing it: the scales of habitat complexity; the diversity of complexity-generating elements; the spatial arrangement of these elements; their sizes and their abundances or densities. In this study, we use Tokeshi & Arakaki's definition to describe habitat complexity and directly assess four out of the five facets they propose, with the exception of the spatial arrangement of complexity-generating elements.

Most of our understanding on habitat complexity in marine systems comes from studies on a few or a single foundation species in its ecosystem. Foundation species are key ecosystem engineers – spatially dominant organisms whose biogenic structure promotes species coexistence through the amelioration of physical and biological stress (Angelini et al., 2011; Ellison, 2019). Most of the available studies on habitat complexity in different types of habitats are of qualitative nature, and there is still a lack of hypothesis-driven quantitative assessments (Bell et al., 1991; Kovalenko et al., 2012; Tokeshi and Arakaki, 2012). This is especially the case for maerl beds. Although some authors have investigated maerl complexity, studies explicitly aiming to quantify it are still rare. When it has been investigated, most studies analysed it qualitatively (Hinojosa-Arango and Riosmena-Rodríguez, 2004; Villas-Boas et al., 2014) or quantified it indirectly only through a single or a few morphological characters specific to rhodoliths (Sciberras et al., 2009; Gagnon et al., 2012; Bernard et al., 2019), with only few very recent attempts on directly quantifying it (Solano et al., 2022; Voerman et al., 2022).

Two main morphometrics have been used as - or linked to - habitat complexity: branching density and sphericity. These are complementary metrics and have both been linked to the associated faunal diversity (de Figueiredo et al., 2007) and environmental conditions (Bosellini and Ginsburg, 1971; Bosence, 1976; Steller and Foster, 1995; Villas-Boas et al., 2014). More complex rhodoliths (higher branching density) have been associated with higher macrofaunal richness and abundance (de Figueiredo et al., 2007) and macrofaunal densities have been shown to increase with rhodolith sphericity (Sciberras et al., 2009). These metrics are also used as tools for paleoenvironmental reconstructions based on maerl facies. Different rhodolith growth forms and shapes found in maerl facies are used as proxies for environmental conditions, usually assuming that higher hydrodynamic regimes allow for more spherical and branched rhodoliths due to constant turning, which would allow for homogeneous growth (Bosellini and Ginsburg, 1971; Adey and Macintyre, 1973; Bosence, 1976; Bassi, 1998; Aguirre et al., 2017; Bassi et al., 2017). Similarly, rhodolith morphology has been shown to vary with water depth, which most authors have related to differences in sediment deposition along depth strata (Bahia et al., 2010; Pascelli et al., 2013; Cabanellas-Reboredo et al., 2018; Otero-Ferrer et al., 2020).

Only since the 1990s, techniques such as interstitial space analysis (Dibble et al., 1996; Warfe et al., 2008) and 2D fractal analysis (Sugihara & May 1990; Gee and Warwick, 1994; Thomaz et al., 2007) have been used to assess habitat complexity without relying on species-specific attributes. Fractal analysis revolutionized this field as it is a means of directly estimating complexity through the fractal dimension (D), which is a measure of the change in detail as a function of the change in scale (Sugihara & May 1990). However, to our knowledge, these methods are yet to be applied to rhodoliths, and quantitative inter-habitat comparisons of structural complexity are still not possible.

In European waters, maerl beds are found from Svalbard (Norway) to Portugal and have also been reported in the Canary Islands (Foster, 2001; Peña et al., 2014). In the Northeast (NE) Atlantic, maerl beds are mostly formed by two foundation species, *Phymatolithon calcareum* and *Lithothamnium corallioides* (Hapalidales). Most of these beds are concentrated in Brittany, France, hence the Breton word maerl being widely used in Europe instead of the counterpart rhodolith. Over 70 beds have been reported in Brittany over the years, and they can be very small (from 10 to 100 m^2) or cover large areas (>20 km^2). The region also contains the thickest known beds in the world, reaching over 10 m in the Glénan Islands (Grall and Hall-Spencer, 2003).

In Brittany, maerl extraction was an ongoing activity for centuries, from the use of maerl sand for soil treatment by Celtic people to the extraction for the construction industry. Although maerl extraction is no longer allowed in most European countries, several conservation threats are still present in the region including invasive species, fishing, aquaculture, and eutrophication (Barbera et al., 2003; Grall and Hall-Spencer, 2003; Dutertre et al., 2015; Hernandez-Kantun et al., 2017; Ragueneau et al., 2018). Of those, oyster and fish aquaculture and, more importantly, dredging for commercial species of scallops and clams are thought or have been shown to extremely impact these habitats by reducing maerl vitality and habitat complexity (Grall and Hall-Spencer, 2003; Ragueneau et al., 2018; Bernard et al., 2019). Ocean acidification and global warming also pose risks to maerl structure and vitality in the long term (Wilson et al., 2004; Nelson, 2009; Kamenos et al., 2013; Martin and Hall-Spencer, 2017; Cornwall et al., 2020). Therefore, a better understanding of how to quantify habitat complexity provided by maerl beds is essential for predicting how different pressures could be impacting it.

Our study aims to fill these gaps and our main objective is to quantify the complexity provided by maerl beds and understand its links to the physical environmental conditions. By investigating different aspects of maerl complexity and linking them to environmental conditions from different beds in Brittany, we aim to explore three main questions: First, we investigate which metrics are necessary to adequately describe maerl structural complexity. While different metrics (rhodolith size, sphericity, branching density, fractal dimension and the density of rhodoliths in each maerl bed) were selected to collectively describe complexity, it is unclear which are complementary or redundant, as they might measure - in different ways - the same aspect of complexity as defined by Tokeshi

and Arakaki (2012). Then, we evaluate how habitat complexity varies along the studied beds. Due to their autecology and since they're found in contrasting environments, we expect that at the maerl beds will present different levels of habitat complexity at a regional level. Finally, we analyse which are the main environmental drivers of maerl habitat complexity and their effects. Since hydrodynamics and depth have been shown to play a major role in determining maerl structural complexity, we expect that high-energy conditions in shallower beds will lead to higher complexity.

2. Methods

2.1. Study area, sampling design and data collection

Rhodoliths of 10 subtidal maerl beds (referred to sites from here on) along the coast of Brittany were sampled between 2019 and 2020 (Fig. 1). These sites were chosen as they are monitored in the context of the ongoing REBENT (Réseau Benthique) monitoring program (2003-present; http://www.rebent.org) and encompass most of the environmental settings found along Brittany's coast, from very shallow (<5 m) to deeper beds (up to 22 m water depth), with varying hydrological and sedimentological characteristics (Grall and Hall-Spencer, 2003; Grall et al., 2006; Boyé et al., 2019). At each REBENT site, three fixed sampling points distributed at least 200 m apart from each other were defined for monitoring since 2003.

Between 2019 and 2020, rhodoliths were sampled at the three sampling points of each site using three Smith-McIntyre grabs of 0.1 m^2. All sampled specimens (rhodoliths) with at least one axis greater than 10 mm were selected. For each sampling point, 12 of them were randomly sorted, totalling 360 specimens analysed. Sediment samples were collected yearly at each sampling point, as additional cores were taken for grain size distribution and organic matter content assessment.

2.2. Habitat complexity metrics

In order to quantify habitat complexity through rhodolith attributes, metrics typically used to describe maerl morphology were taken for each rhodolith (Table 1). Two of them, sphericity and branching density have been related to habitat complexity because they affect faunal communities (Bosellini and Ginsburg, 1971; de Figueiredo et al., 2007; Riosmena-Rodríguez et al., 2017; Sciberras et al., 2009; Villas-Boas et al., 2014). Sphericity was estimated as described by Sneed and Folk (1958) using the longest diameters of the three main axes of the rhodolith,

Table 1
Habitat complexity metrics quantified in this study and the aspect of habitat complexity they assess, following the definition by Tokeshi and Arakaki (2012).

