Large-scale effects of green tides on macrotidal sandy beaches: Habitat-specific responses of zoobenthos

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A B S T R A C T

Sandy beaches are highly dynamic ecosystems mainly driven by physical variables, such as tidal regime. These ecosystems support numerous essential ecological functions and contain a distinctive biodiversity, but are threatened by increasing direct or indirect anthropogenic pressures, among which are green tides composed of free living *Ulva* spp. Studies that have been conducted to understand the effects of macroalgal mats on coastal sediment communities have mostly addressed responses in atidal or microtidal systems, and are often single-site assessments. Using large-scale field surveys across 13 macrotidal sandy beaches of two types (exposed and semi-exposed) distributed along 2700 km of coast for 7 years (REBENT program, Brittany, France), we analysed responses of zoobenthos to the presence of green tides in relation to tidal range, exposure, sediment characteristics, air and seawater temperature, precipitations, wind and salinity. Despite the high variability existing between two distinct categories of sandy habitats and also between macrotidal beaches within the study area, differences in macrofaunal community structure arose from the presence of green tides: mean abundance and species richness of macrozoobenthic invertebrates were higher where green tides occurred. Moreover, macrobenthic assemblages in the two beach-categories respond differently to eutrophication seen as green tides. Surprisingly, the effects of the presence of *Ulva* mats were stronger at exposed sandy beaches than at semi-exposed beaches. Our study also highlights species-specific responses: herbivorous marine invertebrates and suspension feeders were favoured by the presence of *Ulva* mats, whereas large sub-surface deposit feeders and bivalve drifters which surf up and down the shore with the tides were negatively affected by green tides.

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1. Introduction

Sandy beaches line most of the world's oceans and form dynamic environmental transitional areas between land and sea (Defeo and McLachlan, 2005). Several recent studies and reviews in sandy beach ecology (hereafter SB) underline the unique features of beaches (e.g. Defeo and McLachlan, 2005; Schlacher et al., 2007); SB ecosystem functioning provides unique and essential services such as nutrient cycling, filtration of large amounts of seawater, storm buffering, costal fisheries, and feeding-breeding habitats for many species, including commercially important fish species (McLachlan and Brown, 2006; Schlacher et al., 2008; Defeo et al., 2009).

In pristine environments, SB ecosystems harbour diverse forms of life that are all specialized and adapted to live in highly mobile sediments (McLachlan and Brown, 2006). The benthic macrofauna of sandy beaches includes representatives of many phyla, but crustaceans, molluscs and polychaetes are mostly dominant (McLachlan and Brown, 2006). Their habitat is physically structured and defined by 3 factors, namely sediment grain size, waves and tidal currents (McLachlan and Brown, 2006). More specifically, tidal regime determines the nature and the stability of the sediment (Wildish, 1977; Masselink, 1993). Tides directly affect primary

production (Monbet, 1992) and also indirectly influence food supply to benthic organisms (Wildish and Kristmanson, 1979). Tidal regime is thus an important factor shaping the variability of coastal marine systems and sandy beaches in particular.

Despite their ecological importance and their dynamic nature (McLachlan and Brown, 2006), SBs are threatened by multiple human uses, such as fishing, coastal development and pollution (Brown and McLachlan, 2002; Schlacher et al., 2007; Defeo et al., 2009). Regarding the latter, nutrient enrichment of coastal waters that leads to eutrophication (Cloern, 2001) is recognized as a major and worldwide pollution threat (Norkko and Bonsdorff, 1996; Valiela et al., 1997; Raffaelli et al., 1998; Ye et al., 2011).

One of the direct symptoms of eutrophication in shallow areas is mass-development of opportunistic macroalgae (Cloern, 2001). These macroalgae, by definition fine and fragile (Schramm, 1999), can easily be detached and transported by coastal currents and form large mats of drifting algae along beaches or in shallow bays (Grall and Chauvaud, 2002). Such notable algal blooms are increasing in frequency and intensity worldwide (Ye et al., 2011). They often have strong impacts on sediment zoobenthos and greatly modify the functioning of this usually uncovered ecosystem (Bonsdorff, 1992). In exposed macrotidal systems, studies of the effects of eutrophication are few and spatially restricted (Martinetto et al., 2010; Quillien et al., 2015), whereas in sheltered micro- or atidal coastal systems it has been shown that accumulation of drifting macroalgae negatively affects water and sediment, as well as other primary producers (Hull, 1987; Jeffrey et al., 1992; Sundbäck, 1994; Bombelli and Lenzi, 1996). In addition, by modifying the habitat, the presence of drifting algae in such environments affects recruitment, community structure and production of benthic macrofauna (Hull, 1987; Bonsdorff, 1992; Norkko and Bonsdorff, 1996; Raffaelli et al., 1998; Grall and Chauvaud, 2002). The general patterns of macroalgal blooms on a global scale are reviewed in Arroyo and Bonsdorff (2015).

Although our understanding of the ecology of sandy shores has greatly advanced since the 1980's (Defeo and McLachlan, 2005; McLachlan and Brown, 2006; Nel et al., 2014), this habitat is still overlooked in studies of the ecological impacts of global change, e.g. increase in seawater temperature (Schoeman et al., 2014). The effects of macroalgal mats on open sandy beach systems have mainly been assessed using experimental studies based on controlled algal manipulations, which implies important limitations when trying to understand ecosystem-scale response to such perturbations (Bolam et al., 2000; Franz and Friedman, 2002). More generally, studies conducted to understand the effects of macroalgal accumulations on coastal sediment communities have mostly addressed responses in micro- or atidal systems (e.g. Norkko and Bonsdorff, 1996; Thiel and Watling, 1998) and have been conducted in single habitats or sites as relatively small-scale studies (see Raffaelli et al., 1998; Grall and Chauvaud, 2002 for reviews; and Rodil et al., 2007 for later work). Understanding how macrotidal (mean spring tide >4 m, Allaby, 2010) sandy environments respond to seasonal opportunistic macroalgal accumulations is thus a current challenge. Recently, studying the effects of green tides on macrotidal sandy beaches at small spatial and temporal scale, Quillien et al. (2015) found that along a gradient of increasing coverage of stranded Ulva spp. the overall β-diversity and the natural variability in space and time of macrofauna decrease. To support these findings, large-scale (both in space and time), multi-habitat and in-situ studies focussing on macrotidal sedimentary systems are essential.

Such a large-scale monitoring study is currently ongoing in the north-eastern Atlantic Ocean, in Brittany (France): the REBENT program ("REseau BENTHique"). The survey (started in 2003) provides consistent and quality-controlled annual data which allows detection of changes at several spatial and temporal scales (Ehrhold et al., 2006). Two different intertidal sandy habitats are monitored within this program. These two habitats form large and gentle sloped sandy areas where waves break.

The first mobile sandy shore (hereafter Type I SB), typically consisting of clean and fine sediments (median grain size ≈ 180 μm), occur in wave-exposed environment. This biotope typically harbours the bivalves Donax trunculus and Donax vittatus. The second sandy habitat (hereafter Type II SB), typically occurs on shores moderately exposed to wave action. Type II sandy beaches are made of more heterogeneous sediments (median grain size ≈ 380 μm) and are inhabited by polychaetes such as Notomastus latericeus and Scoloplos armiger, as well as the cockle Cerastoderma edule. Within each of the two habitats, several beaches are occasionally or annually affected by drifting macroalgal mats (green tides; hereafter GT), composed of Ulva spp. (Charlier et al., 2007). Other beaches have not been affected by eutrophication symptoms in the form of algal blooms.

The ultimate aim of the present study was to examine whether responses of macrotidal ecosystems were attributable to occurrence of Ulva spp. To reach this objective, we analysed the effects of temporal, spatial and environmental variables, and specifically eutrophication in the form of green tides, on benthic assemblages over hundreds of kilometres and over seven years (2007–2013). Hence, we tested the following research hypotheses: 1) variation in macrofaunal benthic structure is partly and significantly driven by the presence of green tides, and 2) responses of infauna to Ulva spp. blooms differ between the two habitats (Type I and Type II sandy beaches). In addition, these responses are characterized in terms of biology and ecology of the zoobenthos.

2. Material and methods

2.1. Study area

The study was conducted in Brittany (France), which is a marine biogeographical transition zone (Glémarec, 1978; Dinter, 2001; Dauvin, 2006; Quillien et al., 2012) where the limit between the northern and the southern coast (see supplement 1) is mostly defined by hydrodynamics (alternating vs. vortex/gyre currents). Along the 2700 km of Brittany coastline (Fig. 1), sediments accumulate to form sandy beaches ranging from hundreds of metres to several kilometres in width. Among the eighteen beaches that have been monitored within the REBENT, thirteen beaches were selected for this study (Fig. 1) to avoid temporal gaps and match environmental data present in the larger dataset.

