Effects of macroalgal accumulations on the variability in zoobenthos of high-energy macrotidal sandy beaches

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ABSTRACT: Sandy beaches, forming the most widespread coastal habitat in the world, are threatened by the effects of increasing anthropogenic pressure in the context of global change, including the increased occurrence of green tides composed of free-living *Ulva* spp. Sandy beaches are also highly dynamic ecosystems that support numerous essential ecological functions and contain a distinctive biodiversity, but their precise functioning and natural variability (i.e. the disentangling of biological and physical influences) remain under-studied. Our study aimed at determining the effects of space, time, and environmental variables on the natural variability of macrofaunal community structure and at specifically determining the effects of macroalgal accumulations on the observed variability. We followed a high-resolution field sampling design in space and time (261 samples) at non-vegetated and at partially and fully green-tide-impacted macrotidal sandy beaches. We used novel statistical approaches (distance-based Moran's eigenvector maps [dbMEMs] and variation partitioning) to analyse our results. The macrofaunal community structure of the non-vegetated sandy beach was variable in space and time at small scales, and physical environmental variables significantly explained these variations. Our study also highlighted a decrease in this variability along a gradient of increasing coverage of stranded *Ulva* spp. and the increasing importance of biological variables in explaining ecological variability. Compared to a state with no *Ulva*, a large and homogeneous coverage of *Ulva* along a sandy beach shore induced a significant decrease of overall β-diversity. However, macrofaunal responses to macroalgal accumulation were less pronounced than what has been previously shown in micro-tidal and sheltered systems, likely due to the dynamic and unstable nature of high-energy macrotidal sandy shores.

KEY WORDS: Macrotidal sandy beach · Macrofauna · Green tides · Space-time analysis · β-diversity

INTRODUCTION

Sandy beach (SB) ecosystems harbour many organisms that are all specialized and adapted to life in mobile sediments. At regional to global scales, SBs contribute highly to β-diversity and support numerous essential ecological functions such as filtering large amounts of water, mineralizing organic matter, and recycling nutrients, as well as forming nurseries and feeding areas for commercially important fishes (Schlacher et al. 2008). Beach ecosystems make up two-thirds of the world's ice-free coastline (McLachlan & Brown 2006) and provide both resources and recreational opportunities. More than half of the world's human population lives within 60 km of the shoreline (Turner et al. 1996). Hence, SBs are threatened by increasing direct and indirect anthropogenic pressures, such as fishing, coastal development and

Fig. 1. Illustration of green tides in the Bay of Douarnenez, Brittany, France: (a) Sandy beach (SB) that never harbours green tides; (b) SB that harbours green tides during spring and summer. Photo credits: E. Bonsdorff (a) and N. Quillien (b)

pollution (Schlacher et al. 2007, Defeo et al. 2009). One of the most important human-induced pressures is excess nutrient release into water bodies and the resulting eutrophication (Cloern 2001).

One of the direct symptoms of nutrient enrichment in coastal areas is the rapid and important development of assemblages of macroalgae with short life-cycles (Cloern 2001). Such notable blooms are increasing in frequency and intensity worldwide (Ye et al. 2011). In the northeastern Atlantic Ocean, beaches of Brittany (Western France) are particularly affected by stranded *Ulva* spp. (hereafter *Ulva* or green macroalgae) mats (Ménesguen & Piriou 1995, Charlier et al. 2007; Fig. 1); 51 open macrotidal (mean spring tide > 4 m, Allaby 2010) sandy beaches and 33 mud flats hosted green tides in 2013 (CGDD 2014). The presence of such free-living macroalgal mats affects exchange between sediments and water and modifies local hydrodynamics (Hull 1987, Jeffrey et al. 1992), primary production (Sundbäck 1994, Bombelli & Lenzi 1996), and benthic fauna (Hull 1987, Norkko & Bonsdorff 1996). Most of the studies that have been conducted on this issue were carried out in very sheltered environments (i.e. mud flats; see Raffaelli et al. 1998, Ouisse et al. 2011), have involved semi-controlled experiments in the field (Norkko & Bonsdorff 1996, Thiel & Watling 1998), and have mostly addressed the question in non- or micro-tidal systems (Norkko & Bonsdorff 1996, Thiel & Watling 1998). The tidal regime is an additional factor to the variability of coastal marine systems, and much still remains to be discovered and explained regarding the ecological effects of algal accumulations in open macrotidal sandy beach systems.

In their review addressing the threats facing sandy shore ecosystems, Brown & McLachlan (2002) showed that the question of the effects of organic enrichment through eutrophication in sandy shore ecosystems has been mostly studied in sheltered lagoons and in estuaries. The effects of macroalgal mats on open sandy beach systems have mainly been addressed by experimental studies based on controlled algal manipulations, which implies important limitations when trying to understand ecosystem-scale response to such perturbation (Bolam et al. 2000, Franz & Friedman 2002). Thus, to our knowledge, except for meiofaunal communities (Carriço et al. 2013), there is no published research that has studied the effects of green tides on swash zone communities living in highly dynamic sandy systems such as open macrotidal beaches.

Since the 1980s, the understanding of the ecology of sandy shores has greatly advanced (Defeo & McLachlan 2005, McLachlan & Brown 2006, Nel et al. 2014). Numerous studies have described across-shore distribution of benthic macrofauna (e.g. Schlacher & Thompson 2013), and, today, along-shore distribution of specific sandy beach populations is well known (e.g. Lercari & Defeo 1999, Defeo & de Alava 1995, Schoeman & Richardson 2002). In microtidal sandy systems, James & Fairweather (1996) have shown that SB macrobenthic community structure varies along-shore. However, such work has not been conducted in macrotidal systems. Thus, several spatial community patterns and their drivers are still to be fully understood. Regarding temporal variation, seasonal trends have been recorded in macrofaunal assemblages living in intertidal soft-bottom systems (Leber 1982, Degraer et al. 1999, Da

Silva et al. 2008). Yet those studies have been mostly species-specific or used low-frequency sampling designs (ca. 6 mo between samplings), while Addicott et al. (1987) and Botsford et al. (1997) stress that ecological research often requires detailed and fine-scaled knowledge to understand patterns and processes. In addition, ecological processes may be better studied by simultaneous consideration of both spatial and temporal variation (Resh & Rosenberg 1989). Studies that consider both time and space in soft-sediment community ecology remain scarce (Hewitt et al. 2001, Ysebaert & Herman 2002). Regarding sandy beaches, the use of such an approach is still emerging (Veloso & Cardoso 2001, Carcedo et al. 2014).

The limited number of studies assessing how the combination of several factors structures benthic macrofaunal assemblages may be explained by the complexity of analysing multivariate data accounting for effects of time, space, and other environmental variables simultaneously. This issue is an important topic in community ecology (Rundle & Jackson 1996, Anderson & Gribble 1998, Ysebaert & Herman 2002). Hence, biostatisticians and numerical ecologists have developed methods incorporating resampling and permutational functions to answer ecological questions using multivariate and multiscale spatial and temporal data sets (Dray et al. 2012). The present study is one of the first using such an approach to disentangle the effects of time, space, and environmen-

tal factors, including green tides, on sandy swash-zone benthic communities.

The aim of the present study was thus to explain the variation of benthic infauna of macrotidal (mean spring-tide > 4 m) sandy beaches. This was done by studying the following hypotheses: variation in macrofaunal benthic structure is dependent on (1) location at small spatial scale (hundreds of meters) along the swash-zone, (2) time/month (season) of the year, and (3) presence of *Ulva* spp. macroalgal blooms. In other words, we examined whether changes in the community were identifiable by analysing the effects of temporal, spatial, and environmental variables, specifically eutrophication in the form of biomass of *Ulva* spp., on the benthic assemblages over an annual cycle.

MATERIALS AND METHODS

Study area

The study was performed in the bay of Douarnenez (Brittany, France), where sediments accumulate to form kilometre-scale sandy beaches (Fig. 2). Three beaches were selected for this study: one that does not harbour green tides (SB_A) (Fig. 1a), one that harbours spatially heterogeneous green tides (SB_B), and a third one (SB_C) that receives green tides homogeneously along the entire shore (Fig. 1b). Thus, the 3
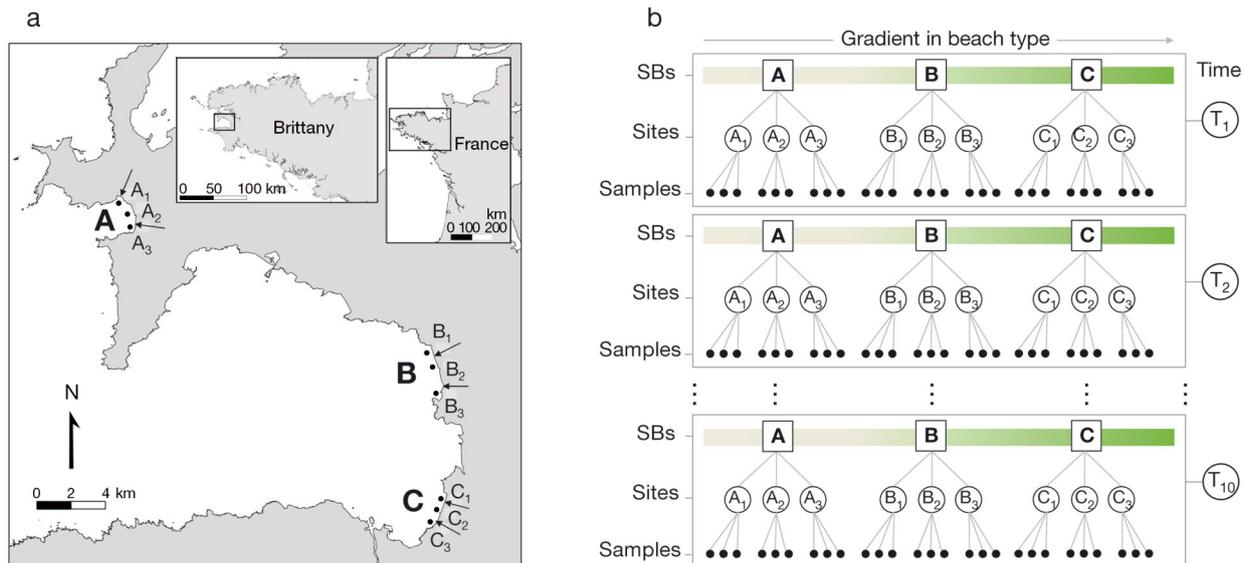

