Original Articles

Reading the heterogeneity and spatial structuring of benthic habitats in macrophyte wracks

Martin Thibault [a,b,1,*], Elisa Alonso Aller [a,b,1], Pauline Poisson [a,b], Christian Kerbiriou [a,b,2], Isabelle Le Viol [a,b,2]

[a] Centre d'Écologie et des Sciences de la Conservation (CESCO), Muséum national d'Histoire naturelle, Centre National de la Recherche Scientifique, Sorbonne Université, CP 135, 57 Rue Cuvier, 75005 Paris, France
[b] Centre d'Écologie et des Sciences de la Conservation (CESCO), Muséum national d'Histoire naturelle, Station de Biologie Marine, 1 Place de La Croix, 29900 Concarneau, France

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ABSTRACT

In coastal socio-ecosystems, the European Commission has proposed a set of indicators that could meet the objectives of the Marine Strategy Framework Directive. Most of them refer to the state of benthic habitats, a marine biodiversity compartment under major threat. However, biodiversity monitoring in the marine environment is logistically, technologically, and economically challenging. One possibility may be the monitoring of marine biodiversity "*ex situ*", *i.e.* thanks to the material transported naturally along the sea to land continuum, but the relationship between benthic donor habitats and beach-casted macrophytes remains unclear. Only few studies have previously explored this relationship and they raised two questions: Could some wrack macrophyte species inform on the composition of proximate marine habitats? What is the contribution of local donor habitats in the composition of macrophyte wrack communities from one site to another? Here we provide answers to these questions from the sampling of macrophyte wracks on 131 beaches and the use of benthic habitat maps from the European Nature Information System. From linear regressions, we first show that the α-diversity of non-floating beach casted macrophytes reflects the heterogeneity of benthic habitats lying in straight marine buffers. Second, using non-linear modelling we show that this correlation peaks at 500 m offshore and maintains up to 1000 m far, which corresponds to the infralittoral seabed along our study coastline. Finally, regressions on distance matrices reveal that dissimilarities in wrack communities of non-floating macrophytes are more the result of differences in proximate benthic habitats rather than geographic patterns. While macrophyte wracks are already considered relevant indicators of geomorphological and ecological processes on coastal socio-ecosystem, this study advocates for their further consideration as *ex situ* indicators of benthic ecosystems.

1. Introduction

Biodiversity decline is already visible in marine ecosystems in terms of local biodiversity, functional diversity, and commercial opportunities (Blowes et al., 2019; Gascuel and Cheung, 2019). This decline is mostly attributed to human activities through overexploitation of marine resources, habitat alteration, and climate change (Díaz et al., 2019). Challenges for marine conservation are particularly enormous and the conflict between development and conservation of coastal ecosystems must be solved urgently at a global scale (Pinheiro et al., 2019a). Development of sustainable management policies thus depends on increased consideration of how terrestrial human activities affect marine ecosystems (Ruttenberg and Granek, 2011).

Development of streamlined European Biodiversity Indicators has been proposed a priority initiative to monitor the progress of policies derived from the Convention on Biological Diversity in Europe (Feest, 2013). These biodiversity indicators should be designed under the driver-pressure-state-impacts-responses scheme to ensure their

relevance in socio-ecosystems (Gari et al., 2015). In coastal socio-ecosystems, the European Commission has already proposed a set of indicators that could meet the objectives of the Marine Strategy Framework Directive (MSFD, Ferreira et al., 2011), most of which are related either directly or indirectly to the state of benthic habitats (Ferreira et al., 2011). Indeed, ongoing alterations of benthic habitats are considered one of the major threats to marine biodiversity (Halpern et al., 2008; Kappel, 2005; McCauley et al., 2015). However, already available benthic indicators within the MSFD should be improved to assess both structural and functional aspects of the "sea-floor integrity" (Van Hoey et al., 2010). The production of ecological indicators is dependent upon the cautious consideration of three components: the biodiversity data that should be sampled, the monitoring design that needs to be implemented and the metrics that should be produced. In the case of benthic ecosystems, biomass and spatial cover of biogenic substrates, occurrence of particular taxa, and multi-metric community indices such as species diversity and richness are already considered relevant biodiversity data (Rice et al., 2012).

The assessment of biodiversity states and threats is then dependent upon biodiversity monitoring (Joppa et al., 2016), which, particularly in the marine environment, is logistically, technologically, and economically challenging (Jacob et al., 2020). Direct *in situ* monitoring of the benthic environment is obviously constraining. Remote technologies such as imagery, photogrammetry and/or robotic are currently in development and offer promising perspectives for the future of long-term and high quality remote monitoring of benthic habitats (Beisiegel et al., 2017; Lim et al., 2020; Ridolfi et al., 2021). Yet, the acquisition and use of such high technologies are still restricted to a set of academic and professional users and inherently limited in geographical scope. Large-scale biodiversity monitoring of benthic habitats therefore require complementary tools to be developed on a low-cost and user-friendly basis (Jones et al., 2018).

The easiest and cheapest way of monitoring marine biodiversity may be "*ex situ*", *i.e.* thanks to the material transported naturally along the sea to land continuum. Indeed, the majority of worldwide ice-free coastlines is made of sandy beaches (McLachlan and Defeo, 2017) where cross-ecosystem transport of materials take place (Fanini et al., 2021). Marine organic and inorganic debris are thereby continuously deposited on these "Littoral Active Zones" (LAZ), in the form of phytodetritus termed "wrack" (Colombini and Chelazzi, 2003). We know that the casting of macrophyte wrack on beaches is driven by external factors such as beach morphology and wave regimes (Barreiro et al., 2011; Gómez et al., 2013; Guerrero-Meseguer et al., 2020; Orr et al., 2005). Study cases such as the beaching events of *Sargassum* in the Caribbean suggest that wind, tides, and currents can transport floating materials over large distances before being shore-casted (Wang et al., 2019) and some species displaying visible buoyancy structures are therefore considered long-distance dispersers (Harwell and Orth, 2002). Still, the relationship between benthic donor habitats and beach-casted macrophytes remains unclear.

To the best of our knowledge, only three studies have directly explored this relationship, based on observations from sites located either along the west coast of the United States or in the gulf of Riga. First, it was suggested that macrophyte wracks may originate from proximate (1 km) benthic rocky donor habitats (Suursaar et al., 2014). Consistent with this idea, further studies showed that the biomass of macrophyte wracks at large spatial scales was driven by the distance to major donor habitats: rocky reefs and estuaries (Liebowitz et al., 2016; Reimer et al., 2018). These early results raise several questions: Could macrophyte wracks inform on the diversity of coastal marine habitats? To what extent? What is the contribution of local donor habitats to the composition of macrophyte wrack communities from one site to another?

