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# Dynamic ecosystems under anthropogenic stress: how does macrotidal sandy beach fauna respond to green tides ?

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l'Environnement Marin (UMR 6539) et à  
Environmental and Marine Biology (ÅAU,  
Finlande)

## Dynamic ecosystems under anthropogenic stress – how does macrotidal sandy beach fauna respond to green tides ?

**Des écosystèmes naturellement  
stressés sous menace anthropique -  
réponses de la faune des plages de sable  
macrotidales aux marées vertes.**

Thèse soutenue le 20 mai 2016  
devant le jury composé de :

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# Dynamic ecosystems under anthropogenic stress – how does macrotidal sandy beach fauna respond to green tides?

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## Sammanfattning (Swedish abstract)

Dynamiska ekosystem, ofta ansedda som motståndskraftiga, karakteriseras av abiotiska och biotiska processer under kontinuerliga och stora förändringar i tid och rum. Denna föränderlighet försvårar identifieringen av överlappande mänsklig negativ påverkan. Dynamiska ekosystem finns i kustområden i form av sandstränder, vilka täcker större delen av världens isfria kustlinje. Det ökade trycket av mänsklig påverkan hotar dessa system, och t.ex. massutveckling av opportunistiska makroalger (huvudsakligen Chlorophyta, s.k. *makroalgblooming*), till följd av kustvattnens övergödning, väcker oro. Effekterna av makroalgbloomingar har tidigare utvärderats i system som är mer skyddade, eller saknar tidvatten. Om mer dynamiska ekosystem, som sandstränder med högt tidvatten, respons till denna påverkan, vet vi mindre.

Denna avhandling syftar till att uppskatta effekterna av antropogen stress, med sandstränder utsatta för makroalgbloomingar som studieobjekt. Avhandlingen omfattar fyra fältstudier, vilka analyserar bentiska samhällens dynamik i naturliga sandsediment i olika skalor i tid (från månatliga till fleråriga) och rum (från lokala till regionala).

I denna avhandling redogör jag för bentiska sandstrandssamhällens långtidsrespons till makroalgblooming, över hundratals kilometer och över en sjuårsperiod; jag lyfter fram den starkare responsen hos zoobentos i exponerade sandstrandssamhällena jämfört med de i halvexponerade områden. I exponerade sandsediment, och på en vertikal skala (från grunda vatten till djupare kustnära områden), identifierar jag en starkare respons hos bentiska evertibratsamhällena i tidvattenszonen, i förhållande till evertibratsamhällena som lever under tidvattennivån, såväl som plattfisksamhällena.

Med fokus på småskaliga variationer i de mest utsatta samhällena (nämligen, bentiska evertibrater i tidvattenszonen), påvisar denna avhandling en minskning av beta-diversitet längs en övergödningsgradient i form av makroalgblooming, liksom den ökade betydelsen av biologiska variabler för den ekologiska variabiliteten hos bentiska makrovertebrat sandstrandssamhällena. För att illustrera den underliggande processen som förklarar de observerade strukturella förändringarna där det skett makroalgblooming, undersökte jag effekten av höga biomassor av opportunistiska makroalger (*Ulva* spp.) på sandstränders trofiska struktur och funktion. Detta arbete lyfter fram den progressiva förenklingen av sandstränders födovävar och en modifikation av energiflöden över tid, via *Ulva*-mattors direkta och indirekta effekter, på åtskilliga trofiska nivåer.

Med denna avhandling demonstrerar jag att högt dynamiska ekosystem reagerar annorlunda (t.ex. förändringar i  $\delta^{13}\text{C}$ , inte i  $\delta^{15}\text{N}$ ) och mer subtilt (hög dödlighet hos bentos observerades exempelvis inte) till mänsklig negativ inverkan än vad som tidigare visats i mer skyddade system, och system som saknar tidvatten. Dessa resultat möjliggjordes av ett mångfacetterat tillvägagångssätt för arbetet; jag presenterar ett ramverk som förenar fältundersökningar med avancerade analyser för att beskriva förändringar i högt variabla ekosystem under mänsklig negativ påverkan.

Nyckelord: Makroalgblooming – *Ulva* spp. – Övergödning – Dynamiska ekosystem – Sandstränder – Tidvatten – Zoobentos – Plattfisk – Samhällsstruktur – Födovävar – Trofisk funktion – Stabila isotoper  $\delta^{13}\text{C}$  och  $\delta^{15}\text{N}$  – Tid-rum analys – Bretagne

## Abstract

Highly dynamic systems, often considered as resilient systems, are characterised by abiotic and biotic processes under continuous and strong changes in space and time. Because of this variability, the detection of overlapping anthropogenic stress is challenging. Coastal areas harbour dynamic ecosystems in the form of open sandy beaches, which cover the vast majority of the world's ice-free coastline. These ecosystems are currently threatened by increasing human-induced pressure, among which mass-development of opportunistic macroalgae (mainly composed of Chlorophyta, so called *green tides*), resulting from the eutrophication of coastal waters. The ecological impact of opportunistic macroalgal blooms (green tides, and blooms formed by other opportunistic taxa), has long been evaluated within sheltered and non-tidal ecosystems. Little is known, however, on how more dynamic ecosystems, such as open macrotidal sandy beaches, respond to such stress.

This thesis assesses the effects of anthropogenic stress on the structure and the functioning of highly dynamic ecosystems using sandy beaches impacted by green tides as a study case. The thesis is based on four field studies, which analyse natural sandy sediment benthic community dynamics over several temporal (from month to multi-year) and spatial (from local to regional) scales.

In this thesis, I report long-lasting responses of sandy beach benthic invertebrate communities to green tides, across thousands of kilometres and over seven years; and highlight more pronounced responses of zoobenthos living in exposed sandy beaches compared to semi-exposed sands. Within exposed sandy sediments, and across a vertical scale (from inshore to nearshore sandy habitats), I also demonstrate that the effects of the presence of algal mats on intertidal benthic invertebrate communities is more pronounced than that on subtidal benthic invertebrate assemblages, but also than on flatfish communities.

Focussing on small-scale variations in the most affected faunal group (*i.e.* benthic invertebrates living at low shore), this thesis reveals a decrease in overall beta-diversity along a eutrophication-gradient manifested in the form of green tides, as well as the increasing importance of biological variables in explaining ecological variability of sandy beach macrobenthic assemblages along the same gradient. To illustrate the processes associated with the structural shifts observed where green tides occurred, I investigated the effects of high biomasses of opportunistic macroalgae (*Ulva* spp.) on the trophic structure and functioning of sandy beaches. This work reveals a progressive simplification of sandy beach food web structure and a modification of energy pathways over time, through direct and indirect effects of *Ulva* mats on several trophic levels.

Through this thesis I demonstrate that highly dynamic systems respond differently (*e.g.* shift in  $\delta^{13}\text{C}$ , not in  $\delta^{15}\text{N}$ ) and more subtly (*e.g.* no mass-mortality in benthos was found) to anthropogenic stress compared to what has been previously shown within more sheltered and non-tidal systems. Obtaining these results would not have been possible without the approach used through this work; I thus present a framework coupling field investigations with analytical approaches to describe shifts in highly variable ecosystems under human-induced stress.

**Keywords:** Green tides - *Ulva* spp. - Eutrophication - Dynamic ecosystems - Sandy beaches - Macrotidal - Zoobenthos - Flatfish - Community structure - Food web structure - Trophic functioning - Stable isotopes  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  - Space-time analyses - Brittany.

## Résumé étendu (French extended abstract)

Note : les légendes des figures auxquelles ce résumé se réfère sont traduites en français.