The thirteen beaches included exposed and semi-exposed sandy beaches (Fig.1), which form two distinct sandy habitats (see supplement 2). These two sandy habitats are also identified (based on grain size, exposure, and benthic community) in the European Union Nature Information System (habitats A2.231 and A2.245 in the EUNIS classification; http://eunis.eea.europa.eu/habitats.jsp). Type I sandy beaches occur on wave-exposed shores, with fine, clean, and well-sorted sand. Their infaunal community is dominated by bivalve species such as Donax spp. and Angulus tenuis, but also contain polychaetes (e.g. Nephtys cirrosa, Owenia fusiformis) and amphipods (Bathyporeia spp., Urothoe spp.). The low-shore of Type I sandy beaches also inhabits some echinoderms, such as Echinocardium cordatum and Acrocnida cf. spatulispina. Type II sandy beaches usually occur in areas sheltered from strong wave action on flats of medium fine sand and muddy sand, which may also contain a proportion of gravel (heterogeneous sediments). The sediment is dominated by polychaetes such as Notomastus latericeus, Lanice conchilega, and Scoloplos armiger. The mud shrimp Corophium arenarium and the Tanaid Apseudes latreilli may be
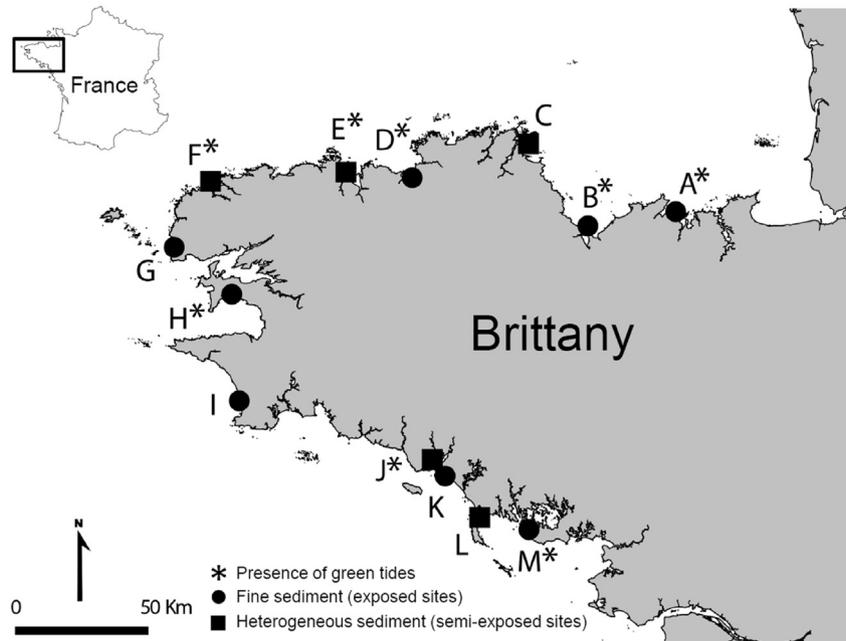
Fig. 1. Locations of the thirteen sandy beaches (A to M), with indication of the exposure (black filled circles = exposed sites; black filled squares = semi-exposed sites) where 3 replicate macrofauna samples were collected yearly (Brittany, France). Sites where green tides occurred are marked with stars.

abundant.

The thirteen SBs show tidal regimes ranging from 5 to 13 m along a gradient from southern to northern Brittany: large areas up to 2400 m wide are laid bare at low tide during spring tides. The two categories of SBs are characterized by a lower shore with mean slope of *ca.* 1.5% and since the tidal regime is macrotidal, these SBs are defined as dissipative beaches (Short, 1996). The presence and development of green tides at SBs along the Brittany coastline are variable, mostly depending on location below agricultural catchment areas and the amount of nutrients locally released (Piriou et al., 1991; Ménesguen and Piriou, 1995; Charlier et al., 2007). Within this region, the amount of stranded *Ulva* spp. is also variable along time and reaches its highest biomass between May and September (Hull, 1987; Quillien et al., 2015). The two types of sandy beaches (Type I and Type II), with or without green macroalgal accumulations (Type I-GT, Type II-GT, or Type I-NoGT, Type II-NoGT), are evenly distributed along the coastline (Fig. 1).

2.2. Sampling design

All samplings conducted within REBENT were carried out systematically (by the authors MM, VLG, BG, JG), minimising variation due to differing sampling approach and use of equipment. In order to cover macrofaunal variability along the shores (Legendre and Legendre, 2012), sampling was conducted at three sites

distributed at the same level along the swash zone (spring low tide) at middle and the two opposite ends of each of the thirteen SBs (Fig. 2); the sampling sites are at least separated by 100 m. All sites (n = 39) were sampled annually in early spring (March) from 2007 to 2013 (Fig. 2).

Macrofauna (larger than 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, three cores (taken 40 cm apart) were pooled to one sample. These pooled core samples were sieved through mesh bags (1 mm mesh size) to separate the fauna from the sediment. At each sampling site within each beach, three such replicate samples were randomly taken 1−2 m apart (Fig. 2). Faunal samples were preserved in 4% buffered formalin for later sorting in the lab where macrofauna were identified to the lowest possible taxonomic level under a stereomicroscope, and counted. Because taxonomy has changed and evolved during the period of the study, we standardized the whole dataset following species nomenclature of the "World Register of Marine Species" (http://www.marinespecies.org/, accessed September 2014).

Species richness is given as the number of species per sample. Abundance is converted to units per m^2. In addition to the quantitative dataset, information on biological traits was linked to each dominant species. Information about the feeding ecology, mobility, size, and reproduction for the dominant species was gathered from peer-reviewed literature and publicly available databases such as
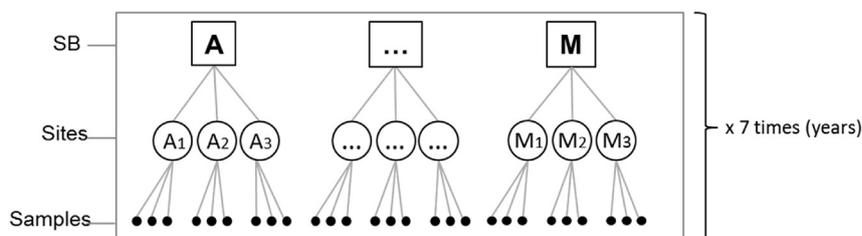

Fig. 2. Sampling design, repeated in time (7 years) showing the thirteen SBs (A to M), the corresponding sampling sites at middle and the two opposite ends of each sandy beaches (e.g. A$_1$ = one opposite end of beach A, A$_2$ = middle of beach A, A$_3$ = the other opposite end of beach A) and the samples (black circles).

MarLIN/BIOTIC and EOL/polytraits (*sensu* Törnroos and Bonsdorff, 2012).

At each site where fauna was sampled (Fig.2), two sediment cores were extracted (in the same way as fauna cores), one for analysis of grain size and the other for organic matter content characteristics. Grain sizes were determined by water- (for 63 μm grain size fraction) and dry-sieving, using a series of 14 sieves from 63 μm to 10,000 μm. Sediment grain size characteristics (median grain size, percentage of gravel, sand, and mud) were calculated with the GRADISTAT software (Blott and Pye, 2001). Gravel is defined as the fraction ranging from 2 mm to 64 mm, sand is the fraction ranging from 63 μm to 2 mm, and mud includes sediment exhibiting grain sizes smaller than 63 μm (according to Blott and Pye, 2001). The sorting index (SI) was 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), and the median (Q50) was equal to the second quartile of sediment grain size values. Beach face slope was calculated for each sampling site by geometry (maximal tide/shore width). The Beach Index (BI) was calculated based on slope, sand and tide ($\log_{10}[sand.tide/slope]$, where slope = beach face slope, sand = mean grain size in phi units +1, and tide = maximum spring tide range in meters). The BI ranges from 0 to 4, from beaches with coarse sand, small waves, and small tides to beaches of fine sand, big waves, and large tides (McLachlan and Brown, 2006). Organic matter content was measured by weight loss after combustion at 450 °C for 5 h. The occurrence of green tides and the percentage of beach covered by stranded *Ulva* were estimated by CEVA (http://www.ceva.fr) through tri-annual aerial surveys (for counting green tides and estimating of surface covered by mats). The surveys occurred during the most productive period (May to September), resulting in a mismatch (circa 8 months) between the aerial surveys and the sampling of macrofauna. Therefore, data on *Ulva* of the year prior to macrofauna sampling was used in the analyses (i.e. *Ulva* data from summer 2006 was used to study variation in fauna sampled in spring 2007). Consequently, we provide conservative estimates of *Ulva*-induced changes in community structure, as faunal responses were not assessed during bloom peaks.