Fig. 2. (a) Location (Brittany, France) of the 3 sandy beaches (SBs: A, B and C), the 9 sampling sites (black filled circles) where 3 replicates were sampled monthly and the coastal rivers' mouths (arrows). (b) Sampling design, repeated in time (10 dates: T_1, T_2, … T_{10}) showing the 3 SBs (A, B and C), the corresponding sampling sites (A_1, A_2, A_3, B_1, B_2, B_3, C_1, C_2, C_3) and the samples (black circles)

SBs form a gradient of beach types (Fig. 2b). We make use of this gradient, and since the performed analyses (see 'Data analyses') are based upon linear regression, they do not require replication of each value along the independent variable (here, the beach type, Fig. 2b). The 3 SBs, open to the west, show large areas (up to 500 m from shore during spring tides) that are uncovered at low tide (mean tidal regime = 6.5 ± 0.5 m). They are characterized by a lower shore with a slope of 1.5 %, and since the tidal regime is macrotidal, these SBs are defined as dissipative beaches (Short 1996, Hénaff 1998). The length of the beaches ranges from 2.1 to 3.0 km. The anthropogenic impacts on SB_A are negligible. Indeed, the continental water inputs are filtered by a wetland area just behind the beach, and the urbanization there is limited. In contrast, SB_B and SB_C are located below agricultural catchment areas and have experienced yearly *Ulva* bloom events since the early 1980s (Ménesguen & Piriou 1995, Charlier et al. 2007).

Field sampling

To assess macrofaunal variability along the shore, sampling was conducted at 3 sampling sites distributed latitudinally at the same level along the swash zone (spring low tide) at the north, middle, and south of the 3 SBs (A_1 = 48° 15.206' N, 4° 33.298' W; A_2 = 48° 15.003' N, 4° 33.051' W; A_3 = 48° 14.109' N, 4° 32.545' W; B_1 = 48° 11.355' N, 4° 18.202' W; B_2 = 48° 11.193' N, 4° 18.149' W; B_3 = 48° 10.132' N, 4° 17.465' W; C_1 = 48° 06.585' N, 4° 17.050' W; C_2 = 48° 06.367' N, 4° 17.145' W; C_3 = 48° 06.105' N, 4° 17.263' W) (Fig. 2). The distance between each adjacent 2 of the 3 sampling sites within a beach ranged from 700 to 1300 m (mean of 900 ± 200 m). To evaluate temporal variability of benthic communities within each of the stations, all sites were sampled monthly from April 2012 to February 2013 (except in December 2012 for SB_C and in January 2013 for all sites due to unfavourable meteorological conditions) within a day for each beach.

Macrofauna (>1 mm) was collected using a tube-corer (inner diameter: 11.3 cm; depth: 15 cm). To obtain faunal samples covering an area of 300 cm^2, 3 cores (circa 40 cm apart) were pooled to obtain 1 sample (Fig. 2b). These pooled core samples were sieved through mesh bags (1 mm mesh size) to separate the fauna from the sediment. At each sampling site (A_1, A_2, etc.), 3 such replicate samples were randomly taken 1 to 2 m apart. Faunal samples were preserved in 4 % buffered formalin for later sorting in the lab where macrofauna were identified to the low-est possible taxonomic level with the aid of a binocular magnifier, counted, and weighed. Species nomenclature follows the 'World Register of Marine Species' (www.marinespecies.org/). Biomass of each taxon was measured by weight loss after combustion at 450°C for 4 h (ash-free dry weight).

Species richness was the number of species per sample. Abundance and biomass were converted to units per m^2. In addition to the quantitative data set, global information on biological traits was linked to each dominant species. Information about the feeding ecology, mobility, size, and reproduction for the dominant species was thus gathered from peer-reviewed literature and publicly available databases such as MarLIN/BIOTIC and EOL/polytraits (*sensu* Törnroos & Bonsdorff 2012).

At each site where fauna was sampled (Fig. 2a, $A_{1,2,3}$; $B_{1,2,3}$; $C_{1,2,3}$), a single sediment core was extracted (in the same way as fauna cores) to obtain grain size and organic matter content characteristics. Grain sizes were measured by dry-sieving, using a series of 16 sieves from 63 to 10 000 µm. The sorting index (SI) was calculated based on the first and third quartile ratio ($\sqrt{Q25/Q75}$, where Q25 and Q75 denote the first and the third quartiles of the sediment grain size, respectively), and the median (Q50) was equal to the second quartile of the sediment grain size value (hereafter referred to as 'median'). Organic matter content was measured by weight loss after combustion at 450°C for 5 h. Beach slope was calculated for each sampling site by geometry (maximal tide/shore width). *Ulva* biomass was estimated by CEVA (www.ceva.fr/fre) through monthly aerial surveys (for estimation of surface area covered by mats) and field sampling (for conversion into biomass). Since CEVA's data were included in a GIS (geographic information system) database, *Ulva* biomass was calculated for 3 at each beach (each polygon was one third of the beach surface and contained 1 sampling site, e.g. site A1, see Fig. 2a) along shore in order to integrate spatial-heterogeneity along SBs.

Seawater temperature, salinity, and dissolved oxygen content were measured on each sampling occasion using a YSI-OMS v2 probe. Monthly mean values for phytoplankton concentrations and for wave height were taken from the publicly available database PREVIMER (www.previmer.org/observations). PREVIMER estimates plankton concentration using the ECO-MARS-3D model (grid = 4 km), and the wave height was calculated using the model WW3 (grid = 200 m). Wind speed was assessed by averaging the values for wind velocity of 5 d before each sampling date using data of the Pointe du Raz

meteorological station (www.infoclimat.fr/observations-meteo/temps-reel/pointe-du-raz/07103.html). The environmental parameters measured at beach scale (seawater temperature, salinity, dissolved oxygen content, plankton concentration, wave height, and wind velocity) were considered homogeneous within each beach (e.g. salinity at SB_A = salinity at Sites A_1, A_2, and A_3).

Data analyses

Effect of site on species richness throughout the SBs was assessed with sample-based rarefaction curves for the 9 sampling sites (from A_1 to C_3). Expected species richness was plotted as a function of the expected number of individuals to allow meaningful comparisons (Gotelli & Colwell 2001) among sites. Macrofauna diversity was assessed using the following primary community variables and diversity indices (Gray & Elliott 2009): abundance (A), biomass (B), species richness (S), and numerical equivalents of Shannon's entropy ($\exp(H')$) and Simpson's ($1/D$) indices following the method of Jost (2006) for unified interpretation of diversity. The temporal (monthly sampling from April 2012 to February 2013) and spatial (along the beach) variation in each of these univariate variables was assessed to extricate diversity trends.

Before performing statistical tests on these univariate characteristics of macrofaunal α-diversity, all faunal and environmental variables were checked for normality (graphically and using Agostino test) and fourth-root, log, or arcsine transformed if necessary. Environmental characteristics between beaches and/or sampling occasions were tested to determine if and how the 3 SBs experienced different environmental conditions. For slope, estimated once from bathymetric maps for each of the 9 sites (see 'Field sampling'), a Kruskal-Wallis test was used. For variables measured repeatedly through time at a single site per beach (seawater temperature, salinity, dissolved oxygen, and wave height), Friedman tests were used to test for consistent differences among beaches over time. Finally, after checking for homogeneity of variance, 2-way ANOVAs with permutations were used for variables measured with replication in both space and time (*Ulva* biomass, sorting index, organic matter, and median). Furthermore, to disentangle the effects of time, environment, and space on the univariate variables (A, B, S, H', and D), 2 recently developed methods were combined: distance-based Moran's eigenvector maps (dbMEMs;

Dray et al. 2006, Legendre & Gauthier 2014) were used in variation partitioning (Borcard & Legendre 1994). First, dbMEM eigenfunctions were generated based on the number of sampling occasions and the number of days between sampling occasions. The generated dbMEM eigenfunctions were used as temporal variables (here called MEMs, see Fig. S1 in the Supplement at www.int-res.com/articles/suppl/m522p097_supp.pdf). MEMs can model both positive and negative temporal patterns, and both models were assessed. Forward selection (Blanchet et al. 2008) was then used to select significant MEMs. The location along the shore was used as a spatial variable and was coded by Helmert contrasts (Legendre & Anderson 1999). Variation in the univariate responses was then partitioned with respect to 3 groups of explanatory variables: environment (the 10 variables describing physical and biological environment of each site after normalization), space (the location along the shore), and time (the selected MEMs). Each fraction of variation, i.e. the explanatory power of each set of the explanatory variables, was tested by multiple and partial (for pure explanatory power, see Fig. S2 in the Supplement, blue section) linear regression (Legendre & Legendre 2012). The importance of each environmental factor (i.e. the 10 variables describing physical and biological environment of each site) in explaining univariate responses was assessed using stepwise selection in multiple regression.

