Constancy despite variability: Local and regional macrofaunal diversity in intertidal seagrass beds

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ARTICLE INFO

ABSTRACT

The importance of seagrass habitat for the diversity of benthic fauna has been extensively studied worldwide. Most of the information available is, however, about α diversity while little consideration has been given to β diversity. To fill the knowledge gaps regarding the variability of epifaunal and infaunal seagrass assemblages at large spatial and temporal scales, we scrutinized an extensive dataset covering five years of monitoring of eight intertidal *Zostera marina* meadows around Brittany (France). High species richness arose at the regional scale from the combination of high local diversity of the meadows and substantial among-meadows β diversity. Epifauna and infauna appeared as distinct self-communities as they displayed different spatial and temporal patterns and varied in their responses to local hydrological conditions. Infauna had higher total β diversity than epifauna due to a tighter link to the great variability of local environmental conditions in the region. Both exhibited substantial variations in species composition and community structure with variations of dominant species that were accompanied by extensive change in numerous rare species. The dominant epifaunal species were all grazers. Changes in species composition were induced mostly by species replacement and rarely by richness differences between meadows. Indeed, species richness remained within a narrow range for all seagrass beds, suggesting a potential carrying capacity for species richness of the meadows. Overall, all meadows contributed equally to the regional turnover of seagrass macrofauna, emphasizing high variability and complementarity among beds at the regional scale. The implications of this substantial within-seagrass variability for the functioning of benthic ecosystems at broad scale and for conservation purposes in habitat mosaics warrant further investigations but our results clearly advocate taking into account within-habitat variation when evaluating the diversity of benthic habitats and the potential effect of habitat loss.

1. Introduction

Seagrasses are marine flowering plants thriving along the world's coastlines from temperate to sub-Antarctic and Arctic regions (Green and Short, 2003). They form widespread meadows that have gained increasing recognition in the past decades as some of the most valuable ecosystems in the biosphere (Costanza et al., 1997; Duarte et al., 2008; Dewsbury et al., 2016). Indeed, seagrasses act as ecosystem engineers (*sensu* Jones et al., 1994). As such, they fulfil key ecological roles in coastal ecosystems and provide high-value ecosystem services including coastal protection and erosion control, carbon sequestration, key contributions to nutrient cycling associated with water purification capabilities, provision of raw materials and food, and maintenance of

important commercial fisheries (Barbier et al., 2011; Fourqurean et al., 2012; Cullen-Unsworth and Unsworth, 2013). Furthermore, they transform bare and relatively homogeneous sediment into structurally more complex, productive and diverse habitats (Hemminga and Duarte, 2000; Duffy, 2006). They provide stable hydrological and sedimentary conditions, abundant resources, higher available surface area and ecological niches, and protection against predation to their associated fauna (Fonseca et al., 1983; Orth et al., 1984; Attrill et al., 2000; Larkum et al., 2006; Heck et al., 2008). Accordingly, seagrasses are typically inhabited by richer and more diverse fauna than bare substrata (*e.g.* Edgar, 1990; Boström and Bonsdorff, 1997; Hily and Bouteille, 1999).

Preventing loss of complexity and homogenisation of benthic

landscape has now become one of the main priorities and challenges for marine biodiversity conservation (Airoldi and Beck, 2007; Airoldi et al., 2008). This concern particularly applies to seagrass meadows as they rank among the most threatened marine habitats (Orth et al., 2006). Indeed, seagrasses are facing increasing pressures from both natural (storms, overgrazing, diseases) and anthropogenic sources (eutrophication, physical damages, over-exploitation, global change; Short and Wyllie-Echeverria, 1996; Duarte, 2002; Orth et al., 2006). This ongoing ecological degradation of coastal waters has led to dramatic shrinkage of seagrass coverage worldwide (Waycott et al., 2009). This has become a major issue as it affects the whole functioning of coastal waters by disrupting the essential linkages between seagrass beds and other habitats and altering the ecological services they provide (Airoldi et al., 2008; Heck et al., 2008; Hughes et al., 2009).

The plethora of studies comparing vegetated bottoms and bare sediment only allow to ambiguously forecast the effects of seagrass loss as they do not fully account for the diversity and variability of seagrass communities (Bell et al., 2006; Airoldi et al., 2008; Boström et al., 2011). By focusing on among-habitat patterns, traditional assessments of seagrass communities have often neglected within habitat variability. Clear evidences of communities variability have however been documented at all spatial scales: within single meadows (Webster et al., 1998; Blanchet et al., 2004; Bologna, 2006; Wong and Dowd, 2015), at the landscape scale (Hovel et al., 2002; Bell et al., 2006; Boström et al., 2011; Carr et al., 2011) and among different locations (Boström and Bonsdorff, 1997; Boström et al., 2006; Borg et al., 2010; Barnes, 2014). Such variability can affect our appreciation of biodiversity distribution and ecosystem functioning and need to be accounted to adequately preserve seagrass biodiversity (Airoldi et al., 2008; Fraschetti et al., 2008; Törnroos et al., 2013).

The need for long-term monitoring and broad scale comparisons is increasingly advocated to apprehend the diversity and variability of seagrass systems and the consequences of their broad spatial and temporal scale disappearance (Duarte, 1999; Airoldi et al., 2008; Boström et al., 2011; Edgar et al., 2016). Broad scale comparisons of seagrass communities among different locations are however scarce with the exception of the Baltic Sea (Boström and Bonsdorff, 1997; Boström et al., 2006). Furthermore, the majority of spatial datasets are "snap shot" that do not include the temporal component of seagrass variability over long periods (Boström et al., 2011). Because there is a positive relationship between the spatial and the temporal scales of variation of ecological phenomena (Wiens, 1989), information on the broad spatial scale variability of seagrass communities should preferably be integrated over long periods. There is increasing evidence that inter-annual variations can be as important as and even blur seasonal patterns (Duarte et al., 2006; Douglass et al., 2010). Inter-annual variations need to be assessed in particular to reveal the long-term effects of wave exposure, tidal currents, or of long-term changes in temperature, salinity or turbidity on seagrass and their communities (Rasheed and Unsworth, 2011; Potouroglou et al., 2014; Lefcheck et al., 2017a, 2017b). These environmental factors can have strong structuring effects on local communities, prone to induce important variability among meadows at broad spatial scale (Boström and Bonsdorff, 1997; Boström et al., 2006; Borg et al., 2010). Yet, most studies have limited spatial and/or temporal extents, often covering between 1 and 50 km^2 or with durations limited to 1 or 2 years (Duarte, 1999; Boström et al., 2011). Therefore, they cannot be used to infer quantitatively how local conditions may shape diversity patterns at regional scale (De Juan and Hewitt, 2011). There are indeed compelling evidences that patterns arising at one scale often do not translate directly at others (Bell and Westoby, 1986; Turner et al., 1999; Balestri et al., 2003; Kendrick et al., 2008). Measuring diversity at regional scales is necessary to guide conservation actions (De Juan and Hewitt, 2011) but the links between regional diversity, local diversity and ecosystem processes requires further studies in seagrass meadows (Duffy, 2006).

One major impediment to our knowledge of seagrass biodiversity at broad scale is that community assessments have traditionally been biased towards the assessment of the local diversity of seagrass meadows (α diversity; Whittaker, 1960), while little interest has been given to the spatial and temporal differentiation and renewal of their communities (β diversity; Whittaker, 1972; Gray, 1997, Airoldi et al., 2008). Yet, assessment of this neglected component is necessary to properly estimate the role of seagrass in promoting coastal diversity and functioning and to adequately define management actions at large spatial scales (Airoldi et al., 2008; Fraschetti et al., 2008; Törnroos et al., 2013). Assessment of β diversity patterns helps in capturing the potential complementarity of communities (Bond and Chase, 2002) and in revealing fundamental facets of community structure and their underlying processes (Whittaker, 1972; Legendre and De Cáceres, 2013). Structurally complex habitats are recognized to favour among-habitat β diversity in comparison to their less complex counterparts (Hewitt et al., 2005; Airoldi et al., 2008). The importance of this facet of within-habitat diversity remains however largely unknown, especially at large spatial and temporal scales. In particular, while the relative contributions of epifauna (organisms living on the surface of the sediment or the seagrass) and infauna (living within the sediment) to the local diversity of seagrass meadows and to among-habitat patterns have previously been described (Boström and Bonsdorff, 1997; Duffy, 2006), there exists no previous assessment of their broad scale patterns and relative importance to within-seagrass β diversity.

In this study we used innovative statistical analysis to scrutinize an extensive dataset arising from a regional survey of intertidal *Zostera marina* beds in order to fill the knowledge gaps regarding β diversity and within-seagrass variability of macrofaunal communities at broad spatial and temporal scale. Data on the epifaunal and infaunal assemblages of eight *Zostera marina* meadows were collected during five years along Brittany as part of the REBENT (Réseau Benthique) monitoring programme. Being a biogeographical transition zone between the North Sea and the Bay of Biscay (Fig. 1), Brittany is of particular interest for its high benthic macrofaunal diversity that is enhanced by the great range of hydrological conditions found in this region (Gallon et al., 2017, this issue). Like most of the eastern Atlantic, Brittany has been severely affected by seagrass disappearance over the last century (Airoldi and Beck, 2007; Godet et al., 2008). The diversity and functioning of these meadows however, have only been locally characterised (Hily and Bouteille, 1999; Hily et al., 2004; Martin et al., 2005). As part of the REBENT programme, molecular approaches have highlighted the variability of Brittany meadows and their communities (Becheler et al., 2010, 2014; Cowart et al., 2015) but their spatial and temporal variation and their underlying structuring mechanisms remain largely to be determined.

