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# Changes in maerl-associated macroalgal community dynamics as evidence of anthropogenic pressure

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## Abstract :

### Background and Aims

Maerl-associated communities have received considerable attention due to their uniqueness, biodiversity and functional importance. Although the impacts of human activities are well documented for maerl-associated macrofauna, the spatio-temporal variations of macroalgae have comparatively been neglected, and the drivers that influence their dynamics are poorly known. We investigate the links between maerl-associated macroalgal communities, anthropogenic pressures and environmental conditions, and hypothesize that sites under human pressure would exhibit different dynamics when compared to reference site.

### Methods

In order to better understand community variation through space and time, four subtidal maerl beds under different pressures were consistently monitored over one year in the bay of Brest, Brittany, France. Both macroalgae communities monitoring and environmental data were acquired through field sampling and available models.

### Key Results

Higher macroalgal biomass was observed within eutrophic sites, especially in summer (more than 10 times higher than in Unimpacted site), caused by free-living forms of opportunistic red macroalgae. The Dredged site also exhibited distinct macroalgal communities during summer from the Unimpacted site. Nutrient concentrations and seasonality proved to be key factors affecting the macroalgal community composition, although dredging and its effects on granulometry also had strong influence. Over the long term, less than half of the species identified during historical surveys were found, indicating major temporal changes.

### Conclusions

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Human pressures have strong impact on maerl-associated macroalgal communities. Nutrient concentrations and dredging pressure appear as the main anthropogenic factors shaping maerl-associated macroalgal communities. Additionally, our results suggest historical changes in maerl-associated macroalgal communities over 25 years in response to changes in local human pressure management. This study suggests that maerl-associated macroalgal communities could be used as indicators of anthropogenic-driven changes in this habitat.

**Keywords** : Beta-diversity, bio-indicators, dredging, eutrophication, long-term changes, maerl beds, rhodoliths, rhodophyta, seaweed, coralline algae

## INTRODUCTION

Marine ecosystems and their communities are under increasing threat and experience rapid changes worldwide (Cloern et al., 2016, Hanley et al., 2023). Indeed, human activities have deep effects on coastal communities, including eutrophication (Cloern, 2001), introduced species (Mineur et al., 2015, Çinar et al., 2014) and water temperature increases and acidification (Barrientos et al., 2020, Martin and Hall-Spencer, 2017, Whalen et al., 2023). Those activities can alter the composition and functioning of marine habitats (Halpern et al., 2008), among which some are much more sensitive than others (Wernberg et al., 2023).

Maerl beds, or rhodolith beds, are complex habitats created by the accumulation of free-living, non-geniculate coralline algae, forming a complex 3D structure of intertwined calcareous branches hosting several microhabitats, making maerl a bioengineer (Foster et al., 2007). These habitats are found worldwide, from polar to tropical seas and are one of the most productive marine habitats, along with kelp forests, saltmarshes and seagrass meadows (Foster, 2001, Bosence, 1983). They are considered biodiversity hotspots, as they provide shelter for various invertebrate species, and a substratum for many macroalgae (Steller et al., 2003, Peña and Bárbara, 2008, Fredericq et al., 2019, Costa et al., 2023).

Maerl-forming species have extremely low growth rate, estimated around  $0.4 \text{ mm.y}^{-1}$  (Foster, 2001, Potin et al., 1990). Fragmentation is considered the primary way maerl-forming species disperse (Foster, 2001, Peña and Bárbara, 2004, Pardo et al., 2019). Due to these characteristics, maerl beds face multiple threats. Dredging as soil amendment (Ray, 1724, Grall and Hall-Spencer, 2003) as well as commercial fishing (Kamenos et al., 2003, Tauran et al., 2020) destroy and bury individuals. Eutrophication (Grall and Chauvaud, 2002) and invasive species (Androuin, 2018) can outcompete and bury coralline algae. Finally, this habitat is also threatened by ocean acidification and global change (Legrand, 2017, Martin and Hall-Spencer, 2017, Qui-Minet et al., 2019).

Maerl beds can be found all around Brittany's coasts, with the largest beds found in the bay of Brest (Hall-Spencer et al., 2008). Maerl exploitation in France has been reported since the 19<sup>th</sup> century (Pruvot, 1897). Although maerl extraction has ceased in French metropolitan waters since 2013 (*loi n°2009-967 relative à la mise en œuvre du Grenelle de l'Environnement, article 35*),

commercial fishing focusing mainly on pectinid and venerid bivalves still threatens Breton maerl beds (Grall and Hall-Spencer, 2003, Tauran et al., 2020).

In the northeast Atlantic Ocean, macroalgal communities associated to maerl beds are mostly dominated by Rhodophyta (BIOMAERL, 1999, Peña and Bárbara, 2010), and some species are only found in this habitat and can be considered maerl-specialists (Peña, 2010, Leliaert et al., 2009, Maggs and Guiry, 1987). In Europe, 368 macroalgae species are found associated with maerl-beds (representing 30 % of the area's macroalgal diversity), with at least 170 species occurring in the bay of Brest (Peña et al., 2014, Helias and Burel, 2023). Maerl beds are characterized by a marked seasonality, with higher macroalgal biomass during summer, particularly in temperate waters (Grall et al., 2006, Peña and Bárbara, 2010, Qui-Minet et al., 2018). However, the spatio-temporal variations (beta-diversity) of maerl macroalgal communities have been neglected in comparison to faunal communities, and the factors that influence their dynamic have not been well documented.

Benthic flora is widely known to respond quickly to anthropogenic perturbations, and is a well-recognized tool to assess ecosystem health (Hansen and Snickars, 2014, Orlando-Bonaca et al., 2008). The structure of coastal macrophyte assemblages is variable in time, depending on the environmental conditions (Piazzi et al., 2002), and can highlight short to long-term changes in benthic habitats (Borowitzka, 1972, Wikström et al., 2016, D'Archino and Piazzi, 2021).

In the bay of Brest, maerl beds have been surveyed since 1992 by the *Observatoire des Sciences de l'Univers de l'Institut Universitaire Européen de la Mer* (IUEM Observatory). The effects of anthropogenic pressures on the macrofaunal communities are well known in the area (Grall, 2003, Tauran et al., 2020). Yet, studies focusing on maerl-associated flora often relies on grey literature, mainly focusing on species lists (Peña et al., 2014, Helias and Burel, 2023).

This study first aims at understanding the links between temporal patterns of maerl-associated macroalgal communities and the environmental and human pressures. We expect macroalgal communities to display higher biomass in eutrophic beds, specifically in spring, due to increased riverine inputs (Qui-Minet et al., 2018), and lower diversity in dredged beds, as the physical impact of the fishing activities can be harmful to many species (Bernard et al., 2019). Then, we quantify the relative importance of different environmental and human pressures driving macroalgal communities and hypothesize that eutrophication and bivalve dredging would be the main driving factors, as both are known to have conspicuous impacts, as it is the case for macrofaunal

communities (Tauran et al., 2020, Grall and Chauvaud, 2002). Finally, we study historical changes in maerl-associated macroalgal communities analysing data acquired 25 years ago in comparison to current conditions in two beds.

## MATERIAL AND METHODS

### *Study area*

Studied maerl beds are located in the bay of Brest, a 180 km<sup>2</sup> semi-enclosed area in Brittany, Western France (**Figure 1**). The bay can be divided into a northern basin, connected to the Iroise Sea and Atlantic Ocean by a narrow strait, and under the influence of the city of Brest and the Elorn river, and a southern basin, under the influence of the Aulne, Daoulas and Camfrou rivers. Maerl beds cover approximately 30 % of the bay, and are mostly consisting of *Lithothamnion corallioides*, often mixed with *Phymatolithon calcareum* and *Lithophyllum incrustans*. Commercial fishing in the bay occurs mostly in the southern basin (**Figure 1**).

### *Sampling*

Four maerl beds were selected and sampled between October 2020 and August 2021. Keraliou is located in the northern basin of the bay of Brest, in the mouth of the Elorn river. This site, close to a highly populated zone (around 200 000 inhabitants in Brest metropole) and to the Brest harbor is considered moderately eutrophic (Hily et al., 1992). Rozegat, Bindy and Roz are all located in the southern basin of the bay. Rozegat has been highly dredged since 2004 (commercial dredging of *Venus verrucosa*), resulting in significant damage to the bed (Bernard et al., 2019). The Bindy bed is located next to Rozegat, in a zone that was not heavily fished, and is thus considered as a reference. The last bed, Roz, is highly eutrophic due to river inputs. All sites shared similar depths (1-2 m), macrotidal regimes, exposure (sheltered), substrata (mud) and photosynthetic active radiations (at least 80 %) (Grall, 2002). In each site, four replicates were sampled a few meters apart, using a 0.1 m<sup>2</sup> Smith-McIntyre grab on board the R/V Albert Lucas. Sifting (1 mm sieve) was performed on board immediately after collecting the samples to remove unwanted sediments. Samples were kept in plastic bags, and fixed using 4 to 7 % formaldehyde before sorting. In the rest of the manuscript, sites will be named according to the different anthropogenic pressures they withstand: Unimpacted for Bindy, Dredging for Rozegat, Moderate eutrophication for Keraliou and High eutrophication for Roz).