To test the null hypothesis of no differences among benthic assemblages through time between the 3 beaches, a multivariate analysis of variance (MANOVA) with permutation tests was computed by redundancy analysis (RDA) based on Hellinger-transformed abundance matrices of the 3 SBs (Legendre & Legendre 2012, Legendre & Gauthier 2014). For all multidimensional analyses, faunal data were first transformed using the Hellinger transformation, which is recommended for analysing abundance and biomass of species data since it does not give high weights to rare species (Legendre & Gallagher 2001). The 2 factors, beach and time, and their interaction, were coded by Helmert contrasts (Legendre & Anderson 1999). Homogeneity of multivariate dispersion was tested prior to this analysis. Principal component analyses (PCAs) were performed to visualize patterns in the distribution of assemblages of macrofauna in space and time within each SB. The total β-diversity (BDTotal) is defined as the total variance of a community matrix (*sensu* Legendre & De Càceres 2013). BDTotal was computed for each of the 3 sites within each sandy beach

(SB_A, SB_B, and SB_C) for each sampling occasion (only 8 sampling events — April to November 2012, i.e. 72 data points — were included to ensure a balanced design in this analysis). To assess if macroalgal accumulations are associated with general losses of β-diversity, BDTotal values were correlated (Kendall rank correlation) with the sum of *Ulva* coverage at each beach. To test if the different regimes of macro-algal accumulations could be linked to overall β-diversity, differences in BDTotal between beaches were assessed using 3 pairwise Wilcoxon-Mann-Whitney tests followed by a Holm probability correction for multiple testing.

Finally, redundancy analysis (RDA) was used to replace the 3 beaches in the overall context and determine how environmental, spatial, and temporal variables constrain the variation of benthic communities in this setting. MEM variables were used to model time, and forward selection was applied as in the previous analyses. To maintain balanced sampling effort in space and time, data from December 2012 were not used in analyses performed on all 3 beaches together. Finally, to circumvent the missed survey of January 2013 and consider data series with regular sampling intervals (1 mo), data from February 2013 were removed from all time-series modelling.

All analyses were conducted within the R environment (R Development Core Team 2013) and relied on the *BiodiversityR* (Kindt & Coe 2005), *vegan* (Oksanen et al. 2011), *PCNM* (Legendre et al. 2013), and *packfor* (Dray et al. 2013) packages.

RESULTS

Environmental characterization

Environmental characteristics for the period April 2012 to February 2013 of SB_A, SB_B, and SB_C are presented in Table 1. Seawater temperature, salinity, and dissolved oxygen content showed no significant differences among the 3 SBs. The environment is fully marine and well oxygenized. Likewise, wave height, beach slope, and chl *a* concentration were not significantly different among the 3 beaches. A significant effect of beach ($SB_{A, B, C}$) was found for the sorting index and median grain size, the latter also varying significantly in time. Finally, a significant interaction of the 2 factors 'beach' and 'time' explained variations of organic matter content and *Ulva* biomass. Significant statistical interaction implies that the effect of a factor (e.g. time) is not constant across the levels of another (e.g. beach).

No *Ulva* was reported from SB_A, while the mean biomass of fresh green macroalgae mats was estimated at approximately 720 and 340 t stranded along SB_B and SB_C, respectively. Particularly large standard deviations were found for *Ulva* biomass (Table 1) due to the temporal variability of stranded macro-algae, which annually occurs in spring and summer. Considering the 3 sampling sites along the shore of SB_B and SB_C, *Ulva* biomass washed ashore was variable both in time (Fig. 3a,c) and space (Fig. 3b,d). Macroalgae biomass measured on SB_B showed a gradient from Site B_1 to Site B_3 with a maximum in June,

Table 1. Environmental characterization of the 3 beaches (SB_A, SB_B, and SB_C) sampled monthly from April 2012 to February 2013 and the associated tests for the effects of beach (Be), time (Ti), and their interaction (Be × Ti) on environmental variables sampled monthly alongshore (*Ulva* biomass, SI, organic matter content, median), monthly at the beach scale (SWT, salinity, dissolved oxygen, wave height, chl *a*), and on a single occasion for the 3 sites along-shore (slope). The table presents the significant effects (p ≤ 0.05); a dash denotes no significant effect. 2w-A: 2-way ANOVA with permutations; F: Friedman test; K-W: Kruskal-Wallis. SWT: seawater temperature; median: Q50 (second quartile of the sediment grain size); SI: sorting index calculated based on first and third quartile ratio ($\sqrt{Q25/Q75}$, where Q25 and Q75 denote the first and the third quartiles of the sediment grain size, respectively); P: physicochemical variable; B: biological variable

Variable	Type	SB_A Mean	SB_A SD	SB_B Mean	SB_B SD	SB_C Mean	SB_C SD	Sources	Test	Effect
Ulva biomass (10^3 kg)	B	0.00	0.00	722.99	401.47	340.21	101.9	CEVA	2w-A	Be × Ti
Sorting index	P	1.24	0.10	1.13	0.06	1.21	0.09	Present study	2w-A	Be
Organic matter (%)	B	4.45	0.47	4.11	0.74	4.14	0.48	Present study	2w-A	Be × Ti
Median	P	180.37	25.07	158.52	11.99	176.87	22.06	Present study	2w-A	Be, Ti
SWT (°C)	P	14.58	3.39	14.68	4.39	15.44	2.82	Present study	F	–
Salinity	P	34.9	0.59	34.86	0.41	34.9	0.42	Present study	F	–
Dissolved oxygen (%)	P/B	103.38	2.23	103.91	2.62	104.05	4.13	Present study	F	–
Wave height (m)	P	1.35	0.43	1.42	0.49	1.59	0.66	Raz Observatory	F	–
Chl *a* (µg l^{-1})	B	15.79	9.86	15.79	9.86	15.79	9.68	PREVIMER	–	–
Slope (%)	P	0.02	0.00	0.01	0.00	0.02	0.00	Present study	K-W	–

while SB_C showed no clear gradient pattern. There, stranding was homogeneous throughout the beach (Fig. 3d).

Spatial-temporal variation in diversity patterns

Over the 10 mo of the study and among the 261 samples, a total of 12 781 macrofauna individuals were identified belonging to 67 different species. Crustacea was the most represented phylum within the community, with 29 malacostraca species, followed by Annelida with 26 polychaete species and Mollusca with 6 species. Other species belonged to Nemertea, Echinodermata, Sipuncula, Platyhelminthes, and Cnidaria. Considering each sampling site and a given number of individuals (n = 720, i.e. the lowest total number for any site), species accumulation curves (Fig. 4) give the highest estimated species richness for Sites B_1 and B_2 (S = 32 and 33 respectively). Sites A_1, A_2, A_3, and B_3 exhibited similar values (26, 27, 28, and 28, respectively). Species richness estimated for sites sampled on SB_C were the lowest, with values ranging from 21 to 24.

The different primary community variables (A, B, S, H', and D) displayed temporal patterns and did not follow the same arrays (Fig. 5; for additional information regarding spatial variation along-shore, see also Fig. S3 in the Supplement) within the SBs (A, B, and C). The development of fauna (abundance and bio-
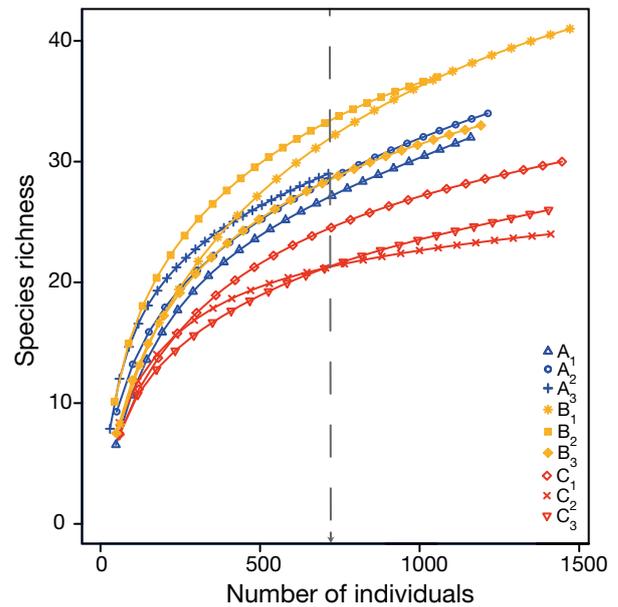