Les écosystèmes dynamiques, caractérisés par des processus biotiques et abiotiques qui varient constamment dans le temps et l'espace, sont souvent considérés comme des systèmes fortement résilients. Ces écosystèmes, terrestres ou aquatiques, sont largement répartis à la surface du globe ; on peut citer parmi eux les dunes de sable des déserts, les zones de haute altitude, les rivières intermittentes, les estuaires ou encore les estrans rocheux de zones battues.

En zone côtière, ce sont les plages de sable macrotidales qui constituent sans doute les systèmes les plus dynamiques. Ces écosystèmes sédimentaires, formés par l'accumulation de particules mobiles soumises à l'action de la houle et des marées (FIG. 1), couvrent 70% des côtes ouvertes à l'océan. L'écosystème « plage de sable » abrite un cortège spécifique unique composé d'espèces toutes adaptées à la vie dans des conditions extrêmement variables, et il assure des fonctions essentielles auxquelles aucun autre écosystème sur la planète ne pourvoit. Par exemple, les caractéristiques physicochimiques des plages ainsi que la biodiversité qu'elles contiennent, forment un excellent système permettant de filtrer des volumes d'eau colossaux et de recycler les éléments minéraux et organiques. Les plages forment aussi des zones de nurserie et de nourricerie pour de nombreuses espèces (en particulier des oiseaux et des poissons d'intérêt commercial ou de conservation). Enfin, cet écosystème constitue, pour plusieurs raisons, un site de premier choix pour l'implantation de sociétés humaines.

La population humaine étant en développement constant, les écosystèmes côtiers sableux sont menacés par de multiples pressions d'origine anthropique, parmi lesquelles l'apport en excès de nutriments, qui constitue une menace majeure. L'eutrophisation des eaux côtières induit un déséquilibre des proportions de nutriments, qui peut se traduire par le développement d'importantes biomasses de macroalgues opportunistes. Ces blooms, communément formés de chlorophycées à court cycle de vie (macroalgues vertes opportunistes) et donc appelées *marées vertes*, se produisent à l'échelle mondiale (FIG. 2, 3). Actuellement, ce phénomène s'amplifie en termes de fréquence et d'intensité en France et dans le Monde.

La plupart des études visant à déterminer les effets des marées vertes sur la structure et le fonctionnement d'écosystèmes sédimentaires ont été conduites dans des environnements abrités, dans des systèmes micro- ou atidaux, ou ont consisté en des expérimentations semi-contrôlées. Elles ont montré que des biomasses importantes d'algues opportunistes détachées (du genre *Ulva* ou appartenant à d'autres taxons) impactent fortement plusieurs compartiments des écosystèmes sédimentaires (biochimie de l'eau, sédiments, macroalgues à long-cycle de vie, faune benthique). Plus particulièrement concernant la faune benthique, il a été montré que l'accumulation d'algues opportunistes provoquait une importante détérioration de la structure des communautés, induite notamment par des mortalités massives d'espèces dominantes ou d'espèces clés pour le fonctionnement du système.

Néanmoins, il reste beaucoup à apprendre et à comprendre des réponses *in situ* (*i.e.* dans des conditions 'naturelles' d'eutrophisation, intégrant la variabilité associée au phénomène) d'écosystèmes, et plus particulièrement d'écosystèmes dynamiques, faisant face à l'accumulation d'algues vertes opportunistes. Cette question est longtemps restée inexplorée en raison des difficultés de mise en place d'expérimentation ou d'échantillonnage inhérentes à la variabilité de ces systèmes. De plus, la détection des effets d'un stress d'origine anthropique sur la structure et le fonctionnement d'un écosystème dynamique est particulièrement complexe. Cette difficulté est liée au fait que la plupart des approches analytiques détectent les variations naturelles – de grande intensité dans le cas de systèmes dynamiques – et celles liées au stress *per se* sans pour autant parvenir à les distinguer.

Cette thèse a pour objectif principal d'étudier les effets d'un stress d'origine anthropique sur la structure et le fonctionnement d'un écosystème dynamique. Pour réaliser cet objectif, les réponses des communautés de plages de sables macrotidales où des marées vertes se produisent ont été étudiées à plusieurs échelles spatio-temporelles et en considérant différents compartiments biologiques (FIG. 4).

Quatre études ont été menées (articles I à IV) pour répondre à cette question générale et plus précisément à quatre sous-questionnements (FIG. 5) :

- Un effet des marées vertes sur la structure des communautés benthiques est-il mesurable à grande échelle spatio-temporelle ?
- L'accumulation d'ulves induit-elle des réponses différentes en fonction du compartiment biologique, de la profondeur ou du type de plage ?
- Quels sont les effets des marées vertes à fine échelle spatio-temporelle le long d'un gradient d'eutrophisation ?
- Une forte biomasse d'ulves induit-elle des modifications de la structure et du fonctionnement trophique des plages ?

Pour répondre à ces questions, des approches *in situ* ont été mises en œuvre. Elles associent des méthodes classiques et émergentes en écologie, et combinent des outils permettant d'analyser des dérives fines du système soumis à une perturbation notamment via l'étude de changements survenant le long d'un gradient de stress ou l'exploration d'interactions et de voie de transfert de carbone au sein d'un réseau trophique (Table 2).

Ce travail a permis de montrer qu'à l'échelle de la région et de manière générale (*i.e.* en intégrant la variabilité de systèmes sédimentaires sur des milliers de kilomètres et sur sept ans) les communautés benthiques de plages macrotidales sont modifiées significativement et de manière conservative (*i.e.* les effets demeurent plusieurs mois après les blooms) par la présence de marées vertes (Table 3). Au cours de cette thèse, j'ai également démontré que les marées vertes impactent différemment la faune benthique en fonction (i) du type d'habitat/de l'exposition (plages semi-exposées composées de sables hétérogènes envasés *vs.* plages exposées composées de sables propres et bien triés), (ii) de la profondeur (médolittoral inférieur *vs.* infralittoral [à 5m de profondeur]), et (iii) du compartiment biologique (macrofaune benthique *vs.* juvéniles de poissons plats). Ces comparaisons m'ont permis d'identifier la faune benthique de médolittoral inférieur des plages exposées comme étant le système le plus affecté par la présence de fortes biomasses d'ulves (FIG. 7). En étudiant plus précisément les effets des marées vertes sur les variations du zoobenthos à petites échelles spatio-temporelles, j'ai montré que selon un gradient de couverture d'algues vertes (de 'pas de marée verte' à 'couverture homogène d'ulves'), les caractéristiques faunistiques - univariées et multivariées - sont significativement modifiées le long de ce gradient. Par exemple, la diversité bêta, correspondant à la variance totale au sein d'une communauté, décroît en présence de marées vertes : la valeur médiane de diversité  $\beta$  du site uniformément couvert d'ulves est significativement inférieure à celle du site non impacté (FIG. 8). Ces réponses correspondent à une dérive de l'écosystème impacté par les marées vertes, qui se traduit par un changement de la structure des communautés au cours du temps. Afin d'explorer les processus pouvant expliquer ces patrons, et déterminer si ces changements ont des répercussions sur le fonctionnement de l'écosystème « plage de sable », j'ai étudié les effets de l'accumulation d'ulves sur la structure et le fonctionnement du réseau trophique à différents niveaux (des sources/producteurs primaires jusqu'aux consommateurs secondaires). Cette étude a révélé qu'une importante biomasse d'ulves induit un changement de la structure entière du réseau trophique (avec un décalage significatif des niches trophiques, spécifiques à une espèce et à la communauté entière) et une modification importante du fonctionnement trophique des plages (avec la simplification du réseau : une seule voie de transfert du carbone en présence d'ulves, contre des voies multiples dans le système non impacté) (FIG. 9). J'ai montré que ces changements étaient liés à des effets directs (consommation directe de débris d'ulves par des consommateurs) et indirects (modifications des autres sources de nourritures liées à l'activité photosynthétique de fortes biomasses d'ulves ou à leur dégradation) de la présence d'ulves à différents niveaux trophiques. Ces changements sont conservés dans le temps et le long de la chaîne trophique, se répercutant ainsi sur la structure et le fonctionnement de la communauté et du réseau trophique dans leur ensemble. Les résultats de cette thèse sont récapitulés et présentés de manière synthétique sous la forme d'un schéma conceptuel (FIG. 10).