### *Sorting and Identification*

After formaldehyde was removed, samples were sorted in order to distinguish the associated macroalgae (including erect, encrusting and free-living species) from maerl fragments. Macroalgae samples were kept in a freezer before identification. All associated species were identified macroscopically and / or microscopically, eventually requiring cross or longitudinal sections, the examination of fertile parts and squashing for crustose species. Post-identification, each macroalgal species was placed in a separate container and dried in an oven at 50°C for two days. Dried samples were then weighed (precision: 0.001 g) in order to estimate the biomass for each species. Encrusting species growing on maerl could not be weighed, but were listed with the minimum weight (0.001 mg) in order to be considered in statistical analysis. Species that were difficult to distinguish due to thallus fragmentation were grouped in categories: “fine foliaceous reds” (corresponding to mats of *Acrosorium ciliolatum*, *Cryptopleura ramosa*, *Nitophyllum punctatum*, *Erythrogloussum laciniatum* and *Rhodophyllis divaricata*) and “cartilaginous reds” (including *Metacallophyllis laciniata* and *Stenogramma interruptum*).

### *Historical data acquisition*

In addition to data collected between 2020 and 2021, a presence-absence dataset from a 1996-1997 survey was analysed (Connan S., Issa R. and Grall J., IUEM Observatory, unpublished data). During this study, two maerl beds were sampled in the bay: Keraliou and Rozegat, corresponding to the Moderately eutrophic and Dredged beds in our survey. In the historical analysis, we will keep the names “Moderate eutrophication” and “Dredging” defined in the sampling section for clarity, even though local pressures of both sites evolved over time and do not necessarily correspond to the conditions in 1997 and 1998. These two beds were sampled 8 times between September 1996 and July 1997, either by a Smith-McIntyre grab (0.1 m<sup>2</sup>), or by a benthic vacuum (0.25 m<sup>2</sup>). The conservation, sorting and identification protocols are identical to the one described above, enabling the use of this dataset for a historical comparison of the maerl-associated macroalgae in the bay of Brest. Data were homogenized to account for observer effect (Kirby et al., 1986, Archaux et al., 2006), in order to be compared to 2020-2021 observations at the same sites. Encrusting species were not considered to avoid false observations as they were not identified in the 96-97 survey, and some species were gathered in groups, or degraded to the genus (*e.g.* fine foliaceous reds and fine Rhodomelacean) [Supplementary Information].

### *Environmental data acquisition*

A large environmental dataset was used to conduct the analyses [Supplementary Information]. Fetch, used as a proxy of hydrodynamics, was defined as the longest distance ranged by the wind before meeting land, and was computed along sixteen segments of up to 200-km in length, radiating around sampled maerl beds using the R package “fetchR” (Seers, 2018). Granulometry indices (Mean grain size ( $\mu\text{m}$ ), skewness, median grain size (D50 in  $\mu\text{m}$ ) and the trask sorting index) as well as percentages of gravel, sand and mud, were obtained by sediment analysis performed in the laboratory or extracted from existing datasets (IUEM Observatory, unpublished data and Toumi (2023)), and computed using the R package “G2Sd” (Fournier et al., 2014). Both fishing data and granulometry were used as proxies of the fishing pressure in each site. The depth of sampled points was measured using the digital terrain model Litto3D (<https://diffusion.shom.fr/>) and was extracted using QGIS.

Dredging data in the bay of Brest was based on AIS (Automatic Identification System) data emitted by every vessel in the study area (only working fishing vessels are kept for the analysis) (Bernard et al., 2019). Vessel id, position and speed are recorded by the AIS. This dataset, computed since 2012, was combined to calculate an accumulated fishing pressure representing the cumulated dredging events. Data were aggregated in  $50\text{ m} \times 50\text{ m}$  cells over the southern basin of the bay of Brest. The surface area of each segment representing the dredged transects was multiplied by 1.8 (equivalent to the dredge width, in m) to get the total surface area covered by each dredging event, and divided by the surface area of a grid cell to get the percent area dredged during the survey. The sum of the distances represented by all points in each grid cell was also divided by the cell length (50 m) to estimate the number of times the square was traversed by a dredge, resulting in a fishing pressure index (see Bernard et al. (2019) for detailed protocol). Cumulated data from 2012 to 2021 was extracted for this study using QGIS 3.12.3 (QGIS.org, 2023). Dredging pressure is expressed for each grid cell as the number of times it was totally dredged between 2012 and 2021

Nutrient concentrations (total nitrate and total phosphorus) were extracted from the “*Objectif-Plancton*” (<https://www.oceanopolis.com/connaitre-nos-missions/conservation/objectif-plancton/>) and “*Pointe du Château*” (Pouvreau S., Ifremer, unpublished data) databases. Finally, the total macroalgal biomass was estimated for each sampling point by summing all biomasses for a given point, to investigate spatiotemporal variations in community size.

### *Statistical analysis*

After checking the normality and homoscedasticity of the data, Kruskal–Wallis and Dunn tests were used to compare the mean macroalgal biomass and species richness among seasons to investigate the intra-site temporal changes. The total beta-diversity (BDtot) (Legendre and De Cáceres, 2013) was estimated among the 4 sampled sites, as the total variance among the dataset for each sampling date. Two additional indices were computed: the species contribution to beta-diversity (SCBD), which highlights the importance of a given species to the total beta-diversity, and the local contribution to beta-diversity (LCBD), measuring the relative contribution of a given site or replicate to the total beta-diversity (Legendre and De Cáceres, 2013). To better understand which species were the drivers of variability among sites and seasons, species with high SCBD values (*i.e.* with a value higher than the mean SCBD value) were selected. High SCBD values can either correspond to rare or abundant species, as both can influence the total variability. Therefore, species were categorized into “rare” (only occurring in one site at a given time) and “common” (occurring in multiple sites at a given time). Then, they were grouped in morphoanatomical groups (cartilaginous, blades, fine foliaceous, filamentous and others) to investigate the influence of morphological groups on the variability. This morphofunctional approach is based on previous classifications made by Steneck and Dethier (1994), Ar Gall and Le Duff (2014) and Helias and Burel (2023).

To assess the main drivers of community composition, redundancy analysis (RDA) of the Hellinger-transformed macroalgal community matrix was performed as a function of anthropogenic and environmental variables (Legendre and Legendre, 2012). The Hellinger transformation, applied on the community matrix, was chosen to downweigh the influence of highly dominant and rare species on the global variability (Legendre and Gallagher, 2001). Forward selection, by permutation of residuals under a reduced model was used to determine the most parsimonious model. The significance of the global RDA model was tested through a permutation test (Legendre et al., 2011). Variation and hierarchical partitioning (Lai et al., 2022) were performed to quantify the overall contribution of each selected variable set to the variation in community data. This statistical method quantifies both unique and shared fractions of the variance explained (semi-partial  $R^2$ ) by each variable or variable set (Borcard et al., 2018). The relative importance of any set of predictors can also be estimated as its unique contribution to the total model plus its average shared contributions with the other predictors through hierarchical



partitioning. For this analysis, the selected explanatory variables were grouped in sets as follows : Hydrodynamics (Fetch), Granulometry (D50, mud), Fishing (dredging pressure), Nutrients (TP, TN), Site, Season and Topography (Depth). Finally, Correspondence Analysis (CA) was used to visualize historical changes (20 years) in the currently Moderately eutrophic (Keraliou) and the dredged (Rozegat) sites, using a Hellinger-transformed presence-absence dataset, after removing the outliers.

All analyses were performed using the software R version 4.0.3 (R Development core team, 2023). Beta-diversity indices were computed using the R packages “adespatial” (Dray et al., 2020). The R package “vegan” (Oksanen et al., 2019) was used to perform the RDA. Variation and hierarchical partitioning was performed using the R package “rdacca.hp” (Lai et al., 2022), and the “UpSetVP” (Liu, 2022) was used for visualization. CA were performed using “FactoMineR” (Le et al., 2008). All other data visualization was created using the R package “ggplot2” (Wickham, 2016).

## RESULTS

### *Spatiotemporal variations of macroalgal communities*

A total of 76 species were identified during this survey, including 6 Chlorophyta, 11 Ochrophyta and 59 Rhodophyta. Only 15 % over the total of 76 taxa identified were found in the 4 beds, representing 11 species. Twenty-seven percent of the species were found only in the Moderate eutrophication bed, 8 % were found only in both the Unimpacted and in the High eutrophication sites, and 4 % were found only in the dredged site. The two eutrophic sites exhibited the largest species richness, with the number of species ranging from 16 to 26 in the Moderate eutrophication site, and from 10 to 18 in the High eutrophication site. The lowest values were found for the Dredged and Unimpacted beds, with species richness ranging from 7 to 16 and 6 to 15 respectively. Total species richness increased between October 2020 and August 2021, with 39 species identified during October and April, 45 species in May, and 52 species in August. However, species richness tendencies remained relatively stable between sampled beds (**Figure 2, A**), and was the lowest in the Unimpacted site ( $7.00 \pm 1.00$  in April, to  $7.33 \pm 1.53$  in August), and the highest in the Moderately eutrophic site ( $19.33 \pm 2.52$  in April, to  $23.67 \pm 2.52$  in August).