Fig. 4. Sample-based rarefaction curves for the 3 SBs (A, B and C) and each site. The dashed grey vertical arrow indicates the chosen number of individuals for comparison between sites (n = 720)

mass) varied only slightly at SB_A, while it showed evident seasonal variability at SB_B and SB_C (Fig. 5a,b). The same overall seasonal trend occurred for the mean species richness for the 3 SBs (Fig. 5c) with the highest mean S observed in August and September for each site. The mean Shannon and Simpson indices showed seasonal variability (Fig. 5d,e) with lower levels at SB_B and SB_C from August to February.
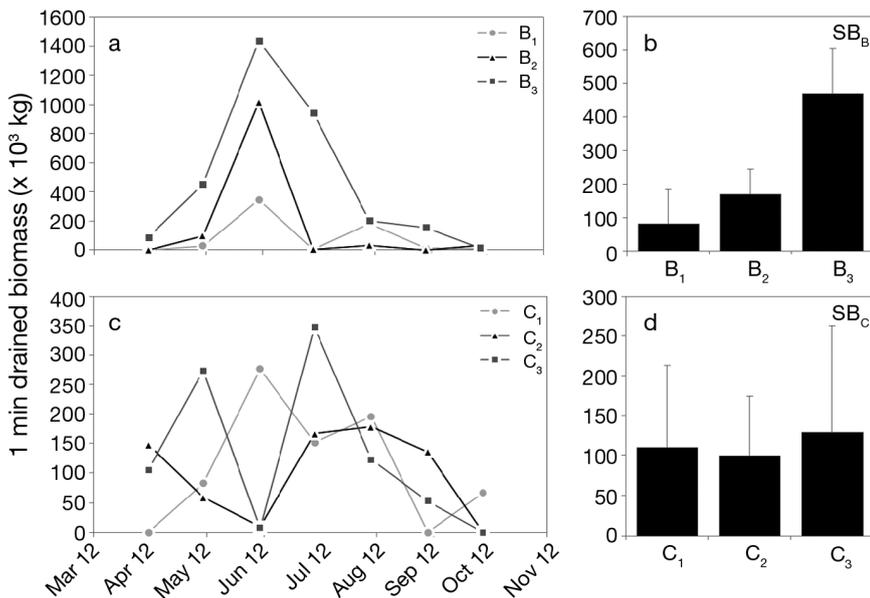
Disentangling effects of time, space, and environment on univariate responses

Variation partitioning revealed the proportion of variation of the 5 univariate community responses (A, B, S, H', and D) explained by temporal variables [**T**], spatial variables [**S**], environmental variables [**E**], and their combinations, for the 3 sandy beaches (Table 2, see Fig. S2 in the Supplement for an example of associated Venn diagram). Taken together, the 3 explanatory variables matrices ([**T**] + [**S**] + [**E**]) significantly explained a large amount (26 to 86 %, p < 0.05) of

Fig. 3. Monthly biomass of stranded *Ulva* throughout the year 2012 estimated at (a) SB_B and (c) SB_C and yearly mean (± SD) at (b) SB_B and (d) SB_C. Note that the scales are not the same on all plots
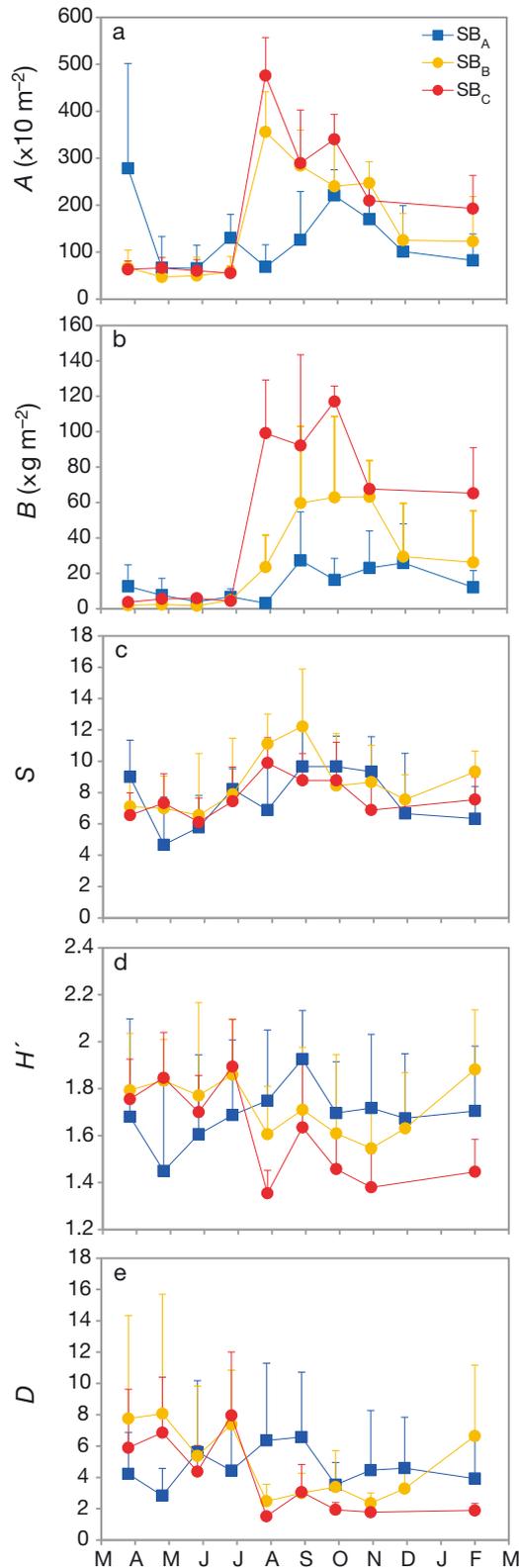
Fig. 5. Mean (+SD) abundance (*A*), biomass (*B*), species richness (*S*), numerical equivalents of Shannon's entropy exp(*H'*) and Simpson's (1/*D*) indices (after Jost 2006) from April 2012 to February 2013 at the 3 beaches (SB$_A$, SB$_B$ and SB$_C$)

the variation observed in univariate responses of the 3 beaches considered in this study, especially for SB$_C$ (Table 2).

Considering the variables separately, temporal, spatial, and environmental variables explained univariate community variables for SB$_A$ and SB$_B$ in the vast majority of situations. Nevertheless, the number of occasions on which the variation explained by spatial explanatory variables was non-significant was higher in SB$_B$ than in SB$_A$, and significant models explained less variation. More remarkably, spatial variables did not significantly explain any variation observed in univariate responses for SB$_C$, where only temporal and environmental explanatory variables significantly explained variations (Table 2).

The small proportions of variation explained by 'pure' explanatory variables (Table 2) indicated that temporal and environmental variables shared high portions of explained variance. The environmental variables [**E**] consisted of both physical and biological factors whose significance in explaining variations in the univariate variables (*A*, *B*, *S*, *H'*, and *D*) was tested for each SB (Table 3). Salinity, dissolved oxygen, mean wave height, and beach slope were the variables most useful to model the variation in the univariate variables observed at SB$_A$. SB$_B$ diversity patterns were best matched with *Ulva* biomass, total organic matter content, phytoplankton, and with the dissolved oxygen content, seawater temperature, and the slope. The same patterns were observed for SB$_C$, but the number of environmental factors fitting the univariate response variation rose.

Community composition and its dynamics related to time, space, and environment

The 21 species presented in Table 4, which mainly belong to molluscs, polychaetes, and crustaceans, made up almost all (99.9%) of the total biomass observed at each of the 3 SBs. The sandy beach community across the 3 SBs is dominated by 3 suspension-feeding bivalves (Table 4) whose contribution to the total biomass differed among the beaches. Where green tides landed on shore (SB$_B$ and SB$_C$), *Donax vittatus* largely contributed to the total biomass, while *D. trunculus* and *Angulus tenuis* were underrepresented, opposite to SB$_A$. The same distinction between beaches was detected for echinoderms (*Acrocnida brachiata*), surface deposit-feeding annelids (*Spiophanes bombyx* vs. *Owenia fusiformis*), and carnivorous polychaetes (*Nephtys hombergii* and *Glycera tridactyla* vs. *Lumbrinereis* sp.).

Table 2. Variance partitioning of total abundance (A), total biomass (B), total species richness (S), Shannon index (H'), and Simpson's index (D) of the 3 beaches (SB_A, SB_B, and SB_C). Variation explained is expressed as a percentage (%) based on adjusted R^2. [T]: selected temporal variables; [S]: spatial location along beaches; [E]: environmental variables; Unexpl.: unexplained variation. Degrees of freedom for [S] = 2, for [E] = 10, and varied from 1 to 6 for [T] due to the forward selection. Grey *italicized* numbers represent non-significant fractions. The shaded cells show the significant ($p < 0.05$) contributions of explanatory matrices that explain the variation observed in the univariate variables

Variable	SB_A					SB_B					SB_C				
	A	B	S %	H'	D	A	B	S %	H'	D	A	B	S %	H'	D
[$T + S + E$]	48	74	42	26	28	68	67	34	25	19	86	84	34	62	73
[T]	26	29	21	4	20	67	63	21	10	22	84	84	28	52	64
[S]	9	36	16	21	*0*	*0*	*1*	8	17	*0*	*0*	*0*	2	1	*5*
[E]	15	50	16	*6*	14	62	62	15	8	18	72	75	33	45	44
[$T \mid (S + E)$]	31	10	17	*0*	14	6	*3*	10	*0*	*0*	13	9	*2*	16	21
[$S \mid (T + E)$]	*0*	7	8	21	*0*	*0*	*1*	12	18	*0*	*0*	*0*	*0*	*0*	*4*
[$E \mid (T + S)$]	11	6	*5*	*0*	8	*0*	*1*	*4*	*0*	*0*	2	*0*	3	7	*1*
Unexpl.	52	26	58	74	72	32	33	66	75	76	14	16	66	38	27