Cette thèse remet en cause la résilience des écosystèmes dynamiques. En effet, ma thèse démontre les effets subtils mais très significatifs d'un stress *per se* sur la structure et le fonctionnement d'un système très variable dans le temps et l'espace. A travers l'étude des réponses de la macrofaune benthique des plages de sable macrotidales impactées par les marées vertes, cette thèse propose donc un cadre de travail visant à mieux détecter les effets de stress anthropiques sur la structure et le fonctionnement d'écosystèmes dynamiques (FIG. 11). Là où des indicateurs de santé/qualité des écosystèmes échouent à déceler les effets d'une perturbation dans un milieu très variable naturellement, je propose d'allier des méthodes de suivi *in situ* dans le temps et le long de gradient de stress, à une approche analytique permettant de tester les interactions espace-temps, afin de mettre en évidence les dérives ténues d'un système dynamique soumis à un stress. Cette démarche pourrait être renforcée par l'étude des performances (d'un point de vue fonctionnel) d'un écosystème impacté ou non par un stress. Cette perspective pourrait s'appuyer sur l'analyse conjointe des traits biologiques exprimés par les espèces formant un écosystème et de leurs interactions trophiques, informant l'identité fonctionnelle sous-jacente d'un système. Dans un contexte de changement global forçant les écosystèmes à faire face à de multiples stress, cette approche pourrait se révéler particulièrement utile pour démêler, comprendre et prédire les effets de perturbations induites par les activités humaines sur le fonctionnement des écosystèmes et constituer une aide à la gestion de ces environnements particuliers dans le cadre de la Directive Cadre pour le Milieu Marin, ou d'Aires Marines Protégées.

Mots-clés : Marées vertes – *Ulva* spp. – Eutrophisation – Ecosystèmes dynamiques – Plages de sable fin – Régime macrotidal - Macrofaune benthique - Poissons plats - Structure des communautés - Structure des réseaux trophiques - Fonctionnement trophique – Isotopes stables  $\delta^{13}\text{C}$  et  $\delta^{15}\text{N}$  - Analyses spatiales et temporelles - Bretagne.

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## List of original papers

**I** Quillien N, Nordström MC, Guyonnet B, Maguer M, Le Garrec V, Bonsdorff E & Grall J (2015) Large-scale effects of green tides on macrotidal sandy beaches: habitat-specific responses of zoobenthos. *Estuarine, Coastal and Shelf Science* 164: 379-391.

**II** Quillien N, Nordström MC, Le Bris H, Bonsdorff E & Grall J (*manuscript*) Green tides on inter- and subtidal sandy shores: differential impacts on infauna and flatfish.

**III** Quillien N, Nordström MC, Gauthier O, Bonsdorff E, Paulet YM & Grall J (2015) Effects of macroalgal accumulations on the variability in zoobenthos of high-energy macrotidal sandy beaches. *Marine Ecology Progress Series* 522: 97-114.

**IV** Quillien N, Nordström MC, Schaal G, Bonsdorff E & Grall J (2016) Opportunistic basal resource simplifies food web structure and functioning of a highly dynamic marine environment. *Journal of Experimental Marine Biology and Ecology* 477: 92-102.

Contributions to the individual papers:

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Design & methods	JG, NQ, EB, MCN	NQ, EB, JG	NQ, OG, MCN, EB, JG	NQ, MCN, JG
Data collection	MM, VLG, BG, JG	NQ, HLB, JG*	NQ, JG*	NQ, GS, JG*
Data analyses	NQ	NQ	NQ, MCN, OG	NQ
Manuscript preparation	NQ, MCN, BG, MM, VLG, EB, JG	NQ, MCN, HLB, EB, JG	NQ, MCN, OG, YMP, EB, JG	NQ, MCN, GS, EB, JG

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## 1. Introduction

Marine soft sediments constitute the most widespread interface environment on the planet (Gray & Elliott 2009). Loose by nature, sediment substratum form three-dimensional habitats harbouring a unique diversity and sustaining essential ecological functions (Schlacher et al. 2008, Gray & Elliott 2009). Often influenced by tides, and reworked by waves within coastal areas, they constitute highly variable systems both in space and time (McLachlan & Brown 2006, Dobson & Frid 2009). Nowadays, coastal ecosystems suffer from significant anthropogenically induced disturbances (Gray 1997, Halpern et al. 2008, Defeo et al. 2009), among which one of the most widespread is the eutrophication of coastal waters (Grall & Chauvaud 2002, Diaz & Rosenberg 2008, Liu et al. 2013, Korpinen & Bonsdorff 2015). One symptom of the release of excess nutrients into the system is the development of high biomasses of opportunistic green

macroalgae, also called “green tides” (Cloern 2001, Ye et al. 2011, Liu et al. 2013), which are currently increasing in frequency and intensity worldwide (Ye et al. 2011). Understanding how coastal sediment ecosystem structure and function are affected by eutrophication in the form of opportunistic macroalgal blooms is thus a current issue in ecology (Lyons et al. 2014, Korpinen & Bonsdorff 2015). Many studies have identified and characterised responses of coastal sediment benthic communities to eutrophication-induced macroalgal blooms, yet most of these studies were conducted within sheltered, non- or micro-tidal systems, or involved semi-controlled experiments in the field (Norkko & Bonsdorff 1996a, b, Bolam et al. 2000, Ouisse et al. 2011). Disentangling the effects of natural variation from anthropogenically induced variability within highly dynamic ecosystems, is far more challenging and require new approaches (Elliott & Quintino 2007).

### 1.1. Physically harsh and dynamic systems

Abiotic and biotic processes under continuous and strong changes in space and time, together form dynamic and resilient ecosystems. Such systems are commonly found, both in terrestrial and aquatic environments. For example, desert sand dunes, high alpine areas, intermediate rivers, estuaries and exposed rocky shores, all constitute highly variable ecosystems (Whitford 2002, Moser et al. 2005, Denny 2006, Elliott & Quintino 2007, Datry et al. 2015). The biota inhabiting these environments experiences extreme variation of most abiotic variables (temperature, exposure to wind and waves, strength of currents, loose nature of substratum), while only few specialized species are adapted to live in such harsh systems (Connell 1978, Defeo & McLachlan 2005). When considering marine environments, studies show that three main abiotic variables predominantly shape communities: the wave energy, the tidal regime, and the nature of the substratum (Dobson & Frid 2009).