Seawater temperature and salinity were extracted for each sampling site and each sampling occasion from datasets provided by the PREVIMER system (www.previmer.org) using the Pypredator software (i.e. Python Previmer Data Extractor) written in Python (https://www.python.org/psf/). PREVIMER estimates seawater temperature and salinity using the MARS-3D model (grid = 4 km). Wind speed, wind direction, air temperature and rainfall measured at coastal stations closest to each beach were assessed by averaging daily measures of three months before sampling occasions (from January to March) using Météo France data (agreement between Université de Bretagne Occidentale and Météo France). The environmental variables measured at beach scale (wind speed, wind direction, air temperature and rainfall) were considered homogeneous within each beach.

2.3. Statistical analysis

Macrofauna diversity was assessed using the following primary community variables and diversity indices (Gray and Elliott, 2009): abundance (A), species richness (S), and Shannon's (H′) and Simpson's diversity (1-D, hereafter D) indices. To test whether macroalgal accumulations and habitat type induce changes in univariate descriptors of macrofauna and to test if the effect of green tides differs depending on type of SBs (interaction of both factors 'Type' and 'Green Tides'), two-way ANOVAs were used. In the case of a significant interaction, we performed pair-wise comparisons using the parametric Student test after performing

Shapiro–Wilk normality tests, and transforming the data when necessary. If, after transformation, data did not meet the normality assumption, the non-parametric Wilcoxon-Mann-Whitney test was used.

For all multivariate analyses, faunal data were first transformed using the Hellinger transformation, which is recommended for analysis of species abundance data since it does not give high weights to rare species (Legendre and Gallagher, 2001). To test if the presence of green tides, the habitat type, as well as the interaction of both factors ('Type' and 'GT'), have significant effects on multivariate responses of invertebrate community, two-way PER-MANOVA (Anderson, 2001) (n permutations = 9999) was performed on a subset of beaches (n = 8, 2 beaches per type harbouring or not harbouring green tides, i.e. 4 groups: Type I-NoGT/Type I-GT and Type II-NoGT/Type II-GT), in order to meet the assumption of equal multivariate dispersion. Principal Component Analyses (PCAs) were performed to visualize patterns in the distribution of assemblages of macrofauna in space and time within each habitat harbouring green tides or not (i.e. the 4 groups). The homogeneity of multivariate dispersion between the four groups (Type I or Type II sandy beaches, with or without green tides) was tested using the function betadisper() with permutations (n = 999). Redundancy analyses (RDA) were also performed for each habitat (Type I and Type II) to determine which environmental variables constrain the variation of benthic communities in this setting.

Temporal (yearly sampling from 2007 to 2013) variation of each of the main classes represented in macrofaunal assemblages for each of the habitats with or without GT (Type I-NoGT, Type I-GT, Type II-NoGT, Type II-GT) was assessed to extricate diversity trends. Furthermore, in order to disentangle the effects of environment (environmental variables not linked to GT), *Ulva* mats, space, and time on the assemblages of macrofauna, two recently-developed methods were combined: distance-based Moran's eigenvector maps (dbMEM, Dray et al., 2006; Legendre and Gauthier, 2014) were used in variation partitioning (Borcard and Legendre, 1994). First, dbMEM eigenfunctions were generated based on the number of sampling occasions (7 years) and on a distance matrix obtained by estimating distances between sandy beaches using the ruler tool in the Geoportail portal (http://www.geoportail.gouv.fr). The generated dbMEM eigenfunctions were used as temporal and spatial variables (here called *temporal MEMs* and *spatial MEMs*, see supplements 3 and 4). MEMs can model both positive and negative temporal and spatial patterns, and the four models were assessed. Forward selection (Blanchet et al., 2008) was then used to select significant spatial and temporal MEMs. Variation of the multivariate responses was then partitioned with respect to four groups of explanatory variables: environment excluding variables related to green tides (18 variables describing physical and biological environment of each beach), *Ulva* (the variables related to the occurrence and coverage of GT), space (the selected spatial MEMs) and time (the selected temporal MEMs). Each fraction of variation, *i.e.* the explanatory power of each set of the explanatory variables, was tested using multiple linear regressions (Legendre and Legendre, 2012).

All analyses were conducted within the R environment (R Development Core Team, 2013) and relied on the *vegan* (Oksanen et al., 2010), *PCNM* (Legendre et al., 2013) and *packfor* (Dray et al., 2013) packages.

3. Results

3.1. Environmental characterisation

General characteristics for the period 2007 to 2013 of the thirteen beaches considered in this study (SBs A to M) are presented in

Table 1. The length of the SBs varied between 400 m and 26 km, the width between 149 m and 2.4 km and the slope between 0.5 and 2.9%. From north-west (SB$_A$) to south-west (SB$_M$), the maximal spring tide decreased from 13.2 to 5.1 m while beach types (I and II) and the presence of green tides were evenly distributed along the coasts of Brittany (Table 1, Fig. 1).

Environmental characteristics for the study period (2007—2013) of the thirteen SBs (SBs A to M) are presented in Table 2. For the biological variables, no *Ulva* was reported from SB$_C$, SB$_G$, SB$_I$, SB$_K$, and SB$_L$, whereas presence of green tides at the other SBs (A, B, D, E, F, H, J and M) varied from 2 to 20 counts on 21 aerial surveys, 3 per year from 2007 to 2013. At SBs harbouring green tides, the mean coverage by *Ulva* spp. varied between 0.6% and 23.1% and 4.3%—19.3% at Type I and Type II SBs, respectively. Organic matter content was low and varied between 0.5 and 2.2% regardless of habitat type.

For sediment variables, differences between Type I and Type II SBs were distinct: mean median grain size and sorting index ranged from 140 to 280 μm and from 1.7 to 3.3 at SBs of Type I, and from 300 to 560 μm and 2.5 to 7.6 at SBs of Type II. In addition, the beach index varied between 2.6 and 3.1, and between 3.0 and 3.6 for beaches of Type I and II, respectively (Table 2). The environment was fully marine at all SBs. Seawater temperatures were the lowest in the western-northern part of Brittany, with no clear gradient over the study area, however. For terrestrial variables, air temperature as well as wind speed and direction did not show any clear patterns through the SBs in the study. In contrast, rainfall was spatially more variable, affecting runoff from land.

3.2. Diversity patterns in relation to green tides and habitat

Differences in community structure between the two habitats were clearly illustrated with a PCA analysis (Fig. 3) integrating the presence of GT. The ordination for Type I showed a shift in the structure of macrofaunal data where green tides occurred (Fig. 3): the dot cloud is more spread out than without green tides (significant difference in multivariate dispersion between the two groups; p = 0.014). A different picture emerged for SBs of Type II (Fig. 3) with no difference in dispersion of the dot clouds, with and without green tides (p = 0.439). The examination of the influence of the factors "Type", "Green Tides" (Fig. 4) and the interaction of both factors on the univariate variables (A, S, H and D) using a two-way ANOVA analysis (Table 3) revealed several patterns. The development of fauna (abundance) and the species richness were significantly higher at Type II-SBs irrespective of the presence of green tides, and these two variables were also higher where green tides

were present (for both SB-types, Table 3, Fig. 4A, B). There were strong significant interactions of the factors 'Type' and 'Green Tides' for the Shannon and the Simpson diversity indices (Table 3). Therefore, individual tests exploring differences in terms of diversity indices within each beach type with or without GT were used. Shannon and Simpson diversity indices were significantly affected by the presence of green tides at SBs of Type I (Fig. 4C, D, p < 0.001), whereas no effect of green tides was found at SBs of Type II (for additional information regarding individual comparison statistical tests, see supplement 4). In addition, analysis of the effects of both factors 'Type' and 'GT', and their interaction (Type × GT), on multivariate responses of macrotidal SB macrofauna using a two-way PERMANOVA (Table 4) revealed a strong significant interaction of the two factors 'Type' and 'GT', suggesting that the effects of the accumulation of *Ulva* spp. on sandy beaches are not the same depending on the type of SB.

3.3. Community composition and its dynamics related to habitat and green tides

Over the 7 years of the study and among the 819 samples, a total of 36,643 macrofauna individuals were identified belonging to 273 different species. Considering each type of SBs, 10,649 and 25,994 individuals that belonged to 153 and 231 species were identified at SBs of Type I and Type II, respectively (temporal trends in mean species richness at each sandy beach is presented in supplements 6 and 7). Annelida was the most common phylum with 100 polychaete species, followed by Arthropoda with 95 malacostraca species, Mollusca with 40 bivalve species, and Echinodermata with 3 ophiuroid species. The four classes Polychaeta, Ophiuroidea, Malacostraca and Bivalvia represented more than 90% (ranged from 94.2 to 100%) of the mean relative abundance from 2007 to 2013 (Fig. 5). At SBs of Type I, the mean relative abundances of Polychaeta and Ophiuroidea were higher where GT occurred compared to pristine SBs (Type I-NoGT). On the contrary, the relative abundances of Bivalvia and Malacostraca were lower where GT occurred at SBs of Type I (Fig. 5). At sandy beaches of Type II, the relative abundance of Malacostraca was higher and the relative abundances of Bivalvia and Polychaeta lower where GT occurred (Fig. 5).