| Variable name	Metric	Aspect of habitat complexity
L	Largest rhodolith diameter (mm)	Size of complexity-generating elements;
I	Intermediate rhodolith diameter (mm)	Diversity of complexity-generating elements
S	Smallest rhodolith diameter (mm)	
Sphericity	Rhodolith shape	Diversity of complexity-generating elements
DR1		
DR2		
DR3		
Broken density	Number of broken apical branches · cm^{-2}	Diversity of complexity-generating elements;
Branching density	Number of apical branches · cm^{-2}	Density of complexity-generating elements
D$_{bin}$	Fractal dimension estimated through binary images	
D$_{gray}$	Fractal dimension estimated through grayscale images	
Maerl density	Number of rhodoliths · m^{-2} at each site	Density of complexity-generating elements; Scales of habitat complexity
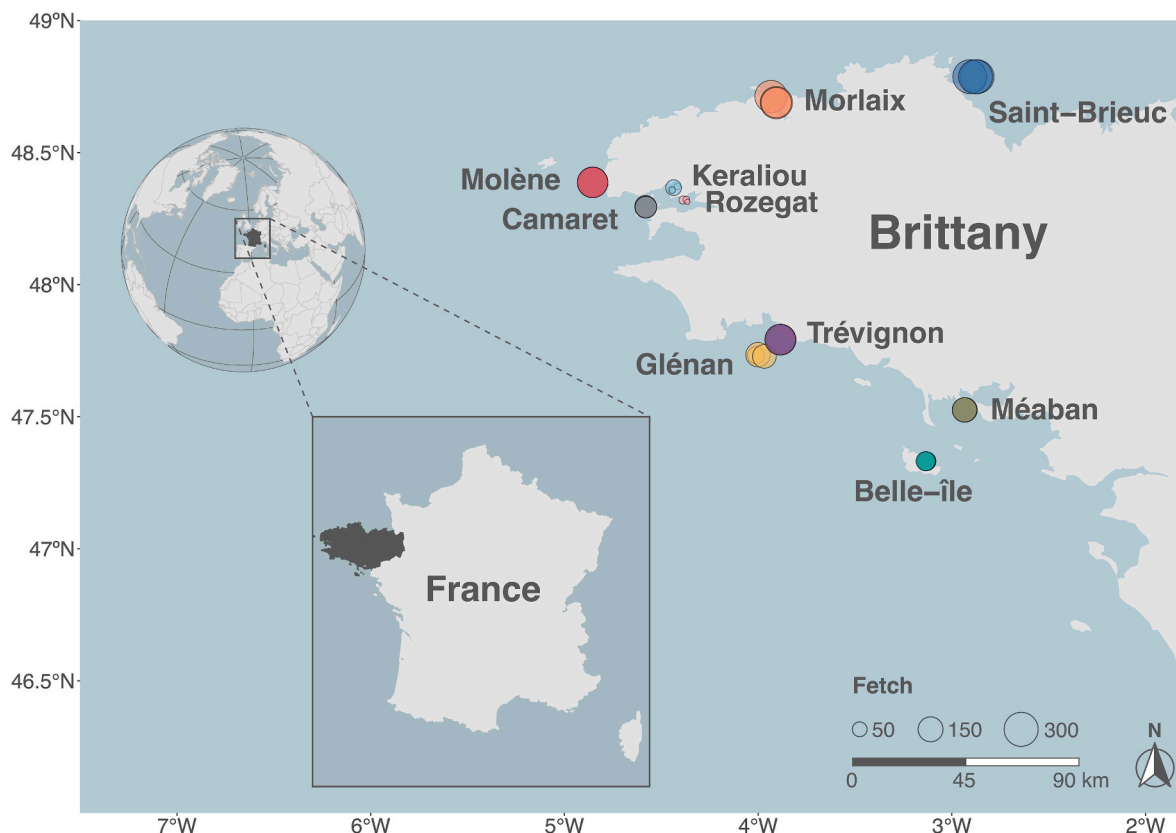
Fig. 1. Map of the study area, containing the 3 sampling points for each site (which overlap in some cases due to small bed size and large fetch values). Each circle represents a sampling point and their areas refer to the maximum fetch values (expressed in km).

which were measured to the closest millimetre using a Vernier calliper. The maximum projection sphericity and three diameter ratios were calculated: $Sphericity = \sqrt[3]{S^2/(L \times I)}$, $DR1 = S/L$, $DR2 = (L - I)/(L - S)$, and $DR3 = I/L$ where L is the longest diameter of the rhodolith, I is the longest diameter of the intermediate size axis, perpendicular to L, and S is the longest diameter of the shorter axis, perpendicular to both L and I. Together, the three measures provide an estimation of rhodolith shape, values of Sphericity are proxies for ellipsoidal (low values) to spheroidal (high values) shapes, DR1 values increase from discoidal to spheroidal shapes and DR2 values increase from discoidal to ellipsoidal values. Branching density was estimated by randomly placing a 1 cm^2 quadrat over each specimen five times and counting the number of apical branches entirely placed inside the quadrat. The average number of apical branches per cm^2 was taken as the final branching density for each specimen (Steller et al., 2003). Shape and growth form were used to classify specimens following Woelkerling et al. (1993) and Bosence (1976, 1983). To visualize the diversity in rhodolith sphericity, shape triplots (Graham and Midgley, 2000) modified as in Bassi et al. (2017) to

Fig. 2. Six of the 12 analysed specimens collected for each sampling point (1–3) at each site. The pictures were used for fractal analysis after treatment. Most specimens are fruticose, with the exception of some lumpy and warty rhodoliths in sites Glénan, Belle-île and Saint-Brieuc.

indicate Bosence's shape classes were performed for each sampling site.

To account for complexity at the habitat scale, the density of rhodoliths (referred to as maerl density from now on) was also estimated. Data available from the *Observatoire Marin de l'IUEM* acquired over the years (from 1997 to 2004) was gathered. Samples were collected using 15×10 cm box-corers, and only rhodoliths bigger than 5 mm and free of sand were taken into account. Six replicates were taken at each sampling site, and the final average maerl density was calculated and expressed in rhodoliths/m^2. It's important to note that these data were collected before the REBENT monitoring program and therefore were not sampled at the same points as the rhodoliths analysed in this study and for which the physical environment measurements were taken. Hence, average maerl density was defined at the site level - with the three points of each site having the same value.

For fractal analysis, an image-based analysis was adapted from methods by Warfe et al. (2008) and Thomaz et al. (2007). A Pentax K–S2 camera with a LAOWA Venus UltraMacro 60 mm lens was mounted on a tripod in front of a black background and each specimen was positioned at the same distance from the camera. The specimens were placed under direct light from two directions to decrease shadow noise. At least five photographs of each specimen were taken, each with a different depth of field. The first was taken focusing on the parts closest to the camera, and each successive photograph was taken focusing back until all structures were completely blurred. The number of pictures with different depths of field necessary for the final focus stack varied due to differences in the rhodoliths attributes such as size, arrangement and density of branches and overall shape (Fig. 2). All images were then edited using Adobe Photoshop 2021, and focus stacks were created in Zerene Stacker (https://zerenesystems.com/) to have a better 3-D representation of the rhodolith structure. The final focus stacks were converted into grayscale for differential fractal analysis and further edited using Fiji for ImageJ (Schindelin et al., 2012) to get an 8-bit binary image with only the outline of each specimen for classical fractal analysis.

Both grayscale and binary images were analysed using the open-source ImageJ add-on FracLac (Karperian, 1999), in which the box-counting method was used to estimate fractal dimensions (D). For binary images, the fractal dimension D_{bin} was determined by the classical box-counting method: estimating the slope of log N(s) as a function of log ($1/s$), in which s represents the grid calibre (the size of each box) and N(s) is the number of boxes containing part of the object in that grid calibre (s). The counting process was implemented by superimposing regular grids of boxes of calibre s over the image of each specimen. A linear series with the minimum calibre of 5 pixels and a maximum of the equivalent of 45% of the image was set, and the maximum number of box calibres was used (100). FracLac repeats the process using different starting grid positions and calculates the mean Fractal Dimension. The default of 12 starting grid positions was set, as recommended by the authors of the software. All images had the same size and were analysed using the same 12 starting grid positions.

For grayscale images, FracLac offers analysis in which the fractal dimension or D_{gray} is calculated from the relationship between the change in average intensity and the change in grid calibre. Instead of counting the number of boxes in which the object is found, FracLac computes the difference in pixel intensity (ranging from 0 to 255) for each box (Sarkar and Chaudhuri, 1992; Karperian, 1999). The greyscale method "Differential Volume Variation Plus 1" was chosen as it yielded the smallest variance between different grid positions for each photograph. The number of calibres and starting grid positions was the same as for binary analysis.

2.3. Physical environmental data

Due to the slow growth rates of the two main maerl species found in the study area and to ensure consistency among sites and points, environmental conditions from the 12 years (2007–2018) prior to specimen sampling were taken into consideration into the analysis.

For granulometry, sediments were dried for 24 h at 60 °C and separated into 15 fractions that were measured for masses. Fractions were afterward grouped from mud (<63 μm) to sand (63 μm–2 mm) and gravels (>2 mm), with R package G2Sd (Fournier et al., 2014). Mean grain size and the Trask Sorting Index, $\sqrt{\frac{Q_{25}}{Q_{75}}}$ (in which Q_{25} and Q_{75} are the first and the third quartiles, respectively), were also calculated for each sampling point. Organic matter content was estimated by mass loss after combustion at 450 °C for 5 h. To avoid excluding entire sampling sites or years, missing data were estimated using k-Nearest neighbour imputation (Acuña and Rodriguez, 2004)t using the median value of the 5 closest neighbours computed on Gower distance. Of the selected years, 27 out of 348 (<8%) observations were missing for granulometry, while 42 out of 348 (12%) observations were missing for organic matter content.

For bathymetry, data was downloaded from the EMODnet Digital Terrain Model 2020 (EMODnet Bathymetry Consortium, 2020; https://www.emodnet-bathymetry.eu/data-products). The model has been generated for European sea regions from selected bathymetric survey data sets, composite Digital Terrain Models (DTMs), Satellite-Derived Bathymetry (SDB) data products, and gaps with no data coverage were completed by integrating the General Bathymetric Chart of the Oceans (GEBCO) Digital Bathymetry. The DTM is a grid of $1/16 \times 1/16$ arc minute of longitude and latitude (around 115×115 m). The bathymetry was extracted at the point level by averaging the model data within a radius of 115 m (equivalent to 1 grid cell) around each sampling point.