The present study was designed to answer these three questions. We first sampled and described macrophyte wracks from 131 sites of variable geomorphology along the coastline of French Brittany under a gradient of environmental conditions. We first hypothesised that the diversity of macrophyte taxa on beaches may positively correlate with the heterogeneity of proximate donor habitats. Therefore, we compared the α-diversity of our macrophyte data with the heterogeneity of benthic habitats maps available through the European Nature Information System (EUNIS, Davies et al., 2004). We hypothesized that non-buoyant macrophyte taxa may have limited movements from donor habitats and that their debris, once stranded, would provide information about proximate donor habitats. Conversely, buoyant macrophyte taxa should not directly provide information on these habitats as they are known to float and drift over long distances (Harwell and Orth, 2002). To test these assumptions, we calculated diversity/heterogeneity correlations between three categories of macrophyte wracks (all taxa, only non-floating taxa and only floating taxa) and benthic habitats lying in a set of coastal buffers encompassing various potential movement trajectories and distances. We also hypothesised that differences in macrophyte wrack composition from one beach to another (Reimer et al., 2018) may originate in the specificity of coastal benthic habitats at each site. To test this, we modelled pairwise dissimilarity matrices of macrophyte wrack communities as a response to both geographical distance and benthic habitat dissimilarity matrices. Results are discussed in terms of promises and steps forward for further uses of macrophyte wracks as a biodiversity monitoring tool in coastal socio-ecosystems.

2. Methods

2.1. Study sites

The study took place in four areas belonging to the European Natura 2000 network for which high resolution habitat maps were available. The coastline of Brittany (France) is mainly rocky and interspersed with rivers, estuaries, and sandy areas so that it encompasses a wide heterogeneity in terms of benthic habitats (Table S1). We applied a stratified random sampling to select study sites in the four areas while maximizing the variability of four habitat features: i) substrate, ii) habitat homogeneity, iii) habitat diversity and iv) habitat stability (Table S2). A total of 131 sites (beaches and creeks) were selected on satellite imagery that covered the coastlines of Archipel de Glenan (N = 30), Baie de Morlaix (N = 28), Roches de Penmarc'h (N = 31) and Trégor Goëlo (N = 42) sites (Fig. 1). Sites were separated by 0.04 up to 152 km, with a median distance between sites of 85 km. The selected sites covered a wide range of conditions in terms of orientation, exposure to wind and swell, proximity to estuaries, and human activities, as well as biotic environment, with environmental marine conditions also being known to differ between the north and the south parts of Brittany.

2.2. Macrophyte wrack sampling

Macrophyte wrack sampling took place in May and June 2020, in absence of strong winds or mass algae-deposition events. For each of the four areas (Glenan, Morlaix, Penmarc'h and Trégor-Goëlo), all sites were sampled within 1–2 weeks to minimise any potential temporal variability in beach wrack composition. Each area was sampled by a single set of observers to minimise observer bias within each area. At each site, the sampling design consisted in a 25 m transect set on the freshest wrack line (closest to shore), along which five 1 m² quadrats separated by 5 m were sampled.

Within each quadrat, all macrophyte fragments were visually identified at the lowest possible taxonomic rank. A large majority of fragments were identified at a species (80 %) or genus level (16 %), and unidentified fragments (6 %) were categorized in groups based on their morphology. Fragments belonging to *Ulva*, *Umbraulva* and *Monostroma* genus classified into two groups based on their morphology, *i.e.* foliose and tubular forms. The abundance of each taxon per quadrat was estimated using a 5–grade scale based on their relative abundance (0 = none; 1 = very rare, one fragment; 2 = rare, a few fragments; 3 =
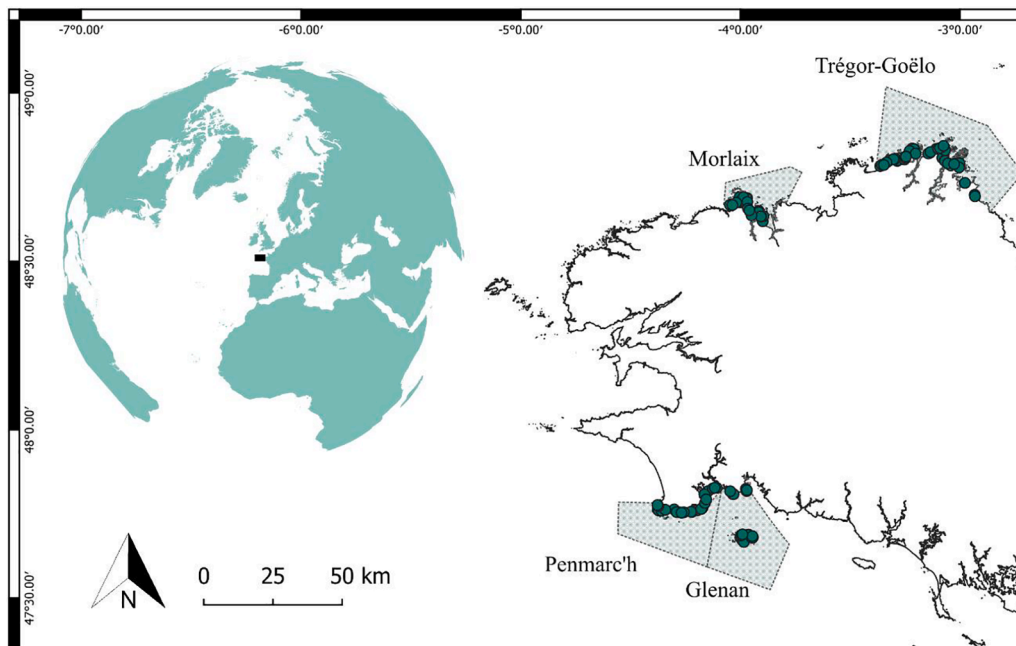
Fig. 1. Location of the four Natura2000 areas as well as the 131 sites sampled for this study.

common, many fragments, 4 = dominant, >50 % of fragments). At 10 out of 131 selected sites, no macrophyte wrack were found.

Macrophyte wrack composition relies on the drifting of macrophyte debris, which can occur over various distances depending on physical conditions and properties of the dispersing species (Gaylord et al., 2006). In particular, the presence of macroscopic buoyancy structures is associated with long-distance drifting (Hawes et al., 2017) and could therefore explain macrophyte wrack composition. To test this hypothesis, we divided sampled macrophyte taxa in two categories. "Floating taxa" (N = 13) were defined as those presenting buoyancy structures (*e. g. Fucus vesiculosus*) or that are known to aggregate and drift on the ocean surface (*e.g. Zostera marina,* Harwell and Orth, 2002). All other taxa (N = 66) were further categorized as 'non-floating taxa'. Note that some non-floating taxa were observed at only one site (N = 9) and therefore not considered in analyses. Overall, 79 taxa were considered for further analyses out of the 88 originally identified on our 131 sites (Table S3).