Concerning total macroalgal biomass (**Figure 2, B**), it was the lowest in the Unimpacted site ( $0.70 \pm 0.50 \text{ g.m}^{-2}$  in April and  $9.47 \pm 2.51 \text{ g.m}^{-2}$  in August), and the highest in the Highly eutrophic site ( $2.99 \pm 1.06 \text{ g.m}^{-2}$  in April and  $197.20 \pm 21.28 \text{ g.m}^{-2}$  in August). Total macroalgal biomass was significantly higher in August for the Unimpacted, Dredged and High eutrophication sites ( $\chi^2$ : 10.675, p-value < 0.05,  $\chi^2$ : 10.675, p-value < 0.05 and  $\chi^2$ : 9.8462, p-value < 0.001, respectively, Kruskal-Wallis). For the Moderate eutrophication site, biomass was also significantly higher in both October and August (F value: 12.129, p-value < 0.001). In the Unimpacted bed, attached species such as cartilaginous red species (*e.g. Chondria dasyphylla*) dominated the community in all sampling dates (More than 70 % of the total macroalgal biomass). The opposite was observed for the High eutrophication site, with free-living species (*e.g. Halopithys incurva*) dominating all year long (nearly 90 % of the total macroalgal biomass). In both the Dredged and Moderate eutrophication beds, the community switched from a free-living species-dominated state in October (more than 70 % of the total macroalgal biomass) to an attached species-dominated community during the other sampling dates. Nevertheless, the Moderate eutrophication site presented consistently higher macroalgal biomass compared to the dredged one.

High spatial variability was observed in all sampling occasions, with similar BDtot values, ranging from 0.48 to 0.52. LCBD values showed no significant differences. However, a total of 17 taxa showed high SCBD values ( $> 0.01$ , the value of the SCBD mean), most of them being rhodophytes (**Figure 3**). Spatiotemporal variability was mainly driven by 7 taxa: *Chondria dasyphylla*, *Halopithys incurva*, *Rytiphlaea tinctoria*, *Solieria chordalis*, *Vertebrata martensiana*, fine foliaceous reds and *Hypoglossum hypoglossoides*. Most of these high-SCBD species belonged to cartilaginous and fine foliaceous species. It is also important to note that all free-living species were important contributors to the variance. However, while these species appear as the most contributing ones at the scale of the whole survey, differences can be observed between the different sampling dates, indicating that the differences among sites (spatial variability) is driven by different species at certain sampling dates. While *C. dasyphylla* was one of the main drivers in all sampling dates, other species showed some variation. In October, *R. tinctoria*, *S. chordalis* and the fine foliaceous reds were also important drivers of the variance. In April, the variance was additionally driven by *R. tinctoria* and *H. hypoglossoides*. Finally, in May and August, *H. incurva* also contributed greatly to the variance, with the addition of *V. martensiana* in August.

#### *Effect of anthropogenic and environmental pressures*

Sites near the mouths of coastal rivers (High and Moderate eutrophication sites) had the highest nutrient concentrations during the study (**Figure 4, A**). Nevertheless, some sites experienced important temporal variations in their nutrient inputs such as the High eutrophication site that had a strong decrease in nitrogen during May and August, following an initial peak in October ( $17.67 \mu\text{mol.L}^{-1}$ ) (**Table 1**). Although the Moderately eutrophic site always showed high nitrogen concentrations, there was a strong increase in August ( $12.67 \mu\text{mol.L}^{-1}$ ) (**Table 1**). The Unimpacted and Dredged sites showed consistently low nitrogen concentrations throughout the study ( $3.09$  to  $4.73 \mu\text{mol.L}^{-1}$ ). Phosphorus concentrations followed a similar trend, but with considerably lower values, with  $0.07 \mu\text{mol.L}^{-1}$  on average during spring, and  $0.18 \mu\text{mol.L}^{-1}$  during late-summer, with a notable peak in the High eutrophication site during summer ( $0.60 \mu\text{mol.L}^{-1}$ ) (**Table 1**).

In the southern basin, the highest cumulated dredging-pressures were found for the Dredged site (4.52 times fully dredged since 2012), while they were considerably lower for the Unimpacted site (0.14 times fully dredged, only corresponding to historical dredging) and null in the High eutrophication site (**Figure 4, B**). No data were available for the Moderate eutrophication bed, but

this area was not historically involved in clam-dredging (IUEM Observatory, unpublished data). Fetch values were relatively low in the bay ( $4.61 \pm 1.20$  km on average, with the highest value for the Moderate eutrophication site (6.30 km) and the lowest for the High eutrophication site with 2.90 km). Depth ranged from -0.78 m for the Unimpacted bed, to -2.26 m for the Moderate eutrophication. The beds substrata (**Table 1**) were mainly composed of gravel and mud ( $43.01 \pm 7.67$  % and  $39.51 \pm 16.67$  % respectively). The Dredged site showed the highest percentages of gravel (51.02 %) and sand (34.50 %), while the Unimpacted and eutrophic sites showed a higher mud percentage (around 48.00 % in the 3 sites).

The RDA of the macroalgal community as a function of environmental and anthropogenic pressures was significant (F-value: 9.44, p-value < 0.001). The first two axes account for *ca.* 45 % of the total variance in the data (**Figure 5, A**). A gradient is underscored by the RDA, which separates the two eutrophic sites (teal and green) characterized by mud and nutrients (TN and TP), and both the Dredged (yellow) and the Unimpacted (red) site, characterized by dredging pressure and depth. Sampling dates, are also separated, as the centroids of the observations made in October and April are distinguished from those made in May and August. Unimpacted and Dredged sites are characterized by the filamentous *Leptosiphonia fibrata* and the cartilaginous *C. dasyphylla* (**Figure 5, A**). Both sites are not clearly separated in the analysis, although there is a higher variability in the Dredged one, with a few observations being more similar to both eutrophic sites. The High eutrophication site is characterized by cartilaginous species such as *H. incurva*, *R. tinctoria* and *Rhodymenia ardissoni*, while the Moderately eutrophic is characterized by *S. chordalis*, fine foliaceous reds and cartilaginous reds. Following the variation and hierarchical partitioning, the different variable sets explained 79.1 % of the spatio-temporal variations in macroalgae communities (**Figure 5, B**). Nutrients contributed the most to macroalgal community variance, with an individual contribution of 26.82 %, followed by date (23.66 %) and hydrodynamics (14.16 %). Dredging (6.31 %), granulometry (4.15 %) and depth (4.05 %) accounted for the least variance explained. The unique effects of date and nutrients explain most of the variance, with 22.10 % and 21.32 % respectively (**Supplementary information Figure S1**).

### *Historical trends*

The dataset from the 96-97 survey included 59 species (8 Chlorophyta, 4 Ochrophyta and 47 Rhodophyta), and the 20-21 dataset included 76 species (6 Chlorophyta, 11 Ochrophyta and 59

Rhodophyta). After combining and homogenising the two datasets, a dataset of 56 species (8 Chlorophyta, 8 Ochrophyta and 40 Rhodophyta) was obtained [Supplementary Information]. Most sampled species were rhodophytes in both surveys. The most abundant species collected in the Moderate eutrophication site in 2020-2021 were *S. chordalis*, Delesseriacean species, and *V. martensiana* while, *C. dasyphylla* was dominant in the Dredged site for the same period. These dominant species seem to differ from those reported in the 1996-1997 survey, which were *Ceramium glandulosum* and *N. punctatum* in both beds, as well as *Dictyota dichotoma* in the eutrophic site.

When comparing the lists of identified species the number of species recorded in the eutrophic site increased between the two surveys (31 in the historical survey and 37 in this study), while this number decreased for the dredged bed (29 in the historical survey and 20 in this study). In the eutrophic site, 51.1 % of the total detected species were found in both surveys, and for the dredged one this number only reached 32.4 %. In both beds, *S. chordalis*, *H. incurva* and *R. tinctoria*, identified during this study, were not found in the 1996-1997 survey. As shown by **Figure 2, B**, maerl-associated biomass tends to significantly increase between fall and summer. Similar trends were observed in both surveys in the dredged bed (0.43 to 12.33 g.m<sup>-2</sup> for the 2020-2021 survey, and 0.20 to 23.03 g.m<sup>-2</sup> for the 1996-1997 survey (**Table 2**). In the eutrophic site, macroalgal biomass in summer was nearly ten times higher during the 1996-1997 survey (615.79 in 1996 and 777.13 g.m<sup>-2</sup> in 1997 over 86.18 g.m<sup>-2</sup> in 2021). Finally, for both sites, the first two CA axes account for a great percentage of the total temporal variance, 68 % for the eutrophic site, and 86 % for the dredged one (**Figure 6**). For the Moderate eutrophication site (**Figure 6, A**) observations from the historical (red) and present (blue) surveys are clearly distinguished in the first axis. A similar pattern can be observed for the Dredged site (**Figure 6, B**). Additionally, both sites display a temporal gradient associated with axis 2, and is visible for the two sampling periods.