The hydrological data were extracted from the Atlantic - Iberian Biscay Irish - Ocean Physics Reanalysis Product (version 3.3) issued from the E.U. Copernicus Marine Service Information (Iberia Biscay Irish Monitoring Forecasting Centre, 2020). The model has a resolution of $1/12°$ (equivalent to ~ 9 km^2 grids). For temperature, seafloor potential temperatures were extracted from the "dataset-ibi-reanalysis-phys-005-002-daily" product which contains daily averages. For currents, data was extracted from the "dataset-ibi-reanalysis-phys-005-002-hourly" product, which contains the hourly values of the Eastward velocity (o) and Northward velocity (vo) components of the current. The hourly current velocity was calculated as $U_{Current} = \sqrt{(uo^2) + (vo^2)}$. The daily average was then calculated for each grid cell. Finally, for the estimate at the point level for both temperature and current velocity, the data was extracted by averaging the models' values within a 9 km radius (one grid cell) of each sampling point of the study. In cases where the sampling point was outside the model's grid, the minimum distance from that point to one of the model's grids was added to a nine km radius.

Fetch is a measure of the unobstructed distance that wind can travel over a surface in a constant direction, in the ocean it represents the area in which ocean waves are generated by the wind and can be used as an overall wind exposure for a specific marine location. Fetch was calculated using land polygon data for the study area manually retrieved through QGIS (QGIS Development Team, 2021) and the fetchR package (Seers, 2020). The maximum wind fetch, referred hereafter to as fetch, was calculated in kilometres as the largest length of nine radiating fetch segments (one every 10°) with a maximum distance for any fetch segment set to 300 km.

2.4. Statistical analysis

In order to investigate how habitat complexity varies along the 10 studied sites, a Principal Component Analysis (PCA) was performed on the standardized box-cox transformed (Box and Cox, 1964) complexity values of each sampling point. A Permutational Analysis of Variance (PERMANOVA - Anderson et al., 2008) was performed on the box-cox transformed complexity metrics as a function of sites and points as fixed factors, with points nested in sites. The assumption of homogeneity of multivariate dispersions was tested prior to the analysis. Additional

pairwise tests with Holm's correction were performed to evaluate the differences between sites.

Similarly, to describe the different environmental conditions among studied beds and identify the main drivers of variance, a PCA was performed containing all environmental variables but mean grain size (Table A1), as it was highly correlated to the percentage of gravel. Again, the box-cox transformation was chosen in order to improve data symmetry, a desired property for linear methods such as PCA. Then, to evaluate which environmental factors could be driving regional differences in maerl complexity, a Redundancy Analysis (RDA - Rao, 1964) of the habitat complexity as a function of the physical environment was performed. After testing for collinearity, and performing variable selection, mean current velocity, fetch, depth, the trask sorting index, and the percentage of mud were selected as explanatory variables. The significance of the RDA was then evaluated through a free permutation test under a reduced model with 9999 permutations, and the adjusted R^2 was calculated to evaluate the model fit (Peres-Neto et al., 2006). Finally, when computing the RDA, variation partitioning was performed to further explore the contributions of each selected variable to the overall complexity. For the variation partitioning, the variables used for the RDA were grouped in three main sets: granulometry (containing the variables mud, trask, and sand), hydrodynamics (containing fetch and current velocity) and bathymetry (depth). Variation partitioning allows to quantify the fraction of the variance explained by each environmental set when combined to the effects of the other variable sets (combined effect), as well as their effect alone, when all other variable sets are controlled for (isolated effect; Borcard et al., 2018).

All analyses were performed using R version 4.2.0 (R Core Team, 2022). The k-nearest neighbour imputation was done using the VIM R package (Kowarik and Templ, 2016). The box cox transformation of explanatory variables was applied with the *EnvStats* package (Millard, 2013). Forward selection was performed using *adespatial* (Dray et al., 2021). All other analyses relied on the *vegan* package (Oksanen et al., 2020).

3. Results

3.1. Maerl morphometrics and habitat complexity

Although species determination (histology and molecular biology) was not conducted, visual identification based only on growth forms and colour of the analysed specimens suggests a higher proportion of *Lithothamnium corallioides*. The great majority of specimens analysed were of fruticose growth forms, although a few specimens were lumpy or warty,
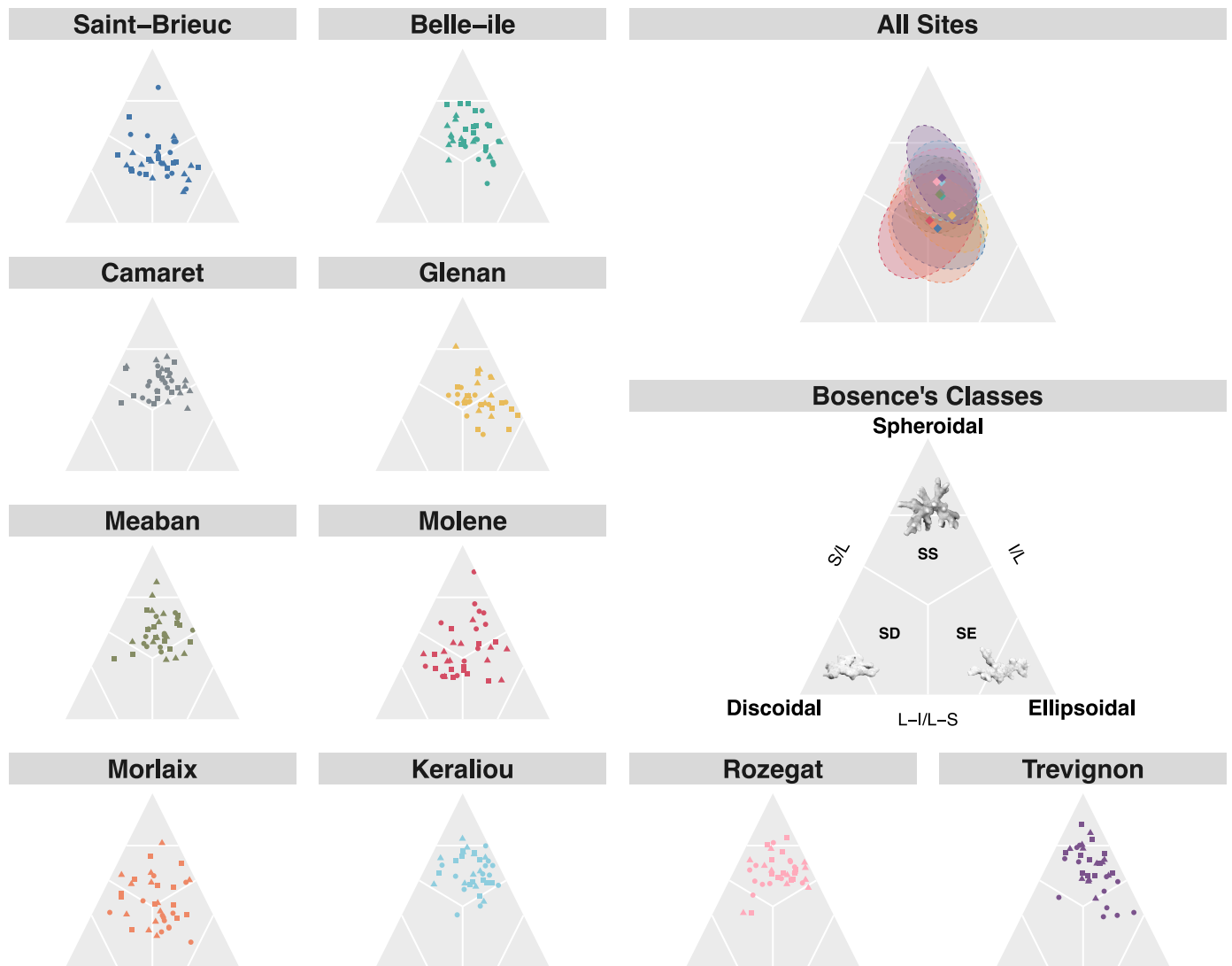

Fig. 3. Triplots of rhodolith sphericity, modified as by Bassi et al. (2017) to indicate Bosence's shape classes (Bosence, 1976, 1983). Left and bottom panels: intra-site variability (different point shapes represent the three sampling points in each site). Top-right panel: inter-site variability with centroids and 75% confidence interval ellipses. Middle-right panel: Bosence's shape classes, where SS = Sub-spheroidal, SD = Sub-discoidal, SE = Sub-ellipsoidal.

mainly in the beds of the Glénan Islands, Belle-île, and Saint-Brieuc (Fig. 2). In regards only to rhodolith shape, the triplots (Fig. 3) show that Keraliou, Rozegat, and Trévignon presented mostly sub-spheroidal to spheroidal rhodoliths. The rhodoliths from Camaret, Belle-île, and Méaban were mostly sub-spheroidal, although a few were sub-ellipsoidal. Molène and Morlaix were the most variable sites in terms of rhodolith shape, presenting both sub-spheroidal, sub-discoidal, and sub-ellipsoidal rhodoliths. Saint-Brieuc and Glénan presented the least spheroidal rhodoliths, with the first containing mostly sub-discoidal and sub-ellipsoidal rhodoliths, and the second presenting the highest amount of sub-ellipsoidal rhodoliths.