In this context, we aim at assessing at the scale of this rich region the α, β, and γ (regional) diversities of seagrass macrofauna and at identifying the sources of community variation within this habitat such as richness differences, species replacement, as well as the role of abundance patterns and the importance of rare species. Barnes (2014) highlighted substantial variations of the infaunal assemblages among three sheltered intertidal meadows of different geographical areas (Australia, South-Africa and United Kingdom) but pointed out that common assemblage structures were found in all three. We hypothesise however, that the capacity of seagrass meadows to promote similar assemblage structures is unlikely in highly contrasted environments (Barnes, 2016), as present in the Brittany region. We expect indeed strong spatio-temporal variability of all components of epifauna and infauna diversity, along with site-specific dynamics. Both compartments are also hypothesised to respond differently (Leopardas et al., 2014). An exploration of the role of the hydrologic regimes, assessed here using sediment characteristics as proxy, will also provide a first insight into the influence of local environmental conditions on the patterns observed.
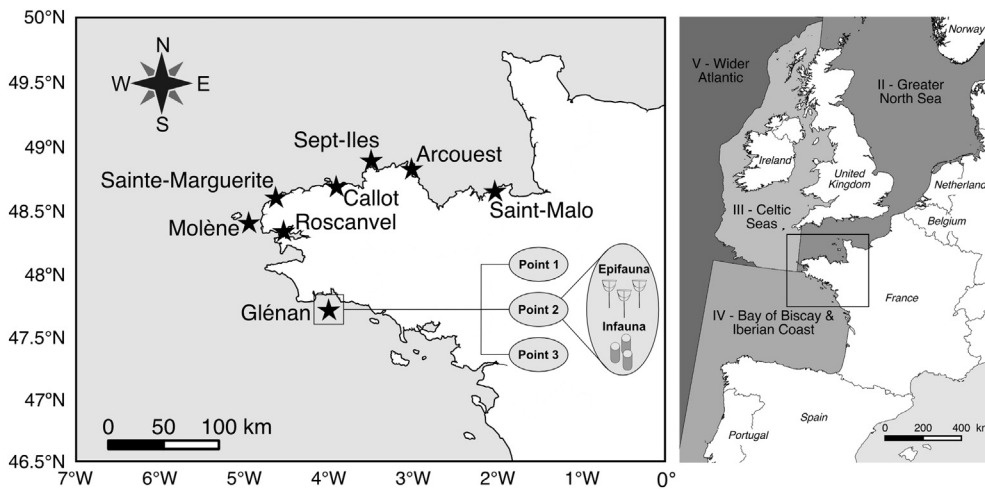
Fig. 1. Localities of the eight *Zostera marina* meadows (black stars) monitored by the RÉseau BENThique (REBENT) in Brittany in 2007 and from 2009 to 2012. Each meadow was sampled at three points located 200 m apart for epifauna (using three dip nets) and infauna (using three sediment cores), as exemplified in the figure for the Glénan meadow. Brittany waters (encompassed by the rectangle in the right-hand map) constitute a marine biogeographical transition zone between two marine regions defined by the OSPAR commission: region II of the Greater North Sea (northern Brittany) and region IV of the Bay of Biscay and the Iberian coast (southern Brittany).

2. Material and methods

2.1. Sampling and processing protocols

In the context of the REBENT monitoring programme, eight intertidal *Zostera marina* beds were sampled in 2007 and from 2009 to 2012 along the coast of Brittany, France (Fig. 1). These eight meadows were chosen to encompass the spectrum of environmental settings in which intertidal *Zostera marina* meadows can be found in Brittany: from sheltered bays and turbid waters to exposed areas and fully marine conditions, through semi-opened habitats (Hily et al., 2003). As a consequence, the eight meadows differ in terms of underlying sediment, densities, biomasses, and distribution areas, which may contribute to the variability of their associated macrofauna. Sampling was consistently performed for all beds around the spring equinox of each year, between the end of February and the beginning of May (Appendix 1). This sampling season correspond to the season of minimum canopy development and was set to limit inter-annual variability that may arise from variation in the growth phase of *Zostera marina* during the spring/summer season (Moore and Short, 2006). This sampling season also follows the winter storms and is therefore the period of minimum macrofaunal densities and diversities in the region (Grall, 2002). Inter-annual variability induced by the seasonal variations of macrofauna and their development or recruitment processes is limited at this time of year.

Three fixed sampling points distributed 200 m apart were visited within each seagrass bed. At each point, epifauna was sampled by three 10 m horizontal hauls of a 1 m width dip net (1 mm mesh size) shortly before low tide. These three samples were pooled to estimate abundances at the point level (illustrated for the Glénan meadow in Fig. 1). Likewise, at each point infauna was sampled using three sediment cores of 0.03 m² that were also pooled to estimate abundances at the point level. Accordingly, macrofaunal densities were estimated based on the 30 m² and 0.09 m² surface sampled per points for epifauna and infauna respectively. Sediment cores were then sieved over 1 mm mesh and fixed in 4% formalin in the laboratory until sorting and morphological identification to the lowest taxonomic levels possible. Despite a constant scientific supervision of the monitoring programme by one of the author (J. Grall) for the duration of the study, several field and laboratory personnel were involved in data acquisition over the years. Hence, to ensure that a consistent taxonomic resolution was used in the study, the distribution in time and space of each recorded species was scrutinized by experts in benthic taxonomy. Degradation to higher taxonomic levels was undertaken for doubtful identifications, safeguarding against major misidentification, differences in identification among operators, or changes in time in given taxonomic groups due to updates in the taxonomic literatures. Particular care was taken for rare

species and decision on their taxonomic degradation was made according to the robustness of the criteria discriminating the species, the level of expertise needed to discern them, and the likelihood of their presence in the studied area given their known distribution range. We favoured the possibility of underestimating the true diversity over that of keeping potential artificial patterns.

Another sediment core was collected at each point for grain size distribution assessment and organic matter content. Sediments were dried in an oven (24 h at 60 °C), separated into 15 fractions (< 63 μm, 63, 80, 100, 125, 160, 200, 315, 500, 800, 1250, 2000, 3150, 5000 and > 10,000 μm) whose masses were measured. Fractions were afterwards grouped into gravels (> 2 mm), sand (63 μm to 2 mm) and silt and clay (< 63 μm; Fournier et al., 2012). Organic matter content was estimated by mass loss after combustion at 450 °C for 5 h.

2.2. Data analyses

Species richness, abundance of individuals and Simpson's inverse ($1/\lambda$), which is Hill (1973) diversity number N_2, were calculated for each sampling point of each seagrass bed for the 5 years of the study to characterise the α diversity of epifauna and infauna and its spatial and temporal variations. Simpson's inverse was chosen for its property to down-weight rare species (Hill, 1973) as these species may not have been properly sampled in such a monitoring programme with large spatial and temporal extents. Additionally, β diversity for each pair of observations was first estimated from presence-absence data, using the Jaccard dissimilarity (Jaccard, 1908), computed for each macrofaunal compartment separately. This is the simplest and the most frequently used of the measures of β diversity described in Table 1 of Koleff et al. (2003). To test whether spatial and temporal variations of epifauna and endofauna composition were predominantly induced by changes of species identity or fluctuations of species richness, β diversity among each pair of samples was partitioned into two components, namely species replacement ($\beta_{Replacement}$) and richness difference ($\beta_{RichDiff}$) following Legendre's (2014) re-description of the Podani family indices (Podani and Schmera, 2011):

$$\beta_{Replacement} = \frac{2\min(b,c)}{a+b+c}$$

and

$$\beta_{RichDiff} = \frac{|b-c|}{a+b+c}$$

with, for any two samples S_j and S_k, a being the number of species found in both samples, b the number of species unique to S_j and c the number of species unique to S_k. $\beta_{Replacement}$ and $\beta_{RichDiff}$ sum to the Jaccard dissimilarity, $(b+c)/(a+b+c)$, hence they represent a full

Table 1

Spatial and temporal variability of species richness, Simpson's inverse ($1/\lambda$) and abundance per m^2 for epifauna (Epif.) and infauna (Inf.). Mean values are displayed with their standard deviations.