## DISCUSSION

The present study shows that maerl-associated macroalgal communities in the bay of Brest display different species compositions in space and time, following spatiotemporal variations in anthropogenic pressures that vary in space and time. The studied sites were representative of four contrasted conditions: the Unimpacted bed of Bindy, the Dredged bed of Rozegat, and the two eutrophic beds, Keraliou (Moderately eutrophic) and Roz (Highly eutrophic). Our results indicate that dredging would have an indirect impact on maerl-associated macroalgae, while eutrophication would be the main driver of taxonomic and morphofunctional diversity.

### *Spatial and temporal variability of the maerl-associated flora*

Most species collected belong to the Rhodophyta which is consistent with findings from other maerl beds in European waters (Peña and Bárbara, 2010, Cabioc'h, 1969, Peña et al., 2014). Moreover, some species were found all year-long, with important seasonal biomass variations (as highlighted in **Figure 3**). Species responsible for temporal and spatial variability (i.e. with high SCBD values), such as *Halopithys incurva*, *R. tinctoria* and *S. chordalis* are uncommon species, that are however characteristic of the bay of Brest, and are likely to form dense populations, as already reported (Cabioc'h, 1969). On the other hand, other species such as *C. ramosa* or *S. interruptum* (respectively classified in the groups “fine foliaceous reds” and “cartilaginous blades”) showed similar seasonal patterns to other European maerl beds (Peña and Bárbara, 2010). Overall, maerl-associated macroalgal communities in the bay of Brest were the most developed during summer, and displayed significantly different communities as a response to anthropogenic factors.

The two eutrophic sites are located near the mouths of Aulne for the High eutrophication site, and of Elorn for the Moderate eutrophication site. Grall (2002) and Qui-Minet et al. (2018) showed that nutrients inputs from the Aulne were important and stable all year-long, with a peak in early-spring such as observed for the High eutrophication site. On the contrary, these inputs peaked during summer in the Moderate eutrophic site at the mouth of Elorn, with inputs from the city of Brest. This explains the high relative importance of both the date and nutrient inputs in the variation and hierarchical partitioning, indicating an interaction between both effects. Such interaction also appears in Figure 5-A as the observations from May and August clearly differ from those from April in the Highly eutrophic site. Nutrient concentrations (total Nitrogen and Total Phosphorus) were negatively correlated with species such as *H. incurva*, *R. tinctoria* and *R. ardissoni*, dominant in the Highly eutrophic site, since these red cartilaginous macroalgae bloom through the consumption of the nutrients.

In contrast, the nutrient concentrations remained high during summer despite the growth of important macroalgal biomass in the Moderate eutrophication site. These high levels of nutrient during summer could explain the high macroalgal biomass observed in this site during October 2021, dominated by fine foliaceous and cartilaginous blade species (e.g. *C. ramosa* and *S. interruptum*). Species in both sites are known to thrive under Moderate eutrophication (Johansson et al., 1998, Eriksson et al., 2002), especially as rhodophytes are highly resistant to sedimentation (Fraser et al., 2017). However, while the flora associated with both eutrophic sites showed similarities, the two sites exhibited different community compositions, with a higher species richness in the Moderate eutrophication bed. Two hypotheses might explain the difference between the two beds associated flora:

(1) Although both beds undergo the same tidal regime, riverine inputs from the Aulne are known to be higher than from the Elorn (Daniel, 1995), and macroalgal-assemblages in the Highly eutrophic site are defined by higher river influxes and by the site's more sheltered position in the bay in comparison to the Moderate eutrophication site (Berthois and Guilcher, 1959, Qui-Minet et al., 2018).

(2) In the southern basin, the singular flora of the High eutrophication site might be linked to continuous nutrient inputs from the Aulne, while the one observed for the Moderate eutrophication site might result from the sudden increases of nutrients during summer. Both beds exhibit different

flora in response to different nutrient regimes, as described in the classical eutrophication succession model (Schramm, 1999): the Moderate eutrophication site presents more seasonal and opportunistic species (stage 2 of eutrophication) that might quickly react to important nutrient inputs during summer, while the Highly eutrophic exhibits more free-living species (stage 3 of eutrophication).

The present study revealed major biomass growth of Gigartinales and Ceramiales during summer in the bay of Brest. Such red macroalgal blooms occur worldwide, and are usually linked with eutrophication (Nelson et al., 2015, Valiela et al., 1997, Austin, 1960). Similar cases showing substantial rhodophyte growth have been documented in Mediterranean lagoons with soft substratum (Battelli and Gregorič, 2020), without an evident link to eutrophication (although occurring in semi-enclosed environments). In case of excessive development, these blooms may be referred to as “red tides”, for example with *S. chordalis* in Southern Brittany (Burlot et al., 2023). Extensive development of Ceramiales might also be considered as indicators, as many species are considered opportunistic (Ar Gall et al., 2016). While not equivalent in scale to the events in Southern Brittany, red macroalgae blooms like those observed in the bay of Brest are community responses to eutrophication, and warrant continuous monitoring.

Dredging has significant known impacts on maerl beds: (1) it decreases the abundance and richness of associated fauna, (2) it alters the habitat by breaking maerl pieces and (3) it stirs up the sediments in the water column (Hall-Spencer and Moore, 2000, Coquereau et al., 2017, Bernard et al., 2019). Considering these major impacts, we expected clear differences between the Dredged and the Unimpacted sites. However, while both sites were separated from the two eutrophic sites in the RDA (**Figure 5, A**), they both exhibited similar biomass trends and were dominated by *C. dasyphylla*. Nevertheless, the Dredged site showed higher intrinsic variability, with a few observations being more dominated by free-living species (mainly *S. chordalis* and *R. tinctoria*), characteristic of the eutrophic sites, mainly in October. Indeed, some individuals of free-living species were identified in the Dredged site for these given sampling occasions, although the site did not exhibit high nutrient concentrations (see **Table 1**).

Therefore, this difference in community composition, could not directly be explained by dredging alone, and may be a consequence of this activity through the mortality of fragile benthic macrograzers. Undeniably, grazing is a key driver for macroalgal communities, and can completely



modify the structure and complexity of a community (Tsirintanis et al., 2018, Piñeiro-Corbeira et al., 2023). Grazers are mostly represented by urchins in Breton maerl beds (Guillou et al., 2002, Grall et al., 2006), which are fragile and highly sensitive to physical impacts and therefore, dredging (Robinson et al., 2001, Hauton et al., 2003). Indeed, urchins are nowadays absent from the Dredged site, while they still occur in the Unimpacted site (IUEM Observatory, unpublished data). Filamentous, cartilaginous and encrusting macroalgae are considered more resistant to herbivory (Mei and Schiel, 2007, Hay, 1981, Lubchenco and Cubitt, 1980, Duffy and Hay, 1991), which would explain the dominance of these species in the Unimpacted site. Thus, although clam dredging does not impact the flora as strongly as it does for the fauna, it enables the colonization of the bed by grazing-sensitive macroalgal species through the removal of large grazers.

It is possible that the dredging variable estimated by the model developed by Bernard et al. (2019), which determines the number of times the cell grid's surface is completely dredged since 2012, might not be suitable to discriminate between the Dredged and Unimpacted beds. The analysis failed to acknowledge that at the Unimpacted site, dredging efforts were primarily sporadic at the beginning of the AIS survey, while dredging has continuously been ongoing at the Dredged site. Furthermore, only one value was available for each site during the current survey period, which may not accurately account for the spatial differences in dredging pressure over time. The priority would be to quantify the effect of dredging on maerl-associated by assessing grazers' density in each sampled beds, for example by counting living urchins in a given area in the vicinity of the sampled beds. Another alternative could be to quantify the maerl morphology, for example by using sphericity estimations (Costa et al., 2021, Jardim et al., 2022), to quantify the effect of dredging on maerl individuals. Moreover, information on the long-term recovery of dredged maerl bed communities remains scarce and mostly relies on short-term (1-2 years) surveys following dredging events (Hall-Spencer and Moore, 2000, Bernard et al., 2019). Clear signs of resilience in dredged maerl communities have been shown using BACI experimental dredging; however, these communities never fully returned to their original (undredged) state (Tauran et al., 2020). Additionally, the historical effects of occasional dredging in our Unimpacted site have not yet been assessed. This site is considered a reference (never or at the most very seldomly dredged) site in the French maerl monitoring program. Such level of impact is not comparable to the intensive regular yearly dredging occurring at the Dredged site since the beginning of the 2000s (IUEM Observatory, unpublished data). Concerning the nutrient data used in this study, they relied on

citizen-science program (*Objectif Plancton*) and archive data (*Pointe du Château*). For future monitorings of maerl-associated flora, nutrients should be more regularly assessed *in situ* in order to build precise series.