The PCA (Fig. 4) showed that while some complexity metrics were redundant (such as Sphericity and the diameter ratios DR1 and DR2, as well as the Largest and Intermediate diameters), others were complementary. The first 2 axes represent around 54% of the variation among and within beds. The analysis confirmed large variations among the maerl beds in Brittany, as well as some intra-bed variations in terms of habitat complexity. The first axis (PC1) was mainly driven by the smaller rhodolith diameter (S), as well as the fractal dimension from binary images (D_{bin}), which were mainly responsible for intra-site variations. The second axis (PC2) was mainly driven by maerl density and the largest rhodolith diameter, but also by sphericity, all of which contributed greatly to differences between sites. The fractal dimension acquired from grayscale images (D_{gray}) and the branching density contributed slightly to both intra and intersite variability, while the density of broken branches had a small effect on the overall variation.

The analysis revealed a clear gradient from Rozegat to Saint-Brieuc, the first being a dense bed with small and spheroidal highly branched and complex rhodoliths and the latter presenting low maerl density and containing mostly large (up to 4.5 cm, Fig. 2) and platy, less complex rhodoliths. A less pronounced gradient is seen from Trévignon - with highly branched, spheroidal and complex (higher fractal dimension) rhodoliths but very low maerl densities - to Glénan, which is a denser bed with less branched, platier, and less complex rhodoliths. The Méaban, Camaret, Belle-île, Morlaix, and Glénan sites were

characterized by average to low values of rhodolith complexity and maerl density and were overall quite similar in terms of complexity, although the rhodoliths from Glénan were less spheroidal.

The PERMANOVA confirmed the differences between sites were significant ($R^2 = 0.31$, F = 18.8, p = 0.001) and that although the intra-site differences were significant, they represented a much smaller part of the variance in the data ($R^2 = 0.09$, F = 2.31, p = 0.001). Both factors explained around 40% of the total variance in the data, confirming extensive regional variability in maerl complexity. The assumption of homogeneity of multivariate dispersions was initially rejected, but a Tukey's pairwise test revealed that the Saint-Brieuc and Molène sites were the ones usually significantly different from a few sites. However, those differences were subtle, and the exclusion of both sites from the PERMANOVA resulted in very slight differences in the model fit suggesting that the differences were indeed due to location and not dispersion effects (Suppl. material).

3.2. Environmental description

The PCA of the physical environmental variables confirmed extensive variations at the regional level, with the first two axes representing around 64% of the variation within and among sites. The first axis highlights a great variety of physical environmental conditions among the studied sites, with a gradient from more exposed, high-energy, and deeper environments (up to ~23 m water depth), to more sheltered, low-energy, and shallower (<5 m water depth) sites (Fig. 5, Tab. AI). The second axis is mostly related to the within-site variation over 12 years, which is explained by changes in sediment granulometry. At one end of this spectrum, Saint-Brieuc is the site with the highest energy conditions, reaching the (arbitrary) maximum limit of 300 km of fetch, exposed to both winds from the East and North (Fig. 1). The three points in that site are also characterized by the second strongest currents in the study area, with mean velocities ranging from 0.51 to 0.6 m·s[1]. It is also the deepest site analysed in this study, with one of its points reaching almost 23 m water depth. In terms of granulometry, the Saint-Brieuc bed
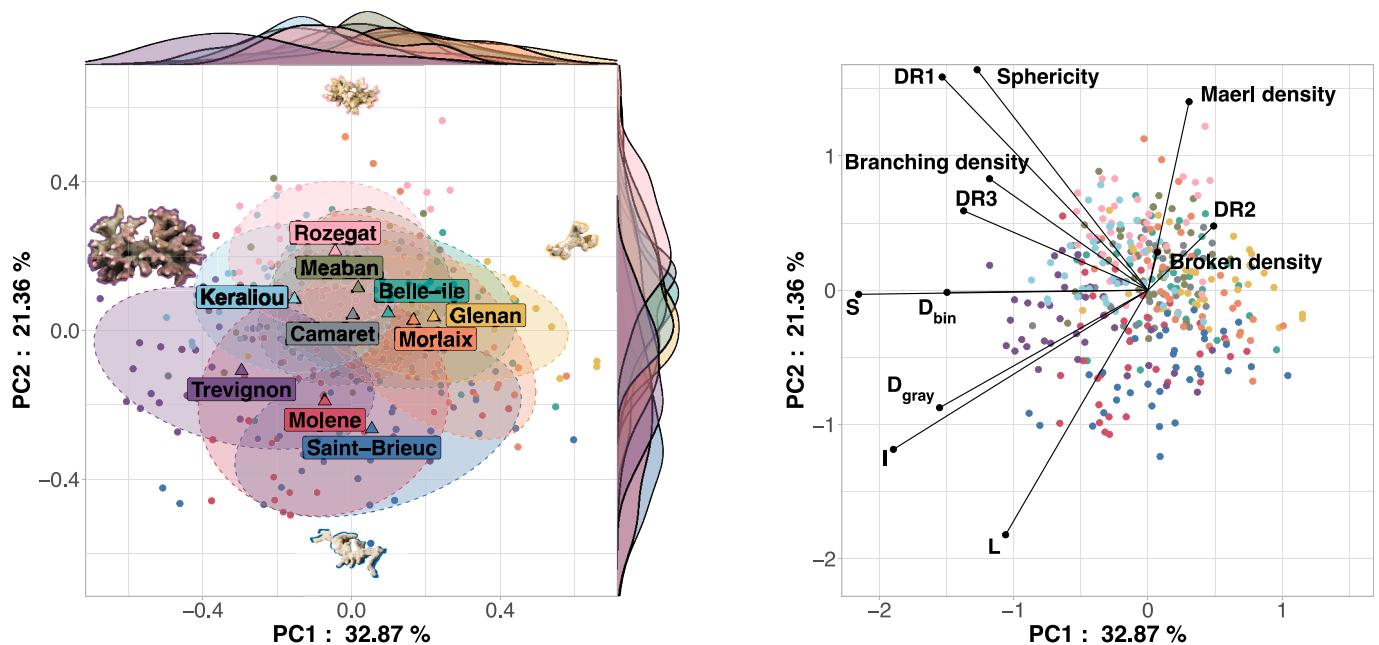

Fig. 4. Principal Component Analysis (PCA) of standardized box-cox transformed habitat complexity variables of the 10 maerl beds analysed in the study. The first two axes account for 54.23% of the total variance in the complexity data. Scaling 1 (distance biplot) in the left panel and scaling 2 (correlation biplot) in the right panel. Circles represent the 360 analysed specimens, while triangles represent each site's centroids with their relative 80% confidence interval ellipses. Specimens from each bed at the end of both gradients are illustrated on the left panel, and their relative scale was preserved. DR1-3: Diameter ratios used to describe maerl shape; D_{bin}, D_{gray}: Fractal dimension estimated from binary and grayscale images, respectively; L, I, S: Larger, Intermediate and Smaller diameter of a rhodolith, respectively; Maerl density: density of rhodoliths; Broken density: Density of broken branches.
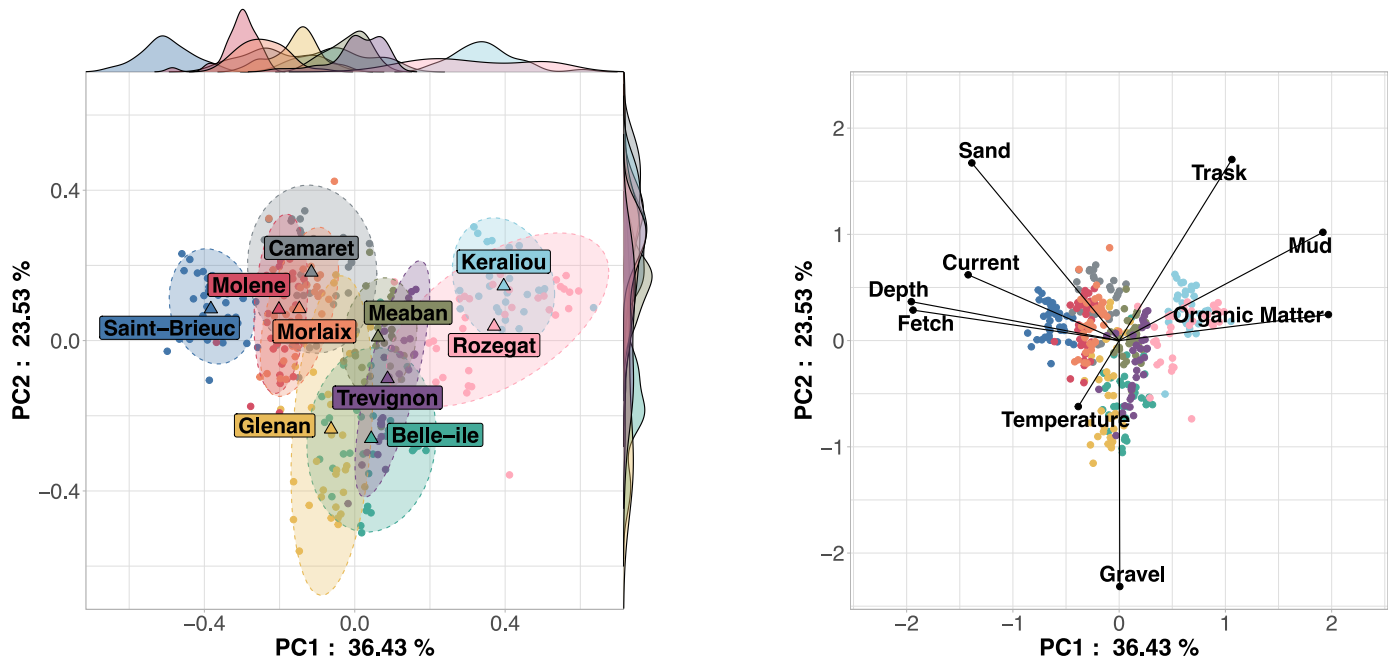
Fig. 5. Principal Component Analysis (PCA) of standardized box-cox transformed physical environmental variables. The first two axes account for around 60% of the total variance in the environmental data. Scaling 1 (distance biplot) in the left panel and scaling 2 (correlation biplot) in the right panel. Round points represent the annual values, while triangular points represent each site's centroids with their relative 90% confidence interval ellipses.