Site		Total species richness	Mean species richness per point						Mean diversity ($1/\lambda$) per point						Mean abundance per m^2
			2007	2009	2010	2011	2012	Mean	2007	2009	2010	2011	2012	Mean	
Saint-Malo	Epif.	108	30	33	30	38	34	33 ± 5	8.8	9.3	8.1	7.4	8.0	8.3 ± 1.5	30 ± 26
	Inf.	119	43	27	32	30	26	32 ± 8	8.9	9.3	13.6	12.8	9.0	10.7 ± 3.4	3196 ± 1862
Arcouest	Epif.	142	40	53	53	46	36	46 ± 10	12.7	8.4	6.8	10.8	3.3	8.4 ± 4.4	40 ± 22
	Inf.	132	43	33	37	39	33	37 ± 5	9.0	7.6	8.7	7.6	10.6	8.7 ± 3.5	4775 ± 1451
Sept-Iles	Epif.	91	22	30	29	29	37	29 ± 7	4.4	4.8	5.6	5.8	4.7	5.1 ± 1.4	31 ± 13
	Inf.	134	47	19	37	38	33	35 ± 12	7.6	5.3	6.7	6.4	6.6	6.5 ± 2.1	6842 ± 4736
Callot	Epif.	155	53	44	50	70	56	55 ± 9	12.9	4.5	3.2	3.4	6.4	6.1 ± 4.2	55 ± 19
	Inf.	187	70	47	51	52	51	54 ± 10	14.0	12.3	13.7	14.5	12.4	13.4 ± 2.9	6609 ± 3161
Sainte-Marguerite	Epif.	127	37	49	36	57	41	44 ± 9	5.4	5.6	5.3	3.1	3.6	4.6 ± 1.4	131 ± 61
	Inf.	118	25	38	30	42	42	36 ± 9	2.1	3.6	3.4	4.3	4.6	3.6 ± 1.3	19429 ± 10457
Molène	Epif.	140	48	41	44	47	43	45 ± 9	13.1	17.8	7.8	18.2	4.9	12.4 ± 5.8	36 ± 28
	Inf.	139	41	29	45	35	40	38 ± 8	4.9	4.4	6.6	5.4	4.7	5.2 ± 2.1	12629 ± 4907
Roscanvel	Epif.	139	39	32	21	49	47	38 ± 14	5.9	4.4	3.2	5.3	5.0	4.8 ± 1.4	40 ± 21
	Inf.	163	59	66	34	51	29	48 ± 16	16.3	16.5	12.3	17.4	8.5	14.2 ± 4.1	6628 ± 3620
Glénan	Epif.	153	45	43	45	65	36	47 ± 14	10.0	6.1	4.5	8.1	5.3	6.8 ± 3.3	66 ± 54
	Inf.	136	42	48	34	38	32	39 ± 7	2.2	1.9	2.9	2.2	1.4	2.1 ± 0.8	24304 ± 12695

decomposition of that index of β diversity. Calculation and decomposition of the Jaccard dissimilarity was performed for each faunal compartment 1) between all samples (all pairwise comparisons possible), 2) between samples belonging to the same sites (within-site variation), 3) between samples belonging to different sites (among-site variation), 4) between samples belonging to the same sampling year (within year), 5) between samples belonging to different sampling years (among years).

In order to account for the species relative importance in the communities, patterns of species abundances were visualised using Principal Component Analysis (PCA) of the Hellinger-transformed data. Hellinger transformation allows for the use of Euclidean-based methods on abundance data and also has, as for the Simpson concentration, the desirable property of not giving excessive weight to the rare species (Legendre and Gallagher, 2001). Additionally, the spatial and temporal patterns observed were quantified using multivariate analysis of variance (MANOVA), which allowed us to test the null hypotheses of no difference among the macrofaunal communities through space and time. The MANOVA was computed by redundancy analysis (RDA; Rao, 1964) on the Hellinger-transformed abundances of epifauna and infauna separately and tested by permutations (Legendre and Anderson, 1999; Legendre and Legendre, 2012). Sites, years and their interaction were coded by Helmert contrasts (Legendre and Gauthier, 2014); homogeneity of multivariate dispersions was tested at the $\alpha = 0.05$ significance level prior to this analysis (Anderson, 2006). Interaction between space and time was measured and tested to estimate if temporal variations were similar across all sites; or expressed differently, if the spatial patterns were constant through time.

Macrofaunal patterns were related to sediment characteristics of the seagrass meadow visually, using triangular plots of the three granulometric fractions defined above. As well, the relationship between macrofauna and granulometric conditions was quantified separately for epifauna and infauna using redundancy analysis with the Hellinger-transformed species abundances. Among the explanatory variables for this analysis, only the sand and the silt and clay fractions were used, as the gravel fraction is highly collinear with the other two. Median grain size and the Sorting-Index, $So = \sqrt{Q_{25}/Q_{75}}$ with Q_{25} and Q_{75} the first and third quartiles of the distribution, were calculated to describe the position and dispersion of the granulometry and were also included in the RDA as explanatory variables along with organic matter content. Missing organic matter data for two points of Roscanvel in 2007 and one point of Glénan in 2010 were estimated beforehand using k-Nearest neighbour imputation (Acuña and Rodriguez, 2004). This prevented the removal of entire sites or years of the analysis while giving neutral weights to these observations.

Finally, total beta diversity (BD_{TOTAL}) was estimated for each faunal compartment as the total variance of the Hellinger-transformed community matrix and expressed as a percentage of the maximum possible value, reached only if all sites have completely different community compositions, which is $BD_{max} = 1$ for this coefficient (Legendre and De Cáceres, 2013). Contributions of individual sampling units to this total β diversity was measured for each point-site-year combination for epifauna and infauna separately using LCBD indices (Local Contributions to Beta Diversity; Legendre and De Cáceres, 2013). LCBD indices indicate the uniqueness of a community sample; they were used to evaluate the relative contribution of each seagrass meadow to the total β variation of each of the faunal compartments (epifauna and infauna) at the regional scale and over the five years of the study.

All statistical analyses were conducted using R (R Core Team, 2015) and relied on the G2Sd (Fournier et al., 2014), VIM (Templ et al., 2015), vegan (Oksanen et al., 2016), adespatial (Dray et al., 2016) and ggtern (Hamilton, 2016) packages.

3. Results

3.1. Spatial and temporal patterns of α diversity in seagrass communities

During the five years of this study, a total of 120 samples were collected in the eight *Zostera marina* meadows. They contained a total of 306,566 individuals within 460 species. Epifauna and infauna shared a total of 190 species while 113 and 157 species were respectively unique to epifauna and infauna. Species retrieved in only one sampling unit over the 120 of this study represented 17% (78/460) of the total number of recorded species. Species represented by a single individual represented 3.5% (16/460) while 179 species (39% of total richness) were represented by 10 specimens or less.

All eight seagrass beds had substantial overall richness over the five years of the study with > 200 species recorded in each of them (Table 1). On average, one sampling point contained between 30 and 55 species for each compartment with epifauna and infauna contributing similarly to total richness. Contrary to species richness that displayed comparable values among seagrass meadows, marked spatial differences were observed for Simpson's inverse and total abundances. Indeed, densities (individuals/m²) revealed the striking predominance of infaunal organisms compared to epifaunal ones and at the regional scale, a factor of 8 was found between the infaunal abundances of the least populated site (infauna, Saint-Malo) and the most crowded meadow (infauna, Glénan). Similarly, high amplitude variations were
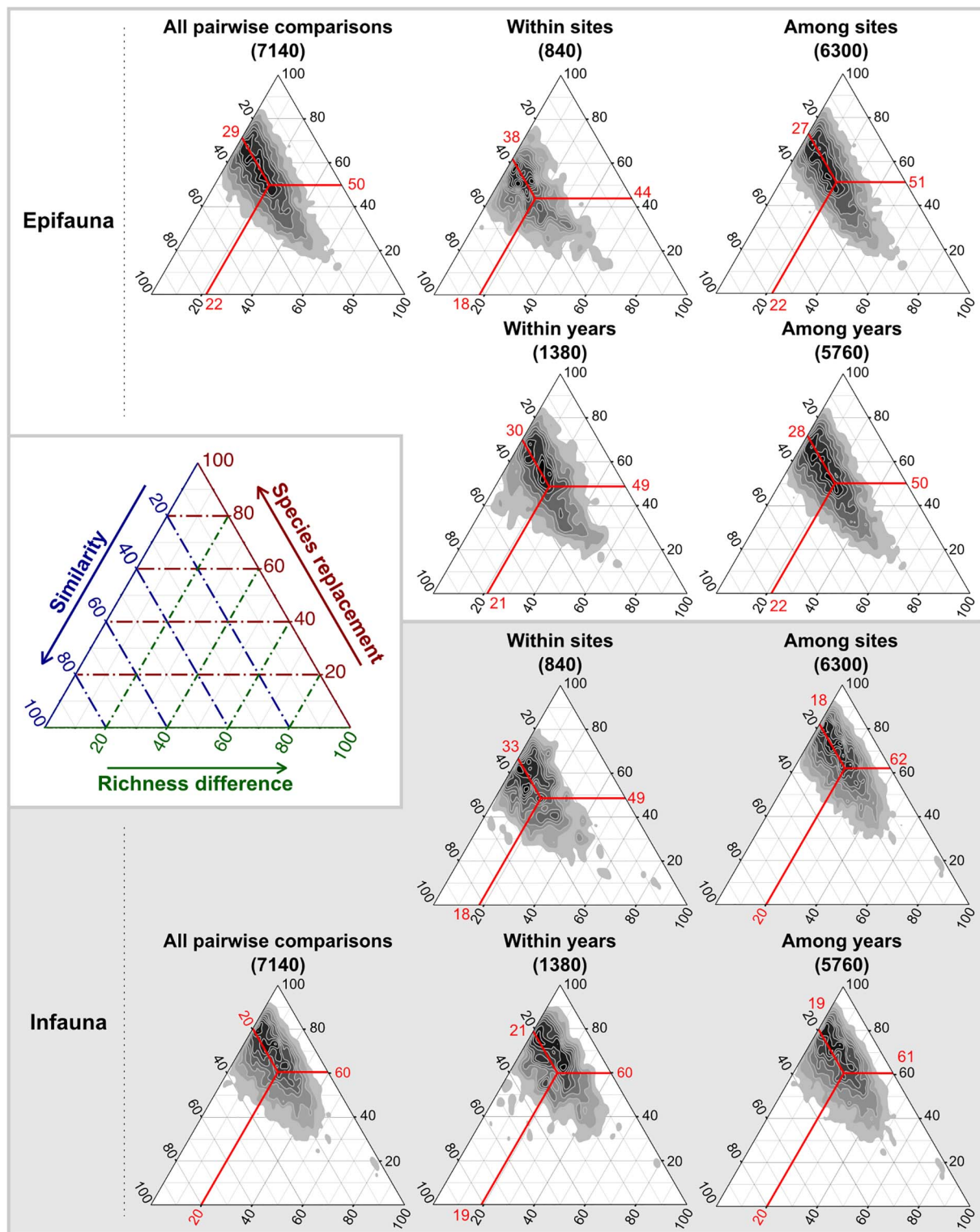
Fig. 2. Triangular plots illustrating the spatial and temporal variations of the Jaccard dissimilarity between the species composition (presence/absence data) of the eight seagrass beds over the five years of the study, and its decomposition into similarity, richness difference (*i.e.* variation in species richness) and species replacement (*i.e.* variation in species identity). Contributions were calculated for each compartment (epifauna and infauna) separately, for all pairwise comparisons and for comparisons between samples belonging: to the same meadow (within site), to different meadows (among sites), to the same year (within year), to different years (among years). Due to the high number of pairwise comparisons, the density of points was estimated by two-dimensional kernel estimations and was represented with darker colour for higher numbers of comparisons. Numbers in parentheses indicate the number of pairwise comparisons used for kernel estimation. Red lines indicate the centroid value for each graph with its associated mean values for the three components of dissimilarity. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