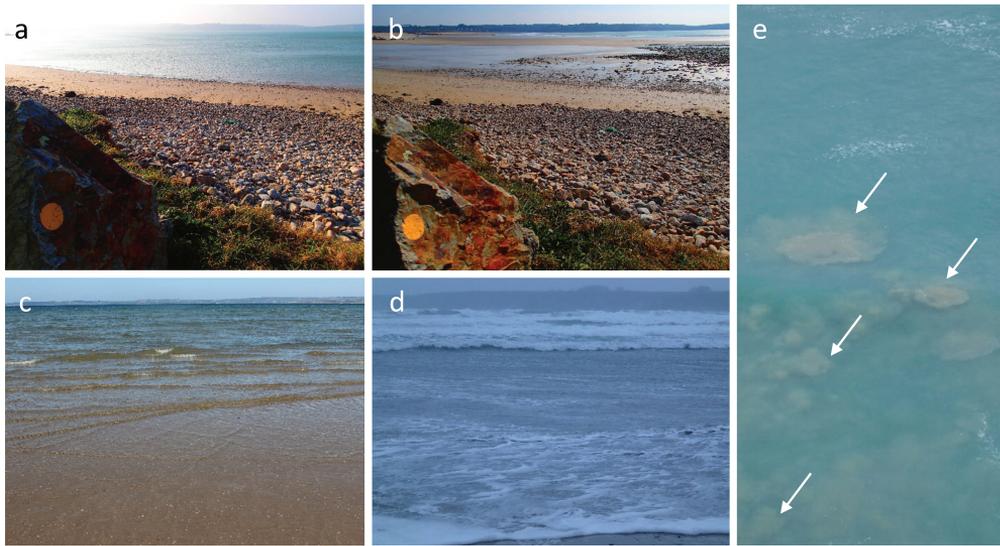
Within coastal ecosystems, the nature of the substratum can be divided into two categories. Non-mobile substrata, also defined as 'hard' substrata, are, contrary to 'soft' ones, composed of non-mobile particles. This structural contrast has profound effects on the composition of communities that develop there (Dobson & Frid 2009). In particular, mobile substrata imply a relatively unstable habitat. In order to withstand such instability, species inhabiting mobile sediments are primarily burrowers that have strong abilities to quickly move among, and maintain themselves in, mobile particles (Scapini 2014). For example, the mollusc bivalves of the genus *Donax* have a large and powerful foot that makes them able to re-settle quickly in the sediment to regain their position after being swept by waves (De la Huz et al. 2002, McLachlan & Brown 2006).

One extreme variation that a marine system can experience, is the cyclic shift between aquatic and terrestrial conditions (Datry et al. 2015), resulting from periodic movements of the sea: the tides (FIG.1 a, b). These shifts occur at different

temporal scales, with flood and ebb tides alternating daily or twice daily, and neap and spring tides alternating every 15 days. Depending on the bathymetry and on the volume of water adjacent to the coast, the tidal range (TR; the difference between spring high and low tides, expressed in meters) may differ. Consequently, non-tidal (TR = 0m), microtidal ( $0 < TR < 4\text{m}$ ) and macrotidal ( $TA \geq 4\text{m}$ ) regimes are distinguished (Allaby 2010). Due to water retention in-between particles, sediment systems are less subject to desiccation compared to hard substratum (McLachlan & Brown 2006). Nonetheless, intertidal sediments face extreme temperature changes, and occasionally drop in salinity. These conditions are constantly fluctuating because of tidal influences. Tides also induce currents that are comparable in magnitude to flows in streams and rivers (Dobson & Frid 2009), but wave energy may exceed such currents in terms of transferred energy in open areas.

Waves are well-known attributes of marine systems, transferring energy from winds at sea to the coastal zone (McLachlan & Brown 2006, FIG.1c, d). When they break on- or near-shore, they impose great hydrodynamic forces on substrate and living organisms (Denny 2006, McLachlan & Brown 2006, Short & Jackson 2013). Wave energy and exposure to wave action have been identified as key explanatory variables of species abundance and diversity across large spatial scales and different ecosystems (McLachlan & Dorvlo 2005, Denny 2006). When breaking on sedimentary systems, waves may induce deep reorganization of particles by resuspension in the water column (FIG. 1e) or movements close to the seabed (McLachlan & Brown 2006), thus increasing the variability of the soft substratum.

Macrotidal sandy beaches, with mobile particles that are effectively reworked by waves, tides and currents, form an ecosystem that is subject to the combination of these three main variables, which makes them highly dynamic and variable environments (FIG. 1).



**FIG. 1.** Photographs of the Anse of Dinan (Brittany, France) showing variation in energy within a macrotidal sandy beach; a) high tide, b) low tide, c) low wave action, d) high wave energy, e) resuspension of particles after a wave has broken, the arrows denote some sedimentary whirls. Pictures: N.Q. *Photos prises dans l'Anse de Dinan (Bretagne, France) illustrant l'énergie diffusée sur une plage macrotidale et ses variations; a) marée haute, b) marée basse, c) énergie de la houle faible, d) énergie de la houle intense, e) mise en suspension de particules après le passage d'une vague, les flèches blanches indiquent les tourbillons sédimentaires. Clichés : N.Q.*

## 1.2. The sandy beach ecosystem

Sandy beach ecosystems constitute 70% of the world's ice-free coastline (McLachlan & Brown 2006). Sandy beaches (SBs) can be defined as accumulations of fine sediment along coastlines (Davis 2015), and this thesis mainly focusses on exposed beaches of pure sand, although the later are compared to more sheltered beaches composed of heterogeneous sediments (mud, sand, coarse sediments). However, this description focussing on the material composing beaches is limited and often unfairly associates these systems with lifeless deserts (McDermott 1983). Conversely, these ecosystems contain a highly specialised fauna and provide ecological functions that are not supported by any other ecosystem on earth (McLachlan & Brown 2006). They also provide prime sites for human recreation and other uses, which turn them into ecosystems under high anthropogenically-induced stress (Schlacher et al. 2007, Defeo et al. 2009).

### *Biodiversity and functioning*

The species inhabiting SBs are uniquely adapted to withstand the natural stress induced by the high variability of physicochemical conditions affecting these systems (McLachlan & Brown 2006, Scapini 2014). One could also say that they

“need/require” this dynamism/harshness to exist, and natural stress can thus be viewed as a subsidy, *i.e.* a perturbation with a positive effect on the system (Costanza et al. 2002). This effect ensures the development of a diverse fauna: a sandy beach can hold hundreds of species of invertebrates when their smallest forms are included (Armonies & Reise 2000). Most non-symbiotic marine phyla are represented in coastal sands, while polychaete annelids, bivalve and gastropod molluscs and crustacean arthropods are those most commonly found within sandy beaches. The absence of attached macrophytes, together with the presence of a rich surf-zone phytoplankton production and of macrophyte wrack subsidies (Dugan et al. 2003, McLachlan & Brown 2006, Rodil et al. 2008), both dictate dominant feeding traits of biota (McLachlan & Brown 2006) within SB systems. Most SB invertebrates are filter- and/or deposit feeders, while fewer are scavengers and predators (Schlacher et al. 2008).

Sandy beach organisms form assemblages that are shaped by not only physical variables, but by biological interactions and coastal processes related to food availability (Defeo & McLachlan 2005, Lastra et al. 2006, Barboza & Defeo 2015). Sandy beach species inter-specific relationships and

biological traits, together with intrinsic physico-chemical characteristics of SB ecosystems, sustain a large spectrum of essential functions (McLachlan & Brown 2006, Schlacher et al. 2008). For instance, SB porous sands form an excellent “digestive and incubating system” that filters large amounts of water, and along with the SB biota, processes organic material and recycles nutrients (Schlacher et al. 2008). In addition, sandy beaches assume key biological and conservation roles by linking coastal dune and nearshore sandy systems, as well as by providing essential nursery and foraging areas for many species (in particular for fish, birds and turtles) (McLachlan & Brown 2006). SB ecosystems also support many commercial and artisanal/recreational fisheries, most notably for bivalves (*e.g.* Donacidae) and fishes (*e.g.* Moronidae).