is mostly composed of coarse sediment: sand and dead maerl fragments (gravel - Fig. 5). It presents some of the largest mean grain sizes in the study area and is relatively well sorted (Mean Trask values ranging from 2.37 to 2.5). There was a very slight variation in mean bottom temperature within and among sites (Table A2).

On the other end of the gradient, the sites located in the Bay of Brest - Keraliou and Rozegat - are the shallowest (<3 m deep) and sheltered, presenting the lowest fetch values (14–21 km - Fig. 1) and relatively slow mean current velocities (ranging from around 0.13 to 0.22 m·s^1). These sites present the highest percentage of fine sediment in the study - and are sometimes composed of over 60% of mud. Rozegat, however, presents the highest variability in terms of granulometry, with one of its points being mostly composed of gravel (mostly dead rhodoliths in this case) and sand, a second of gravel and equal parts sand and mud, and a third mostly of gravel and mud (Fig. 6).

3.3. Environmental drivers of maerl morphometrics and habitat complexity

The RDA showed that the selected physical environment constraints explained 31.5% of the variation in habitat complexity among beds ($R^2_{Adjusted} = 0.315$, $F = 28.526$, $p < 0.0001$). Around 30% of the variance is contained in the two first RDA axes (Fig. 7). Once more, a gradient from Saint-Brieuc to Rozegat can be seen in the first axis. It's mainly driven by differences in maerl density, which was highly negatively correlated with depth, wind exposure (Fetch) and current velocity. Similarly, both maerl sphericity, branching density and the binary fractal dimension increased with the percentage of mud and the sorting index, which in turn decreased with higher energy conditions (negatively correlated with both Fetch and currents). The largest rhodolith diameter and the grayscale fractal dimension both increased with fetch and depth.

Variation partitioning (Fig. 8) revealed that around 17% of the differences in maerl complexity were linked to granulometry (combined effects with both variable sets). 13% of the variance was explained by granulometry alone (isolated effect), while 2.6% were related to the combined effects of granulometry and hydrodynamics, and only 1.5% were explained by the combined effects of bathymetry, granulometry, and hydrodynamics. The isolated effect of depth accounted for 5.6% of the variance in the data, while its combined effects with hydrodynamics explained 7.8% of the variance, and the effect of hydrodynamics alone accounted for the least amount of variance - 1.2%. When sites were added to the model as a factor, an additional 9% of the variance was explained, explaining in total 41.3% of the variance. However, variation partitioning revealed that the effect of sites accounted for over 40% of the variance, completely masking the isolated effects of the environmental variables, which are bound to be related to the sites (Supp. material II). Therefore, we decided to keep the simpler model as it was more informative.
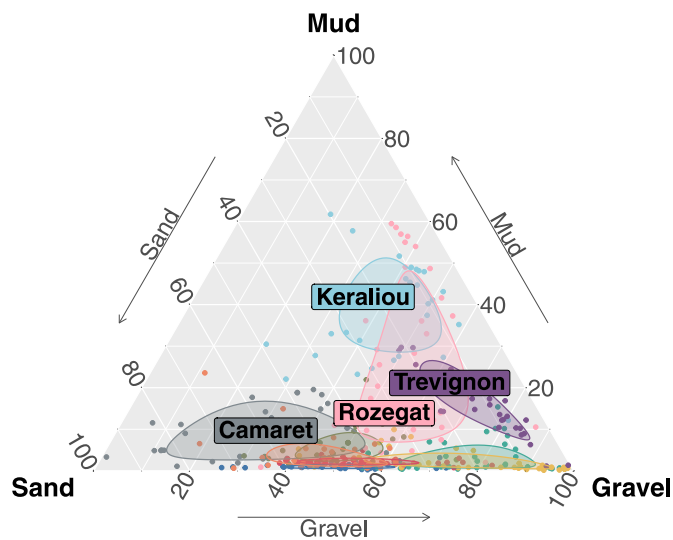

Fig. 6. Grain size distribution variation over a 12-year span in the 10 studied beds. Ellipses were calculated using the mean and variance of the ternary data. Note that the gravel component represents mostly alive and dead rhodoliths.
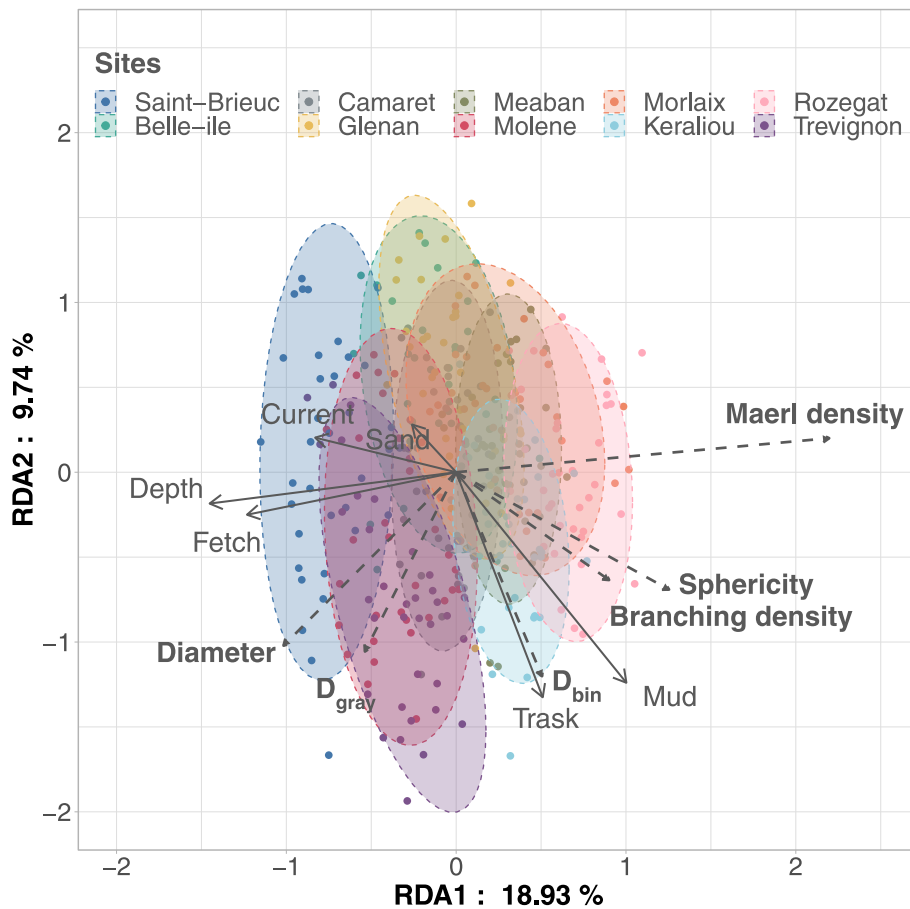
Fig. 7. Redundancy Analysis (RDA) triplot of the standardized box-cox transformed complexity metrics as a function of the mean physical environment constraints. Variables are scaled proportional to eigenvalues (Scaling 2). Gray, dashed bold lines represent the response variables, while black lines indicate environmental constraints. 95% interval ellipses are shown for each site. The first two axes represent 28.67% of the variance in habitat complexity (unadjusted).

4. Discussion

4.1. Maerl habitat complexity quantification

Although habitat complexity varies over time for different systems (Smith et al., 2014), since the main maerl forming species *P. calcareum* and *L. corallioides* have very slow growth rates (~0.4 mm.y^{-1}), temporal variability in maerl complexity is probably irrelevant between the sample dates of our study, assuming no severe physical disturbances happened during this period. We were able to show that some of the most commonly used metrics were important in driving differences among sites, and that maerl-specific morphometrics and fractal dimension are somewhat complementary.