Table 3. Variation in total abundance (A), biomass (B), species richness (S), transformed Shannon index (H'), and transformed Simpson index (D) for the 3 beaches (SB_A, SB_B, and SB_C) explained by stepwise regression models constructed with all environmental variables. **Bold** variables are those that enter at least 2 distinct models. SWT: seawater temperature; P: physicochemical variable; B: biological variable; *$p < 0.05$, **$p < 0.01$, ***$p < 0.001$

	Type	A	B	S	H'	D
SB_A	**Adj R^2:**	14.2	35.9	7.0	1.6	13.0
SWT (°C)	P					
Salinity (psu)	**P**	**	**	**		
Dissolved O_2 (%)	**P/B**	**				***
Ulva biomass (t)	B					
Mean wave height (m)	**P**		**	*		
Sorting index (unitless)	P					
Slope (%)	**P**	*	***			
Organic matter (%)	B		*			
Phytoplankton (µg l^{-1})	B		***			
Median (µm)	P					
SB_B	**Adj R^2:**	59.7	59.9	11.3	11.1	14.0
SWT (°C)	P	***	***			
Salinity (psu)	P					
Dissolved O_2 (%)	**P/B**	***	***			
***Ulva* biomass (t)**	**B**	**	**	**	*	**
Mean wave height (m)	P	***				
Sorting index (unitless)	P					
Slope (%)	**P**		***		*	**
Organic matter (%)	**B**				**	*
Phytoplankton (µg l^{-1})	**B**	***	***	**		
Median (µm)	P					
SB_C	**Adj R^2:**	66.9	72.0	30.8	36.3	33.5
SWT (°C)	**P**	***	***	***		
Salinity (psu)	**P**	***	***	***		
Dissolved O_2 (%)	**P/B**	***	***	***		
***Ulva* biomass (t)**	**B**	*	*		**	*
Mean wave height (m)	**P**	***	***	***	**	**
Sorting index (unitless)	P					
Slope (%)	P					
Organic matter (%)	**B**			**	***	***
Phytoplankton (µg l^{-1})	**B**	***	***	***		
Median (µm)	P					

A significant interaction between time and beach on macrofauna community structure was revealed by the 2-factor MANOVA ($F_{14, 48} = 1.42$, $p = 0.006$). Consequently, we focused on each of the 3 beaches separately to look at the spatio-temporal changes in the benthic communities.

BDTotal varied among the 3 beaches. There was no significant Kendall correlation between total β-diversity and *Ulva* coverage ($\tau = -0.08$, $p = 0.30$, $n = 24$) considering all sampling events. However, a significant difference in β-diversity was found between SB_A (no green tide present during any of the sampling times) and SB_C (uniform *Ulva* coverage along the shore; $W = 54$, corrected $p = 0.021$). The median of total β-diversity was the highest when *Ulva* never occurs on shore, and the lowest was found where green tide occurs homogeneously along the shore (Fig. 6). SB_B, with a local persistent gradient in *Ulva* coverage along the shore, had an intermediate BDTotal value and exhibited a greater dispersion than SB_A and SB_C (Fig. 6). SB_B did not significantly differ from SB_A ($W = 46$, corrected $p = 0.321$) or SB_C ($W = 45$, corrected $p = 0.321$).

Shifts and differences in community structure between the 3 beaches are illustrated with PCA analyses (Fig. 7), integrating time (range of grey scale) and space in the representation (3 different shapes for sites). On one hand, the ordination for SB_A showed the absence of a clear temporal pattern and both distinct and overlapping spatial structuring of macrofaunal data (Fig. 7A). On the other hand, a different picture emerges for SB_B and SB_C (Fig. 7B,C) with a shift in benthic community composition over time and a spatial structuring for SB_B macrofauna communities. No discernible spatial patterns appeared at SB_C.

Table 4. Percentage dominance in terms of biomass for the major species (threshold = 99.9%) living in the sampled sites (A_1, A_2, A_3, B_1, B_2, B_3, C_1, C_2, and C_3). **Bold** numbers show contributions that are >0.70%. Taxonomic group and selected biological traits (cohort, feeding strategy, mobility, size, and reproduction/development) are given for each species. Cohorts: Ad.: adults; Juv.: juveniles; s-Ad.: sub-adults. Feeding strategy: P: predators; SDF: surface deposit feeders; SSDF: selective surface deposit feeders. Mobility: B: burrowers; C: crawlers; D: drifters; nS: night swimmers; S: swimmers; T: tube-builders. Reproduction/development: BE: brooded eggs; BS: broadcast spawners; Cut.: Cuttings; Ov.: oviparous; Pel.: pelagic. Data set excludes December 2012 samples; species that were not weighted because of their scarcity were also excluded. Traits data collected from MarLIN, EOL, polytraits, and BIOTIC databases, and personal observations. Max. size: maximal size (mm); Rep./dev.: Reproduction/development; values in parentheses are a less-expressed trait; –: zero values (biomass dominance) or no data available (cohorts and max. size); [a]diameter of central disc; [b]length of carapace

Species	Taxonomic group	Biomass dominance (%)									Functional characteristics				
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		A_1	A_2	A_3	B_1	B_2	B_3	C_1	C_2	C_3					
Donax vittatus	Mollusca: Bivalvia	**24.73**	**46.83**	**35.94**	**85.88**	**65.68**	**90.42**	**85.64**	**83.69**	**87.22**	Ad., Juv.	SF	D, C, B	38	BS/Pel.
Donax trunculus	Mollusca: Bivalvia	**9.14**	**19.12**	**39.79**	**2.79**	**10.98**	**4.32**	**10.41**	**10.17**	**4.06**	Ad.	SF	D, C, B	45	BS/Pel.
Angulus tenuis	Mollusca: Bivalvia	**36.07**	**27.14**	**5.60**	**2.17**	**3.77**	**0.75**	**2.19**	**3.49**	**5.05**	Ad., Juv.	SDF	B	20	BS/Pel.
Acrocnida brachiata	Echinodermata: Ophiurida	**4.38**	**3.39**	**6.74**	0.58	**4.74**	**1.30**	0.53	0.32	0.41	Ad., Juv.	SDF, P	B	12[a]	BS/Pel.
Spiophanes bombyx	Annelida: Polychaeta	**12.60**	**0.91**	**4.82**	0.03	0.01	0.01	0.20	0.02	0.01	Ad.	SDF	T	60	BS/Pel.
Owenia fusiformis	Annelida: Polychaeta	0.69	0.02	0.08	**5.82**	**7.10**	**1.40**	0.18	**0.74**	**1.62**	Ad., Juv.	SDF, SF	T	100	BS/Pel.
Nephtys assimilis	Annelida: Polychaeta	**2.81**	**0.77**	**3.09**	**0.79**	**2.71**	0.60	0.19	**0.72**	0.61	Ad., Juv.	P	B, C (S)	115	BS/Pel.
Nephtys hombergii	Annelida: Polychaeta	**5.03**	0.30	–	0.28	–	–	0.15	–	0.15	Ad.	P	B, C (S)	200	BS/Pel.
Urothoe poseidonis	Arthropoda: Malacostraca	0.35	0.52	0.03	0.26	**1.01**	0.36	0.16	0.33	0.27	Ad.	SSDF	B (nS)	6	Ov./BE
Nemertea sp.	Nemertea	**1.31**	0.09	0.69	0.31	0.43	0.11	0.13	0.10	0.06	–	P	B	–	Cut.
Lineus acutifrons	Nemertea: Anopla	**0.90**	0.44	0.69	0.20	0.49	0.16	0.04	0.04	–	Ad., s-Ad.	P	B	250	Cut.
Glycera tridactyla	Annelida: Polychaeta	**0.84**	0.11	0.50	0.04	0.23	0.05	0.02	0.06	0.02	Ad., Juv.	P	B (S)	50	BS/Pel.
Sigalion mathildae	Annelida: Polychaeta	0.42	–	0.41	0.18	0.57	–	–	–	0.05	Ad., s-Ad.	P	B, C (S)	150	BS/Pel.
Nephtys cirrosa	Annelida: Polychaeta	0.18	0.10	0.32	0.10	0.40	0.05	0.04	0.10	0.12	Juv.	P	B, C (S)	100	BS/Pel.
Magelona filiformis	Annelida: Polychaeta	0.13	0.00	0.02	0.18	**0.77**	0.13	0.01	0.05	0.06	Ad.	SDF	B	80	BS/Pel.
Lumbrinereis sp.	Annelida: Polychaeta	–	–	–	–	0.48	0.16	–	0.13	0.25	Ad.	P	B	150	Ov./BE
Diogenes pugilator	Arthropoda: Malacostraca	0.20	0.02	0.49	0.09	0.05	0.08	–	–	–	Ad., Juv.	P	C (B)	7.5[b]	Ov.
Bathyporeia pelagica	Arthropoda: Malacostraca	0.05	0.02	0.17	0.05	0.08	0.01	0.00	0.00	0.00	Ad.	SDF	B (nS)	8	Ov./BE
Scolelepis cantabra	Annelida: Polychaeta	0.03	0.01	0.10	0.02	0.06	0.01	0.01	0.01	0.02	Ad.	SDF, SSDF	T	80	BS/Pel.
Eocuma dollfusi	Arthropoda: Malacostraca	0.05	0.02	0.14	–	0.01	0.00	0.00	–	–	Ad.	SDF, SSDF	B (nS)	15	Ov./BE
Cumopsis fagei	Arthropoda: Malacostraca	0.02	0.01	0.14	0.01	0.03	0.00	0.00	0.00	0.00	Ad., s-Ad.	SDF, SSDF	B (nS)	6	Ov./BE

Partitioning of the variance of macrofauna at the 3 SBs with respect to temporal, spatial, and environmental explanatory variables is presented in Fig. 8. The proportion of variation explained by the combination of the 3 sets of explanatory variables was always significant and increased from SB_A to SB_C (35 to 42%, $p < 0.05$). This increase is mainly attributable to a better fit of the temporal and environmental variables to the variation in the macrofauna community observed at sandy beaches harbouring green tides, and may be illustrated by the increase in the explanatory power of the intersection of time and environment from SB_A to SB_C (12 to 28%, $p < 0.05$). Spatial variables (total and pure fractions) also significantly explained the variation observed in macrozoobenthic assemblages. However, the spatial explanatory power decreased from SB_A to SB_C (9 to 3%, $p < 0.05$).