observed between meadows for Simpson's inverse with most values found between 2 and 13 for both epifauna and infauna. Meadows that displayed high diversity for a compartment rarely exhibited concomitant high values for the other. Overall, all three community measures displayed major temporal variations. They mostly exhibited punctual and abrupt changes and their year-to-year variations often differed between the two compartments of the same meadow and for the same compartment in different meadows. Furthermore, temporal

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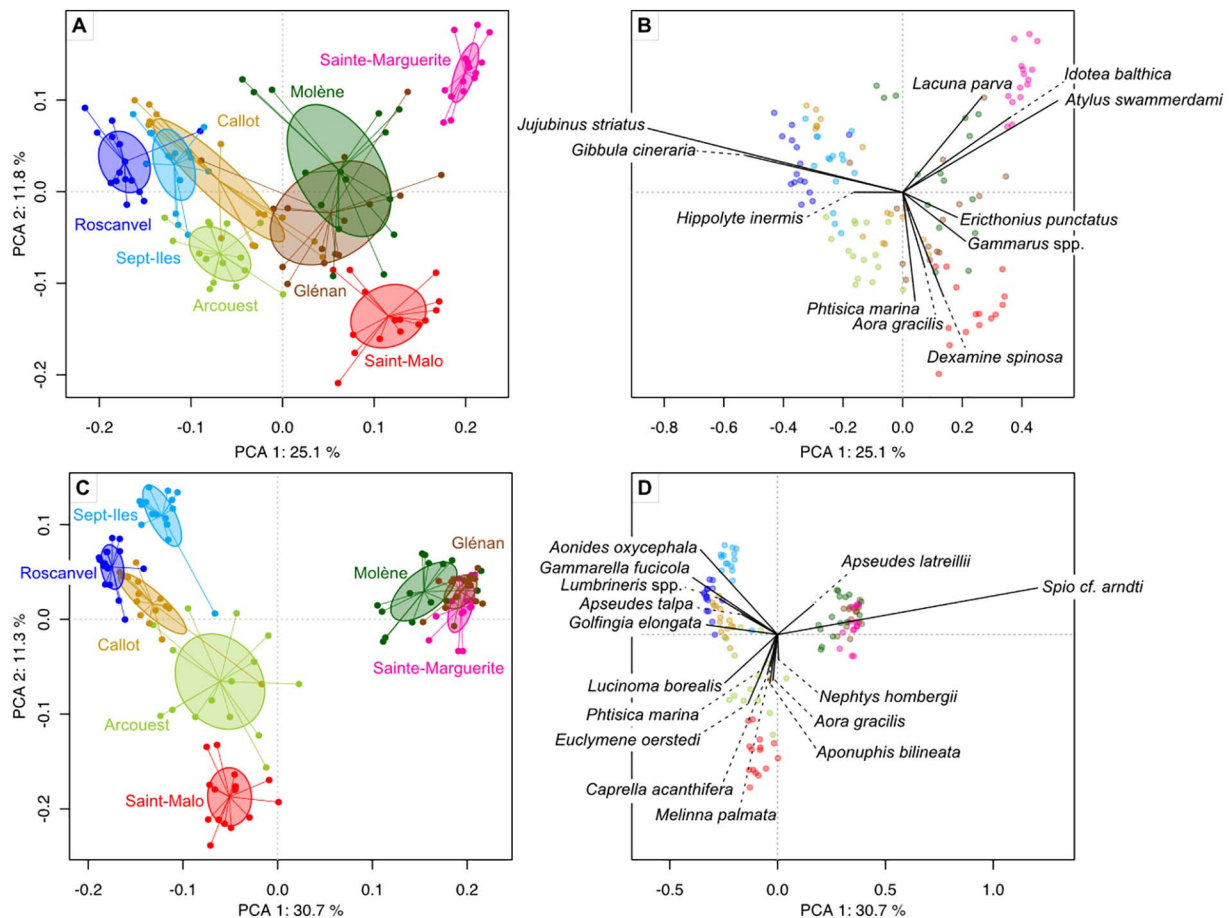
Fig. 3. Principal component analyses of the Hellinger-transformed abundances for the epifauna (A and B) and the infauna (C and D) of the eight *Zostera marina* beds over the five years of the study. The first two axes represent 36.9% and 43% of the total variation of epifaunal and infaunal communities respectively. A and C: the sites for each point sampled during the 5 years of the study with their 95% confidence dispersion ellipses. Within-site dispersions represent temporal variability and variation of the communities among the three points sampled per year. B and D: positions of the species for which the two first axes represented at least 40% (cumulative R^2) of their variance, ensuring that these species were well represented and contributed to the patterns observed in the ordination. A and C are represented in scaling 1 (distance biplot) preserving the distances among the sites. B and D are represented in scaling 2 (correlation biplot) preserving the covariances among the species. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

variations of Simpson's inverse (Table 1) appeared unrelated to changes observed in species richness or in abundances (Appendix 2).

3.2. Quantification and decomposition of the variation of species compositions among meadows

The β diversity of the macrofauna of *Zostera marina* meadows was first investigated with presence/absence data through pairwise comparisons between the 120 samples of each compartment (Fig. 2). Calculation and decomposition of the Jaccard dissimilarity between samples belonging to the same site provided information on within-site variations: temporal variation of the community at the site on the one hand, and variation among the three points sampled within the meadow on the other hand (Fig. 2 – Within sites). Calculation between samples belonging to the same year provided information on the spatial variations of the communities within each time step (Fig. 2 – Within years). Finally, among-years comparisons provided information on overall temporal variation, regardless of sampling site, and among-sites comparisons provided information on overall spatial variation, regardless of sampling year (Fig. 2 – Among years & Among sites).

Over the whole spatial and temporal extent of this study, epifaunal communities shared on average 29% of their species, with most pairwise similarities lying between 20 and 50% shared species (Fig. 2 – All pairwise comparisons). Comparatively, infaunal communities displayed higher compositional changes with an average of only 20% shared

species over the whole extent of the study. Similarity values among the infaunal communities ranged mostly from 10 to 40% shared species. Substantial changes in species composition were observed within sites with mean similarity values of 38% shared species for epifauna and 33% for infauna (Fig. 2 – Within sites). Hence there is, on average, more similarity (less dissimilarity) within sites for epifauna than for infauna albeit the difference is not very large and both compartments mostly ranged from 20% to 60% of shared species within meadows. The amplitude of these similarity values indicated important differences among meadows in terms of their fine-scale heterogeneity and/or temporal variability. Yet, despite these low proportions of shared species within meadows, within-site comparisons still displayed higher similarities than among-site comparisons, indicating even more extensive variations of species composition among meadows. The importance of the spatial variation of community compositions was confirmed by the low similarities observed for within-year comparisons with mean values of 30% shared species for epifauna and 21% for infauna. Hence again, there is, on average, more similarity (less dissimilarity) within years for epifauna than for infauna, indicating more important compositional changes among sites for infauna. Ultimately, this substantial spatial variation emerged as dominant compared to the temporal variation as, for both compartments, within- and among-years comparisons displayed the same patterns.