While several typologies have been proposed for other macrophyte-dominated benthic habitats such as eelgrass meadows (Boyé et al., 2022), subtidal rocky macroalgal communities (Derrien-Courtel et al., 2013, Soltan et al., 2001) and intertidal macroalgal communities (Burel et al., 2022), no such typology has been published for maerl beds yet. In this paper, we showed that distinct macroalgal communities occur in the different maerl beds, supported by the redundancy analysis (**Figure 5**), and that they can be structured by anthropogenic pressures. Characteristic species, can be grouped in functional categories such as proposed by Steneck and Dethier (1994). The Unimpacted bed exhibits a community dominated by filamentous (*e.g. L. fibrata*), cartilaginous species (*e.g. C. dasyphylla*) and encrusting species (*e.g. Cruoria cruoriiformis, Peyssonnelia* spp.). Therefore, we hypothesize that species falling under these morphological groups could be characteristic of unimpacted maerl beds. Those assemblages are mainly driven by biotic interactions such as grazing. Indeed, the Dredged bed exhibits a similar community as the Unimpacted bed, mainly differing from the addition of corticated free-living, and foliaceous species (*e.g. H. incurva, R. tinctoria* and *C. ramosa*). Those assemblages may be driven by the absence of grazers, and their low macroalgal biomass in our study may only be explained by the absence of nutrient-enrichments. Finally, the two eutrophic beds are characterized by free-living (*e.g. H. incurva, V. martensiana* and *S. chordalis*), cartilaginous blades (*e.g. M. laciniata, R. ardissoni* and *S. interrupta*) and foliaceous (*e.g. C. ramosa*) rhodophyte species. Those assemblages are mainly driven by the nutrient inputs, usually in the vicinity of cities and coastal rivers. Maerl beds in the bay of Brest develop in a semi-enclosed bay, and mainly on muddy bottoms (Grall, 2002). We here propose the description of three functional approach-based macroalgal community types for maerl beds on muddy bottoms under various anthropogenic pressures (**Figure 7**):

- (1) Communities with low species richness and biomass, mainly composed of seasonal filamentous, cartilaginous and encrusting species characteristic of unimpacted maerl beds.

- (2) Communities with intermediate to low species richness and biomass, composed of seasonal filamentous, cartilaginous and encrusting species to which are also added more complex and free-living species characteristic of dredged maerl grounds.
- (3) Communities with high species richness and biomass dominated by free-living species, with foliaceous and cartilaginous rhodophyte species, characteristic of eutrophic beds.

#### *Historical changes in maerl-associated macroalgal communities in the bay of Brest*

Our results show that maerl-associated macroalgal communities in the bay of Brest have changed in over 25 years, between the 1996-1997 and 2020-2021 surveys.

Long term changes in macrophyte-dominated communities are often associated with changes in water temperature (Barrientos et al., 2020, Brodie et al., 2014, Eriksson et al., 2002, Harley et al., 2012, Whalen et al., 2023). Maerl beds themselves are threatened by acidification and rises of water temperature (Qui-Minet et al., 2019, Legrand et al., 2017). Indeed, the recent high biomass of warm affinity species such as *R. tinctoria* in the bay, which was not detected in the historical survey, may be explained by higher temperatures (Ardre, 1970, Phillips and De Clerck, 2005, Helias and Burel, 2023). Nevertheless, both in the past and the present, maerl beds in the bay of Brest experienced a range of anthropogenic pressures (Grall and Hall-Spencer, 2003). Small scale anthropogenic pressures in the bay (eutrophication and dredging) were some of the main drivers of present maerl-associated macroalgal communities, thus, those pressures might as well drive long-term changes.

The decrease in biomass since the 1996-1997 survey could indicate a decrease in the eutrophication process in the nowadays Moderately eutrophic site. Indeed, a study near the Brest harbor in the vicinity of a newly built water treatment plant in 2004, showed an improvement in water quality (Quillien and Grall, 2012). Similar improvements were also observed in subtidal macroalgal assemblages associated with rocky-substrata (Soltan et al., 2001). However, while they have greatly decreased over the last decades (Pommepeuy et al., 1979, Guillaud and Bouriel, 2007), nutrient inputs from coastal rivers are still important in the bay (Mènesguen, 2007, Mènesguen et al., 2006, Qui-Minet et al., 2018). The inputs might originate from agriculture and the city of Brest (Qui-Minet et al., 2018, Neilson and Cronin, 2012), causing important rhodophyte developments during summer.

While the Dredged site displayed a dredging-characteristic assemblage in 2020-2021, the 1996-1997 survey detected an unimpacted-characteristic assemblage. Before 2004, this site only faced

minor dredging pressures and was considered as a reference for maerl studies in the bay (Grall and Glémarec, 1997). However, it has been impacted by intensifying dredging practices since 2004 (Bernard et al., 2019, Coquereau et al., 2017). Therefore, we can assume that the nowadays dredged site could have been unimpacted in 1996-1997. Our study showed that grazers might be one of the main drivers of macroalgal communities and are also very sensitive to dredging, therefore, we hypothesize that their loss is the cause of historical changes in the associated flora.

### *Conclusion*

Our findings suggest that anthropogenic pressures, particularly nutrient inputs and dredging through the loss of grazers, account for a greater degree of community changes in comparison to natural processes. Additionally, our results revealed historical changes in the community, indicating historical disturbances. Therefore, the monitoring of macroalgal communities might be a time and cost-effective complementary approach to benthic macrofaunal monitoring. Moreover, red macroalgae blooms (*e.g.* Fine foliaceous reds, *Halopithys incurva*), while reported from various places including the bay of Brest, are still greatly undocumented, and should be monitored as indicators of eutrophication. The morphofunctional approach proposed in this study might be suitable for comparison between macrophytes-dominated soft-substrate habitats worldwide.

### FUNDING

This work was supported by the *IUEM Observatory*, made possible by the French Oceanographic Cruises, and supported by *l'Agence de l'Eau Loire-Bretagne*, Région Bretagne and DREAL Bretagne.

### ACKNOWLEDGMENTS

We thank the crew of the *Albert-Lucas*, M. Maguer and the divers from the GMAP (Groupe Manche Atlantique de Plongée): P. Praud, U. Cadour, S. Carlo, J.C. Jézequel, and F. Ferellec, for the sampling. Thanks are due to V. Peña, R. Issa and S. Connan for sharing their data. We thank A. Tauran for providing fishing pressure data. We thank M. Le Duff and A. Bizien for reviewing the manuscript. Authors would like to thank the handling editors of *Annals of Botany* as well as the anonymous reviewers for their valuable comments.

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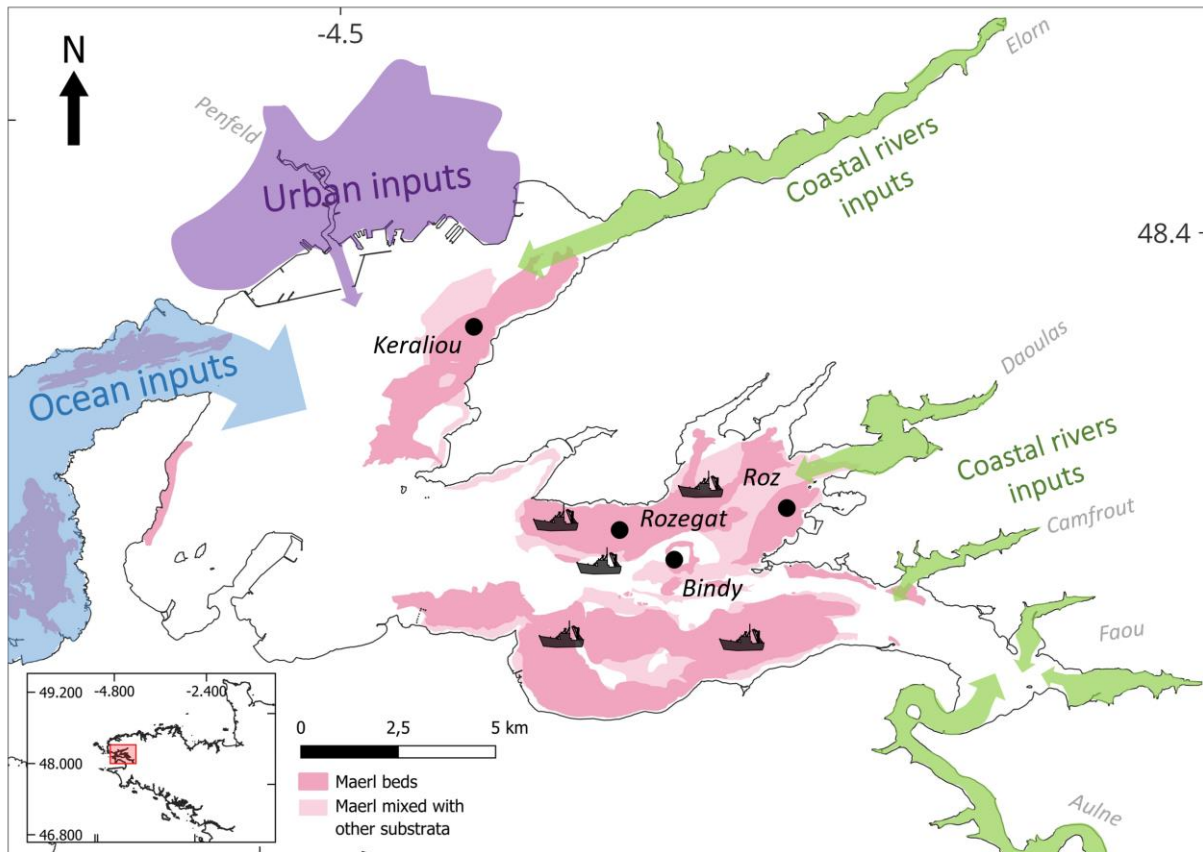
## Tables