Total species richness over 7 years at SBs of Type I was 153 (128 and 84, with and without green tides respectively) and at SBs of Type II 231 (187 and 168, with and without green tides respectively). The 46 species presented in Table 5, which belong to the four main classes presented in Fig. 5, made up >90% of the total abundance at each of the four categories of SBs (TI and TII, with and

Table 1
General characteristics of the thirteen sandy beaches (from SB$_A$ to SB$_M$), with indications relative to the presence of green tides and to the Type of beaches (I or II).

Beach	Beach code	Beach type	Latitude	Longitude	L (km)[a]	W (m)[b]	S (ha)[c]	Spring tide (m)	Slope (%)
Saint-Cast	A[d]	I	48.63	−2.25	1.7	2410	403	13.2	0.5
Saint-Brieuc	B[d]	I	48.55	−2.69	26.4	1520	4014	11.9	0.5
Arcouest	C	II	48.82	−3.02	0.4	403	14	11.8	2.9
Saint-Efflam	D[d]	I	48.68	−3.60	3.0	1536	457	10.05	0.7
Callot	E[d]	II	48.68	−3.93	4.9	760	372	9.7	1.4
Sainte-Marguerite	F[d]	II	48.61	−4.61	1.6	1287	208	8.4	0.7
Blancs-Sablons	G	I	48.37	−4.76	1.4	325	45	7.6	2.3
Aber	H[d]	I	48.23	−4.45	1.9	392	74	7.4	1.9
Audierne	I	I	47.88	−4.37	11.6	342	398	5.8	1.7
Gàvres	J[d]	II	47.70	−3.33	1.6	461	76	5.6	1.2
Erdeven	K	I	47.69	−3.33	7.3	320	234	5.6	1.8
Plouharnel	L	II	47.56	−3.12	3.2	1025	324	5.7	0.6
Kerjouanno	M[d]	I	47.53	−2.87	1.9	149	28	5.1	3.7

[a] Length of beach.
[b] Width of beach.
[c] Surface of beach.
[d] Presence of green tides.

Table 2

Environmental characteristics of the thirteen sandy beaches (from SB_A to SB_M) yearly sampled from 2007 to 2013 with indications relative to the presence of green tides, to the type of beaches. The environmental variables are ordered in regards to their nature: marine, terrestrial, biological, or relative to sediment.

Variables	Beach	Saint-Cast	Saint-Brieuc	Arcouest	Saint-Efflam	Callot	Sainte-Marguerite	Blancs-Sablons	Aber	Audierne	Gâvres	Erdeven	Plouharnel	Kerjouanno
	Beach code	A[j]	B[j]	C	D[j]	E[j]	F[j]	G	H[j]	I	J[j]	K	L	M[j]
	Beach type	I	I	II	I	II	II	I	I	I	II	I	II	I
Biological var.	GT occurrence[a]	7	19	0	20	18	18	0	4	0	5	0	0	2
	Ulva coverage[b]	0.6 ± 0.9	7.7 ± 2.9	0	23.1 ± 5.4	19.3 ± 9.3	4.3 ± 2.3	0	2.8 ± 5.5	0	13.6 ± 17.2	0	0	1.3 ± 2.2
	OMC[c,d] (%)	1.4 ± 0.3	1.0 ± 0.2	1.1 ± 0.4	2.2 ± 0.3	1.0 ± 0.9	1.3 ± 0.3	0.7 ± 0.1	1.4 ± 0.6	1.0 ± 0.1	0.7 ± 0.1	0.5 ± 0.1	0.5 ± 0.1	0.4 ± 0.2
Sediment var.	Median[c] (μm)	155.5 ± 28.3	174.6 ± 24.6	301.1 ± 67.1	140.1 ± 13.8	368.0 ± 317.7	310.7 ± 75.6	217.4 ± 38.2	158.9 ± 13.3	207.7 ± 38.8	563.6 ± 329.1	153.6 ± 21.6	355.5 ± 467.0	280.4 ± 426.9
	Sorting Index[c]	2.7 ± 0.8	3.2 ± 1.4	4.1 ± 1.1	1.7 ± 0.1	4.3 ± 1.6	2.5 ± 1.0	1.9 ± 0.2	2.9 ± 1.2	1.8 ± 0.1	7.6 ± 5.6	2.7 ± 0.5	3.2 ± 3.1	3.3 ± 1.3
	Beach Index[c]	3.9 ± 0.1	3.1 ± 0.1	3.6 ± 0.1	3.8 ± 0.0	3.2 ± 0.2	3.5 ± 0.1	3.0 ± 0.0	3.1 ± 0.1	3.0 ± 0.1	3.0 ± 0.1	3.0 ± 0.0	3.4 ± 0.2	2.6 ± 0.2
	Gravel[c] (%)	3.5 ± 3.0	6.6 ± 5.4	11.3 ± 7.0	0.2 ± 0.2	15.3 ± 8.3	5.8 ± 8.3	0.3 ± 0.2	4.9 ± 4.2	0.8 ± 0.6	20.1 ± 13.5	5.1 ± 2.7	7.3 ± 13.6	10.9 ± 11.7
	Sand[c] (%)	94.5 ± 3.4	92.0 ± 5.3	83.8 ± 7.1	97.3 ± 0.6	80.2 ± 11.1	92.3 ± 8.5	98.6 ± 0.3	93.9 ± 4.2	98.2 ± 0.6	77.3 ± 13.3	93.8 ± 2.7	91.4 ± 13.5	88.1 ± 11.5
	Mud[c] (%)	2.0 ± 0.9	1.4 ± 0.8	4.9 ± 2.9	2.5 ± 0.6	4.5 ± 10.8	1.8 ± 0.7	1.1 ± 0.2	1.1 ± 0.3	1.0 ± 0.2	2.6 ± 0.6	1.0 ± 0.1	1.3 ± 0.3	0.9 ± 0.2
Marine var.	SWT[e,f] (°C)	9.0 ± 0.9	9.6 ± 0.9	10.1 ± 0.9	10.2 ± 0.8	10.8 ± 0.8	11.4 ± 0.7	11.7 ± 0.5	9.9 ± 0.9	11.7 ± 0.6	11.6 ± 0.7	11.6 ± 0.7	11.4 ± 0.9	11.4 ± 0.9
	Salinity[e] (‰)	35.2 ± 0.2	35.2 ± 0.2	35.2 ± 0.2	35.2 ± 0.2	35.3 ± 0.1	35.4 ± 0.1	35.5 ± 0.1	35.0 ± 0.2	35.4 ± 0.1	35.3 ± 0.2	35.3 ± 0.2	35.1 ± 0.2	35.1 ± 0.2
Terrestrial var.	Air Temp.[e,g] (°C)	6.8 ± 1.2	6.5 ± 1.1	6.5 ± 1.1	7.4 ± 1.0	7.5 ± 1.0	7.9 ± 1.0	8.5 ± 0.9	7.6 ± 1.1	8.7 ± 1.1	7.2 ± 1.3	7.4 ± 1.2	7.4 ± 1.2	7.3 ± 1.2
	Wind speed[e] (1/10 m/s)	1.3 ± 0.3	1.4 ± 0.3	1.4 ± 0.3	1.3 ± 0.2	1.5 ± 0.3	1.5 ± 0.2	2.4 ± 0.3	1.3 ± 0.4	2.0 ± 0.5	1.4 ± 0.2	1.4 ± 0.2	1.4 ± 0.2	0.7 ± 0.3
	Wind speed[e] (1/10 m/s)													
	Wind dir.[e,h] (/360°)	193.8 ± 20.6	186.6 ± 21.3	186.6 ± 21.3	188.1 ± 21.4	193.9 ± 16.2	192.7 ± 14.2	200.2 ± 17.1	192.1 ± 20.0	203.5 ± 14.5	178.6 ± 18.1	178.6 ± 18.1	178.6 ± 18.1	179.0 ± 17.6
	Rainfall[i] (mm)	158.9 ± 58.2	185.9 ± 72.8	185.9 ± 72.8	426.2 ± 121.8	228.1 ± 78.4	255.5 ± 71.3	218.9 ± 63.7	275.5 ± 77.3	206.3 ± 65.3	246.5 ± 75.4	244.0 ± 76.9	243.9 ± 76.9	175.5 ± 41.5