Relative contributions of species replacement and richness difference to species composition renewal in space (Fig. 2 – Within years)

were comparable with those for temporal changes (Fig. 2 – Within sites). On average, when considering all pairs of epifaunal assemblages together, 70% of the species were found in only one assemblage: 50% of them changed in terms of species identity (replacement) and 20% were unique to the richest assemblage and thus linked to the richness difference (Fig. 2 – All pairwise comparisons). Likewise, for all pairs of infaunal assemblages, on average 80% of the species were found in only one assemblage with 60% changing identity due to species replacement and 20% linked to richness differences. The contributions of richness difference were on average similar in both compartments albeit they appeared more variable in epifaunal than in infaunal communities. Indeed, more comparisons implying extremely important changes of species richness were observed for epifaunal communities than for infauna. Yet, for each compartments, richness differences constituted > 60% of the dissimilarity in > 2% of the total pairwise comparisons. In all these cases, it involved comparisons with few specific samples where important drops in richness had occurred such as in Roscanvel 2010 for the epifauna or in one point of Sept-Iles in 2009 for the infauna. Overall, variations of species composition within and among seagrass meadows were mostly driven by changes in species identity and were rarely induced by important changes in species richness.

3.3. Variations of the community structures of seagrass epifauna and infauna and relationship with sediment conditions

Principal component ordinations of the Hellinger-transformed abundances confirmed extensive spatial and temporal variations of the seagrass macrofaunal assemblages (Fig. 3). These patterns were consistent with those obtained with presence-absence data (Appendix 3). Besides, removing the 179 species represented by < 10 specimens over the whole study had little impact on the observed patterns, even for presence/absence analyses (Appendix 4). Overall, predominance of spatial over temporal variation and differences in spatio-temporal structures between epifauna and infauna emerged from the two PCAs. Spatial and temporal variations were further tested and quantified with two-way MANOVAs in which significant space-time interactions were found for both compartments. The interaction was more important for the epifaunal communities ($F = 4.05$, $p = 0.001$, $R^2 = 27\%$) than that of their infaunal counterparts ($F = 2.47$, $p = 0.001$, $R^2 = 18\%$), confirming the visual conclusions drawn from the PCA. Indeed, Glénan, Molène and Callot meadows exhibited extensive within-site variation in terms of epifauna whereas, comparatively, infaunal communities showed more homogeneous within-site variation with the exception of the Arcouest meadow. Furthermore, epifauna and infauna not only displayed different heterogeneity level among meadows in terms of their temporal variations but also exhibited distinct spatial patterns. Epifaunal assemblages expressed a main gradient that separated the sites of Roscanvel and Sept-Iles on one side from the meadows of Sainte-Marguerite and Saint-Malo on the other. Further differences were also found between the communities of the latter two meadows on the second axis. The main gradient observed in epifaunal communities was also retrieved in infauna but was eclipsed by the important differences of the three meadows of Glénan, Molène and Sainte-Marguerite with the other beds. Consequently, the gradient between the infaunal communities of Sept-Iles and Saint-Malo was relegated to the second axis.

The main gradient within epifaunal assemblages of the seagrass meadows was mainly expressed through changes in the dominant grazers. It particularly opposed the trochid-dominated meadows of Roscanvel and Sept-Iles, highly dominated by *Jujubinus striatus*, *Gibbula cineraria* and *Gibbula pennanti*, to communities dominated by other mesograzers. Identity of these other mesograzers was also at the basis of the distinction between Sainte-Marguerite, displaying high abundances of *Lacuna parva*, *Idotea balthica* and *Atylus swammerdami*, and Saint-Malo's epifauna, exhibiting instead high abundances of *Dexamine spinosa*, *Phtisica marina*, *Aora gracilis* and of *Gammarus* species. The singularity of the infaunal communities of the Glénan, Sainte-Marguerite

and Molène meadows arose from the high dominance of *Spio cf. arndti* that represented respectively 36%, 14% and 9% of the total abundances observed in these sites during the five years of the study. Comparatively, this polychaete represented < 0.5% of the total abundances in the other sites. The lower abundances of *Golfingia elongata* contributed to their distinction as well. All other meadows displayed weaker dominance. The seagrass beds of Sept-Iles and Roscanvel were characterised by high abundances of the polychaetes *Aonides oxycephala* and of the *Lumbrineris* genus, the amphipod *Gammarella fucicola* and the tanaid *Apseudes talpa*, which distinguished them from the communities of Arcouest and Saint-Malo. The latter were differentiated by high relative abundances of the polychaetes *Euclymene oerstedi*, *Melinna palmata*, *Aponuphis bilineata* and *Nephtys hombergii*, the two bivalves, *Lucinoma borealis* and *Loripes lacteus*, and the amphipods *Phtisica marina*, *Caprella acanthifera* and *Aora gracilis*.

Sediment granulometry displayed a gradient similar to the one retrieved for the epifauna and infauna between the meadows of Roscanvel and Sept-Iles on one side and of Sainte-Marguerite and Saint-Malo on the other (Fig. 4). Indeed, it separated the sites with heterogeneous sediments, with high contents of silt and clay or gravel, from the meadows composed of well-organized and homogenous sediments characterised by high sand content. Particularly, the important distinction of the infauna of Glénan, Molène and Sainte-Marguerite matched with the uniqueness of their sediment as all three displayed extreme sandy characteristics over the 5 years of the study. In comparison, all other sites displayed greater variability in time and more heterogeneity. Overall, redundancy analysis (RDA) of the community data against sediment properties explained 27.1% of the variation of infaunal communities (adjusted R^2, $F = 9.8$, $p = 0.001$) whereas 18.0% only of the epifaunal variation was related to the sediment conditions of the seagrass beds (adjusted R^2, $F = 6.2$, $p = 0.001$). Hence, variation among the macrofaunal communities could not be entirely explained by sediment properties alone. This is especially the case for the two sites of Roscanvel and Sept-Iles, which displayed similar communities while having completely opposed granulometry with a dominance of fine and coarse sediments, respectively. Moreover, within-site community variability did not coincide with sediment variability of the sites, especially in terms of epifauna as exemplified by the Molène meadow.
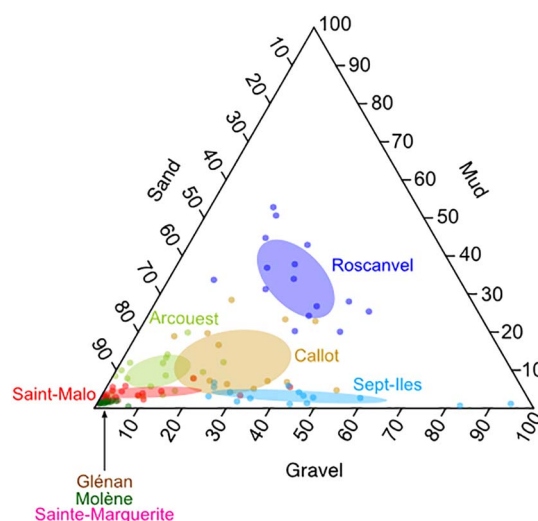

Fig. 4. Granulometry of the points sampled on each of the eight *Zostera marina* beds during the five years. 95% confidence ellipses are drawn for the points corresponding to each site. Within-site dispersion represents temporal variability during the 5 years of the study and variability among the three points sampled per year. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)
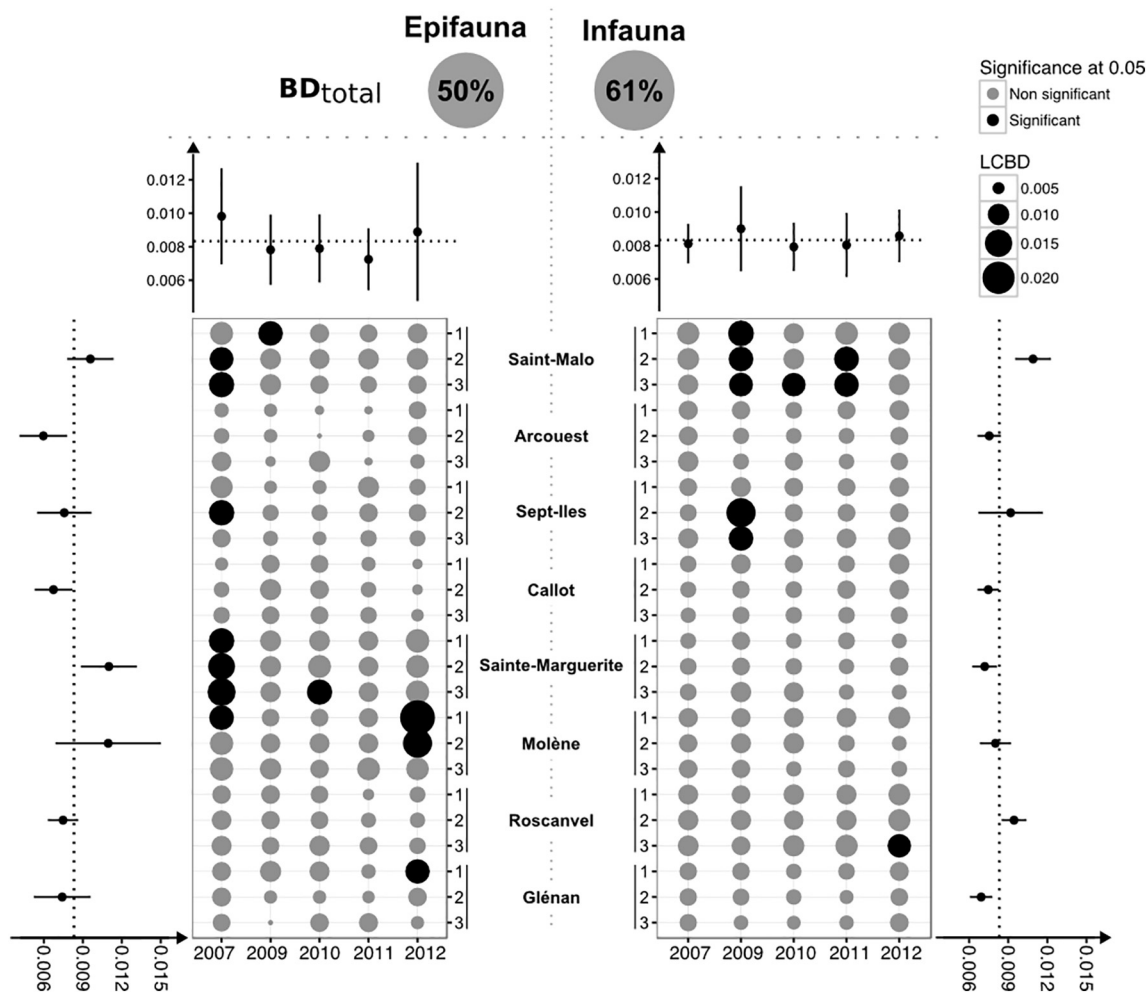
Fig. 5. Spatio-temporal map of the Local Contributions to Beta Diversity (LCBD) of the three points of each site for the 5 years of the study. LCBD values were calculated using Hellinger-transformed data for the epifauna (on the left) and the infauna (on the right) separately. They indicate the extent to which each local community is unique in terms of its composition. Circle surface areas are proportional to the LCBD values. Circles in black indicate significant LCBD indices at the $\alpha = 0.05$ significance level. Marginal diagrams indicate mean LCBD values associated with their standard deviations per year (upper margin) and per site (left margin for epifauna and right margin for infauna). Dashed line in marginal diagrams indicates the expected LCBD value if all samples contributed equally (*i.e.* 1/120). Total β diversity, quantified as the variance of the Hellinger-transformed abundance data, is expressed in the upper panel as the percentage of its maximum possible value for Hellinger-transformed data, which is 1.