#### *An environment under multiple stresses*

Contrary to natural subsidy, sandy beaches suffer from a wide range of anthropogenically induced disturbances. As the human population is constantly growing, and because SB systems are highly valued by society (Davis 2015), these ecosystems are under high anthropogenic pressure (Schlacher et al. 2007, Defeo et al. 2009). Along with many other ecosystems, SBs are expected to be negatively affected by global change (Schoeman et al. 2014). In addition, the exploitation of beach systems and the development of coastal areas affect both morphodynamics and species assemblages of SBs (Defeo & de Alava 1995, Dugan et

al. 2008). Sandy beach ecosystems are also affected by various pollutions either constituting sporadic events, or occurring more widely and more frequently.

### 1.3. Green tides: major threats to coastal ecosystems

Among the multiple human-induced threats affecting marine ecosystems, the release of excess nutrients to coastal waters is of major concern (McClelland & Valiela 1998, Cloern 2001, Diaz & Rosenberg 2008, Liu et al. 2013, Lyons et al. 2014, Korpinen & Bonsdorff 2015). This alteration of water quality is mainly induced by the shift to artificial fertilisers in agriculture during the past fifty years, wastewater treatment plants, and urban runoff, all related to growing human population in coastal areas (Bricker et al. 2008, Korpinen & Bonsdorff 2015). Increased concentrations in nitrogen and phosphorous induce changes in nutrient ratios, and lead to the eutrophication of coastal ecosystems (Nixon 1995). This process is reflected by three main symptoms: the development of (i) short-lived macroalgal blooms, (ii) harmful microalgal blooms, and (iii) the reduction of oxygen content in the seawater leading to coastal hypoxia (Cloern 2001, Diaz & Rosenberg 2008). The eutrophication of coastal water occurs worldwide (FIG. 2), and especially coastlines from developed countries. Along these particularly populated areas, the three eutrophication symptoms often occur together, but are rarely studied

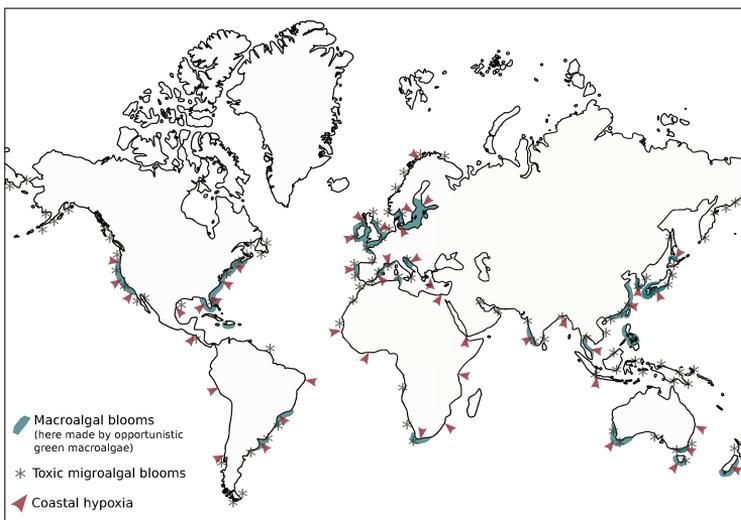
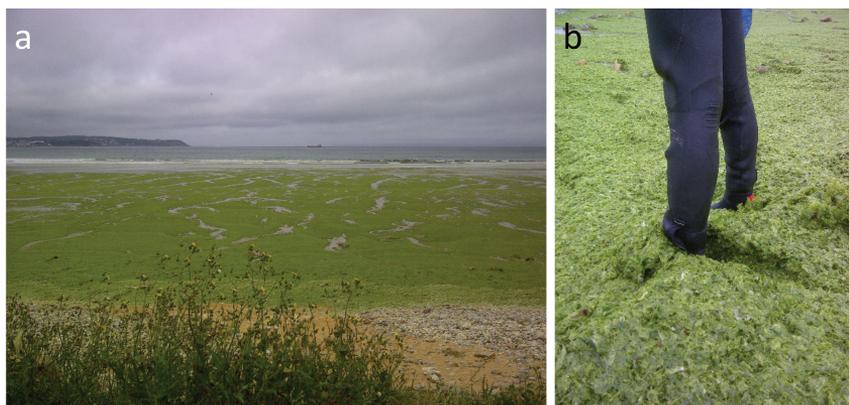


FIG. 2. Worldwide blooms formed by green macroalgae (*i.e.* green tides), toxic microalgal blooms, and coastal hypoxia distribution during the past three decades; information shown here is the combination of several maps presented in the following publications: in Anderson et al. (2015), Ye et al. (2011), Diaz & Rosenberg (2008), Korpinen & Bonsdorff (2015). Répartition mondiale des blooms de macroalgues vertes opportuniste (*i.e.* marées vertes ; zones de couleur turquoise), microalgues toxiques (astérisques) et d'hypoxie côtière (flèches). Les informations présentées ici sont issues de plusieurs cartes publiées dans les articles suivants : Anderson et al. (2015), Ye et al. (2011), Diaz & Rosenberg (2008), Korpinen & Bonsdorff (2015).

**FIG. 3.** Photographs of green tides in Brittany, France. (a) *Ulva* spp. stranding on a sandy shore in the Bay of Douarnenez at low tide. (b) Progressing by feet in stranding green algae before sampling. Pictures: N.Q. *Photos de marées vertes prises en Bretagne, France. (a) Des ulves échouées sur une plage en Baie de Douarnenez à marée basse. (b) La traversée d'une marée verte pour se rendre sur un point d'échantillonnage. Clichés : N.Q.*



simultaneously. However, as shown on the map (FIG. 2), macroalgal and microalgal blooms, and hypoxia, do not always co-occur. This suggests that the concept of multiple secondary effects of eutrophication is valid, and thus the study of the effects of one specific symptom is important. In the present work, special focus is given to macroalgal blooms, which are mainly composed by opportunistic Chlorophyceae, and thus called green tides. Green tides (hereafter GT) are defined as “vast accumulations of unattached green macroalgae” (Ye et al. 2011) (FIG.3). More specifically, GT are formed by green opportunistic macroalgae (mainly the taxa *Ulva*, *Chaetomorpha* and *Cladophora*), which are fine and fragile (Schramm 1999) and can easily be detached and transported by coastal currents, and ultimately strand on or float along beaches or in shallow bays (Grall & Chauvaud 2002). Such accumulations far exceed, in terms of extent/coverage and biomass (FIG. 3a, b), seaweed wrack subsidies that commonly strand in the supralittoral zone (Rodil et al. 2008). The development of green macroalgal blooms is controlled by nutrient concentrations, light and temperature. Eutrophicated sandy beaches are ideal places for the development of GT as they offer shallow, well mixed waters, which may warm up easily during spring in temperate systems (Ménesguen & Piriou 1995).

The persistency, frequency and intensity of opportunistic macroalgal blooms have dramatically increased since the 1980's in many regions along the global coastlines (Sfriso et al. 1992, Ménesguen & Piriou 1995, Valiela et al. 1997). Massive blooms of *Ulva* spp. have for example developed in China covering large part of the

Yellow Sea (Liu et al. 2013), as well as in Brittany (northwestern France), where GT affect more than 80 sites and have started to expand to other regions in France (Normandie, Aquitaine) during the past five years (CGDD 2014). Globally, this phenomenon is currently spreading and increasing worldwide (Ye et al., 2011).