Fractal analysis provides a comparable framework for habitat complexity studies, allowing for analysis across different environments and/or foundation species (Sugihara & May 1990; Gee and Warwick, 1994; Commito and Rusignuolo, 2000; Kostylev et al., 2005; Kovalenko et al., 2012; Tokeshi and Arakaki, 2012), and therefore is a preferred method for generalizing the effects of complexity. We have shown that the fractal dimension estimated from binary images of the rhodoliths was highly correlated to rhodolith sphericity and branching density. This could be evidence that fractal dimension is indeed a promising comparable metric for describing rhodolith complexity, as it captures, at least partially, two important rhodolith traits. However, the 2D fractal analysis applied here most certainly leads to the loss of very important elements of 3D complexity, even if our methods aimed to minimize those losses by using macro photography and focus-stacking. Additionally, while we decided to standardize the distance between the rhodoliths and the camera, and, therefore, picture magnification, Warfe et al. (2008)

showed that fractal dimensions depended greatly on the magnification level of pictures. This also seems to be the case in our study as both methods of fractal dimension estimation were correlated to rhodolith diameter.

Therefore, further studies should be conducted to perfect fractal analysis on rhodoliths, preferably investigating novel techniques such as 3D modelling and fractal analysis, which have shown to provide an optimal description of highly structurally intricate organisms such as corals (Reichert et al., 2017; Zawada et al., 2019; Zawada et al., 2019). Alternate promising techniques have recently been developed using three-dimensional models of macrophytes for quantifying available interstitial space and available shelter from predators and could provide an alternative comparable framework (Ware et al., 2019). None of those methods would, however, provide information on the spatial arrangements of the rhodoliths on the seafloor, which is another crucial component of habitat complexity at the bed level. Therefore, we suggest that in situ metrics such as interstitial space approaches on Sediment Profile Imagery (SPI, Bernard et al., 2019) or 3D reconstruction at the habitat level in situ (Torres-Pulliza et al., 2020) or *in silico* (Sadcha-theeswaran et al., 2019) should be evaluated as well. Additionally, the fractal analysis of the interface between the rhodoliths and water, such as what has been done for mussel reefs and rocky shores (Commito and Rusignuolo, 2000; Kostylev et al., 2005) might prove effective alternatives.

Maerl density was one of the main factors driving intra-site variability and seems to be an important metric for complexity at the habitat level. However, we highlight that, ideally, maerl densities and their variability should be measured at the point level in the specific locations surveyed in the REBENT context. This should either be done through
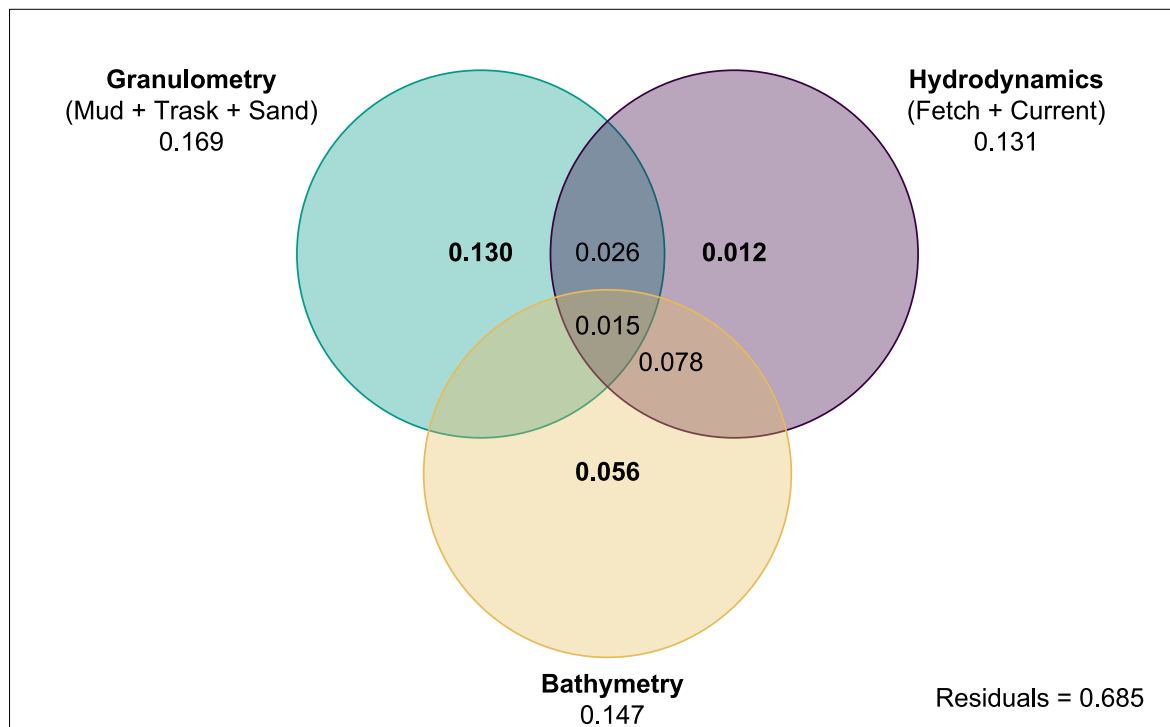
Fig. 8. Venn's diagram with the adjusted R-squareds from the variation partitioning of the habitat complexity data as a function of the physical environmental constraints. The variables were grouped in 3 environmental sets and their combined and isolated effects (in bold) are shown. Values < 0.001 are not shown.

direct counts of rhodoliths over standardized sampled areas, as the measures that have been used in this study, or through image analysis (Amado-Filho et al., 2012; Pereira-Filho et al., 2012). Indeed, more recent image analyses of maerl percentage cover in most beds in Brittany were complementary to the maerl density data used in our study: while our data revealed that the Trévignon bed had some of the lowest maerl densities, Dutertre et al. (2015) found that it was the bed with the highest maerl coverage. However, in both studies, the maerl beds in the Bay of Brest presented the highest maerl quantities, both as maerl density or coverage. These inconsistencies further suggest that both techniques should be taken into consideration when assessing habitat complexity at the bed level.

Most of the commonly used metrics for describing rhodolith morphology and complexity have been applied in this study, except for rhodolith volume. Although it has also been widely used as a measure of maerl structure (Steller et al., 2003; Bahia et al., 2010; Gagnon et al., 2012), the high porosity and reduced size of the rhodoliths sampled in this study did not allow for an accurate estimation of displaced water volume using graduated cylinders. Additionally, estimates of spheric volume wouldn't be informative as the rhodolith shapes were mostly fruticose with sparse branches and would be highly correlated with sphericity measurements. Therefore, volume was discarded as a complexity metric in this study.

Nonetheless, the analysis confirmed extensive variability both among and within beds, when collectively considering the different metrics at the rhodolith level. Rhodolith size (diameter or volume), shape (sphericity), and branching densities have historically been studied (Amado-Filho et al., 2007; Bahia et al., 2010; Cabanellas-Reboredo et al., 2018; Otero-Ferrer et al., 2020) to describe maerl beds, and seem to be good indicators of overall rhodolith complexity in this study as well. The PCA reveals that most metrics are complementary, and further confirms that a holistic approach is preferred in order to describe maerl beds' habitat complexity. For instance, in the first two axes of the PCA the vector representing rhodolith diameter is almost orthogonal to those of branching density and sphericity, showing that the variability in size differs from that of

rhodolith shape and growth pattern. However, other metrics were redundant, such as the diameter ratios DR1 and DR3 and sphericity, or not very informative, such as the density of broken branches or DR2. Finally, some metrics showed similar regional patterns although they measure different facets of complexity, such as branching density and sphericity.

4.2. Regional variation in habitat complexity

The analysis confirms both high within and among beds variations in maerl habitat and rhodolith complexity, and the PERMANOVA suggests that the variability among sites is greater. With a few exceptions focused on maerl occurrence, density, and vitality (Carvalho et al., 2020; Dutertre et al., 2015), most authors described differences in rhodolith morphometrics among beds at a local scale, and usually in fewer locations than in our study (Steller and Foster, 1995; Steller et al., 2003; de Figueiredo et al., 2007; Sciberras et al., 2009; Sañé et al., 2016; Neves et al., 2021). Our results provide new evidence that maerl morphometrics and habitat complexity can be extremely variable at both very small (200 m) and larger scales (up to 400 km).

Maerl density and rhodolith diameter were two of the main metrics driving differences among sites. They were also negatively correlated - with beds with bigger rhodoliths being a lot less dense. Complexity is thought to increase with a larger density of repeating small structuring elements (Sugihara & May 1990), in our case those elements could be best represented by the rhodoliths themselves, the rhodolith branches or even the spaces between branches and rhodoliths. Beds such as Saint-Brieuc, where maerl density is very low and rhodoliths are large but the least spheroidal and branched, can be described as low-complexity habitats, as they present the least amount of larger structuring elements. However, in beds such as Trévignon or Molène, which have large rhodoliths that are also complex, but low maerl densities, one question remains: are those beds more or less complex than those with smaller, highly complex rhodoliths and low densities? Theory suggests that these beds are indeed less complex than Kéraliou or Rozegat, which present high densities of small but highly complex

rhodoliths.