3.4. Contributions to overall β diversity

The contribution of each meadow to the overall spatial and temporal renewal of seagrass macrofaunal communities was evaluated using LCBD indices calculated for each of the faunal compartments separately (Fig. 5). Infaunal communities displayed greater overall variation than epifauna with a BD_{total} reaching 61% of its maximum possible value while it was 50% for epifaunal communities. Contributions to total β diversity displayed little variation across the different meadows or the different years, albeit the variation was more pronounced for epifauna than for infauna. Indeed, mean contributions for the five years were similar for infauna and lied near their expected mean if all communities had equal contributions. Comparatively, the years 2007 and 2012 contributed more than the three others for the epifauna, mainly due to high contributions in these two years of the Saint-Malo, Sainte-Marguerite and Molène communities. All meadows did not contributed equally to the total variation of epifauna but higher average contributions of some meadows mainly arose from punctual events. For instance, Molène's contribution appeared mainly linked with the high and significant LCBD scores registered in 2012 and related to the drop of diversity – as recorded by Simpson's inverse – observed in that year. The 11 significant LCBD scores observed among the 120 sampling units represent a 9% rejection rate that remains near the

expectation level of type I error for a significance threshold of 5% if all LCBD values were drawn from the same statistical population. This also applies to the 9 significant LCBD scores observed for the infauna, which represent a 7.5% rejection rate albeit the highest LCBD scores were repeatedly found in the Saint-Malo meadow. With the exception of the latter bed, similar average LCBD contributions were observed across the different sites with values near the expected mean for most of the infaunal communities. As for epifauna, punctual high contributions could be related to important drops of diversity such as in Sept-Iles in 2009 or in Roscanvel in 2012, but overall, contributions to total β diversity of infauna were even more homogenously distributed across sites and across years than for the epifauna.

4. Discussion

Local studies can only evidence a subset of ecological patterns. Apprehending the general laws that underlie diversity structures in ecosystems often requires the combination of a variety of observations at various scales of analysis (Whittaker et al., 2001). For that reason, authors increasingly advocate the expansion of the scales of ecological studies for both marine conservation and theoretical purposes (Witman et al., 2015; Edgar et al., 2016). Here, using an extensive dataset covering eight seagrass meadows surveyed during five years, we provide

the first estimation of the substantial spatial and temporal variability of the species-rich macrofaunal communities in mid-Atlantic meadows at a regional scale.

Seagrass meadows form a highly productive habitat (Heck et al., 2008). We observed important densities of macrofaunal organisms, which correspond to values reported from both sides of the Atlantic and from the Baltic and Mediterranean seas (mostly ranging from 2000 to 50,000 ind·m^{-2}; Orth, 1973, Blanchet et al., 2004, Boström et al., 2006; and references therein). Mean species richness in these *Zostera marina* beds was higher than in the meadows of the Baltic Sea (often < 10 species in 0.002 m^2 samples with 0.5 mm mesh size; Boström and Bonsdorff, 1997, Boström et al., 2006) but were comparable to values reported for infauna in the North-Eastern and Western Atlantic (mostly from 10 to 60 species in samples ranging from 0.004 to 0.27 m^2 with 0.5 or 1 mm mesh size; Orth, 1973, Stoner, 1980, Edgar et al., 1994, Blanchet et al., 2004 and references therein). In addition to this high local richness often reported for individual seagrass meadows (Hemminga and Duarte, 2000), our estimates of BD$_{total}$ (Fig. 5) indicate extensive variation of communities at the regional scale. Hence, regional richness was enhanced by a combination of high α and β diversities, in agreement with the recent description of Brittany waters as a hotspot for macrobenthic richness in Western Europe (Gallon et al., 2017, this issue).

The invertebrate communities differed among sites and years although the 120 sampling units (8 sites × 3 points × 5 years) presented the kind of variation in composition expected for sampling units drawn from a large statistical population such as the broad-scale metacommunity of invertebrates of the *Zostera* beds of Brittany with year-to-year variation. There is indeed strong variation in community composition and α diversity among sites and years. These changes were both dependent on the meadow and the faunal compartment considered. In particular, extensive variations of species composition were observed among sites, confirming that faunal composition of seagrass meadows is not a fixed or constant attribute. Similar variations among meadows were indeed observed in the Baltic Sea by Boström and Bonsdorff (1997), with Jaccard similarity ranging from 0.32 to 0.72 for both the epifauna and infauna associated with *Zostera marina* beds. Likewise, Edgar et al. (1994) found Jaccard similarities ranging from 0.1 to 0.59 among seagrass infauna of different sites in South East Australia.

Removing the 179 species represented by < 10 specimens over the whole study had little impact on the major patterns described by the ordinations, even when considering presence/absence data. However, the β diversity decompositions, computed with all species, indicated extensive species turnover even within meadows with renewals often > 50%, which primarily suggests important fluctuations of the numerous rare species observed in this study. Marine datasets usually contain large numbers of rare species that may partly be attributed to sampling methodology (Gray et al., 2005). Yet, they may also be favoured by the increased niche availability and surface area provided by structurally complex habitat such as seagrass (Boström and Bonsdorff, 1997; Attrill et al., 2000; Lürig et al., 2016). Rare species are often characterised by limited niche breadth, and studies with large spatial and temporal extents – such as the present study – encompass large-scale environmental gradients that inherently favour the discovery of rare species (Gaston and Kunin, 1997; Legendre and Legendre, 2012). As these rare species may be of prime functional importance (Hooper et al., 2005; Ellingsen et al., 2007; Mouillot et al., 2013), further work is needed to disentangle whether they may be attributed to sampling methodology or to underlying ecological causes (Chase and Myers, 2011) and evaluate to what extent the important compositional changes may affect seagrass functioning.

Interestingly, despite important community composition changes, species richness remained within narrow limits. Indeed, species replacement predominated while richness differences were of limited extent, implying that changes in species composition were induced by simultaneous gain and loss of species among meadows. A similar case of varying assemblage composition accompanied by constancy in associated diversity measures was previously reported over 1.5 ha of an intertidal meadow in South Africa (Barnes, 2013) but this is the first report at such broad spatial scale and across such contrasted environments. Barnes (2013) suggested extending the theoretical framework for temporal constancy of biodiversity measures to the spatial context of seagrass meadows. This would require constant levels of productivity and resource availability despite spatially variable environmental conditions, and an open system with opportunity for compensatory mechanism among species to exploit all resource spectra while withstanding varying conditions (Brown et al., 2001; Barnes, 2013). Provided that similar functional spaces are available across the different meadows, the rich regional pool of species available to colonise these North-East Atlantic meadows may provide foundation for portfolio effects (Schindler et al., 2015). Indeed, spatial and/or temporal stability of community's organisations may theoretically arise from independent dynamics among species that perform similar ecosystem functions (Tilman et al., 1998; Schindler et al., 2015). Such ecological equivalence may arise at regional scale among species that only vary subtly in their ecological niches such that their partially overlapping niches make believe that they fulfil similar roles in the communities at such scales of study (Shmida and Wilson, 1985; Munoz and Huneman, 2016). Biogenic habitats often harbour similar functional groups across different locations while displaying high levels of redundancy within each groups (Hewitt et al., 2008; Barnes and Hamylton, 2015). For instance, several mesograzers can coexist through micro-habitat partitioning in seagrass (Lürig et al., 2016), nonetheless they are generally regarded as occupying equivalent trophic positions and feeding niches (Duffy, 2006). Accordingly, we observed important local changes in the identity and preferences of dominant mesograzers among beds but their functional space was invariably occupied. Thus, in a species-rich region such as Brittany, some are able to thrive in the different local conditions while occupying similar functional spaces. High species replacement together with low richness differences may indicate that the studied meadows share essential properties in terms of niche and resource availability despite varying local conditions (Cornell and Lawton, 1992). These shared properties may constrain their diversity and the narrow range of species richness described in this study may therefore correspond to the species richness carrying capacity for seagrass (*sensu* Hansen et al., 2011).