[a] Count over 21 flight overs (3 per year from 2007 to 2013).
[b] Mean estimation of GT coverage of the measured values from 2007 to 2013 (CEVA).
[c] Mean ± SD of the measured values from 2007 to 2013.
[d] OMC = Organic Matter Content.
[e] Mean ± SD of the measured values between January and March from 2007 to 2013.
[f] SWT = Sea Water Temperature.
[g] Temp. = temperature.
[h] Dir. = direction.
[i] Mean ± SD of sums of rainfall felt between January and March from 2007 to 2013.
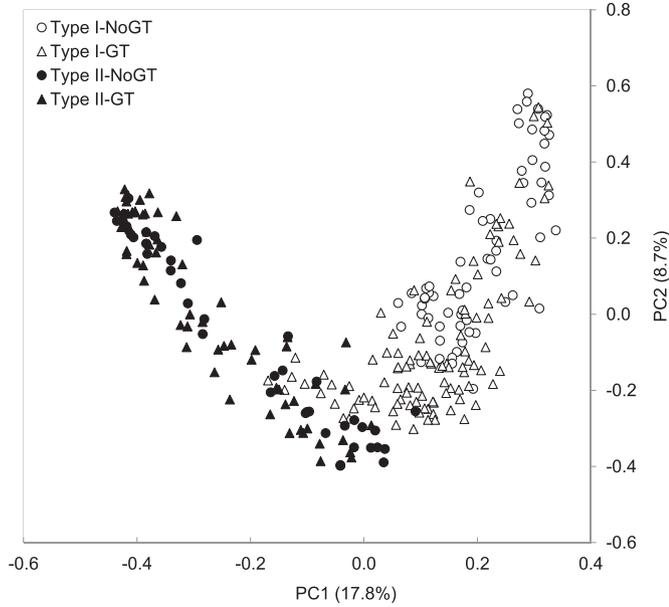[j] Presence of green tides.

Fig. 3. Principal component analysis (PCA) of sites Type I–NoGT (open circles), Type I–GT (open triangles), Type II–NoGT (filled circles) and Type II–GT (filled triangles), based on Hellinger transformed abundance of benthic community sampled at the thirteen sandy beaches from 2007 to 2013. With GT = Green Tides.

Table 3
Results of 2-way ANOVAs of univariate variables calculated based on abundance data of the thirteen SBs yearly sampled from 2007 to 2013. Total number of observations was 273. Significant values at p ≤ 0.05 are shown in bold; *p ≤ 0.05,***p ≤ 0.001.

	df	MS	F	p
log(A)				
Type	1	167.51	178.94	**<2.10^{-16} *****
GT	1	4.53	4.84	**2.87.10^{-2} ***
Type* GT	1	0.8	0.86	3.55.10^{-1}
Res.	269	0.94		
S				
Type	1	10,622	348.56	**<2.10^{-16} *****
GT	1	698	22.89	**2.83.10^{-6} ******
Type* GT	1	108	3.56	6.10^{-2}
Res.	269	30		
H				
Type	1	18.48	27.57	**3.08.10^{-7} ******
GT	1	9.38	14	**2.24.10^{-4} ******
Type* GT	1	13.33	19.89	**1.21.10^{-5} ******
Res.	269	0.67		
D				
Type	1	0.032	0.77	3.81.10^{-1}
GT	1	0.23	5.36	**2.13.10^{-2} ***
Type* GT	1	0.63	14.96	**1.38.10^{-4} ******
Res.	269	0.04		

without green tides). The Type I sandy beach community was dominated by the suspension-feeding bivalve *D. vittatus* (Table 5), which contribution to the total abundance by almost 50% in beaches where no green tides occurred. However, the relative abundance of *D. vittatus* did not exceed 26% at sandy beaches with green

tides. Other species were also negatively affected by green tides at sandy beaches of Type I, namely the selective surface-feeder *Spiophanes bombyx*, the burrower amphipods *Bathyporeia elegans* and *Bathyporeia pelagica* as well as other crustaceans (*Cumopsis* spp. and *Eurydice affinis*). On the other hand, the omnivorous ophiuroid *Acrocnida* cf. *spatulispina*, the tube-dweller polychaete *Owenia fusiformis* and the selective surface feeder *Tellina tenuis* were positively affected by the presence of green tides at SBs of Type I.
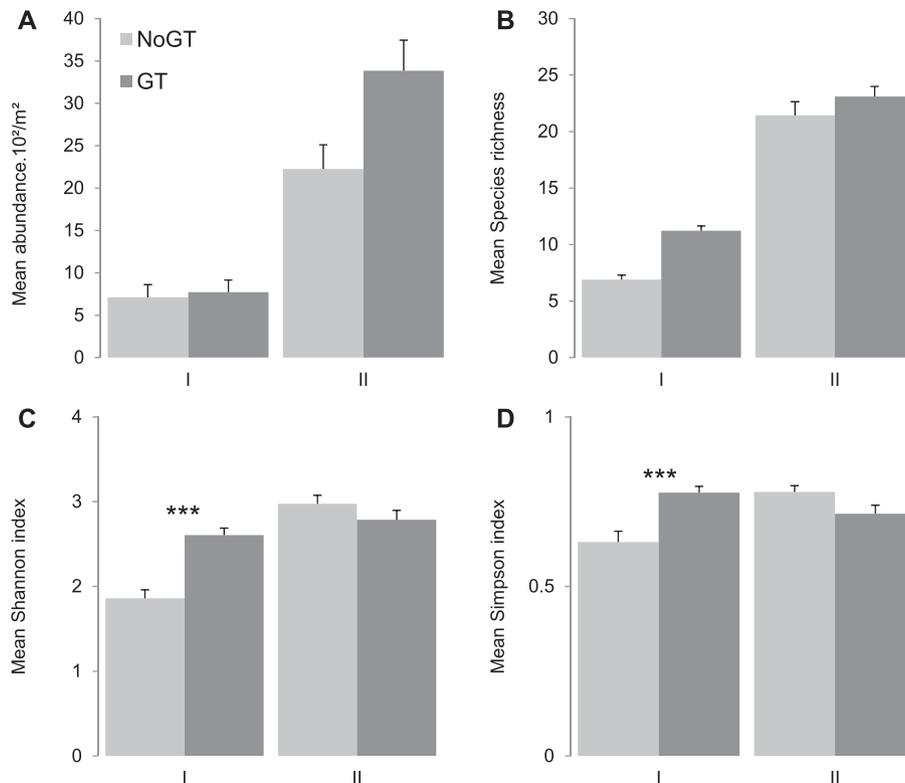

Fig. 4. Mean + SE abundance (A), species richness (B), Shannon index (C) and Simpson index (D) of zoobenthos sampled in the thirteen sandy beaches which take part of two habitats (I & II, fine and heterogeneous sediment in light grey and dark grey respectively) around Brittany. GT = Green Tides. Level of significance: *p ≤ 0.05, ***p ≤ 0.001.

Table 4
Results of 2-way PERMANOVA of multivariate responses of macrofauna based on abundance data of a sub-sample of 8 beaches yearly samples from 2007 to 2013. Total number of observations was 168. Significant values at $p \leq 0.05$ are shown in bold; ***$p \leq 0.001$.

	df	MS	F	p
Type	1	24.91	41.00	1.10^{-4} ***
GT	1	3.48	5.73	1.10^{-4} ***
Type* GT	1	3.20	5.27	1.10^{-4} ***
Res.	164	0.61	0.76	

The Type II sandy beach community was dominated by the herbivorous tanaid *Aspeudopsis latreillii*, which showed a relative increase from pristine to eutrophicated beaches. The same pattern was observed for the amphipod *C. arenarium*, which went from being almost completely absent to reaching 8% in the presence of green tides. Three large polychaete species were negatively influenced by the presence of GT (*Euclymene oerstedi*, *Lanice conchilega* and *Notomastus latericeus*) (Table 5).

3.4. Disentangling the effects of the environment, space and time

The two correlation triplots of redundancy analyses of macrofaunal data from all SBs for each habitat constrained by environment (Fig. 6) revealed contrasting responses in the different types of SBs. At SBs of Type I, two dot-clouds were identified: the bulk of unvegetated sites were largely separated from sites where green tides occurred. The divergence of these communities was associated with the explanatory variables Rainfall, *Ulva* (cov. and occ.), Tide and Width (of beach). The ordination diagram (Fig. 6) also showed strong and positive association between coverage by green tides (*Ulva* cov.) and *Owenia fusiformis* and *Acrocnida* cf. *spatulispina*. Patterns were less evident at SBs of Type II, where sediment variables (percentage of Sand and Gravel) and Slope, Tide and Width of beaches drove the ordination.