This further confirms the necessity of better assessment of maerl densities and other metrics of complexity at the habitat level. Nevertheless, it is also important to keep in mind that the different scales of the structuring elements might have different effects on different taxa. Therefore, studies on the role of these different facets of complexity on driving biodiversity are necessary to truly understand what is indeed a complex habitat (Kovalenko et al., 2012). Quantifying the interstitial space between rhodolith branches and individual rhodoliths would further help answering those questions as it is a direct measure of available space which can also inform about the arrangement of the structuring elements in space.

Sphericity strongly differed among beds, with some showing a very homogeneous distribution of only sub-spheroidal rhodoliths, such as Camaret, and others presenting very heterogeneous shapes, like Morlaix and Molène. There was an overall prevalence of sub-spheroidal rhodoliths in most sites, with the exception of the beds in Saint-Brieuc and the Glénan Islands. This pattern has already been reported in different regions worldwide (Aguirre et al., 2017; Bassi et al., 2009; Neves et al., 2021; Pascelli et al., 2013; Steller and Foster, 1995). Alternatively to the pattern observed by Bahia et al. (2010), branching density covaried with sphericity in our study, with more spheroidal rhodoliths usually presenting high branching densities, while less branched rhodoliths were usually sub-ellipsoidal or sub-discoidal. This has been previously found in Brittany (Qui-Minet et al., 2018) and could indicate that both characters are driven by similar environmental or autecological processes. The fractal dimension measured through binary images was also correlated with both sphericity and branching density, suggesting that although some part of the 3D complexity might be lost with this metric, it seems to capture rhodolith complexity at least partially and further studies should investigate it, as it would allow for comparison among different habitats (Warfe et al., 2008; Kovalenko et al., 2012).

4.3. Environmental drivers of maerl habitat complexity

The PCA of environmental drivers and the RDA of habitat complexity as a function of the physical environment evidence that the previously mentioned gradient in habitat complexity follows, at least partially, the environmental gradient. Around a third of the variation in habitat complexity (31.5%) was related to hydrodynamics, bathymetry and granulometry combined. Several studies have shown differences in rhodolith morphometrics following bathymetric gradients (Bahia et al., 2010; Pascelli et al., 2013; Cabanellas-Reboredo et al., 2018; Otero-Ferrer et al., 2020) and suggested the importance of hydrodynamics in driving maerl growth patterns. In our study most of the variance was explained by the sediment granulometry (13.5%), namely the presence of mud. However, it should be noted that the hydrodynamic model has a 9 km^2 resolution, while the granulometry was measured in situ.

Although the granulometry is also influenced by the hydrodynamics of each site, the percentage of mud seems to have an intrinsic effect on maerl complexity. For example, the high proportions of mud in Rozegat and Keraliou are not only related to the fact that they are sheltered and under weak currents, but also reflect their location in a semi-enclosed system under strong influence of riverine inputs (Le Pape et al., 1996; Chauvaud et al., 2000; Ragueneau et al., 2018). Similarly, one could expect less mud percentage in Trévignon due to its high exposure to wind-generated waves, but the sedimentary profile of the region is reminiscent of a fossil delta, with a paleo-valley filled with fluviatile and estuarine Pleistocene deposits, and is under the influence of riverine inputs (Baltzer et al., 2017).

The presence of mud was mostly related to rhodolith shape and complexity: the most spheroidal, highly branched rhodoliths with the highest values of D_{bin} were found in sites with higher proportions of fine sediments. Bosence (1976) showed that more complex and densely branched rhodoliths are more easily transported by water motion independently of rhodolith shape, and that more spheroidal and

ellipsoidal (when their largest axis disposed in the direction of the wave) rhodoliths are more easily transported than discoidal ones. For that reason, one could expect that an exposed site such as Trévignon would present mostly discoidal forms due to high exportation rates of more spheroidal forms - but the exact opposite pattern is found. On the other hand, Saint-Brieuc, which is very exposed and contains close to 0% of mud, presents some of the least spheroidal and branched rhodoliths. Therefore, we argue that the intricate matrix formed when maerl is found in muddy and poorly sorted sediments (Bernard et al., 2019) highly increases the cohesion between rhodoliths and the overall bed stability, keeping more complex rhodoliths to be exported from the system by strong bottom currents and waves. This could also explain why several field studies have not found clear relationships between hydrodynamics and rhodolith shape, as revised by Aguirre et al. (2017).

Bioturbation is another possible cause for higher sphericity in beds with finer sediments, as bioturbation intensity increases in sediments with smaller grain sizes and higher cohesion (Dashtgard et al., 2008). Bioturbation and the overall movement of rhodoliths by associated macro-megafauna have been previously reported as being related to higher sphericities, as it promotes an evenly distributed growth by frequent turning (Prager and Ginsberg, 1989; Marrack, 1999; James, 2000; Foster, 2001). However, these possible positive effects of finer sediment on rhodolith complexity and maerl densities go against the generally accepted idea that higher mud content, usually associated with higher sedimentation rates and fouling, can affect maerl vitality, densities and growth by rhodolith burial (Adey and Macintyre, 1973; Bosence, 1976; Foster, 2001; Wilson et al., 2004). We consider that other possible important factors such as nitrate concentrations could explain the observed relationship between mud percentages and rhodolith complexity, as studies had found that higher nitrate concentrations promote maerl growth and density (Dutertre et al., 2015; Carvalho et al., 2020). However, higher nutrient concentrations could also negatively affect maerl through light competition due to epiphyte blooms and eutrophication (Qui-Minet et al., 2018; Ragueneau et al., 2018).

Overall the combined effects of hydrodynamics (Fetch and bottom currents) and bathymetry were mostly related to complexity at the habitat level, with lower maerl densities in deeper, high-energy environments. In terms of depth, similar results have been previously reported (Amado-Filho et al., 2007; Pascelli et al., 2013). However, Bahia et al. (2010), found that in northeastern Brazilian beds, maerl densities increased with depth, a difference they attributed to the variations in the continental shelf morphology and higher sedimentation rates at the shallower sites.

Differences in the effect of water motion on maerl densities between shallow and deeper waters have already been reported. In shallow waters, strong water motion has been shown to reduce maerl coverage due to rhodolith breakage, while in deeper beds lower energy conditions can lead to maerl burial through sedimentation (Marrack, 1999; Wilson et al., 2004; Pascelli et al., 2013; Villas-Boas et al., 2014; Otero-Ferrer et al., 2020). In our study, however, this generalization was not observed. Stronger water motion had a negative effect on maerl density in both deep and shallow beds. For instance, the two deeper beds - Saint-Brieuc and Camaret - which have different energy conditions, showed very different maerl densities. The first, which is under high hydrodynamics, has the lowest densities of the region, while the second, which is under relatively slower currents and is less exposed to wind-generated waves, is at least four times denser. In the Northeast Brazilian coast, the occurrence of maerl beds in deep shelf conditions sheltered from sediment deposition seems to be favoured by slow currents, but their occurrence in shallower sites under stronger sediment deposition seems to be favoured by stronger currents (Vale et al., 2022). This further suggests that the effects of hydrodynamics and bathymetry on maerl densities are dependent on local levels of sediment deposition, and this might also explain our findings. However, our study has a relatively small depth gradient, due to the nature of Brittany's continental shelf which extends several kilometres from the coast (Castaing

et al., 1999), which could also explain the small effect of depth in driving maerl densities.

Despite the lower contribution of depth to the overall variation of rhodolith size (diameter), shape (sphericity), and complexity (branching densities and fractal dimension) in our study (Fig. 8), the role of depth on driving some of these morphometrics has been frequently discussed (Amado-Filho et al., 2007; Bahia et al., 2010; Cabanellas-Reboredo et al., 2018; Otero-Ferrer et al., 2020; Neves et al., 2021). The maerl beds in the Pontine Archipelago, Italy, present similar rhodolith morphological composition to those of our study - with smaller, highly branched and spherical rhodoliths in shallower beds (Sañé et al., 2016). Another study found that sphericity decreases with depth, and the authors attributed that to possible higher sediment deposition in deeper sites that could negatively affect rhodolith downward growth (Peña and Criado, 2008). The effects of depth on rhodolith size, however, are not easily generalized, and studies showed contrasting results. While some found similar trends to the ones in our study (Amado-Filho et al., 2007; Otero-Ferrer et al., 2020; Pereira-Filho et al., 2012), others have found that rhodolith size decreased with depth.

Most of the accepted interpretations of the effects of depth on both maerl vitality, density and rhodolith morphometrics, depend on assumptions that deeper environments are under lower energy regimes and higher sedimentation rates (Foster, 2001). This is not the case for most of the deepest beds (with the exception of Camaret) which are mainly highly exposed to currents and wind-generated waves and have almost no mud content, and therefore suggest low sedimentation. Therefore, the role of depth in driving maerl habitat complexity should be assessed carefully and in combination with measurements of sedimentation rates, light intensity and water motion.