Such macroalgal accumulations have strong impacts on several faunal groups of soft-sediment ecosystems (see Raffaelli et al. 1998, Grall & Chauvaud 2002, Lyons et al. 2014, Korpinen & Bonsdorff 2015 for reviews). The accumulation of high biomasses of opportunistic macroalgae modifies the biochemistry of the water column through significant uptakes of dissolved oxygen at night (Sundbäck et al. 1996) and light carbon ( $^{12}\text{C}$ ) during photosynthesis (Van Alstyne et al. 2015). Macroalgal blooms also change sediment characteristics, and impact other primary producer (such as perennial macrophytes, eelgrass, and salt-marsh plants) communities (Cloern 2001, Hauxwell et al. 2001, Watson et al. 2015, Green & Fong 2016). At high biomasses, opportunistic macroalgal accumulations also alter the recruitment, community structure and production of benthic fauna, including meiofauna, macrofauna, and flatfish (Hull 1987, Baden et al. 1990, Bonsdorff 1992, Raffaelli et al. 1998, Franz & Friedman 2002, Pihl et al. 2005, Nordström & Booth 2007, Lyons et al. 2014). For instance, changes in macrofauna community structure have been investigated by Norkko and Bonsdorff (1996a) in an experimental study. The authors showed that structural differences between assemblages sampled at control and algae-covered plots appeared after 9 days, and that the sediment benthic com-

munity broke down after 16 days of algal cover. Structural changes in benthic communities were mainly induced by massive die-offs of dominant and key players (Norkko & Bonsdorff 1996b).

However, most of the studies focussing on the effects of eutrophication induced macroalgal accumulations on marine ecosystems have been conducted within sheltered environments (e.g. mud flats; Ouisse et al., 2011; Raffaelli et al., 1998). They also have involved semi-controlled experiments in the field (Norkko & Bonsdorff 1996a, b, Bolam et al. 2000), and have mostly addressed the question within micro- or non-tidal systems (Norkko & Bonsdorff 1996a, Thiel et al. 1998). Much still remains to be understood regarding the effects of human-induced pressures within highly dynamic systems, such as open macrotidal sandy beaches, where tidal regime is an additional factor to the variability of coastal marine systems (see section 1.1).

#### 1.4. Detecting anthropogenic stress within dynamic systems

When human-induced pressures overlap with highly variable and naturally harsh systems, the constantly changing characteristics of these dynamic systems make it difficult to distinguish variability due to natural subsidy (Costanza et al. 2002) from anthropogenically induced variation. More specifically, even though many numerical methods have been developed to identify effects of anthropogenic pressure through the study of benthic communities (see for example Grémare et al. 2009, and Culhane et al. 2014 for a review), the approaches still detect natural and anthropogenic forcing without distinction. This leads to a decrease in the ability of detecting the signal (stress *per se*) to noise ('natural' variation) ratio (Elliott & Quintino 2007). The difficulty of detecting human-induced stress in harsh and dynamic systems is defined as the 'Estuarine Quality Paradox', first described by Dauvin (2007), then theoretically

developed by Elliott & Quintino (2007). This paradox has recently been extended to sandy beach systems (Daief et al. 2014).

In order to identify anthropogenic impacts on dynamic ecosystems, the authors of the above mentioned studies propose that the manifestation of subsidy (i.e. natural dynamic system biological characteristics) needs to be separated from signs of the stress *per se* (i.e. anthropogenic dynamic system biological characteristics). Achieving such a separation is not effortless, and according to Elliott and Quintino (2007), the best way to distinguish between natural and human-induced variability is the *in situ* study of structural and functional aspects of benthic communities within both pristine and impacted dynamic systems. Indeed, creating or maintaining harsh conditions within mesocosms or experimental settings is hardly feasible (but see Kraufvelin et al. 2009) and may produce unrealistic results and interpretations. Furthermore, the assessment of food webs provides a quantitative framework that combines both community and ecosystem ecology approaches, and thus unifies the study of biodiversity and ecosystem function (Thompson et al. 2012). Given that carbon transfer may be affected by some anthropogenically induced disturbances (e.g. green tides; Valiela et al. 1997), investigating trophic relationships in impacted dynamic environments would also be valuable to understand functional shifts in such environments. Finally, a way of disentangling anthropogenic and natural forces acting in a system is the simultaneous investigation of spatial and temporal variation within communities, aiming at understanding spatial variations through time, or conversely temporal variation among sites (Legendre & Gauthier 2014). The combined use of the approaches listed here would help at answering the non-trivial question of how highly dynamic ecosystems respond to anthropogenic stress, as has been done in some other systems (Thrush et al. 1998, Hewitt et al. 2007).

## 2. Aims of the thesis

The overall aim of my thesis was to investigate the effects of anthropogenic stress on the structure and the functioning of highly dynamic ecosystems. This was achieved by determining the responses of benthic communities inhabiting open macrotidal sandy systems to the presence of green tides. I have explored how dynamic system benthic communities respond to the presence of high biomass of *Ulva* across different spatial and temporal scales, and between habitats, as well as across two different biological compartments (FIG. 4).

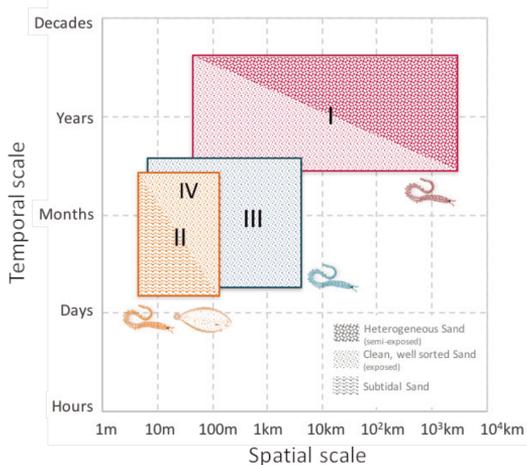


FIG. 4. Spatial and temporal scales covered by the specific papers presented in this thesis (I-IV). The colours of boxes refer to those used in the conceptual diagram illustrated in FIG. 5, except for paper II. The illustrations denote the communities studied in each paper: macroinfauna and flatfish (papers II, IV), or exclusively macroinfauna (papers I, III). *Schéma montrant les échelles temporelles et spatiales couvertes par les différentes études menées au cours de cette thèse (I-IV). Les couleurs des boîtes utilisées ici font référence à celles employées dans le diagramme conceptuel de la FIG. 4, à l'exception de celle utilisée pour l'article II. Les symboles illustrent les différents compartiments benthiques étudiés : macrofaune et poissons plats (articles II et IV), et seulement la macrofaune (articles I et III).*

First, to answer the overall question of the PhD thesis (*i.e.* do green tides impact dynamic ecosystem communities?), I focussed on the responses of macrofauna inhabiting sandy systems in early spring (several months after blooms of *Ulva*), across large spatial and temporal scales (paper I). I thus investigated long-lasting effects of green tides on benthic community structure, despite the high variability existing between study sites. Additionally, I explored potential differential responses of benthic communities to the presence of *Ulva* mats (*i.e.* dense accumulations of stranding or floating *Ulva*), depending on (i) the beach

type/the exposure (heterogeneous muddy- vs. well-sorted clean- sands, paper I), and (ii) the depth (shallow subtidal vs. low-intertidal, paper II). Further, I examined the responses of two different faunal groups, namely macroinfauna and flatfish, to the presence of GT (paper II). The results of papers I and II lead me to specifically focus on responses of macrofauna inhabiting well-sorted sand at low-shore of macrotidal sandy beaches. Considering this habitat, I investigated the variability in zoobenthos at small spatial and temporal scales, along a gradient of eutrophication by *Ulva* (paper III). And within this habitat, I ultimately assessed the effects of green tides on the functioning of highly dynamic ecosystems, studying trophic relationships and food web structure (paper IV). More specifically, I explored direct and indirect influence of *Ulva* at several trophic levels (from basal resources to predators) and complexity levels (from species-specific to community-wide responses) in order to highlight potential impact on carbon transfer in eutrophicated macrotidal sandy beaches (paper IV). These four interlinked studies explore how highly dynamic systems respond to anthropogenic pressure (FIG. 5).