These results all corroborate the hypothesis that time and space play a major role in explaining benthic assemblage structure at SB_A and SB_B, while the location along the shore does not explain macrofauna community structure observed at SB_C, which has the most uniform cover of *Ulva*.

The correlation triplot of redundancy analysis of macrofaunal data from all 3 beaches, constrained by time, space, and environment (Fig. 9), revealed 3 dot clouds: a triangular polygon on the top-right contained the SB_A sites, and 2 diagonals in the centre and in the lower part of the diagram were formed by SB_C and SB_B sites. The separation of the 3 sites is associated with the explanatory variables SI, oxygen content, and *Ulva* biomass. The ordination diagrams (Fig. 9) also showed strong and positive association of the SI and *Angulus tenuis* and *Spiophanes bombyx*, of wave height and *Donax vittatus*, and of *Ulva* biomass and *Magelona filiformis*.
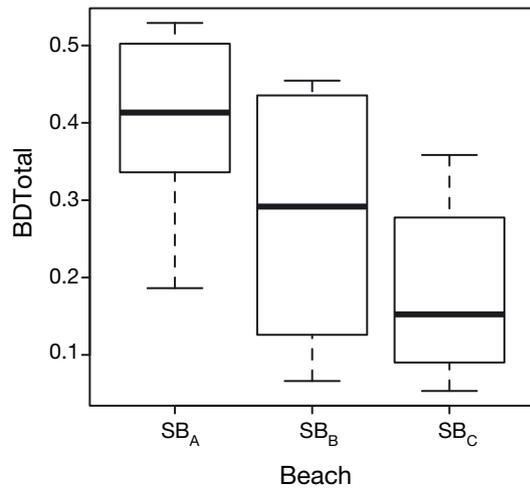
Fig. 6. Total β-diversity (BDTotal) across space and time at the 3 beaches (SB_A, SB_B and SB_C). Box plots show the median (line in box), the first and third quartiles (hinges), and the most extreme data points which are 1.5 times the interquartile range from the box (whiskers)

DISCUSSION

Macrozoobenthic assemblages of the ocean-exposed sandy beaches considered in this study were mainly composed of molluscs, polychaetes, and crustaceans, which is consistent with other studies in the same ecoregion (Leber 1982, Degraer et al. 1999, Rodil et al. 2006) and worldwide (e.g. McLachlan 1983). The SBs had a rich benthic community, composed of >60 species, and it was highly variable along the shore and through time. Spatio-temporal changes in the overall community composition support our hypotheses 1 and 2, indicating that macrotidal SB macrofauna community structure is dependent on site at small spatial scales (hundreds of meters) and time of the year (monthly to seasonal intervals).

More precisely, the 3 sites that we studied along the swash zone of SB_A (no green tides present at any time of the year on any site) showed similar rarefied species richness, while other biological variables, such as biomass and abundance, varied among sites. Similar species richness among sites may be explained by homogenisation, which is an important factor in determining intertidal macrobenthic community patterns (de Juan & Hewitt 2014). Along-shore patterns observed in abundance and biomass have also been described for other sandy shores (Defeo & de Alava 1995) and may be associated with gradients in physical (e.g. swash climate) and biological (e.g. competition or predation) factors (Defeo & McLachlan 2005).
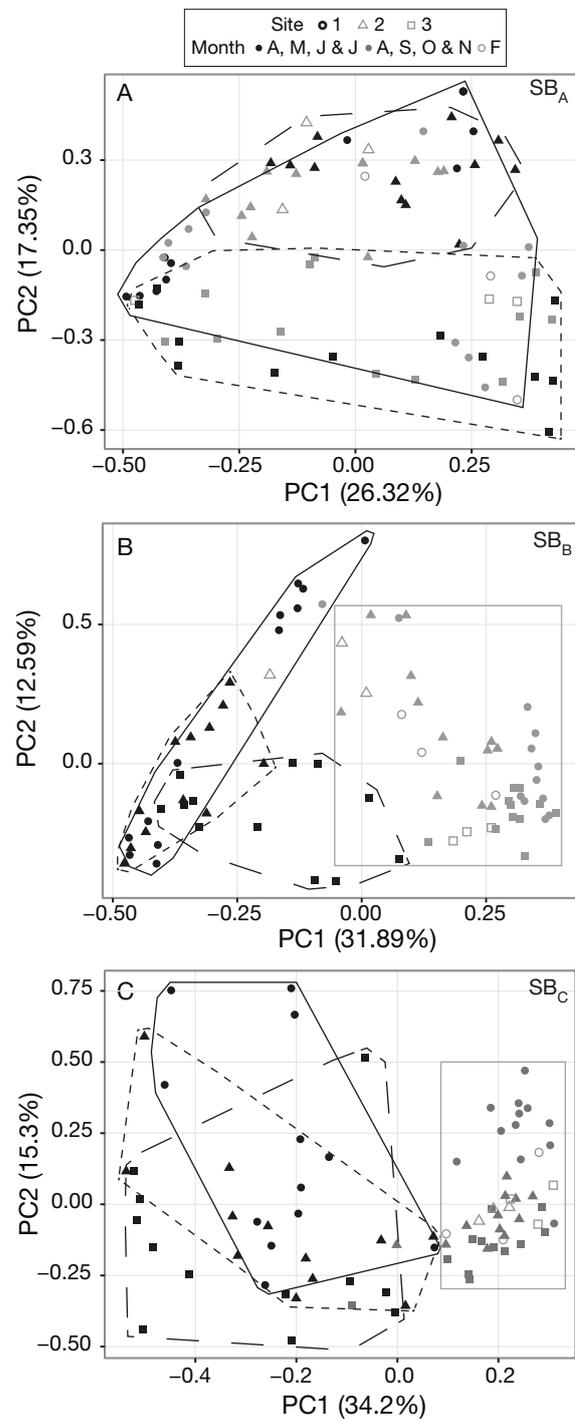