2.3. Coastal buffers

To determine the extent to which the diversity of beach wrack macrophytes reflects the heteregeneity of coastal benthic habitats, we defined buffers (N = 48), varying in size and shapes, around all sample sites. These buffers first considered two shapes accounting for various macrophytes dispersal directions (Fig. 2). The circular shape assumed that debris could come from anywhere around each site through long distance drifts: i) The "round" buffer included all benthic habitats lying at 360° around the sampling site while ii) the "round direct" buffer excluded habitats separated from the sampling site by physical barriers such as islands, peninsulas, or harbours (21 % of round buffers). The rectilinear shape, 250 m wide or the width of the beach if <250 m, assumed that macrophyte debris originate from local donor ecosystems and drift primarily with tidal and shoreline currents: iii) the "straight" buffer included all habitats within a band defined as perpendicular from the sampling sites while iv) the "straight direct" buffer excluded habitats separated by physical barriers (4 % of straight buffers). Buffer shapes were applied at 12 distances to the coast (from 250 to 3000 m at 250 m intervals), as we expected close proximal donor habitats to better explain macrophyte wrack diversity as compared to distant ones. All GIS
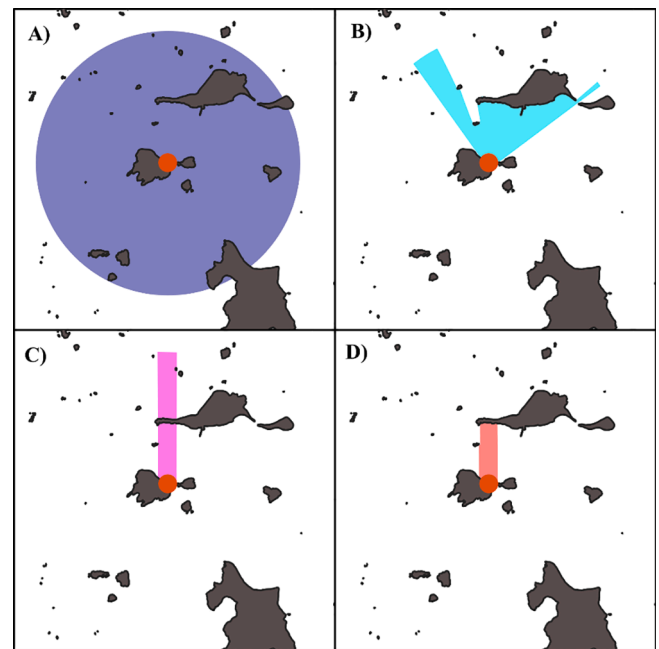

Fig. 2. Depiction of the four types of marine buffers considered: A) round, B) round direct, C) straight, and D) straight direct. Dark grey polygons represent islets of the Glenan archipelago, an original context that we highlight to illustrate the maximum extent encompassed by the four buffer shapes.

analyses were carried out in QGIS 3.14 (QGIS.org, 2020).

2.4. Benthic habitats

To correlate macrophyte wrack α-diversity from *in situ* samplings with the number of habitats and the Shannon diversity of coastal benthic habitats, we utilized marine habitat maps made from the standardized EUNIS classification (Bajjouk et al., 2019, 2018,2017; Bajjouk and Hamdi, 2017). EUNIS classification takes substrate, depth, exposure, and biological composition into account within a comprehensive

hierarchical classification of habitats (Davies et al., 2004). In our four study areas, EUNIS habitat polygons were available at a resolution down to one square kilometer. For convenience in merging the habitat lists from each area, we only considered habitat types up to the third level of resolution in this classification. Habitats available at higher resolution levels were included in the nearest category at this third level resolution. Habitats that were present in only one out of the four areas (N = 3) were reclassified in the nearest habitats category at the higher resolution level. Fauna dominated habitats (N = 6) were excluded from analyses. Thereby, 46 habitat types were considered for further analyses out of the 55 originally available at our four study areas (Table S1).

2.5. Diversity metrics

We calculated two α-diversity indices, richness and Shannon index, from macrophyte wrack samplings. Taxa richness is the number of taxa in each site per quadrat and the taxa Shannon index was calculated for each transect based on the relative abundance of taxa in each quadrat. If a sample included observations of taxa identified to genus level and taxa of the same genus identified to species level, only species level taxa were included in the calculation of diversity indices (*e.g.* if both Laminaria sp. and *Laminaria hyperborea* were identified, only *Laminaria hyperborea* was included).

From EUNIS marine habitat maps, we calculated two 'habitat heterogeneity' indices. We first calculated a proxy of the biological habitat richness as the number of EUNIS habitat categories present in each site per buffer shape and distance. Similarly, a proxy of habitats Shannon index was calculated from the percent cover of each EUNIS habitat categories within each buffer shape and distance. Shannon indices were calculated using the "vegan" package in R (Oksanen et al., 2019).

2.6. Identifying relevant marine buffers

We conducted our analyses in three steps (Figs. 3 and 4). The first step aimed at estimating correlations between the heterogeneity of benthic habitats maps and the α-diversity of macrophyte wracks depending on their floating potential. To that end, we used linear mixed-effects models (LMMs) to assess how macrophyte wrack α-diversity was correlated to the heterogeneity of habitats found in a variety of coastal buffers. Individual models were run for each buffer shape and distance, with habitat heterogeneity as a predictor of taxa α-diversity. The models also included 'Natura 2000 area' (factor, 4 levels) and site (nested within 'Natura 2000 area') as random factors (random intercept only), to account for uncontrolled variability at both scales (*e.g.* observer and date). Spatial autocorrelation was controlled by applying a Gaussian auto-correlation structure to our geographic covariates (Pinheiro and Bates, 2006). Models were run separately including (i) all taxa, (ii) only non-floating taxa and (iii) only floating taxa. Potential type-1 errors associated with the testing of multiple non-independent hypotheses on each taxa subset were accounted for by applying Hochberg corrections to *p* values (Andrade, 2019; Hochberg, 1988). LMMs were run using the 'nlme' package (Pinheiro et al., 2019b) and model R^2 values were obtained using the 'MuMIn' package (Bartoń, 2019). Statistical analyses were performed using R v. 4.02 (R Core Team, 2020). Models were run for the two measures of diversity (*i.e.* richness and Shannon index), the three taxa subsets (all, non-floating and floating), the four buffer shapes and the 12 distances, for a total of 288 models. AIC were calculated for each model (Akaike, 1987). Response variables were checked for normality and homogeneity of variance before analyses. Model fit and residual structure were visually inspected to ensure that statistical assumptions were met.