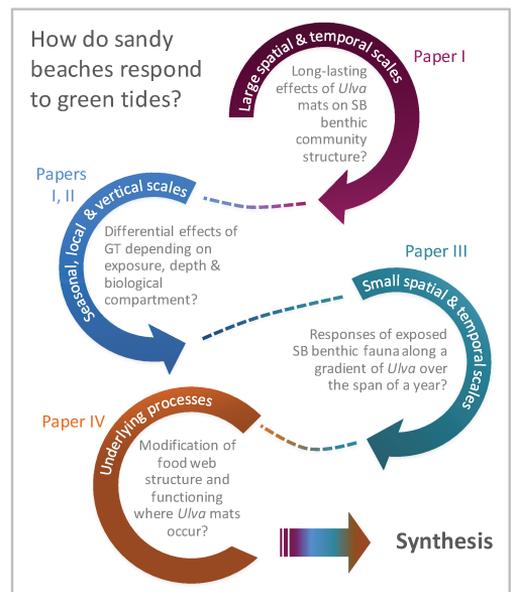


FIG. 5. Conceptual diagram showing the main questions addressed in the four papers (I-IV), as well as the logical links between each study, which build up upon each other at several scales. *Diagramme conceptuel montrant les principales questions traitées dans les articles I-IV, et illustrant la logique générale de cette synthèse, précisant notamment les liens entre chacune des questions et des études.*

In order to answer the main questions (FIG. 5), *in situ* integrative studies were designed, and classic, as well as novel approaches in ecology were used; they are described below.

### 3. Material and methods

As the questions asked in this thesis are intricate, data were required on a number of spatial and temporal scales, including abiotic and biotic variables. The following section provides overall information on data collection, on the study areas and communities, and briefly describes the analytical techniques used in papers I-IV. The basic field- and analytical methods were the same in all of the studies. However, for certain questions, specific custom-made sampling designs were used. Detailed descriptions of materials and methods are found in the individual papers.

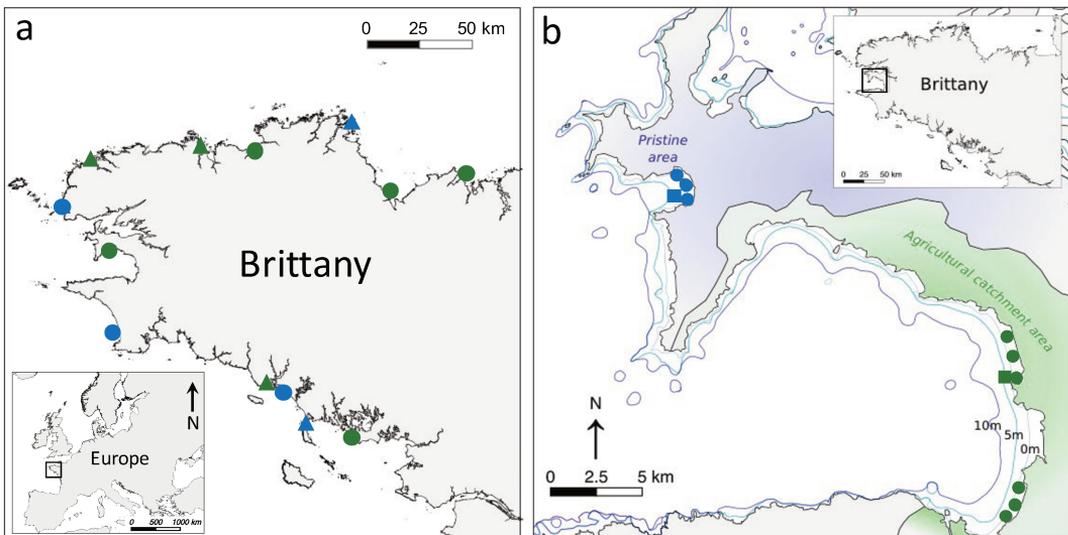
#### 3.1. Multiscale study areas

The studies for papers I-IV were conducted at 24 different sites, spread across different spatial scales, both vertical and horizontal (Fig. 5, 6). The studies were all designed to examine temporal patterns (from month to multi-year), *i.e.* they encompass large temporal variability, and intend to investigate dynamic responses of an ecosystem

under anthropogenic stress, rather than steady states. In addition, the four studies were all conducted in the field, under “natural” conditions. Such a setting, embracing broad spatial and temporal scales *in situ*, leads to an increase in generality (Hewitt et al. 2007). The study sites were selected based on the availability of data (paper I), the research history of some specific areas and the occurrence of gradients of anthropogenic stress (papers II-IV).

#### Across wide coastal areas (the regional scale)

The studies were all conducted in Brittany (Fig. 6a, b); the first one was designed to encompass patterns in this whole area (paper I) (Fig. 6a), which is located in northwestern France, with a total coastline spanning 2730km (<http://www.bretagne-environnement.org>). Greatly indented, the coast of Brittany harbours numerous sandy beaches ranging from hundreds of meters to several kilometres in length and width. This region’s extensive shoreline shows a macrotidal regime, which ranges from 5 to 13m. The area also constitutes an occidental cape of the European continent, and SBs lining its coasts are actively influenced by big, unhindered, Atlantic waves. Coastal sediment ecosystems are there dominated by highly dynamic, open macrotidal sandy beaches.



**FIG. 6.** Location in Brittany (NW France) of the 24 exposed (circles/squares) and semi-exposed (triangles) sandy sites sampled in this thesis (papers I-IV); at low-intertidal (circles) and at shallow subtidal (squares) sites impacted (green) or not (blue) by green tides. (a) Location in Brittany of the 13 sandy beaches investigated in paper I. (b) Location of the 9 study sites sampled in paper III, of the four study sites (squares and adjacent circles) sampled in paper II, and of the two study sites (circles adjacent to squares) sampled in paper IV. Localisation (Bretagne, Nord-Est de l'Europe) des 24 sites échantillonnés durant cette thèse (articles I-IV) en mode battu (cercles/carrés) ou semi-battu (triangles) au niveau du médiolittoral inférieur (cercles) et de l'infralittoral supérieur (carrés) impactés (vert) ou non (bleu) par les marées vertes. Plus précisément, les 13 plages étudiées dans l'article I sont localisées le long des côtes bretonnes (a), les 9 sites échantillonnés dans l'article III sont représentés par des cercles (b) et les quatre sites échantillonnés dans l'étude II sont symbolisés par les carrés et les deux cercles adjacents à ces derniers (b).

Located at mid latitudes between the English Channel and the Atlantic Ocean, as well as at the boundary between Northern European Seas and Lusitanian provinces within the ‘temperate Northern Atlantic’ realm, Brittany is an area where Nordic and Mediterranean influences meet. This geographical characteristic makes this region a marine biogeographical transition zone (Glémarec 1978, Dauvin et al. 2006, Spalding et al. 2007). There, an abstract boundary appears where species with both “warm” and “cold” affinities inhabit the same region, which is an interesting feature in a global change context (Spalding et al. 2007).