Fig. 7. Principal component analysis (PCA) distance biplots (i.e. scaling 1) of Sites 1 (circles), 2 (triangles), and 3 (squares), based on Hellinger-transformed abundance of benthic community sampled at SB_A, SB_B, and SB_C from April 2012 to February 2013 (excluding December 2012 for balanced design) with superimposed indicative clusters for spatial (solid line [Site 1], dashed line [Site 2] or long-dashed line [Site 3] polygons) and/or temporal structuring (grey boxes and symbols for autumn/winter, highlighting the difference from spring/summer [black polygons and symbols])
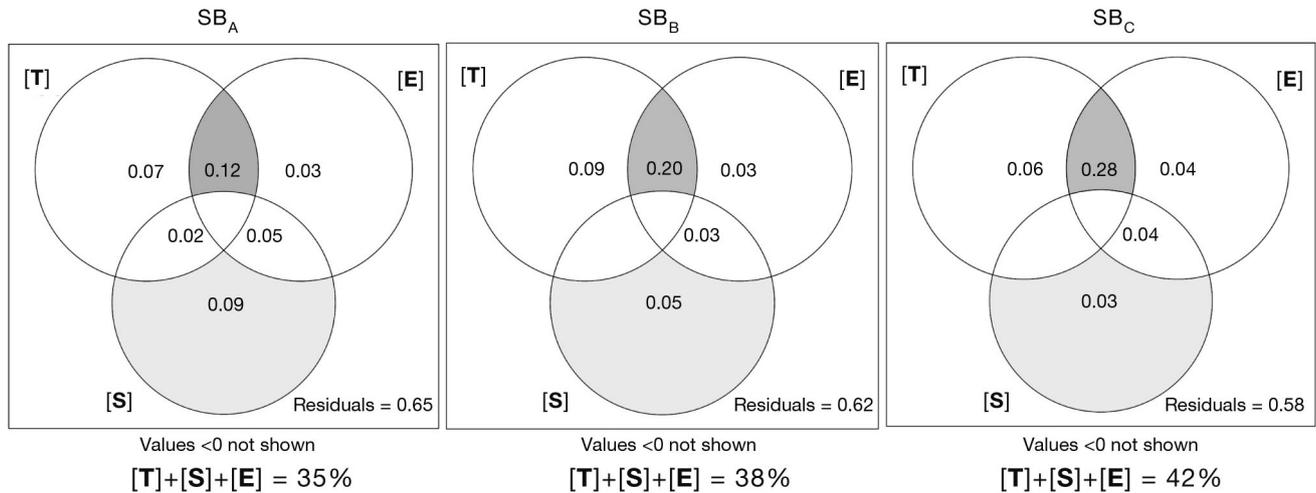
Fig. 8. Venn diagrams illustrating the result of variance partitioning of the macrofauna time series at SB$_A$, SB$_B$, and SB$_C$ with respect to environmental (physical and biological variables), spatial (location along shore), and temporal (distance-based Moran's eigenvector maps [dbMEMs]) explanatory variables. Variation explained is expressed as a percentage (%) based on adjusted R^2. [**T**]: selected temporal variables, [**S**]: spatial location, [**E**]: environmental variables, Residuals: unexplained variation
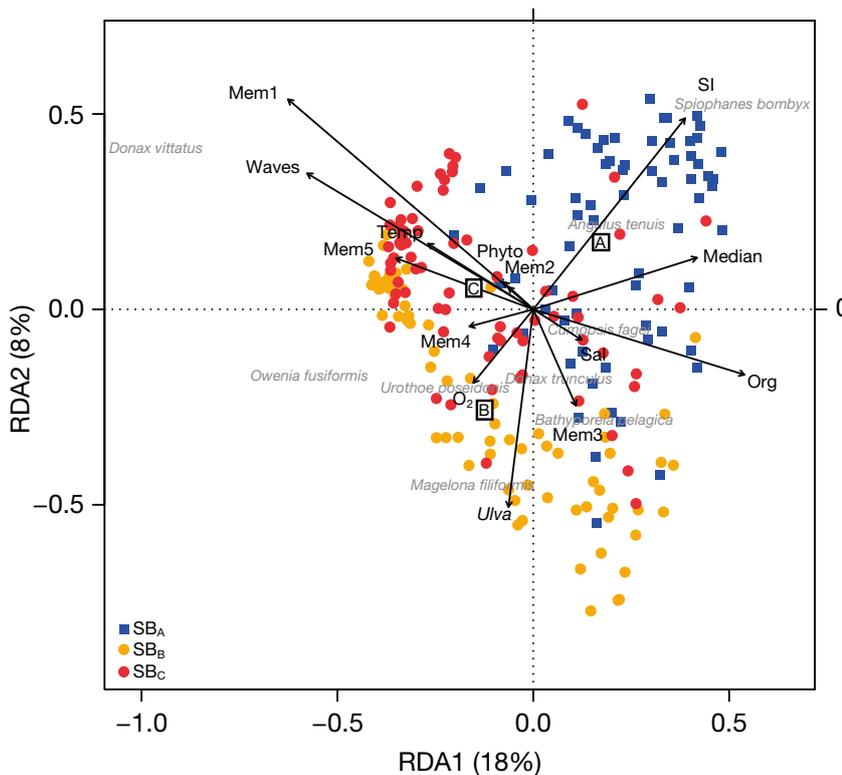

Fig. 9. RDA correlation triplot (scaling 2) of macrofaunal communities data and all explanatory variables (environmental, spatial, and temporal) of the 3 sandy beaches together: A (blue), B (orange), and C (red). Org: total organic matter; Sal: salinity; O$_2$: dissolved oxygen; Temp: temperature; Phyto: phytoplankton concentration; Median: Q50 (second quartile of the sediment grain size); SI: sorting index calculated based on first and third quartile ratio ($\sqrt{Q25/Q75}$, where Q25 and Q75 denote the first and the third quartiles of the sediment grain size, respectively); *Ulva*: stranded *Ulva* biomass; Waves: wave height; Mem*x*: temporal variable *x* generated dbMEM eigenfunctions, *x*: centroid for SBs

Variation partitioning also revealed the significant importance of spatial variables in explaining the variation observed for univariate variables calculated from macrofaunal data. Along-shore variations of the primary community variables and diversity indices were due to changes in the relative abundance (recruitment) of key species such as *Donax vittatus* and *Owenia fusiformis*. These changes in the spatial variation of the univariate variables of the benthic community are consistent with the findings of James & Fairweather (1996), who highlighted significant along-shore variation in the abundance of individual taxa. More recently and at smaller spatial scales (transects about 10 m apart), Veiga et al. (2014) also found variability in the abundance, diversity, and structure of macrobenthic assemblages. Our study argues in favour of small spatial (hundreds of meters) along-shore structuring of macrotidal SB macrofauna. Taking into consideration along-shore variation through entire open sandy beaches is thus crucial for ecological studies aiming at understanding the functioning of such systems at the mesoscale.
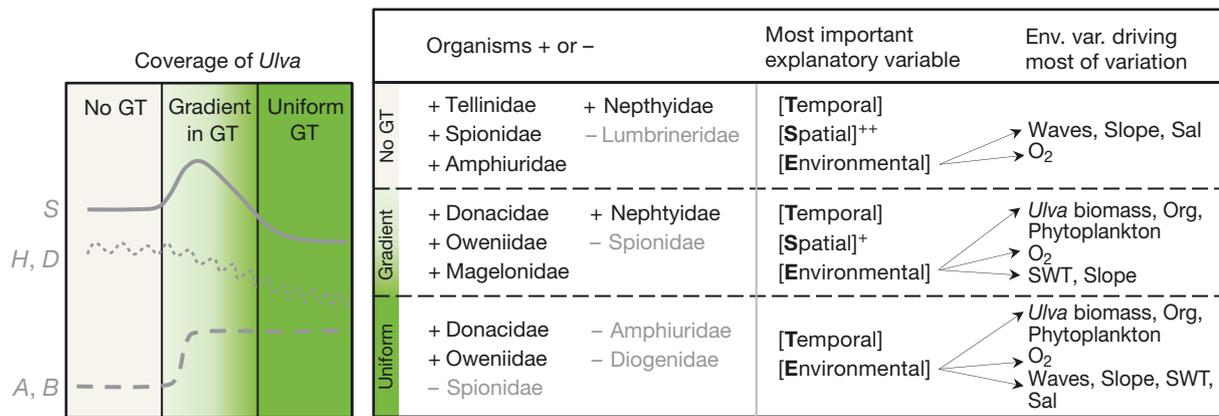
Coverage of *Ulva*				Organisms + or −		Most important explanatory variable	Env. var. driving most of variation
No GT	Gradient in GT	Uniform GT	No GT	+ Tellinidae + Spionidae + Amphiuridae	+ Nepthyidae − Lumbrineridae	[**T**emporal] [**S**patial]⁺⁺ [**E**nvironmental]	↗ Waves, Slope, Sal ↘ O₂
			Gradient	+ Donacidae + Oweniidae + Magelonidae	+ Nephtyidae − Spionidae	[**T**emporal] [**S**patial]⁺ [**E**nvironmental]	↗ *Ulva* biomass, Org, Phytoplankton → O₂ ↘ SWT, Slope
			Uniform	+ Donacidae + Oweniidae − Spionidae	− Amphiuridae − Diogenidae	[**T**emporal] [**E**nvironmental]	↗ *Ulva* biomass, Org, Phytoplankton → O₂ ↘ Waves, Slope, SWT, Sal

Fig. 10. Conceptual model of the effects of green tides on macrobenthic characteristics of sandy beaches. GT: green tide; Env.: environmental; var.: variable; +: stimulated; −: stifled; SWT: seawater temperature; S: species richness; H', D: Shannon and Simpson indices; A, B: abundance and biomass; Waves: wave height; Sal: salinity; Org: total organic matter

Also, temporal variables influenced abundance, biomass, and species richness at SB$_A$. These observations are in accordance with other studies in comparable environments (Leber 1982, Degraer et al. 1999), although such studies often do not take small temporal scale into consideration. Our results highlight real seasonal patterns (Morrisey et al. 1992) in the benthic community as we sampled intensively (monthly) during each season. The seasonal variations observed are mainly due to recruitment of the dominant species during summer (Guillou 1982, McLachlan & Brown 2006) as well as mortality and migrations offshore due to lower temperature and storms during winter (McLachlan & Brown 2006). Furthermore, temporal changes in the benthic macrofauna structure may be modified by variations in the food supply and by trophic interactions within the zoobenthos (Defeo & McLachlan 2005). Our results emphasize the importance of covering the small temporal scale (month).

Our third hypothesis, regarding changes occurring in the presence of *Ulva* macroalgal mats, was verified (Fig. 10). Our results support the hypothesis that patterns and differences in macrofaunal community structure observed arose from an *Ulva* accumulation gradient on sandy shores rather than from other environmental factors. Indeed, most of the environmental variables (wave height, seawater temperature, salinity, dissolved oxygen, slope, and phytoplankton) did not show any significant differences among the 3 beaches or over time. Median grain size and sorting were significantly different, but the effect sizes are negligible when placed in an ecological context: both characterized fine and well-sorted sediments (Blott & Pye 2001). Furthermore, organic matter content differed among the 3 SBs due to temporal variations (see Fig. S5 in the Supplement at www.int-res.com/articles/suppl/m522p097_supp.pdf) that may be linked to the presence of *Ulva* stranded ashore. Indeed, accumulations of drifting macroalgae cause direct shading of sandy shores, which limits the growth of microphytobenthos (Corzo et al. 2009). A loss of microalgal mats may thus result in a decrease in total organic matter content, and since microphytobenthos support grazing trophic levels (Miller et al. 1996), it may also affect deposit-feeding macrofauna. The 3 beaches are part of the same regional macrohabitat (Glémarec 1969), but despite being located in the same regional water body and showing high similarities in terms of physical characteristics, the 3 beaches showed different nutrient concentrations in the inshore water (Dussauze & Ménesguen 2008). Due to agricultural activity in the catchment area, coastal rivers draining at SB$_B$ and SB$_C$ bring nutrients. There, the eutrophication and the associated *Ulva* blooms originating from nutrient inputs remain highly local, i.e. hundreds of meters from the shore at the mouths of coastal rivers (Ménesguen & Piriou 1995).