Ecological equivalence among species may have a large stochastic component (Munoz and Huneman, 2016) so that the processes underlying this apparent richness constancy remain unclear (Barnes and Hendy, 2015). Accordingly, efforts should be made to disentangle the biotic and abiotic structuring factors of epifaunal and infaunal communities. Seagrasses form intricate structures that vary at a series of hierarchical levels, generating complex interplay between the scales at which their associated fauna responds (Turner et al., 1999). This study confirms that the structuring factors underlying epifauna patterns may differ from those shaping infauna, as shown at more local spatial scale than the present study by Leopardas et al. (2014). Indeed, PCAs showed that epifauna and infauna did not display the same patterns and MANOVA results revealed that these patterns where different with respect to space and time. Hence, despite sharing a substantial number of species, epifauna and infauna may not respond in similar ways and be sensitive to the same prevailing forces. Both compartments have considerable amount of unique species that are most likely the ones inducing the differences observed. A community is most often defined as group of interacting species occurring together in space and time (Stroud et al., 2015). Accordingly, the differences between epifauna and infauna spatial and temporal patterns described here support the hypothesis that they may be considered as distinct self-communities (Hemminga and Duarte, 2000; Törnroos et al., 2013; Leopardas et al., 2014). This statement however, does not preclude that these two communities may be closely linked in their fate and depend on their respective functional roles, nor does it challenge the trophic

relationships that may exist between some of the species composing the two communities (Orth et al., 1984).

Epifauna was characteristically dominated by grazers (Duffy, 2006). Variation of epifauna was partly related to sediment characteristics implying a relationship between local hydrological conditions and aboveground communities. This relationship may operate through direct effects of currents on epifauna (Hovel et al., 2002), or through indirect effects *via* modification of the *Z. marina* beds' architecture and characteristics under the influence of substrate and hydrodynamic conditions (Frederiksen et al., 2004; Moore and Short, 2006). For instance, epifauna has often been related to variation in seagrass aboveground biomass (Attrill et al., 2000; Leopardas et al., 2014). The present epifaunal assemblages were dominated by trochids and crustacean mesograzers that generally feed on epiphytic algae associated with *Z. marina* blades but have different feeding behaviour (Hily et al., 2004; Duffy, 2006; Rueda et al., 2008; Mancinelli, 2012). These behaviours may induce different responses to variations in epiphyte availability linked with seagrass biomass as well as to differences that may exist among beds in terms of epiphytic composition (Saunders et al., 2003; Borg et al., 2010). They may also be influenced by external phenomena such as provision of transient food sources. Accumulation of drifting algae may represent an important food supply for benthic invertebrates (Norkko et al., 2000). Such input was for instance commonly observed in the Sainte-Marguerite meadow since the beginning of its monitoring by the REBENT programme in 2004. This can explain the dominance of species such as *Idotea balthica* in this meadow, as these isopods are often associated with drifting algae (Duffy, 2006). The role of environmental variables not accounted for in the present analysis such as temperature, salinity or primary productivity (Snelgrove, 1998) remain however to be unveiled. In particular, *Zostera marina* displays a large phenotypic plasticity in Brittany (Becheler et al., 2010). Variation in seagrass morphology can certainly influence associated macrofauna but the role of seagrass structure has mostly been explored in terms of among-habitat patterns (Airoldi et al., 2008). Its influence on within-seagrass community variability remain however to be fully apprehended, in particular regarding its relative importance compared to abiotic factors and its underlying mechanisms (Attrill et al., 2000; Sirota and Hovel, 2006; Ávila et al., 2015). Likewise, the influences of dispersal patterns, of historical events and macroevolutionary processes, and of local scale processes such as predation, facilitation, resource partitioning and competitive exclusion are largely unknown at such scales (Ricklefs, 1987; Wagner and Fortin, 2005; Boström et al., 2010).

Sediment conditions and the forces that shape them are often the main factors structuring infaunal communities (Gray, 1974). The Glénan, Sainte-Marguerite and Molène communities were clearly distinguished by the great dominance of *Spio cf. arndti* that is characteristic of fine sand conditions (Dauvin, 1989). All other meadows displayed more heterogeneous sediments with characteristic species such as *Golfingia elongata* (Gibbs, 2001) and *Nematonereis hebes* (George and Hartmann-Schröder, 1985). While the effects of local conditions on epifauna may be dampened by their adult dispersal capabilities (Thrush and Whitlatch, 2001), infauna is more sedentary and often displays a tight relationship with its proximate environment (Pearson and Rosenberg, 1978). Accordingly, infauna showed a stronger response to the local hydrological characteristics of the meadows than epifauna and therefore displayed a higher BD_{total}. As hypothesised by Gallon et al. (2017), the great range of local hydrological conditions found in Brittany may explain the important spatial renewal observed for infaunal communities, promoting high overall richness at the regional scale. Thus, while seagrass epifauna has been described as an important local addition to infauna diversity and as playing an important role in among-habitat diversity (Boström and Bonsdorff, 1997), the present study reveals that infauna may be more variable at the regional scale and thus contribute more importantly to within-habitat β diversity of seagrass communities. Further work is needed to refine our understanding of the relative roles of epifauna and infauna on regional diversity in habitat mosaics, taking into account the within-habitat contribution of the infauna.

Management actions should vary, for sites with similar local α diversity, depending on their local contributions to β diversity (Noss, 1983). Despite a growing interest in measuring and understanding β diversity (Koleff et al., 2003; Legendre et al., 2005; Anderson et al., 2011; Legendre and De Cáceres, 2013), only a few studies have explicitly focused on spatial or temporal turnover of marine communities. These studies mainly concerned fish communities (*e.g.* Belmaker et al., 2008; Lamy et al., 2015) and macrofauna of rocky habitats (*e.g.* Balata et al., 2007) and soft sediments (*e.g.* Hewitt et al., 2005; Josefson, 2009; Zajac et al., 2013). High β diversity was observed in the PCAs and LCBD analyses, implying that the studied *Zostera marina* meadows differed markedly from one another, each one containing but a small fraction of the regional richness (Koleff et al., 2003). Exceptional contributions to β diversity were only punctual and these high LCBD values were mostly related to drops in local diversity. These drops may be linked to catastrophic events such as the sand dune movement that covered the Molène meadow in 2012 (personal observation) but this remains to be determined for the other high LCBD scores, and in particular for the Saint-Malo meadow that repeatedly had significant LCBD scores. Overall, all seagrass meadows had fairly similar contributions to the high β diversity. They consequently have equivalent conservation values (Legendre and De Cáceres, 2013). This conclusion is strengthened by the weak species richness differences observed among the sites, while the substantial community replacement among meadows confers them high complementarity. Future work will need to evaluate the relevance of this extensive within-seagrass variation in a multi-habitat context. This variability, however, undoubtedly needs to be accounted for in management schemes to fully preserve the regional diversity (Fraschetti et al., 2008; Törnroos et al., 2013). In particular, a significant space-time interaction was found, indicating that spatial patterns have changed over time or, conversely, that the year-to-year variations of the meadows were location-specific (Legendre et al., 2010). These spatial and temporal interactions seem to be a common feature in seagrass (Boström et al., 2011; Carr et al., 2011). Accordingly, to preserve this high regional diversity, management actions should focus on site-specific rather than broad-scale measures. These measures should foster the maintenance of the local diversity of meadows but also their complementarity at broad scale. If local diversity seems to be a good predictor of the functioning of seagrass meadows (Duffy et al., 2015), the important variations observed in species composition, and especially of rare species, and the equal contribution of the different meadows to regional diversity, raise questions about their functional complementarity at regional scale (Bond and Chase, 2002). Life trait analysis of these seagrass communities would be of particular interest to deepen our understanding of the processes underlying their apparent carrying capacity for species richness. It may give insights into the role of species and on how functional space may vary among these meadows in relation to environmental filters (Villéger et al., 2011; Mason et al., 2013).

Large scale analyses of marine biodiversity have traditionally focused on surrogates of species-level pattern such as mapping habitat feature (Ferrier, 2002; Fraschetti et al., 2008). The ability of these approaches to grasp the biodiversity of different seagrass species have however been challenged in previous work (Hamilton et al., 2012). In agreement, we illustrate here, through an important monitoring effort, the existence of not negligible ecological patterns among meadows that remained concealed with these approaches (Edgar et al., 2016). In the context of benthic homogenisation and loss of complexity on the sea floor, this study argues for a better consideration of all components of diversity in marine studies (Gray, 1997; Airoldi et al., 2008). It emphasizes in particular the importance of taking β diversity patterns into account to fully grasps the richness of benthic habitat at broad scale (De Juan and Hewitt, 2011; De Juan et al., 2013). Efforts in the broad scale acquisition of ecological data have long been thwarted by various

logistical or methodological impediments (Edgar et al., 2016). However, appropriate analytical tools are becoming increasingly available and the present study illustrates the potential contributions of broad spatial and temporal monitoring programmes combined with innovative statistical analyses. Further broad scale analyses in contrasted environments will help to deepen our understanding of biodiversity patterns and their underlying ecological processes, and in turn will help guide management actions.