In a second step we explored the distance to coast as a continuous predictor of the correlation between beach wrack macrophyte diversity and benthic habitats heterogeneity. To this end, we ran generalized additive mixed models (GAMMs) including the slopes of correlation obtained from the LMMs as response variables and the buffers' distance as a spline smoothing function with a basis dimension (k) of three. GAMMs were run only for the diversity indices calculated on the "straight direct" buffers, based on outputs of the LMMs models. Just like before, models were run separately including (i) all taxa, (ii) only non-
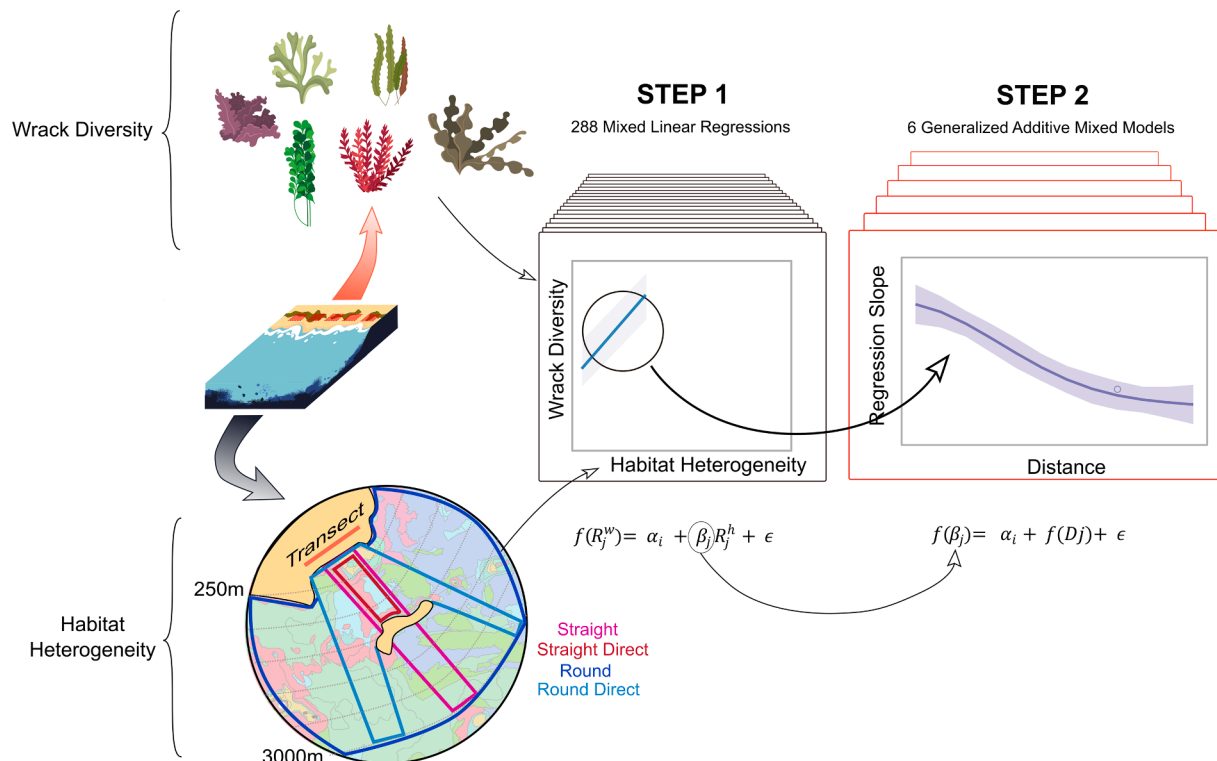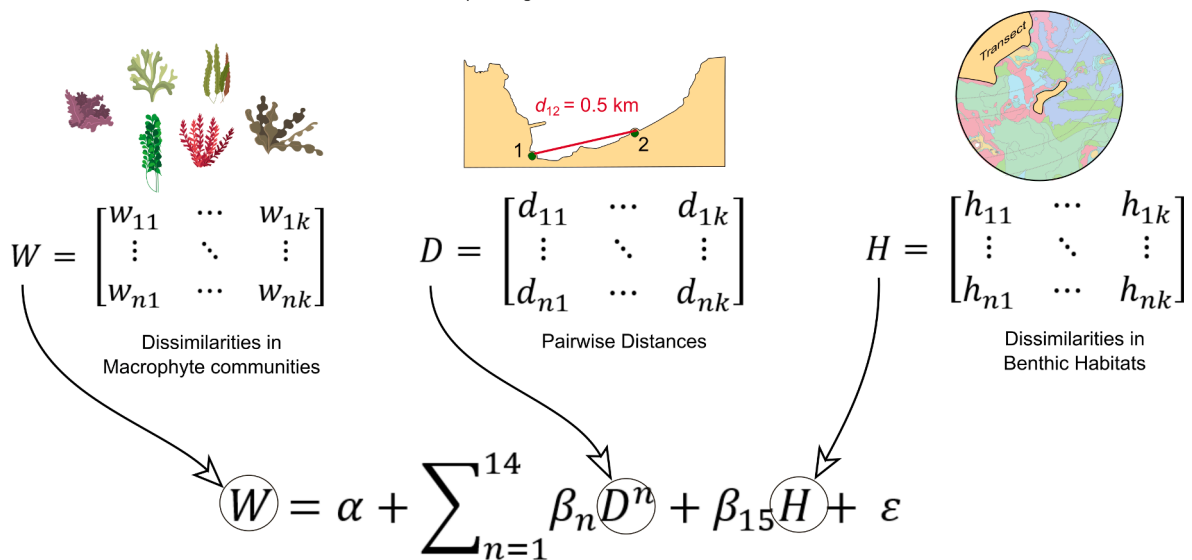

Fig. 3. Workflow of analyses to (i) explore correlations between macrophyte wracks α-diversity and benthic habitats heterogeneity (ii) evaluate the contribution of buffers' distance to the coast as a correlation predictor.

STEP 3

2 Multiple Regressions on Distantce Matrices

Fig. 4. Workflow of analyses to evaluate the contribution of benthic habitat communities' dissimilarity to pairwise site dissimilarities in macrophyte wrack at short and large spatial scales.

floating taxa and (iii) only floating taxa. GAMMs were run with the 'mgcv' package (Wood, 2011).