**Table 1:** Concentrations of total phosphorus (TP) and total nitrogen (TN) in  $\mu\text{mol.L}^{-1}$  and percentages of gravel, sand and mud in % for the four sites and the four sampling occasions. \* The High eutrophication site was not sampled in October 2020.

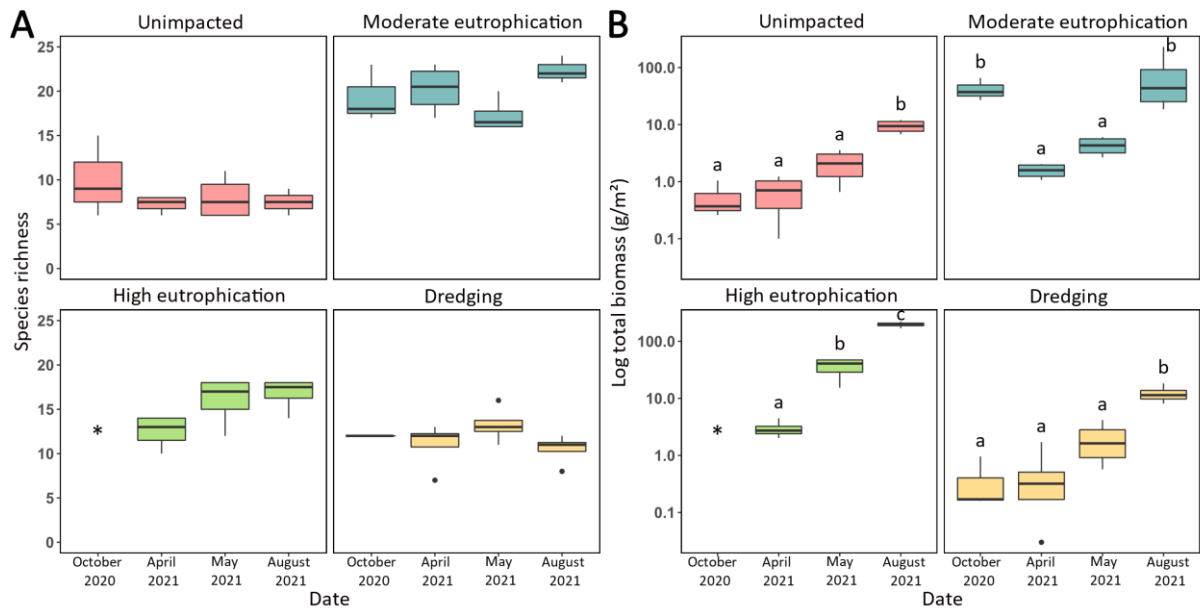
Sampling occasion	Site	TP ( $\mu\text{mol.L}^{-1}$ )	TN ( $\mu\text{mol.L}^{-1}$ )	Gravel (%)	Sand (%)	Mud (%)
October 2020	Unimpacted	0.39	3.09	43.95	7.97	48.08
	Moderate eutrophication	0.37	7.34	34.85	15.99	49.16
	High eutrophication	0.60	17.67	*	*	*
	Dredging	0.39	3.09	51.02	34.51	14.47
April 2021	Unimpacted	0.02	4.73	44.39	7.33	48.29
	Moderate eutrophication	0.05	5.20	49.28	11.76	38.96
	High eutrophication	0.05	11.66	32.18	6.50	61.32
	Dredging	0.02	4.73	28.69	34.76	36.55
May 2021	Unimpacted	0.02	4.73	44.39	7.33	48.29
	Moderate eutrophication	0.05	5.20	41.79	8.14	50.07
	High eutrophication	0.01	0.66	34.74	15.08	50.19
	Dredging	0.02	4.73	55.03	38.78	6.20
August 2021	Unimpacted	0.07	4.06	44.39	7.33	48.29
	Moderate eutrophication	0.10	12.67	41.79	8.14	50.07
	High eutrophication	0.21	0.21	43.85	21.36	34.79
	Dredging	0.07	4.06	55.03	38.78	6.20

**Table 2:** Compiled mean macroalgal biomass ( $\text{g}\cdot\text{m}^{-2}$ ), for the dredged and eutrophic sites over the two sampling periods (1996-1997 and 2020-2021). Condition refers to the pressure associated with the two beds during a given sampling occasion (U: Unimpacted, D: Dredged, HE: High eutrophication and ME: Moderate eutrophication).

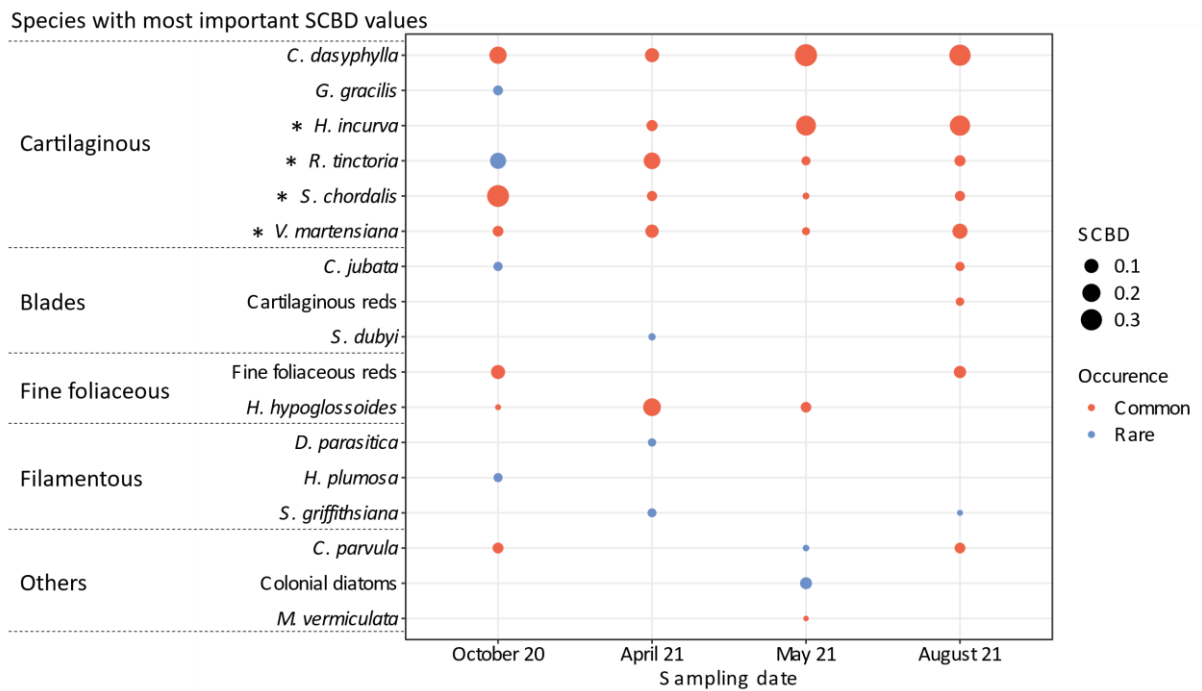
Sampling occasion (year + season)		Dredging	Moderate eutrophication
1996	Summer	1.28	615.79
	Autumn	0.36	20.76
	Winter	0.2	1.71
1997	Spring	2.74	118.31
	Summer	23.03	777.13
2020	Autumn	0.43	43.28
2021	Spring	1.33	2.99
	Summer	12.33	86.18



**Figure 1:** Map of the bay of Brest showing the location of the studied sites in black points. Maerl beds are described in pink colors, light pink indicating heterogeneous beds whereas dark pink is used for homogeneous beds. Green arrows represent inputs from coastal rivers (names in light gray), the purple arrow represents inputs from the city and harbor of Brest (sewage and pollution) and the blue arrow represents the inputs from the Iroise Sea, twice a day via tidal currents. Schematized fishing boats in the southern basin indicate the location of clam-fisheries in the bay, hence fishing pressure.