In order to specifically evaluate the explanatory power of

environmental variables as well as spatial and temporal variables in the context of this large scale study, we partitioned the variance of macrofauna in the two habitats with respect to environment (variables not related to GT), presence of *Ulva* mats (*Ulva* occurrence and coverage), spatial and temporal explanatory variables (Table 6). The proportion of variation explained by the combination of the four sets of explanatory variables was always significant and higher for Type II SBs compared to Type I SBs (30.8 and 41.7%, $p < 0.05$). This higher proportion of variation explained is mainly attributable to a better fit of environmental variables to variation in the macrofauna community observed at sandy beaches of Type II, as the explanatory power of the set of environmental variables was lower in Type I than Type II SBs (25.4 and 40.7%, $p < 0.05$). Explanatory variables related to *Ulva* explained significantly 7.8 and 6.7% ($p < 0.05$) of the variation in macrofauna at Type I and Type II SBs respectively. Spatial variables also significantly explained high proportions of variation observed in macrozoobenthic assemblages (23.2 and 29.8% for Type I and II respectively, $p < 0.05$). However, the proportion of variation explained by temporal variables was low regardless of habitat (2.1 and 1.1% for Type I and II respectively, $p < 0.05$).

4. Discussion

Our large-scale field study revealed a general regional response of macrotidal sandy beach macrofauna to the presence of drifting macroalgal mats and also showed habitat- and species-specific responses to the occurrence of green tides. Overall, our results demonstrate that eutrophication by macroalgae modify the structure of highly dynamic environments, such as macrotidal sandy beaches, despite a large natural and regional variability.

4.1. Sandy beach macrofauna large spatial and temporal scale dataset

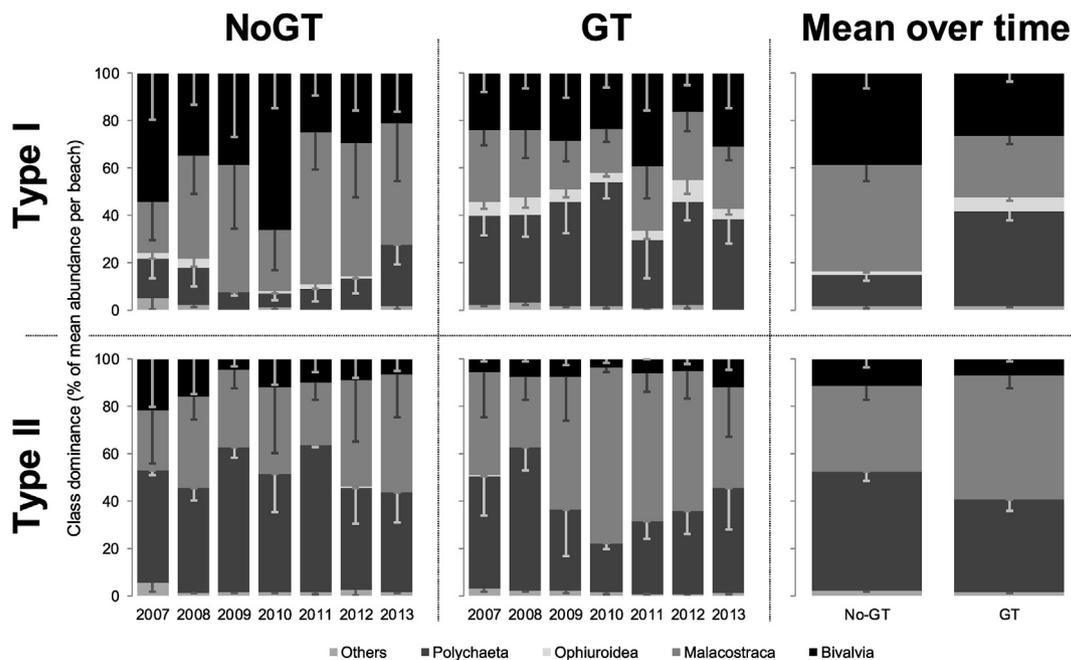By using a long-term dataset (7 years) covering a large area

Fig. 5. Relative abundance of the dominant class — SE at SBs of Type I without green tides (top-left panel), Type I harbouring green tides (top-middle panel), Type II without green tides (down-left panel), Type II harbouring green tides (down-middle panel) at each sampling occasion (from 2007 to 2013) and the mean relative abundance — SE over time (7 years) at SBs of Type I (top-right panel) and of Type II (down-right panel) harbouring (GT) or not (no-GT) green tides.

Table 5
Percent dominance in terms of abundance for the major species (threshold = 90%) living at the sandy beaches of Type I and II harbouring or not green tides (GT or no-GT). Bold face type numbers show contributions that are higher than 1%. Taxonomic group and selected biological traits (feeding habit, feeding strategy, mobility, maximal size and reproduction/development) are given for each species. Traits data collected from MarLIN, EOL, polytraits, and BIOTIC databases, and personal observations.

Species	Taxonomic group	Abundance dominance (%)				Functional characteristics				
		TI		TII		Feeding habit	Feeding strategy	Mobility	Maximal size (mm)	Reproduction development
		No GT	GT	No GT	GT					
Ampharete sp.	Annelida polychaeta	–	–	–	0.9	D	SF, SPF	T	~20	Ovi
Aonides oxycephala		–	0.0	0.1	**1.7**	D	SuF, SPF	T	81	Ovi
Caulleriella alata		–	–	0.3	0.7	D	SuF, SPF	T	12	Ovi
Chaetozone gibber		–	**1.6**	0.3	0.5	D	SuF, SPF	T	20	Ovi
Euclymene oerstedi		–	0.2	**7.8**	**1.9**	D	SuF	T	100	Ovi
Glycera tridactyla		–	0.8	0.2	0.3	Ca	SPF	B, (S)	50	Ovi
Lanice conchilega		–	0.5	**3.9**	0.9	D	SF, SPF	T	300	Ovi
Leiochone leiopygos		–	**1.6**	**1.7**	**1.4**	D	SuF	T	200	Ovi
Macroclymene santandarensis		–	0.0	**1.4**	0.7	D	SuF	T	150	Ovi
Magelona filiformis		0.5	**1.6**	0.1	–	D	SuF, SPF	B	80	Ovi
Marphysa bellii		–	0.0	0.2	0.5	Ca	SPF	B	200	Ovi (Ovo)
Nephtys cirrosa		**3.1**	**3.2**	**1.6**	0.2	Ca, Sc	SPF	B, C, (S)	100	Ovi
Nephtys hombergii		0.1	0.7	0.7	0.7	Ca, Sc	SPF	B, C, (S)	200	Ovi
Notomastus latericeus		–	**1.7**	**13.8**	**9.1**	D	SuF	B	300	F, Ovi
Oligochaeta spp.Oligochaeta spp.		0.0	0.1	–	0.6	D	SuF	B		F, Ovi
Owenia fusiformis		0.2	**8.0**	0.4	0.0	D	SuF, SF, SPF	T	100	Ovi
Paradoneis sp2Paradoneis sp2		–	–	**1.9**	0.1	D	SPF	B	15	Ovi
Phyllodoce mucosa		0.2	0.1	0.1	0.6	Ca	SPF	B, C, (S)	100	Ovi
Poecilochaetus serpens		–	–	**1.2**	0.1	D	SF, SuF, SPF	T	55	Ovi
Scoloplos armiger		0.2	0.6	**3.8**	**3.9**	D	SSF	B, C	120	Ovo
Sigalion mathildae		0.4	**2.1**	0.0	–	Ca	SPF	B, C, (S)	150	Ovi
Spio spp.Spio spp.		0.1	0.4	**1.8**	**1.0**	D	SPF	B	~150	F, Ovi
Spiophanes bombyx		**3.9**	0.4	0.1	0.0	D	SuF, SPF	T	60	Ovi
Ampelisca brevicornis	Arthropoda Malacostraca	0.0	–	0.5	0.7	D	SF	T	12	Ovo
Apseudopsis latreillii		0.0	–	**36.1**	**49.2**	D, H	SPF	S, (C)	7	Ovo
Bathyporeia elegans		**2.7**	0.4	–	0.1	D, Hµ	SPF	B	6	Ovo
Bathyporeia pelagica		**4.1**	**1.2**	0.2	0.1	D, Hµ	SPF	B, (nS)	8	Ovo
Corophium arenarium		–	–	0.0	**8.1**	D, H	SuF, SF, SPF	B, C	7	Ovo
Cumopsis spp.		**6.3**	0.4	0.2	0.0	D	SSF, SPF	B (nS)	~6	Ovo
Diogenes pugilator		0.6	**1.6**	0.0	–	Ca	SPF	C, (B)	20	Ovo
Eurydice affinis		**9.0**	0.3	–	–	Ca	SPF	S, B, (nS)	7	Ovo
Leptocheirus hirsutimanus		–	0.4	0.8	0.1	Hµ	SF	T	8	Ovo
Leucothoe incisa		–	0.6	0.4	0.3	D	SuF, SPF	B, C	7	Ovo
Siphonoecetes kroyeranus		–	**6.9**	0.6	0.8	D, Hµ	SuF, SPF	T, C	5	Ovo
Synchelidium maculatum		**3.8**	0.2	–	–	Ca	SPF	B	5	Ovo
Urothoe poseidonis		0.1	**3.4**	**1.6**	**1.0**	Hµ	SSF	B (nS)	6	Ovo
Urothoe pulchella		0.6	**5.9**	**3.3**	**1.2**	Hµ	SSF	B (nS)	5	Ovo
Acrocnida cf. spatulispina	Echinodermata Ophiuroidea	**1.0**	**5.5**	0.0	–	O, (Ca)	SPF	B	12*	Ovi
Cerastoderma edule	Mollusca bivalvia	–	**1.2**	0.6	0.6	Hµ	SF	B	20	Ovi
Donax trunculus		**6.2**	**2.2**	–	–	D, Hµ	SF, SPF, (SuF)	D, C, B	45	Ovi
Donax vittatus		**48.4**	**25.8**	0.0	–	D, Hµ	SF, SPF, (SuF)	D, C, B	38	Ovi
Kurtiella bidentata		0.3	**4.2**	0.1	**1.0**	D, Hµ	SF, SuF	C, B	6	Ovi
Loripes lacteus		–	0.0	**3.0**	**1.6**	Sy, D	SF, Sy	B	22	Ovi
Lucinoma borealis		–	0.0	0.3	0.9	Sy, D	SF, Sy	B	39	Ovi
Tellina tenuis		**2.4**	**7.5**	0.6	0.2	D, Hµ	SuF, SPF	B	20	Ovi
Nassarius reticulatus	Mollusca gastropoda	0.0	0.3	0.7	0.3	Sc	SPF	C	30	Ovi