2.7. Determinants of pairwise dissimilarities in macrophyte wrack communities.

The third step of our analyses aimed at determining if the spatial structuring in macrophyte wrack communities is only the result of broad scale geographical patterns or determined by site specific assemblages of benthic habitats. We modelled the response of between-sites dissimilarities in beach wrack macrophyte communities (non-floating and floating) to both habitat dissimilarities and geographical distances (Fig. 4). These analyses were only performed on sites with macrophyte wrack present, *i.e.* on a subset of 121 sites for floating taxa, and 119 sites for non-floating taxa. Geographic distances between all sites were first computed in a matrix using the "geosphere" package in R (Hijmans et al., 2021). The spatial structuring of benthic habitats was computed as a matrix of pairwise Bray-Curtis dissimilarities between sites in terms of the percentage cover of all benthic habitats. A focus was made here on the buffer shape and distance highlighted by the first analysis step, *i.e.* "straight direct" buffers within 500 m off sampled beaches. This focus reduced the list of potential donor habitats to 31 (Table S1). Macrophyte communities were first aggregated at the transect scale as lists of relative abundance per taxa, which was calculated as the frequency of occurrence in the five quadrats. Two Bray-Curtis dissimilarity matrices were then calculated from pairwise differences in communities of i) non-floating (N = 66 taxa) and ii) floating (N = 13 taxa) macrophyte taxa.

We then evaluated the performance of the habitat matrix and geographical distances matrix in predicting dissimilarities in macrophyte wrack communities. This was achieved by computing two multiple regressions on distance matrices, following the procedure presented in Lichstein (2007) to remove spatial autocorrelation. First, a mantel correlogram was fit with the "ecodist" package (Goslee and Urban, 2007) to describe spatial patterns in the habitat dissimilarities, to the specifications set forth by Legendre (2000). This function uses a mathematical data partitioning rule (Sturge's rule, Legendre and Legendre, 2012) to determine the number of distance lags that best highlights the general patterns of correlation between biological and spatial distance pairs (Lichstein, 2007). Here, dissimilarities between macrophyte wrack

communities were partitioned into 14 spatial distance classes containing various pair numbers. The function then runs Mantel tests on each of the 14 distance classes and provides Pearson correlations along with Bonferroni corrected *p* values (Table S4). Accordingly, we then remodelled the geographical distance matrix into 14 sub-matrices that were all used as predictors in the multiple regressions (Lichstein, 2007). The lack of spatial autocorrelation in the two final models was finally controlled by refitting a Mantel correlogram on the models' residuals (Lichstein, 2007). Results are presented as compilations of predictors with corresponding regression coefficients and *p* values from 1000 permutations (Legendre et al., 1994). Percentages of explained variance provided for each predictor matrix were computed as individual adjusted R^2 using Ezekiel's formula through variation and hierarchical partitioning with the R package "rdacca.hp" (Lai et al., 2022).

3. Results

We identified 88 macrophyte taxa, of which 79 were observed on multiple sites (Table S3). When considering all macrophyte taxa together, the mean species richness per site was of 17.5 ± 9.3 while the mean Shannon index was of 2.3 ± 0.8. Non-floating taxa (N = 66) were observed on 89 % of sampled beaches. They were characterized by a large species richness of 12.3 ± 8.3, and a mean Shannon diversity of 1.9 ± 0.8. Floating taxa (N = 13) were slightly more frequent on sampled beaches (91 %), while their mean richness was half (6.9 ± 2.1) that than for non-floating taxa. Their relative diversity accounted by Shannon index appeared similar on average (1.7 ± 0.4) than that of non-floating taxa. Pairwise Bray-Curtis dissimilarities in benthic habitats found within "straight direct" buffers up to 500 m off the coasts (N = 31) were in the range $3 \times 10^{-4} - 1$ with an average of 0.8 ± 0.2. Similarly, communities of non-floating taxa were highly dissimilar on average (0.8 ± 0.2), while those of floating taxa were more similar from one site to another (0.5 ± 0.2).

3.1. Identifying relevant marine buffers

We found significant correlations between macrophytes wrack α-diversity and benthic habitats heterogeneity. The sign and consistency of correlations varied with buffer shape and distance, as well as with the

type of taxa considered (all, non-floating and floating taxa; Tables S5 and S6). This extensive screening produced three major results: 1) non-floating taxa α-diversity is positively correlated with benthic habitats heterogeneity, 2) this correlation is best explained by models considering the heterogeneity of benthic habitats lying within "straight-direct" buffers (Table 1), and 3) this correlation is strongest with the heterogeneity of benthic habitats within short distance (<750 m) buffers (Table 2).

Non-floating taxa were good predictors, as expected. The heterogeneity of benthic habitats was best reflected by the α-diversity of non-floating beach-casted macrophytes as compared to floating taxa (Table 1). Out of 96 models, 19 showed significant positive correlations between non-floating taxa α-diversity and benthic habitats heterogeneity. Conversely, only four were significant for "floating" taxa and they were all negative. The combination of the two taxa subgroups provided nine significant positive correlations with benthic habitats heterogeneity in straight and straight direct buffers.

Straight rectangle in front of the beach appeared the most relevant marine extent of the wrack/habitat correlation. "Straight-direct" (i.e. found in front of beaches) was the buffer shape for which the correlation between the α-diversity of non-floating macrophyte wracks and the heterogeneity of habitats provided the lowest AIC values (Tables S5 and S6). This buffer shape revealed correlations between the α-diversity of non-floating macrophyte wracks and the heterogeneity of benthic habitats that peaked at short offshore distances for both the richness and Shannon diversity indices (Table 2). In comparison, correlations estimated from round shaped buffers showed up at various distances depending on the consideration of either the species richness or the Shannon diversity. We therefore focused on "straight-direct" buffers in following analyses. The full list of model outputs for the two diversity indices and per taxa group, buffer shape and distance are provided in Tables S5 and S6.

Habitats lying at short distance to the shore best correlated with the diversity of casted macrophytes. Overall, regression slopes higher than 0.5 with 99 % confidence (p < 0.001) were all found within 250, 500 m and 750 m off the beaches (Table 2, Tables S5 and S6). Generalized additive models revealed that slopes of correlations between macrophyte wrack and benthic habitat diversity gradually decreased with distance to the beach (Fig. 5). Buffer distance was found to be a significant predictor of the correlation calculated from both indices when considering non-floating taxa only, explaining up to 78 % of the correlation slope variance for the richness model on non-floating taxa. Further, models revealed two patterns. First, correlation slopes peaked at a very short range from the sampled beaches, *i.e.* 500 m for richness and 750 m for Shannon index. Second, correlation slopes were relatively high at both short and long distances compared to intermediate

Table 2
Highlights of results from LMM screening, showing strong correlations between the diversity of non-floating taxa and heterogeneity of benthic habitats lying within 3 distance buffers for the straight direct buffer.