Acknowledgement

Appendix 1. Sampling dates of each site in the 5 years of the study. Date format: day/month/year (DD/MM/YY). Sampling dates may vary from one year to another due to tide conditions or logistic constraints.

| Sites	Sampling dates
Arcouest	2/19/2007
Arcouest	3/12/2009
Arcouest	3/1/2010
Arcouest	3/22/2011
Arcouest	4/4/2012
Callot	2/21/2007
Callot	3/11/2009
Callot	3/2/2010
Callot	4/19/2011
Callot	4/8/2012
Glénan	4/17/2007
Glénan	3/11/2009
Glénan	4/20/2010
Glénan	4/18/2011
Glénan	5/7/2012
Saint-Malo	2/20/2007
Saint-Malo	3/28/2009
Saint-Malo	4/1/2010
Saint-Malo	4/18/2011
Saint-Malo	3/8/2012
Sainte-Marguerite	2/20/2007
Sainte-Marguerite	2/12/2009
Sainte-Marguerite	2/3/2010
Sainte-Marguerite	3/19/2011
Sainte-Marguerite	3/9/2012
Molène	4/18/2007
Molène	2/11/2009
Molène	2/2/2010
Molène	3/22/2011
Molène	5/8/2012
Roscanvel	4/17/2007
Roscanvel	2/10/2009
Roscanvel	2/1/2010
Roscanvel	3/21/2011
Roscanvel	3/8/2012
Sept-Iles	4/18/2007
Sept-Iles	3/10/2009
Sept-Iles	3/1/2010
Sept-Iles	3/21/2011
Sept-Iles	5/7/2012

Appendix 2. Total abundances per m² per site (sum over the 3 points) in the 5 years of the study. Epifauna in black, infauna in gray.

Site		Mean abundance per point				
		2007	2009	2010	2011	2012
Saint-Malo	Epif.	11	78	20	17	24

	Inf.	5889	4193	2444	1981	1470
Arcouest	Epif.	15	48	62	36	40
	Inf.	6422	4541	4807	5378	2726
Sept-Iles	Epif.	31	39	33	19	30
	Inf.	13,763	2156	8156	5522	4611
Callot	Epif.	42	40	86	55	51
	Inf.	12,289	5296	5615	3585	6259
Sainte-Marguerite	Epif.	76	188	96	203	94
	Inf.	32,178	26,000	9578	7944	21,444
Molène	Epif.	26	19	73	12	48
	Inf.	13,141	12,630	16,511	7441	13,422
Roscanvel	Epif.	22	28	38	67	45
	Inf.	8422	12,274	4348	5267	2840
Glénan	Epif.	37	89	32	144	27
	Inf.	18,185	41,941	6696	25,830	28,867

Appendix 3. Principal coordinates analyses (PCoA) of presence/absence data based on the square root of Jaccard dissimilarity. The square root of Jaccard dissimilarity was used because distances calculated in this way are fully embeddable in Euclidean space and the distance matrix does not produce negative eigenvalues (Legendre and Legendre, 2012). The analysis of epifaunal communities is represented in panel A and of the infauna in panel B. The first two axes represent 10.9% and 12.1% of the total variation of epifaunal and infaunal community compositions respectively. 95% confidence ellipses are drawn for the points corresponding to each site. Within-site dispersions represent temporal variability during the 5 years of the study and variation of the communities among the three points sampled per year.
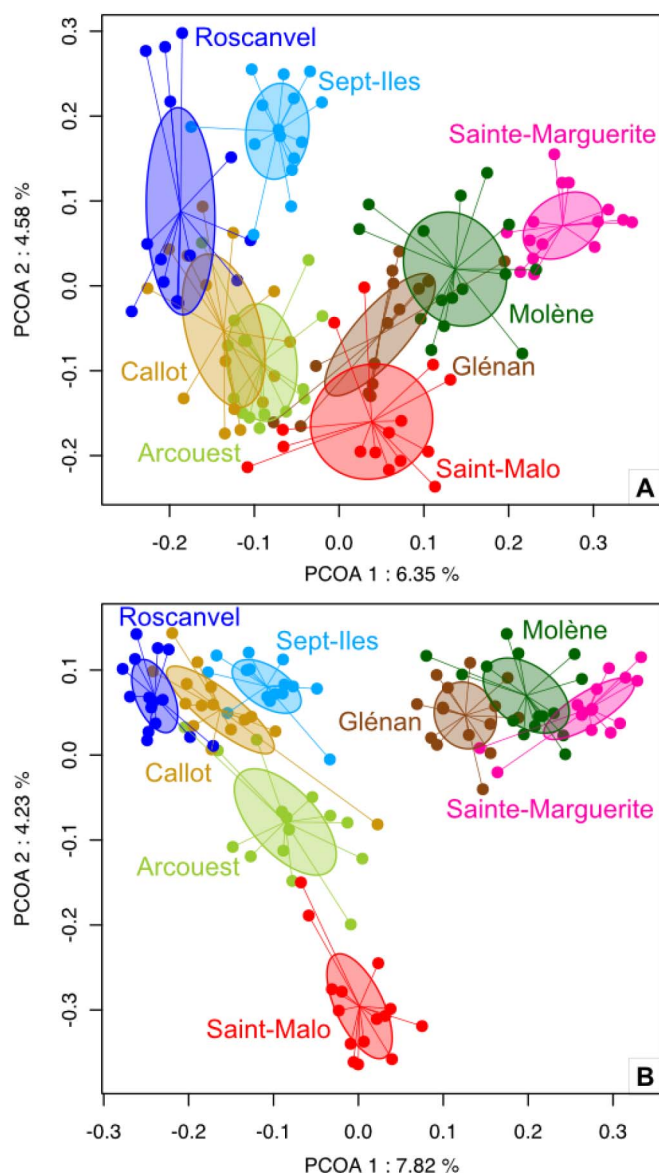
Appendix 4. Principal coordinates analyses of presence/absence data based on Jaccard dissimilarity. Species represented by < 10 specimens over the whole study (representing 179 species over the epifauna and infauna together) were removed from these analyses. The square root of Jaccard dissimilarity was used because distances calculated in this way are fully embeddable in Euclidean space and the distance matrix does not produce negative eigenvalues (Legendre and Legendre, 2012). The analysis of epifaunal communities is represented in panel A and of the infauna in panel B. The first two axes represent 11.9% and 13.1% of the total variation of epifaunal and infaunal community compositions respectively. 95% confidence ellipses are drawn for the points corresponding to each site. Within-site dispersions represent temporal variability during the 5 years of the study and variation of the communities among the three points sampled per year.
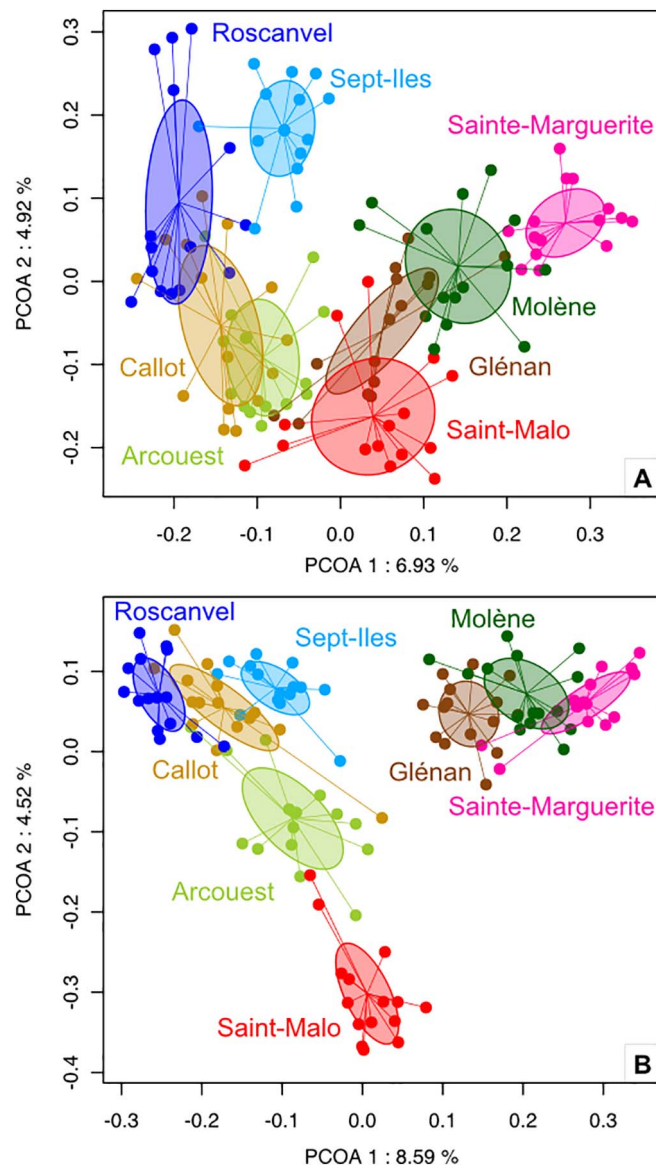
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