Similarly, our results contradict the overall accepted idea that hydrodynamics is the main factor driving maerl morphology. The isolated effects of bottom currents and exposure to wind-generated waves accounted for the least amount of the explained variance in the complexity data (1.3%), and its combined effects with sediment granulometry explained 2.6% of it, further suggesting the intrinsic importance of the sediment composition. Although slight, its effects were overall negative in both maerl sphericity, branching density and complexity. The opposite pattern has been observed in most studies, encompassing different species and growth forms (Bosellini and Ginsburg, 1971; Bosence, 1976; Cabanellas-Reboredo et al., 2018; Carvalho et al., 2020), although a few others have also found highly branched spheroidal rhodoliths in quiet waters (Reid and Macintyre, 1988; Prager and Ginsberg, 1989).

4.4. Eco and paleoecological implications

The use of rhodolith shape in facies as proxies for hydrodynamics is still widely accepted (Aguirre et al., 2017; Bassi et al., 2017). However, our results further support Foster's statement that interpretations of hydrodynamic conditions based on rhodolith shape found in the fossil record should be carefully considered (Foster, 2001). We have shown that most of the assumptions necessary for inferring water motion are not met in 10 beds in a large scale study on one of the world's regions with the highest density of maerl beds (Grall and Hall-Spencer, 2003; Peña et al., 2014; Hernandez-Kantun et al., 2017).

Additionally, the very small amount of the variance in maerl habitat complexity explained by hydrodynamics and depth in this study had already been suggested by Adey and Macintyre (1973). The authors propose that the main forces driving rhodolith shape and growth forms are species biology and autoecology. Indeed, the main maerl-forming species in the NE Atlantic mainly disperse through vegetative reproduction and breakage, and sexual gametophytes have rarely been detected in Brittany (Peña et al., 2014). Recent work has shown that *P. calcareum* rhodoliths, spores, and gametes have low dispersal potential and that high clonality leads to strong genetic differentiation between beds even in small scales (Pardo et al., 2019; Jenkins et al., 2021).

Therefore we argue that the biology (mainly the high clonality potential) of these algae might play a more important role in driving the rhodolith complexity than the physical environmental constraints, considering that only 31% of the variance was explained by granulometry, depth and hydrodynamics combined.

On top of the possible effects of bioturbation already discussed, other interactions with maerl associated organisms could also explain the large amount of unexplained variance in our study. For instance, epiphytic algae can have important effects on maerl vitality due to competition, but could also affect rhodolith mobility and export (Carvalho et al., 2020; Peña et al., 2014; Qui-Minet et al., 2018). Additionally, encrusting and boring organisms can also affect rhodolith morphology through bioerosion, for example (Nitsch et al., 2015; Bassi et al., 2020).

Another possible explanation, which could be related to the additional 10% of the variance explained when sites were added as a factor in the analysis, could be the sites' histories. Until the late 70's, around 300,000 tonnes a year of maerl were commercially collected in Brittany, with the main areas of extraction being the Glénan islands and in the Gulf of Saint-Malo, in which the Saint-Brieuc bed is included (Blunden et al., 1977). Those two beds present the least branched and complex rhodoliths in our study, with a high density of broken branches in the Glénan islands, which could reflect this activity. Although the latter has been highly exploited, maerl deposits in the area have been reported to be up to 10 m thick, being the thickest maerl beds known, which could explain their reminiscent high densities (Barbera et al., 2003). This further suggests that human activities such as maerl extraction and dredging can indeed decrease habitat complexity (Bernard et al., 2019).

The habitat complexity gradient shown among maerl beds in Brittany provides a unique opportunity to test several hypotheses on its role on biodiversity. Instead of only binary and qualitative comparisons between complex and less complex habitats, these different complexity levels could allow for quantitatively testing if the generally accepted hypothesis of the facilitative role of habitat complexity on the associated biota also holds within a habitat at the regional level. Additionally, the macrofaunal communities of the studied sites in our study have been monitored yearly since 2003 in the context of the REBENT program, which would allow us to investigate in-depth the role of habitat complexity in community trajectories and stability (Cáceres et al., 2019). The data available also allow for trait-based approaches (Boyé et al., 2019) that could verify the role of habitat complexity in ecosystem functioning, a question that only recently has been given attention (Mocq et al., 2021; Soukup et al., 2021).

5. Conclusions and future directions

The elements presented in this study allowed us to answer our initial three main three questions. First, we have shown that some classical morphometrics used to describe maerl, such as rhodolith diameter, branching density and sphericity adequately quantify rhodolith complexity when taken into account collectively. Similarly, maerl density partially quantifies complexity at the habitat level, and sampling protocols should be improved to better quantify it. Our study provides a first attempt of using fractal dimension to quantify maerl complexity, and shows that it captures at least two aspects of rhodolith structure: sphericity and branching density. Therefore, this comparable metric needs to be perfected in order to better describe maerl complexity, and holistic 3D approaches at the habitat level seem promising and should be preferred in future studies.

We have shown that maerl morphometrics and habitat complexity vary greatly both at the local and regional level, with beds relatively close to each other presenting very different structures and high within-site variability. These differences are partially driven by physical constraints, namely granulometry, depth, and hydrodynamics. We provide evidence that the complexity of rhodoliths is promoted by poorly sorted sediments with higher proportions of mud, which in most cases is a

result of low energy conditions, but can also be related to sites geological histories and riverine inputs. In our study, the beds with the highest mud contents presented the most spheroidal, complex and highly branched rhodoliths. This could also suggest that bioturbation also plays a role in driving rhodolith complexity, and this question should be further explored.

Depth and hydrodynamics individually explained only a small portion of the variance in habitat complexity at both the rhodoliths and bed levels, further suggesting that other aspects such as maerl species biology and autoecology, as well as interactions with other species and the sites histories, might play a more important role. Alternatively to what has been commonly hypothesized in paleoecology, we found evidence that strong currents may lead to less spheroidal and branched rhodoliths, which we attribute either to export facilitation of more spheroidal rhodoliths by water motion, or unbalanced maerl growth due to unidirectional currents. These results could have important implications for paleoenvironmental studies, which should interpret rhodolith shape in the fossil record carefully and in combination with other environmental proxies.

Further work aiming to understand the links between habitat complexity, environmental conditions, human impacts and community ecology in these ecosystems is essential for biodiversity conservation. Quantifying the role of the complexity provided by foundation species, which are under increasing threats, might provide valuable insights. By quantifying this gradient in habitat complexity on different maerl beds surveyed by a long-term monitoring program, our work provides a unique opportunity for further elucidating fundamental ecological questions related to habitat complexity and biodiversity.

Author statement

Victor Leite Jardim: Conceptualization, Data curation, Investigation, Methodology, Visualization, Writing - Original Draft, Writing - Review & Editing.

Chirine Toumi: Data curation, Methodology, Resources.

Olivier Gauthier: Conceptualization, Supervision.

Jacques Grall: Conceptualization, Funding acquisition, Resources, Supervision.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be made available on request.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.marenvres.2022.105768.

Annex.

Table A1
Physical environmental variables selected for the PCA.

Variable name	Metric
Gravel	Percentage of gravel in the sediment
Mud	Percentage of mud in the sediment
Sand	Percentage of sand in the sediment
Trask	Trask Sorting Index
Organic Matter	Percentage of organic matter in the sediment
Current	Mean current velocity (m·s^{-1})
Fetch	Maximum exposure to wind generated waves (km)
Temperature	Mean water temperature at the bottom (°C)
Depth	Water depth (m)

Table A2
Hydrology and bathymetry of the studied sites. Mean current velocity and bottom temperature values comprise 12 years of observations. Values for each sampling point are shown. Sites are ordered by the median water depth over the three sampling points.

Site	Mean current velocity (m·s^1)	Mean Bottom Temperature (°C)	Depth (m)
Rozegat	0.14	11.94	1.30
	0.17	11.94	1.60
	0.22	11.90	1.80
Keraliou	0.18	12.08	2.00
	0.22	12.08	2.25
	0.22	12.08	2.45
Belle-île	0.17	12.84	3.50

(*continued on next page*)

Table A2 (*continued*)

Site	Mean current velocity (m·s^1)	Mean Bottom Temperature (^{o}C)	Depth (m)
	0.17	12.84	3.68
	0.19	12.83	4.00
Morlaix	0.27	12.52	5.04
	0.27	12.52	5.48
	0.33	12.71	9.24
Méaban	0.05	12.50	5.88
	0.05	12.43	5.88
	0.05	12.50	6.23
Glénan	0.20	12.71	7.48
	0.21	12.75	8.40
	0.21	12.75	10.65
Trévignon	0.08	12.65	11.88
	0.08	12.65	12.12
	0.08	12.65	13.03
Molène	0.59	12.65	11.70
	0.59	12.65	12.16
	0.59	12.65	12.68
Camaret	0.23	12.66	16.07
	0.23	12.43	16.40
	0.23	12.43	19.07
Saint-Brieuc	0.51	12.29	13.44
	0.60	12.33	20.15
	0.60	12.33	22.68

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