	Richness			Shannon		
Distance	*Slope*	*SE*	*p_value*	*Slope*	*SE*	*p_value*
250 m	**0.765**	0.196	**0.004**	**0.561**	0.141	**0.003**
500 m	**1.014**	0.182	**<0.001**	**0.767**	0.138	**<0.001**
750 m	**0.654**	0.155	**0.001**	**0.835**	0.148	**<0.001**

distances when considering all taxa with both diversity indices. When considering all taxa, slopes of correlation decreased up to 1750 m and increased again from 2250 m and further. However, looking at the models accounting for floating and non-floating taxa separately revealed that this pattern was artefactual. Accounting for the significant, negative slopes found in floating taxa between 1000 and 1500 m off the beaches likely accentuated the shift in correlation when considering all taxa within this distance range. When considering non-floating taxa only, the slope gradually decreased with the distance until a plateau was reached between 1500 and 2000 m off beaches. Details of all GAMM models are provided in Table S7.

3.2. Dissimilarities in macrophyte wrack communities explained by spatial structuring of benthic habitats

Exploring the correlations between macrophyte wrack communities and benthic habitats in term of spatial dissimilarities highlighted a positive relationship for non-floating taxa only. Outputs of the two multiple regression models are presented in Table 3. The combination of benthic habitat dissimilarities and distance classes explained 12 % (R^2) of the variance observed in communities of non-floating taxa found in macrophyte wracks (p = 0.001). Dissimilarity in benthic habitats was the third best predictor, accounting for 15 % of the variance explained by this model. The best predictors, *dist13* and *dist14*, both accounted for 22 % of the model's variance. These two distance matrices represented the highest distance classes that were considered here, *i.e.* between 130 and 152 km. Overall, this shows dissimilarities in wrack communities of non-floating macrophytes are more the result of differences in proximate benthic habitats rather than geographic patterns, except for the most distant of Northern and Southern sites. It is worth mentioning that all distance predictors were found to be significant in this model, except for *dist4* and *dist8* which included the distance "gaps" between our four study areas. The correlogram fitted on the model's residuals is provided in Figure S1a and shows that no spatial autocorrelation remained unexplained.

Table 1
Summary of results from LMM screening. Number of models tested predicting taxa diversity from habitat diversity for each buffer shape and predictor and their statistical significance and sign of significant effects.

	Richness			Shannon index		
Buffer shape	Non-significant	Significant +	Significant -	Non-significant	Significant +	Significant -
All Taxa						
Round	12	0	0	12	0	0
Round direct	12	0	0	12	0	0
Straight	10	2	0	9	3	0
Straight direct	10	2	0	10	2	0
Non-Floating taxa						
Round	12	0	0	11	1	0
Round direct	8	4	0	10	2	0
Straight	9	3	0	9	3	0
Straight direct	9	3	0	9	3	0
Floating taxa						
Round	12	0	0	12	0	0
Round direct	12	0	0	12	0	0
Straight	12	0	0	12	0	0
Straight direct	9	0	3	11	0	1
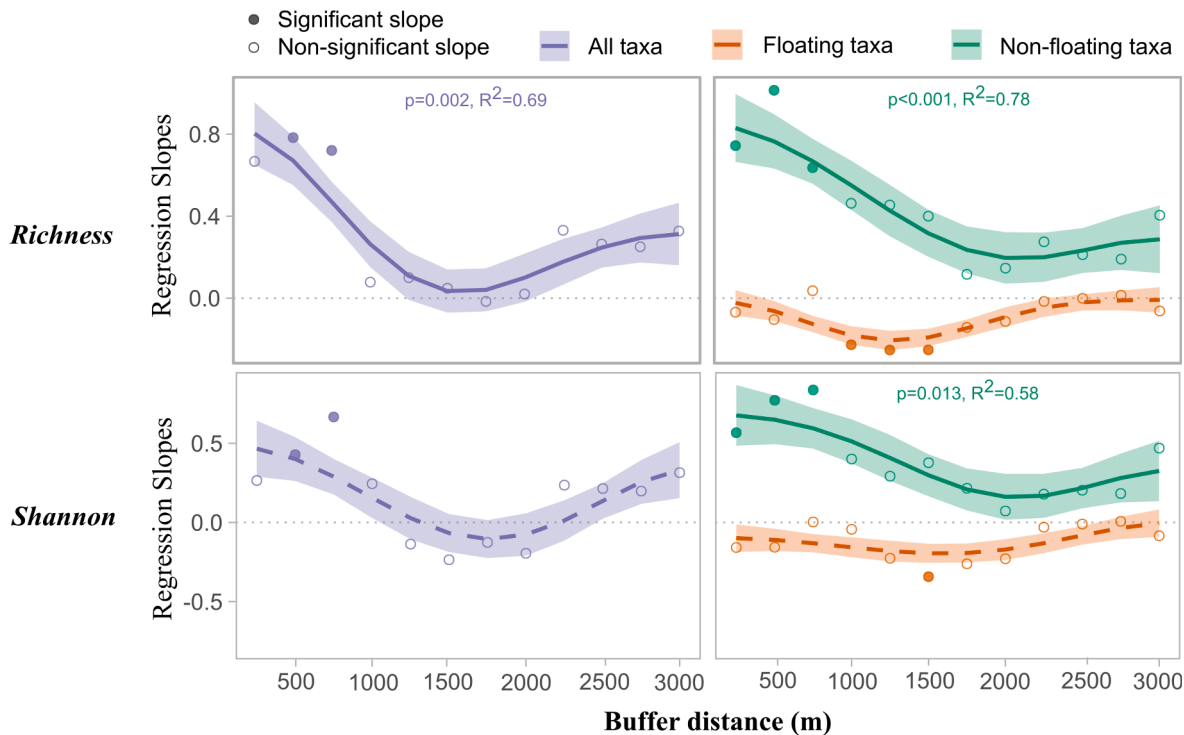
Fig. 5. Change in slope of correlation between taxa and habitat found for straight direct buffers depending on the distance to shore, inferred from richness and Shannon indices. Colours mark data subsets considered: all macrophyte taxa (purple), non-floating taxa only (green), and floating taxa only (orange). Filled points represents significant correlation slopes and empty points mark non-significant correlations. Dashed lines represent non-significant trends. Shaded areas are 95% confidence intervals. *P* and R^2 values are shown only for significant correlation slopes. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Table 3

Results from the multiple regression models for pairwise dissimilarities in i) non-floating and ii) floating taxa found in macrophyte wrack and benthic habitats located on straight direct buffers, 500 m off the sampling sites. *% Variance* indicates the percentage of individual effects towards total explained variation for each matrix. *Scale Interpretation* provides the relevant scale corresponding to each distance submatrices.