Feeding habit: Ca = Carnivore; D = Detritivore; H = Herbivore; Hµ = Micro-Herbivore; O = Omnivore; Sc = Scavenger; Sy = Symbiosis.
Feeding strategy: SF = Suspension feeder; SPF = Selective particle feeder; SSF = Sub-surface feeder; SuF = Surface feeder; Sy = Symbiosis.
Mobility: B = Burrower; C = Crawler; D = Drifter; nS = night Swimmer; S = Swimmer; T = Tube dweller.
Reproduction development: F = Fragmentation; Ovi = Oviparous; Ovo = Ovoviviparous.

(thousands of kilometres), we integrated temporal and spatial variability of sandy beach assemblages. Our study also embraced the great variability of abiotic conditions and characteristics (bio-physical variables, Tables 1 and 2) of macrotidal sandy beaches along the coasts of Brittany. Considering spatial, temporal and environmental variability of macrofaunal assemblages enables robust analysis of possible responses of the benthic community to changes in sandy beach ecosystems (Magurran et al., 2010; Schoeman et al., 2014). Spatial and temporal large-scale comparison of assemblages sampled where eutrophication stress may be high (i.e. presence of green tides, Ménesguen & Piriou 1995; Charlier et al., 2007) with ones sampled in pristine macrotidal SBs allows us to detect changes that can be attributed to anthropogenic activities. These changes were investigated in exposed and semi-exposed macrotidal SBs, which form two habitats made of clean fine sand and of more heterogeneous sediments, Type I and Type II sandy beaches respectively.

4.2. Overall response of zoobenthic communities

Firstly, our hypothesis regarding the influence of green tides on macrofaunal benthic structure was verified for a subset of variables, namely abundance and species richness, which were affected in both beach types. Our results support the hypothesis that differences in macrofaunal community structure observed arose, to some extent, from the presence of green tides on shore. This is consistent
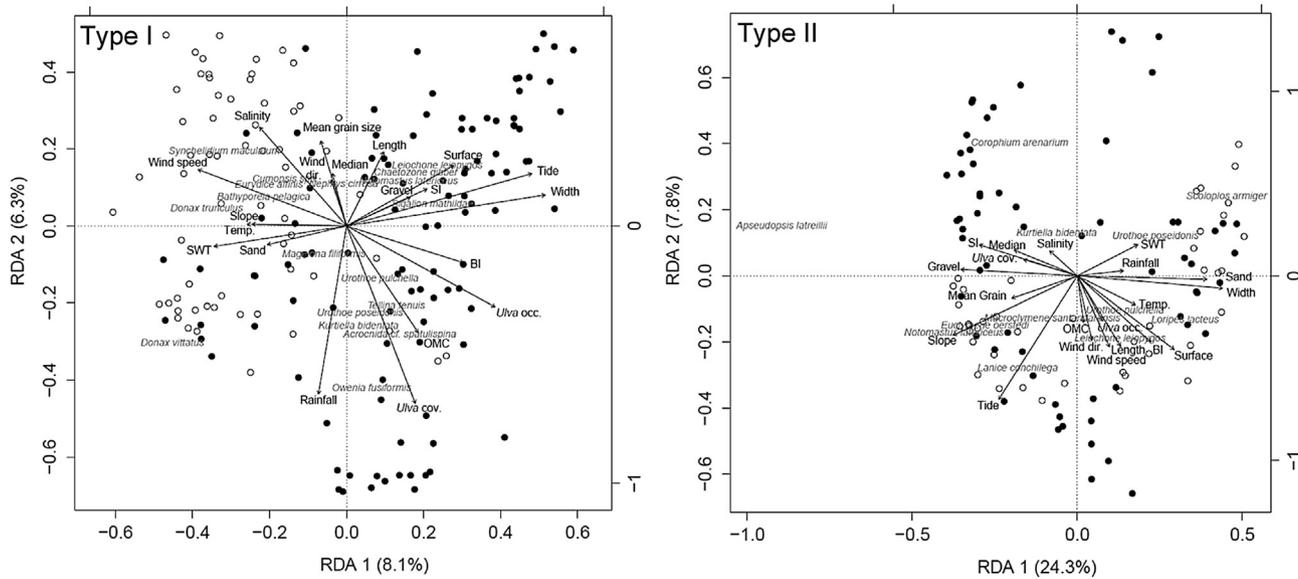
Fig. 6. RDA correlation triplot of macrofaunal community data and all environmental variables of the sandy beaches of Type I (left panel) and of Type II (right panel) harbouring or not green tides (filled and open circles respectively). Ulva cov. = Ulva coverage, Ulva occ. = Ulva occurrence, BI = Beach index (log$_{10}$[sand.tide/slope], where slope = beach face slope, sand = mean grain size in phi units +1 and tide = maximum spring tide range in meters), OMC = organic matter content, Wind dir. = wind direction, Temp. = air 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), Sand = % of sand, Gravel = % of gravel.

Table 6

Results of variance partitioning of the macrofauna time series at SBs of Type I and II with respect to environmental (physical and biological variables except Ulva variables), Ulva (green tide occurrence and coverage), spatial (spatial MEMs) and temporal (temporal MEMs) explanatory variables. Variation explained expressed as a percentage (%) based on adjusted R^2. [E] = environmental variables except the ones relative to green tides, [U] = Ulva variables, [S] = selected spatial variables, [T] = selected temporal variables, Residuals = unexplained variation.

Var.	Type I		Type II	
	Df	%	Df	%
[E + U + S + T]	25	30.8 **	21	41.7 **
[E + U]	20	26.2 **	20	41.4 **
[E]	18	25.4 **	18	40.7 **
[U]	2	7.8 **	2	6.7 **
[S]	7	23.2 **	4	29.8 **
[T]	2	2.1 **	1	1.1 *
Unexpl.		69.1		58.2

** = p < 0.01.

with previous studies assessing the responses of macrofauna to eutrophication by drifting macroalgae (e.g. Hull, 1987; Norkko and Bonsdorff, 1996). In the present study, abundance and species richness were significantly higher at beaches where green macroalgae blooms occurred. As we detect an influence of green tides on SB fauna over larger spatial and temporal scales despite the temporal mismatch between Ulva and fauna sampling, this suggests long-lasting effects of Ulva accumulation on SB zoobenthos. In other words, we see effects on the macrofaunal community even after it has had time to recover following the disintegration/ disappearance of the green tide. Our study provides conservative estimates of Ulva-induced changes in community structure, as we do not assess faunal responses during bloom peaks. In this respect, our results on zoobenthos of macrotidal sandy beaches under the influence of eutrophication are novel. Furthermore, it raises the question of the magnitude of impact on macrotidal sandy beach ecosystem during the actual green macroalgae bloom (i.e. from spring until late summer under these latitudes) as addressed by Quillien et al. (2015).