In the present study, the rarefied richness differed among beaches. The beach where a gradient in *Ulva* stranding occurred (SB$_B$) exhibited higher rarefied species richness than was found at SB$_A$ which did not harbour green macroalgal blooms. Where *Ulva* mats occurred homogeneously along the shore (SB$_C$), the rarefied species richness was lowest (Fig. 4). The observed patterns are in line with what would be expected from the benthic successional paradigm on the effects of increasing organic-matter inputs on communities of benthic macrofauna (Pearson & Rosenberg 1978). This model shows an increase in

benthic species richness, numerical abundance, and biomass with moderate perturbation and then a decrease when disturbance increases, which is in accordance with the concept of intermediate disturbance (Connell 1978).

While it is well recognized that accumulation of macroalgae has strong negative effects on sedentary infauna (Raffaelli et al. 1998, Grall & Chauvaud 2002), such as widespread mortality in zoobenthic communities (Everett 1994, Norkko & Bonsdorff 1996, Bolam et al. 2000), our results contradict this paradigm for the intertidal flats of exposed macrotidal sandy beaches (Fig. 10). In our study, in the highest eutrophic conditions, i.e. under very dense *Ulva* mats (~1.5 kg m^{-2}, Fig. 1), the community response was not as evident as one would have expected. The subtle response of SB macrofauna to eutrophication by *Ulva* accumulation is probably due to the highly dynamic nature of SBs. To highlight these elusive, but real, changes in SB communities, classical ecological and statistical approaches have proved to be inefficient. Our study shows that the combination of a fine spatial-temporal monitoring of the benthic community reaching a high number of samples together with novel statistical approaches (dbMEMs and variation partitioning; Borcard & Legendre 1994, Dray et al. 2006, Legendre & Gauthier 2014) were essential in understanding the changes occurring in SB systems under eutrophication stress.

Following the approach described above, our results also suggest that increasing coverage of stranded *Ulva* along the shores induces a homogenization of the forces driving the swash-zone benthic community structure (Fig. 10). Compared to a state with no *Ulva*, a large and homogeneous coverage of *Ulva* along the shore induces a significant decrease of overall β-diversity and, eventually, a complete lack of spatial pattern in community composition. Where no green tides occurred, 3 main drivers [**T**, **S**, and **E**] influenced the responses of the benthic community, while where algal mats stranded homogeneously along the shore (SB$_C$), community structure was mainly driven by time and environment, including the macroalgae. To fully distinguish ecological patterns observed at macrotidal sandy beaches where green tides have occurred, a longer time-span of the sampling would be required.

Furthermore, a stepwise regression model for univariate diversity indices supports the idea that in regions where no green tide occurred, the main retained environmental variables were physical factors, which is in accordance with previous studies (e.g. Defeo & McLachlan 2005, McLachlan & Dorvlo 2005, McLachlan & Brown 2006). However, our results also highlight the increasing contribution of biological factors along a gradient of increasing coverage of stranded *Ulva*, which corroborates the hypothesis that sandy beach community structure is not only driven by physical factors but also explained by factors linked to general coastal processes (Lastra et al. 2006), competition (Dugan et al. 2004), predation (McLachlan & Brown 2006), and other biological interactions at small spatial and temporal scales.

While our results highlight the subtle nature of the responses of sandy beach systems to strong eutrophication, community composition varied among the 3 beaches considered in this study. Fewer species dominated where green tides occurred, an observation that may be linked to 'biotic homogenization', defined as the process by which human-induced disturbances increase the taxonomic or functional similarity of environments (Smart et al. 2006). In this respect, our results are consistent with other studies showing the effects of algal accumulation on benthic communities (e.g. Hull 1987, Raffaelli et al. 1998, Bolam et al. 2000). The species-dominance patterns also changed with increasing algal cover (Fig. 10). The densities of *Donax trunculus* were lower where green tides occurred. Because this species is of commercial importance (Augris et al. 2005, McLachlan & Brown 2006), the green tides also negatively influence human use and value of the beaches. Moreover, sandy beaches are essential habitat for flatfish recruitment and nursery (Besyst et al. 1999, Rabaut et al. 2013). Spionids are considered essential polychaete prey and important trophic support in fish nursery grounds (Speybroeck et al. 2007). Considering that spionid abundance is impacted negatively by the presence of *Ulva* mats, the nursery-area function of SBs could be affected. Consequently, questions may arise about the potential indirect cascading effects of the presence of algal mats on clam and flatfish fisheries.

Our results also suggest that the high abundance of *Donax vittatus*, which is not a commercial species, at SB$_B$ and SB$_C$, is probably linked to the presence of *Ulva* mats. In the early 1980s, the recruitment was defined as 'very important', with densities reaching 1000 ind. m^{-2} at SB$_C$ (Guillou 1982). Similar densities for *D. vittatus* recruits were found at Ile d'Oléron (French Atlantic coast) over the same period (Ansell & Lagardère 1980). Thirty years later, when green tides are common at eutrophic SBs (Ye et al. 2011), we found densities comprised 1800 to 5000 ind. m^{-2} at each of the 6 sites influenced by green tides. The abundance peak of *D. vittatus* may be attributable to

the influence of macroalgal mats on local hydrodynamics favouring higher recruitment, as suggested by Hull (1987). In addition, because the presence of *Ulva* mats induced a decrease in *D. trunculus* (Table 4) and because interspecific competition for space exists between the 2 Donacidae species (Guillou 1982), *D. vittatus* could find an available niche at SBs where macroalgae get stranded. Also, macroalgal mats induce a decrease of the foraging success of juvenile flatfish (Nordström & Booth 2007) and of the biomass of polychaete predators (Table 4; results in line with Weston 1990); consequently, predation pressure on *D. vittatus* recruits decreases, which may explain the high abundance of the bivalve where green tides occurred.

Besides these shifts in benthic community composition, changes in terms of biomass dominance of species within SBs where detached *Ulva* was washed ashore indicated changes in community biological trait expression (Table 4). For example, animals defined as surface-deposit feeders or suspension feeders dominated the community at SBs with green tides, while predators consistently contributed to SB communities where no green tide occurred. These results, although subtle, are in line with the biomass profile drawn by Weston (1990) showing the relative dominance of the major polychaete trophic groups with increasing organic matter inputs. More explicit hypotheses of shifts in marine community functioning could be tested using appropriate tools, such as stable isotopes and biological trait analysis (Grall et al. 2006, Törnroos & Bonsdorff 2012).

The effects of macroalgae accumulation on highly dynamic systems such as macrotidal sandy beaches are poorly known, but our results are in line with those from Hull (1987) and with those on wrack (i.e. stranded near-shore macroalgal and seagrass accumulations) subsidies studies at upper-shore regions (Soares et al. 1997, Colombini et al. 2000, Dugan et al. 2003). For example, Gonçalves et al. (2009) discussed possible effects of detritus accumulation on the structure of sandy beach benthic communities and the influence of exogenous supply on the structure of macrofauna assemblages. To our knowledge, our work is the first to demonstrate that detritus/macroalgal deposits influence low-shore communities.

CONCLUSIONS

The present study demonstrates that swash-zone macrobenthic community structure in macrotidal sandy beaches is dependent on both location along the shore (at small spatial scale, hundreds of meters apart) and on seasonal variations (monthly). Our results thus clearly recommend taking into account interacting spatial and temporal variation in the study of SB macrofauna assemblages. Moreover, our work highlights the importance of biotic interactions in environments characterized by strong physical forces and fluctuating conditions. This result is important because sandy beach ecology often considers that biological processes do not play a fundamental role in explaining macrofaunal community structure, in contrast to physical factors. Furthermore, our study shows that the presence of *Ulva* mats induces (1) an homogenization of the community living at lower-shore of SBs, (2) a stimulation of the recruitment of some dominant species, and (3) a decrease in the abundance of species assuming key roles for the functioning of SB ecosystems. However, the responses of macrofauna to *Ulva* accumulation are dependent on the type of green tide stranded along the shore (with a gradient in biomass of stranded macroalgae or not) and were not as distinct as in more sheltered systems. The effects of strong eutrophication on benthic community structure vary considering hydrodynamics, from a distinct deterioration (sheltered environments) to more subtle impacts (open systems). Thus, our study highlights the context-dependency of effects of macroalgal mats on coastal ecosystems. Habitats such as open macrotidal sandy beaches should therefore be taken into account in the development of indices and regulation of eutrophication by macroalgal mats. Finally, our conclusions raise questions regarding the functioning of such dynamic systems under eutrophication stress.

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