Scale Interpretation		Variable	Distance (km)	Non-Floating			Floating		
				coef	*p*	*% Variance*	coef	*p*	*% Variance*
		Habitats		0.045	0.016	15	0.041	0.06	8.2
		dist1	[0.0-10.9]	0.009	0.001	7.5	0.013	0.001	6.7
Within any area	South Vs South	dist2	[10.9-21.7]	0.006	0.001	2.2	0.011	0.001	13.9
		dist3	[21.8-32.6]	0.003	0.001	1.2	0.006	0.001	2.3
		dist4	[32.6-43.4]	-0.001	0.566	2.1	0.003	0.010	0.1
	North Vs North	dist5	[43.6-54.3]	0.002	0.001	0.8	0.003	0.001	1
		dist6	[54.4-65.1]	0.001	0.014	4	0.001	0.149	8.8
		dist7	[65.2-76.1]	0.002	0.001	3.7	0.001	0.011	4.5
		dist8	[76.2-81.3]	0.000	0.919	1.1	0.003	0.005	0.6
	North Vs South	dist9	[88.6-97.8]	0.001	0.001	1	0.002	0.001	7.7
		dist10	[97.8-108.7]	0.001	0.001	2.2	0.002	0.001	5.8
		dist11	[108.7-119.5]	0.001	0.001	5.1	0.001	0.003	5.8
		dist12	[119.6-130.4]	0.001	0.001	9.1	0.002	0.001	16.1
		dist13	[130.4-141.3]	0.001	0.001	22.6	0.002	0.001	15.6
		dist14	[141.3-152.1]	0.001	0.001	22.2	0.001	0.001	2.8
		Overall model:		$R^2 =0.12$ $p=0.001$			$R^2 =0.16$ $p=0.001$		

Dissimilarities in communities of floating taxa outlined a different pattern. The variance explained by the whole model (16 %) was slightly higher than that of the non-floating model. However, dissimilarities in benthic habitats did not significantly explain spatial dissimilarities in floating macrophyte wrack communities (p > 0.05). Looking at the percent contribution of individual predictors to the model's variance, habitat dissimilarities turned out as the fifth predictor only. Further,

distance was a better predictor of dissimilarities in floating macrophytes at all geographical scales, as suggested by the higher contribution of *dist2* (10–20 km), *dist6* (55–65 km), and *dist12-13* (120–140 km). This highlights that dissimilarities in floating macrophyte wrack communities are more the results of geographic patterns at various scales than a response to dissimilarities in proximate benthic habitats. The correlogram fitted on the model's residuals is provided in Figure S1b and shows

that no spatial autocorrelation remained unexplained. Regression plots of spatial dissimilarities between both floating and non-floating taxa in macrophyte wrack and those of benthic habitats are presented in Figure S2.

4. Discussion

We provide a quantitative and qualitative description of macrophyte wracks sampled on a heterogeneous set of beaches. From this stratified sampling, we then answer two determinant questions for further considerations of macrophyte wracks as *ex situ* indicators of benthic ecosystems. Our results first show that the diversity of non-floating macrophyte species in wracks correlates with both the richness and relative diversity of benthic habitats. Second, this correlation is particularly strong within 1000 m in front of beaches. Finally, the heterogeneity in non-floating macrophyte wrack communities from one site to another substantially reflects the heterogeneity in proximal benthic donor habitats.

4.1. Non-floating macrophytes are more diverse and unevenly distributed along Brittany coasts

Floating taxa were less represented in terms of richness as compared to non-floating taxa on our study sites. On the other hand, the mean Shannon diversity index of floating and non-floating taxa in macrophyte wracks was very similar and floating taxa were found at more sites than non-floating ones. This testifies for a high evenness in a low number of floating taxa throughout our study area. Here, very few correlations between the α-diversity of floating taxa and the heterogeneity of benthic habitats were significant and they were all negative. Conversely, the richness of non-floating taxa was twice as high and varied more consistently with the diversity of benthic habitats at various buffer shapes. This first observation supports the fact that buoyancy substantially affects the stranding dynamic of marine macrophytes. From an evolutionary perspective, increased buoyancy coupled with adaptation to sea surface conditions is associated with increased dispersal range in marine macrophytes (Rothäusler et al., 2020). Species presenting buoyant vesicles such as *Fucus vesiculosus* can float and move over distances beyond 200 km (Rothäusler et al., 2015). Even some taxa without visible buoyant structures such as *Zostera marina*, are known to disperse over hundred kilometres (Harwell and Orth, 2002). This capability is however counterbalanced in the face of natural selection by a reduction in potential depth niche and increased sensitivity to environmental fluctuations (Fraser et al., 2020). If buoyancy appears neutral toward selection processes, maintaining a diversity of traits, it certainly represents a key feature to understand the transport of macrophyte debris along the sea to land continuum.

4.2. Coastal non-floating macrophytes travel short and straight

We tested whether macrophyte wracks originate from distant and spread, or close and restricted benthic donor habitats. Our results suggest that most macrophytes travel straight from donor habitats to the beaches on which they cast. In all cases, benthic habitats heterogeneity in our straight shaped buffers showed many more significant correlations with the α-diversity of macrophyte wracks as compared to round-shaped buffers. Also, these correlations were much higher within a kilometer off beaches and reached a plateau beyond 1500 m. This is consistent with previous observations suggesting that algae fragments could either quickly beach-cast or enter an offshore drifting journey subject to a combination of tidal and wind regimes (Hawes et al., 2017). Direct monitoring of algal movements in nearshore waters has shown that nearly all fragments exposed to onshore winds beach-cast after one tidal cycle, moving by <400 m on average (Hawes et al., 2017). Further, *in-situ* transect sampling of benthic habitats held in the Gulf of Riga (Baltic sea) previously suggested that benthic donor habitats occur

mostly within 4 km off the coasts (Suursaar et al., 2014). The authors reported that this distance corresponded to the maximum depth at which they observed benthic macrophytes, *i.e.* 10 m. At our study sites, a 1.5 km marine buffer distance corresponded to an average depth of 7.3 ± 6.6 m, and a maximum of 30 m (Figure S3). Along the coast of Brittany, such depth indeed corresponds to the limit between infralittoral and circalittoral benthic communities, the latter being characterized by a reduced access to light and the quasi absence of photosynthetic macrophytes (Derrien-Courtel et al., 2013). This second assessment thereby outlines that the diversity of macrophyte wracks, particularly in non-floating taxa, informs on the diversity of infralittoral habitat communities.