4.3. Habitat specific response to accumulation of Ulva spp.

Our second hypothesis regarding the different responses of infauna to Ulva spp. blooms depending on the habitat (Type I or II sandy beaches) was also verified, considering diversity indices and community composition. The present study shows that the two types of sandy beaches with two distinct macrobenthic assemblages, respond differentially to eutrophication measured as green tides. More importantly and surprisingly, open sandy beaches made of clean fine sands (Type I) respond more pronouncedly to the presence of Ulva mats than more sheltered beaches with heterogeneous sands (Type II). Indeed, our study shows that diversity indices were significantly higher where green tides occurred compared to beaches that never harboured Ulva mats at exposed SBs (Type I), while this was not true for semi-exposed SBs (Type II) (as shown in Fig. 3 and Table 3). In addition, our results highlight different shifts in benthic community structure where detached Ulva spp. was washed ashore depending on the Type of SBs (Fig. 6). These multivariate responses were in line with the significant interaction found using the 2-way PERMANOVA analysis (Table 4). These results, both considering univariate and multivariate responses of macroinvertebrates, suggest that eutrophication by green tides is an important factor stressing and structuring zoobenthos living at macrotidal sandy beaches of Type I, whereas the influence of GT on benthic communities was different, i.e. less pronounced, but nevertheless detectable at SBs of Type II (Table 6). This contradicts what has been previously shown in micro- or a-tidal sheltered shores regarding the effects of eutrophication by macroalgal mats on zoobenthic communities (e.g. Hull, 1987). Further research at a finer spatial and temporal scale would be required to follow effects of drifting macroalgal mats on macrotidal sandy beach benthic communities, especially at SBs of Type II. Also the fact that the two sandy habitats studied respond differently to drifting macroalgal mats is ecologically interesting and may have implications for 1) the understanding of macrotidal sandy beach functioning as such, and 2) the conservation of these environments. And since wrack subsidies are common across sandy shores

worldwide (Dugan et al., 2003; McLachlan and Brown, 2006) it would be interesting to compare responses of surf zone benthic communities at a global scale (c.f. Arroyo and Bonsdorff, 2015).

4.4. Other important drivers

Besides the shifts in zoobenthic community structure linked to the presence of green tides, our study also shows that "natural" environmental variables play a key role in explaining variation of benthic fauna inhabiting macrotidal sandy shores (Table 6, Fig. 6). Intrinsic features of beaches, such as tidal regime, slope, and width, as well as several environmental characteristics, such as the percentage of sand and gravel, are essential variables shaping macro-invertebrate communities within sandy beaches. Interestingly, rainfall (which may indirectly drive the eutrophication process) is also an important variable influencing zoobenthos responses. These results are in line with those of other studies linking environmental variables to sandy beach macrofauna in the same ecoregion (Lastra et al., 2006) and worldwide (Defeo and McLachlan, 2005 & 2013, and reference therein).

In addition, our results highlight the importance of location along the coast of Brittany (i.e. spatial variables), which are significant forces driving the swash-zone benthic community structure (Table 6). This pattern may be explained by the hydro-climatological peculiarities that exist along the coasts of Brittany (see Tréguer et al., 2014). The influence of temporal variables on the responses of the benthic communities was lower but still significant. In a context of increasing seawater temperature through time (Tréguer et al., 2014), the significant influence of temporal variables on sandy beach macrofauna community structure could be linked to a possible effect of climate change (Schoeman et al., 2014). Further research and analyses would be needed to test the hypothesis of changes in benthic community structure due to global warming, also raised in other studies within this biogeographical transition area (Quillien et al., 2012; Derrien-Courtel et al., 2013; Gallon et al., 2014).

4.5. Species-specific responses of sandy beach marine invertebrates

The ultimate aim of our study regarding the characterization of SB macrofauna responses to presence of drifting macroalgae mats in terms of biology and ecology was also met. The SBs in our study had a rich benthic community, composed of nearly three hundred species, and was highly variable between the two habitats as well as in time and space. Macrozoobenthic assemblages were mainly composed of polychaetes, crustaceans, molluscs and ophiurids, which is consistent with other studies (Leber, 1982; McLachlan, 1983; Degraer et al., 1999; Rodil et al., 2006). Our results show that the zoobenthos of macrotidal sandy beaches respond differently to the occurrence of green tides.

On one hand, some species are stimulated by the presence of *Ulva* spp. mats. This is the case of the polychaete *Owenia fusiformis*, which can survive long hypoxia periods (Watson, 1901). In addition, *Owenia* feeds in two distinct ways, either by removing small suspended particles form the water column in a ciliary manner, or by taking up much larger particles with its labial palps (Dales, 1957), which may be a way to ingest wave-smashed *Ulva* spp. *Acrocnida* cf. *spatulispina* is also stimulated by the presence of green tides possibly because they feed on deposit-feeding bivalves (Glémarec, 1979), whose recruitment may be enhanced by the presence of algal mats (Hull, 1987; Quillien et al., 2015). *Apseudopsis latreillii* was also found in greater abundance at SBs where green tides occurred compared to non-impacted beaches. This tanaid has been reported to be a tolerant species (Grall and Glémarec, 1997; de Juan et al., 2007) and a subsurface deposit feeder, which mostly eats

macrophyte detritus. *C. arenarium*, which exhibits the same feeding habits than *A. latreillii* (Table 5), seems to benefits from the presence of GT, too.

On the other hand, several species inhabiting sandy beaches seem to respond negatively where green tides occur. This is, for example, the case of the large tube-dweller polychaetes *Euclymene oerstedi* and *Lanice conchilega*, which are sensitive to low oxygen conditions mainly because of their lack of mobility. In contradiction with its reported opportunistic nature (Giangrande and Fraschetti, 1993), *Notomastus latericeus* abundance was also lower at SBs where GT occurred compared to beaches that did not harbour algal mats. This pattern may be due to a lack of recruitment and to competition with other polychaete species (Giangrande and Fraschetti, 1993), as both processes can be influenced by the presence of *Ulva* (Hull, 1987). Similarly, the abundance of *Synchelidium maculatum* diminished where GT occurred. This amphipod feeds on meiofauna (Yu et al., 2003), and Carriço et al. (2013) have shown that the diversity of meiofauna inhabiting macrotidal sandy beaches is negatively affected by the presence of green tides. Thus, accumulation of *Ulva* spp. has most likely an indirect negative effect on *S. maculatum*. Green tides also negatively influence other crustaceans, which are invertebrates especially sensitive to lack of oxygen (Gray et al., 2002), namely *Bathyporeia elegans*, *B. pelagica*, *Cumopsis* spp. and *E. affinis*, perhaps due to hypoxia induced by the presence of macroalgal mats. Finally, green tides negatively affect one of the main structuring genera for macrotidal sandy beaches (Guillou, 1982) and an important food source for juvenile flatfish (Speybroeck et al., 2007), namely *Donax* spp. and *Spiophanes bombyx* respectively (Table 5).

More generally and in a biological/functional trait perspective, it seems that macroalgal mats favour herbivorous and suspension feeding benthic invertebrates, whereas sub-surface deposit feeders, large size species, as well as bivalve drifters, which surf up and down the shore with the tides, appear to be negatively affected by the presence of the green alga on the beaches. One way to explore further the effect of GT on the functioning of macrotidal SBs is the Biological Trait Approach, which has proved its utility at large spatial and temporal scales and in relation to anthropogenic pressures (Törnroos, 2014).

5. Conclusion

Our study shows that despite tremendous physical constraints, the ephemeral nature of *Ulva* spp. mats, and the temporal mismatch between fauna and *Ulva* samplings, macrotidal sandy beach zoobenthos respond to presence of drifting macroalgae suggesting that the ecology of sandy beaches has some predictability. Our results also suggest that biological forces may have a stronger effect on macrobenthic communities inhabiting sandy beaches than was previously described in the literature (Defeo and McLachlan, 2005; McLachlan and Dorvlo, 2005; McLachlan and Brown, 2006), even at very large spatial and long temporal scales. Our study also reveals that, interestingly, the effects of green tides on macrobenthic assemblages were stronger at exposed sandy beaches than at semi-exposed beaches. The shifts observed in macrofauna community structure are also reflected in the responses in terms of biology and ecology of the zoobenthos, suggesting that the functioning of such dynamic systems is directly and indirectly under the influence of eutrophication. To our knowledge, our work is the first to demonstrate that macroalgal accumulations influence low-shore zoobenthos at large spatial and temporal scale within high-energy macrotidal sandy ecosystems. These results are of particular importance considering that green tides are increasing in intensity and frequency worldwide (Ye et al., 2011; Arroyo and Bonsdorff, 2015) and are currently spreading and accumulating

on coasts of adjacent regions of France (CGDD, 2014). The continuance of large-scale surveys in a context of a changing ocean is thus crucial.

Statement or authorship

J.G. designed the study, B.G., M.M., V.L.G. and J.G. analysed samples, N.Q., M.C.N., E.B. and J.G. performed the analyses, N.Q. wrote the first draft of the manuscript, and all authors contributed substantially to revisions.

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Appendix A. Supplementary data

Supplementary data related to this article can be found at http://dx.doi.org/10.1016/j.ecss.2015.07.042.

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