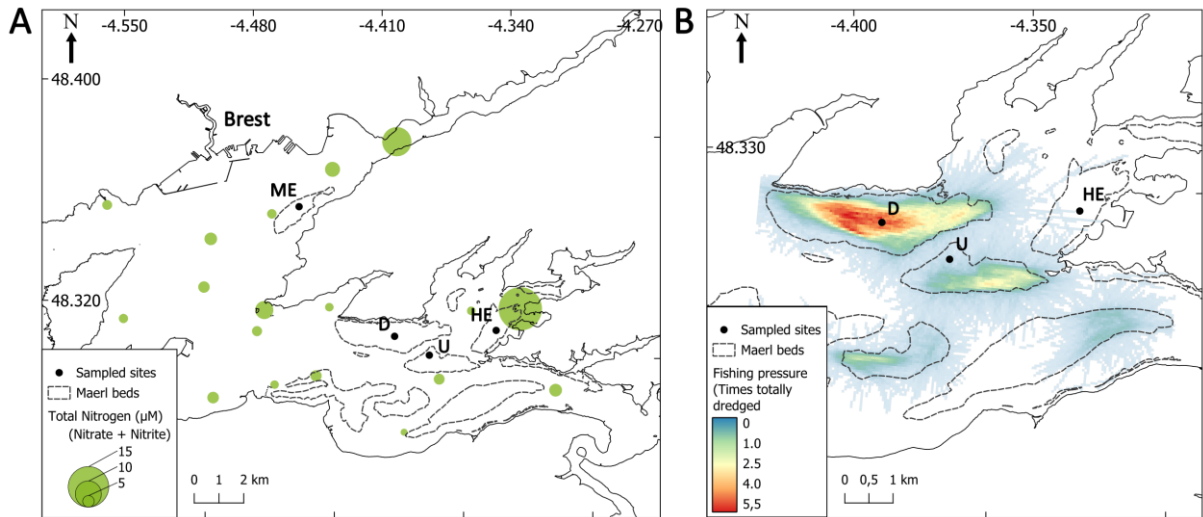


**Figure 2:** Characteristics of the macroalgal communities found in the 4 sampled sites (red for Unimpacted, teal and green for Moderate and High eutrophication respectively and yellow for Dredging) for each sampling period. **A:** Mean species richness. **B:** Mean total macroalgal biomass. Intra-site differences, indicated by lowercase letters, are tested through Kruskal-Wallis and Dunn tests. \* Absence of data.

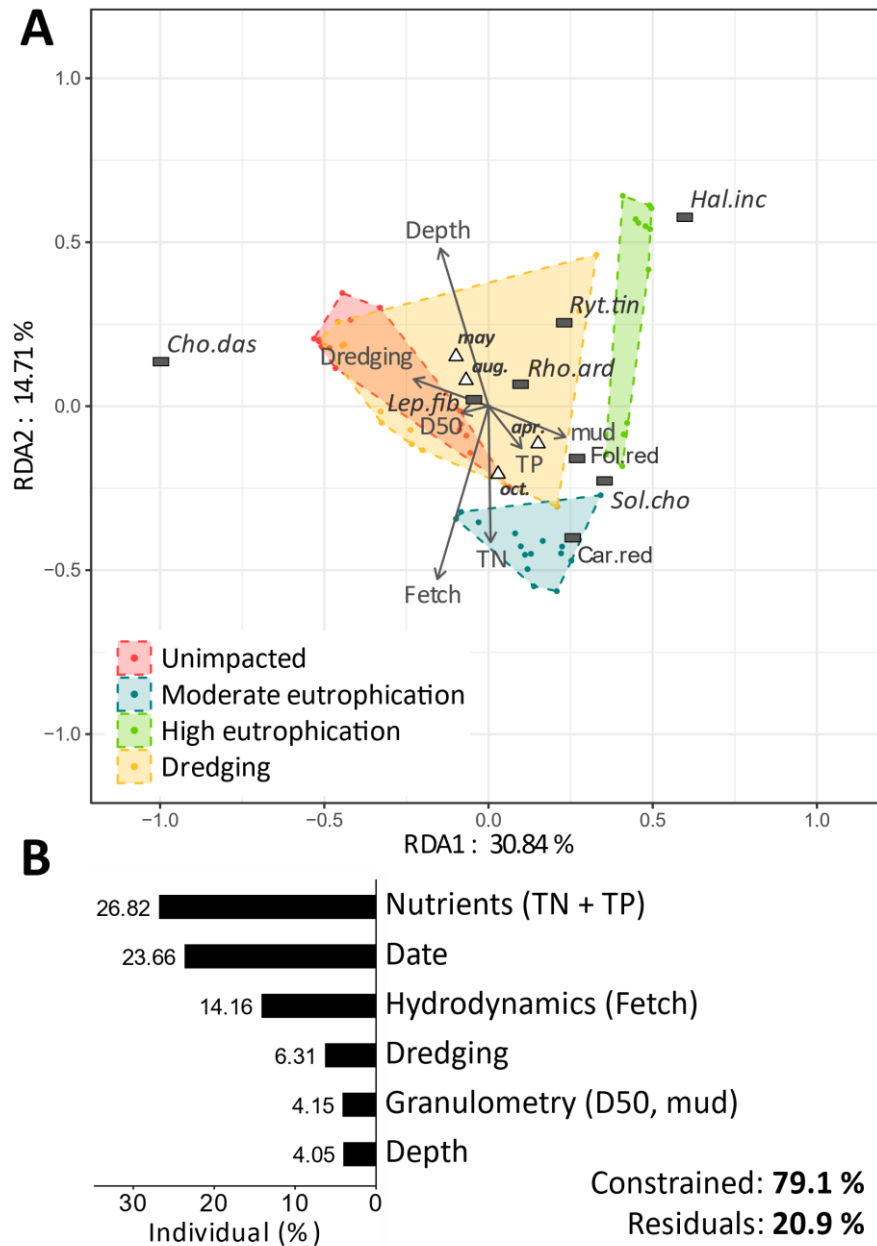


**Figure 3:** Species with the most representative contribution to beta-diversity index (SCBD) for each sampling period. Species are grouped in morphoanatomical groups: cartilaginous, blades, fine foliaceous, filamentous and others (see main text for the definitions). Free-living species are specified by an “\*”. Species that are classified as common (red points) were found in at least two sites for a single sampling period, while rare species (blue points) were only found in one site for a single sampling period.