We tested whether taxa richness and Shannon index of macrophyte wracks could be used as correlates of the heterogeneity in benthic habitats. We found that they can, to a certain extent. Our results suggest that both metrics could be measured on macrophyte wracks to infer the heterogeneity of benthic habitats present in straight direct buffers; although estimations focussing only on non-floating macrophytes were more efficient. This output is especially relevant within the scope of European strategic directives for the marine environment (Mee et al., 2008). Changes in marine macrophyte abundance and community composition are indeed already considered relevant indicators of both direct and indirect effects of seawater eutrophication by the European Commission (Ferreira et al., 2011). The diversity of non-floating macrophytes in beach wracks thus appears a promising indicator within this regional framework (Canonico et al., 2019; Dreujou et al., 2021). Obviously, a quantitative definition of its statistical power and sensitivity at various scales is needed (Van Hoey et al., 2010). Particularly, an effort should be dedicated in evaluating the sensitivity of non-floating macrophyte wracks to variations in the state of benthic habitats resulting from anthropogenic pressures.

4.3. Local benthic habitats predict site variations in macrophyte wrack communities

Macrophyte wrack deposition on beaches is known to vary in space (Orr et al., 2005). Then, using macrophyte wracks as indicators of benthic habitats diversity would only make sense if spatial variations in the casted material correlates with that of benthic donor habitats. This is what our exploration of between-sites dissimilarities suggests. At almost all spatial scales, variations in local benthic habitats appeared a better predictor of site variations in non-floating macrophyte wracks as compared to distance *per se*. Distance appeared to be a better predictor only for differences between the most distant sites (*i.e.* Southern sites Glenan, and Penmarc'h vs Northern sites Morlaix and Trégor-Goëlo, Fig. 1). A plausible explanation for that is the biogeographical zoning of subtidal communities along the coast of Brittany (Derrien-Courtel et al., 2013). Cold and homogeneous waters of the Western Channel favour a different community of benthic habitats along the Northern coast (here Morlaix and Trégor-Goëlo) as compared to the warmer and stratified waters of the Atlantic to which the Southern coast (here Glenan and Penmarc'h) is exposed (Derrien-Courtel et al., 2013; Le Fèvre, 1987). Macrophyte wrack communities at the most distant sites of the Southern and Northern coasts may therefore vary beyond the differences encompassed by our local habitat predictor. This would agree with the findings of Reimer et al., (2018) who presented a spatial structuring of macrophyte wracks with geographical distance to the nearest rocky reefs or estuaries.

Obviously, a substantial part of spatial variation in macrophyte wrack communities remained unexplained, which likely lies in the complexity of nearshore hydrodynamics. We know for example that abiotic environmental predictors such as swell exposure, beach slope, or width contribute to the spatial variance in cover of some macrophyte taxa in wracks (Liebowitz et al., 2016). It is also possible that either the resolution or classification of EUNIS-derived habitat predictors misses part of the spatial heterogeneity in benthic algae communities or micro-

habitats. Still, our third result successfully outlines a direct relationship in spatial variations between benthic habitats and macrophyte wracks, providing an estimate of its predictive power as well as a spatial resolution at which it may be particularly relevant.

4.4. Promises and ways forward

Macrophyte wracks offer promising opportunities for cost-effective and replicable monitoring of infralittoral ecosystems free of the numerous constraints of direct underwater ecosystem monitoring. Thereby, it represents an opportunity for broad scale benthic biodiversity monitoring. On land, features of macrophyte wracks are already considered bioindicators of sandy-beach ecosystems (Gonçalves et al., 2013; Schooler et al., 2019) with regard to their geomorphological and trophic functions (Colombini et al., 2000; Dugan et al., 2011; Garden and Smith, 2015; Nordstrom et al., 2011). Our assessment suggests that this value extends to their benthic donor habitats. We provide a first direct evaluation of i) macrophyte wrack taxa that should be used to that end, ii) the extent of benthic habitats they encompass and iii) how much they both correlate in space. Further research may provide quantitative evaluations of how temporal variations in deposition of macrophyte wracks (Weinberger et al., 2021) could be used to monitor changes in nearshore benthic habitats. Should this hypothesis be validated, one would next want to demonstrate that the intricated effects of environmental fluctuations and anthropogenic pressures on benthic habitats could both be read in the composition of macrophyte wracks. Reaching this further objective would certainly require going lower than the community level, *e.g.* by considering functional or biogeographical traits within species Ecological Indicator Values (EIVs) (Hellegers et al., 2020; Scherrer and Guisan, 2019). For example, spatiotemporal variations in the beach casting of rare and cryptic species may affect the relevance of α-diversity metrics. If our results proved the usefulness of such community scale proxies for identifying the marine extent of the indicator value of macrophyte wracks, species specific indicators would certainly reinforce the strength of macrophyte wracks' indicators of coastal benthic ecosystems (Ferreira et al., 2011).

4.5. A citizen-science opportunity

Thanks to indicator values applying to the whole land-sea continuum, and because of a socioeconomic value inherited from management stakes on beaches, macrophyte wracks could finally be good candidates for citizen-helped biodiversity monitoring. Citizen-science programs have already demonstrated their relevance for many taxa/ecosystem (Chandler et al., 2017; Pocock et al., 2018), and are currently mobilized for the production of structural and sustainable development indicators such as the European Farmland Bird Indicator (EFBI) adopted by the European Union (Gregory et al., 2005). The potential of macrophyte wrack-derived marine indicators is all the more important as they provide the opportunity to build such programs, allowing for biodiversity monitoring at large spatiotemporal scales (D'Archino and Piazzi, 2021). Design of a citizen-based monitoring of beach wrack macrophytes would require i) the identification of key species/taxa that would hold enough information on benthic habitats, ii) the training of volunteers to the identification of these taxa and iii) a cautious handling of the citizen-based sampling effort. The present study is part of the "Plages Vivantes" program which pursues these objectives.

CRediT authorship contribution statement

Martin Thibault: Methodology, Visualization, Formal analysis, Writing - original draft, Writing - review & editing. **Elisa Alonso Aller:** Methodology, Formal analysis, Visualization, Writing – original draft, Writing – review & editing. **Pauline Poisson:** Conceptualization, Investigation, Resources, Data curation. **Christian Kerbiriou:** Conceptualization, Methodology, Validation, Investigation, Writing – review & editing, Supervision, Project administration, Funding acquisition. **Isabelle Le Viol:** Conceptualization, Methodology, Validation, Investigation, Writing – review & editing, Supervision, Project administration, Funding acquisition.

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.

Competing interests

We declare we have no competing interests.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.ecolind.2022.109279.

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