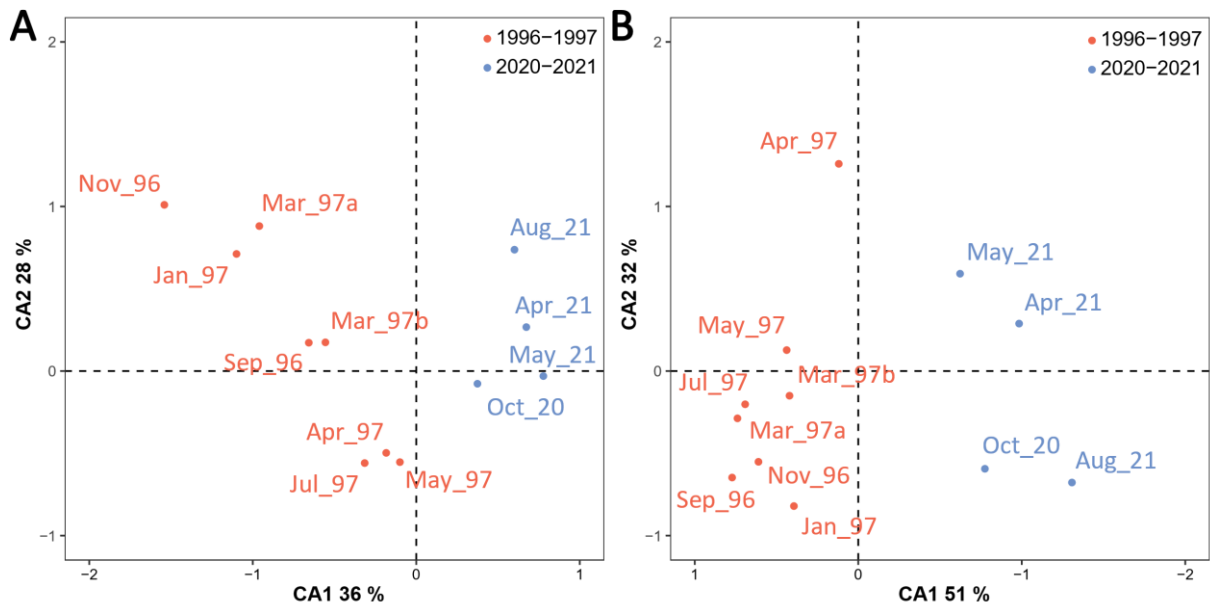




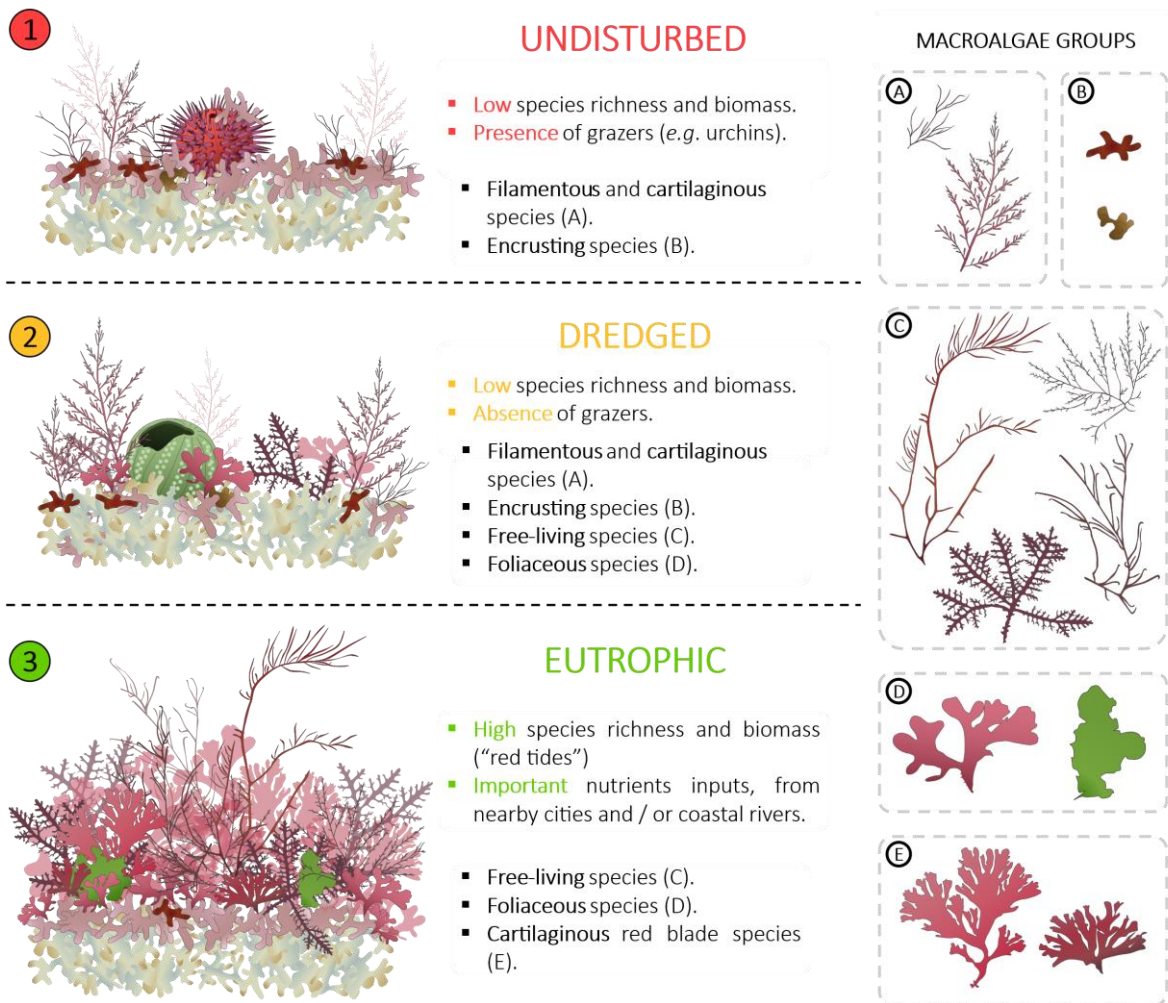
**Figure 4:** Maps of the bay of Brest showing the location of the maerl beds (dashed line). Sampled sites are represented by black dots, ME (Moderate eutrophication), D (Dredging), U (Unimpacted) and HE (High eutrophication). **A:** Nitrogen concentrations (data from “Objectif Plancton” and “Pointe du Château”) during Spring 2021. **B** illustrates the fishing pressure, as the total number of dredging occasions between 2012 and 2021. As the Moderate eutrophication site was not dredged during the 2012 to 2021 period, and is not figured in B.



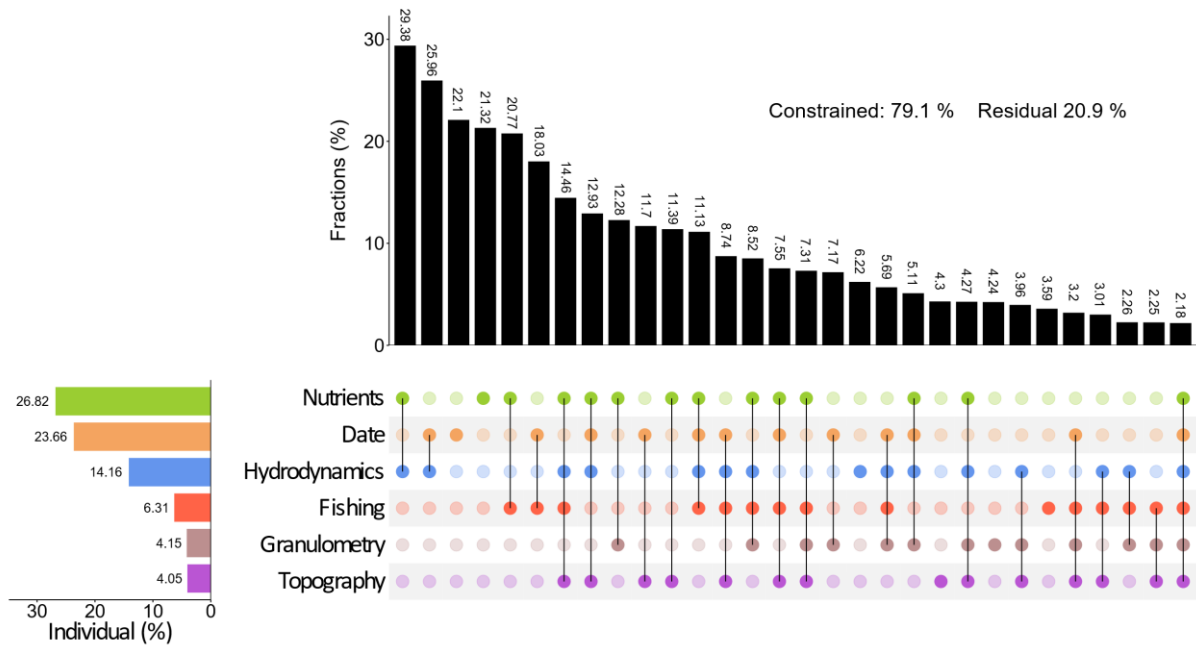
**Figure 5:** **A:** Redundancy analysis (RDA) triplot of the Hellinger-transformed community matrix and of the environmental matrix. Black rectangles represent the taxa and arrows represent the environmental constraints. The centroids of the observations for each sampling date are represented by triangles (oct: October, apr: April, may: May and aug: August). Sites are delimited by polygons (Red: Unimpacted, yellow: Dredged, teal: Moderate eutrophication, green: High eutrophication). TP: total phosphorus, TN: total nitrogen, *Hal.inc.*: *H. incurva*, *Ryt.tin.*: *R. tinctoria*, *Rho.ard.*: *R. ardissoni*, *Fol.red*: fine foliaceous reds, *Sol.cho.*: *S. chordalis*, *Car.red.*: cartilaginous reds, *Lep.fib.*: *L. fibrata* and *Cho.das.*: *C. dasyphylla*. **B:** individual contribution of each explanatory variable matrix assessed by hierarchical partitioning. TN and TP have been gathered as “Nutrients”, and mud and D50 as “Granulometry”.



**Figure 6:** Correspondence Analysis (CA) for the Moderate eutrophication site (**A**) and the Dredged one (**B**) constructed using a presence-absence dataset compiling data from 1996-1997 (red dots) and from 2020-2021 (blue dots). Jan: January, Mar: March, Apr: April, Jul: July, Aug: August, Sep: September, Oct: October, Nov: November.



**Figure 7:** Schematized representation of the 3 main macroalgae community types described in this study. 1) Unimpacted maerl beds, 2) dredged maerl beds and 3) eutrophic maerl beds. For each type, the main characteristics are listed, as well as the type of macroalgae expected, and some examples of species.



**Supplementary information Figure S 1:** Variation and hierarchical partitioning between the Hellinger-transformed community matrix and an explanatory variable matrix. The bottom left barplot shows the individual contribution of each explanatory matrix assessed by hierarchical partitioning. The histogram in the upper part represents the percentage of variation (adjusted R<sup>2</sup>) explained by the different matrices in variation partitioning (fractions < 0 are not represented). The lower panel indicates which fraction of the variance partitioning is considered. Fractions less than 2 % are not shown.