For instance, two mollusc bivalve species from the Donacidae family (*Donax trunculus* and *D. vittatus*) coexist in Brittany as they respectively have their northern and southern distribution limits there. As a whole, breton macrotidal sandy beaches thus harbour a rich biodiversity (Deniel 1973, Glémarec 1973), while they also provide essential feeding and nursery habitats for commercially important species such as the clam *D. trunculus* and the flatfishes *Scophthalmus maximus* and *Pleuronectes platessa* (Guillou 1980, Quiniou 1986). The REBENT program is a large-scale monitoring of Brittany’s coastal ecosystems that was initiated through the water framework directive, and investigates sandy beach biodiversity since 2003. This program provides constant and quality-controlled annual data, which I have used in **paper I**.

Because of the large establishment of intensive livestock farms in Brittany, this area at the same time registers the highest nitrogen surplus amounts in France, and, together with the Netherlands, in Europe (Campling et al. 2005). This great load of nutrients on land directly affects Breton coastal water quality and nutrient ratios through runoff. Due to the great number of small catchment areas, eutrophication occurs locally along Brittany’s coastline, but is widespread, as the intensive agricultural activity is highly developed in the region. Thus, more than fifty open macrotidal beaches and thirty mud flats showed *Ulva* accumulations in 2013 (CGDD 2014). Brittany thus offers a great study location for investigating the effects of the accumulation of opportunistic macroalgae on the structure and the functioning of highly dynamic ecosystems such as macrotidal sandy beaches.

### *Studying variability along sandy beaches (the local scale)*

Studies conducted for **papers II-IV** took place in the Bay of Douarnenez (Fig. 6b). Located in the west of Brittany, the bay harbours fine siliceous sands, greatly reworked by hydrodynamics, which provide suitable habitats for many species (Augris et al. 2005). This area was a key study site four decades ago, when researchers from the Laboratoire d’Océanographie Biologique of the University of Brest conducted surveys in both intertidal and subtidal areas, with the aim of characterizing benthic communities (meiofauna, macrofauna, flatfish) living within sandy systems (Guillou 1980, Bodin 1984, Quiniou 1986). The site is also locally threatened by the occurrence of green tides, which have appeared there both in intertidal and subtidal areas (Merceron & Morand 2004) and approximately a decade after the first blooms of noticeable importance in northern Brittany (*i.e.* 1980’s). Sandy shores located below the agricultural catchment area (FIG. 6b) experience annual *Ulva* bloom events (from spring to autumn) (Mènesguen & Piriou 1995, Charlier et al. 2007).

### *From inshore to nearshore sands (the vertical scale)*

Shallow subtidal and low-shore intertidal habitats are connected, both structurally (with seasonal exchange of sand and organic debris between the two habitats) and biologically (with tidal and seasonal migration of species) (McLachlan & Brown 2006, Schlacher et al. 2008). Because the eutrophication in the form of *Ulva* mats affect both intertidal and subtidal habitats, this thesis also investigated benthic community responses along an inshore-nearshore gradient, thus exploring vertical scale processes. Within the bay of Douarnenez, two sites were sampled at 5m depth, one did not have green tides, the other was regularly impacted by *Ulva* accumulations. These two sites were directly connected with two other sites located at low-intertidal, which were sampled simultaneously (Fig. 5b).

### *Elucidating processes over time (temporal scales)*

Different benthic community responses to the occurrence of green tides were explored over temporal scales: intra- as well as inter-annual successional patterns were analysed throughout **papers I-IV**. Thus, this thesis not only encom-

passes spatial variation, but also considers and integrates temporal variation in the study of dynamic system responses to anthropogenic stress. This approach enabled the use of some innovative methods to test space-time interactions (Legendre et al. 2010), which offers ways to detect and characterize subtle responses of communities to changes in their environment.

### 3.2. Communities studied

One of the most effective ways to track anthropogenically induced changes in an ecosystem is the study of multispecies ecological communities (Legendre et al. 2010). More specifically, as many zoobenthic organisms have relatively sedentary habits and long lifespan, and live at a strategic position at the water/sediment interface, benthic assemblages may exhibit clear responses to changing environmental conditions (Pearson & Rosenberg 1978, Grall & Glémarec 1997, Nyitrai et al. 2012). In addition, considering several biological faunal groups that are linked (through trophic interactions for example) is crucial to assess potential knock-on effects of environmental stress within an entire system. In this thesis, a large range of species from several groups that are part of sandy ecosystems were sampled: macroinfauna (I-IV), flatfish (II, IV), and meiofauna (nematodes only, IV). In total, the work is based on the study of 360 species from 9 phyla (Table 1) and thus encompasses a large spectrum of species- and community-level structural and functional responses.

**Table 1.** List of the phyla and their respective number of species or taxa included in the four studies (I-IV). *Nombre d'espèces ou de taxons appartenant aux huit phylums échantillonnés dans les quatre études menées pour cette thèse (articles I-IV).*

	Paper I	Paper II	Paper III	Paper IV
Annelida	102	44	26	13
Arthropoda	95	42	29	15
Chordata	-	6	-	6
Cnidaria	12	7	3	3
Hemichordata	-	1	-	1
Mollusca	58	20	6	10
Nematoda	-	-	-	1
Nemertea	5	5	4	6
Sipuncula	3	1	1	-
Total n of taxa	275	126	69	54

### 3.3. Field sampling

Sampling design and methods were consistent across the four studies, depending on the biological compartment and the habitat considered. Across papers I-IV, environmental variables were also measured or gathered from publicly available data set. Details regarding the sampling methods are provided below.

#### *Benthic communities*

At intertidal sandy beaches, macroinvertebrates (animals larger than 1mm) were sampled using a tube-corer (inner diameter: 11.3cm; depth: 15cm). To obtain faunal samples covering an area of 300cm<sup>2</sup>, three cores (taken ca. 40cm apart) were pooled to one sample. At each sampling site, three such replicate samples were randomly taken 1 to 2m apart. At subtidal sites, infauna was sampled using a Smith-grab (surface = 0.1m<sup>2</sup>), and five replicate samples were randomly taken at each site within an area of a few m<sup>2</sup>.

The intertidal pooled core samples, as well as the grab samples, were sieved through mesh bags (1mm mesh size) to separate the fauna from the finer sediments. 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. Taxonomy follows species nomenclature of the World Register of Marine Species (<http://www.marinespecies.org/>). Species richness is given as the number of species per sample, and abundance is converted to units per m<sup>2</sup>. Biomass (ash-free dry weight) of each taxon was measured by weight loss after ignition at 450°C for 4h for studies III and IV. Meiofauna (animals smaller than 1mm) was sampled using similar methods, but adapted for this group (see paper IV for details).

Flatfishes were sampled using a beach trawl (5 m wide, 0.3m high, with an 8mm stretched mesh net in the cod-end) in the intertidal, and using a beam trawl (2m wide, 0.5m high, with a 4mm stretched mesh net in the cod-end) in the subtidal. At intertidal sampling sites, beach trawls were carried out during the day at rising tides, at least once along 80 to 260m long latitudinal transects (sampled surface: 400 to 1300m<sup>2</sup>). Beam trawls were carried out during the day, at neap tide, along 500m transects (sampled surface: 1000m<sup>2</sup>).

at least twice at each site within the subtidal zone. The flatfish were sorted, identified and measured (total length) on board and released immediately after the investigations. For each species, individuals were classified into age groups based on their size and on peer-reviewed literature and research-reports on flatfish growth (including Deniel, 1973; Gibson and Ezzi, 1980; Nottage and Perkins, 1983).

#### *Material for stable isotope analyses*

The low-shore community trophic structure of macrotidal sandy beach systems was assessed by sampling biota for stable isotope analyses ( $^{13}\text{C}$ : $^{12}\text{C}$  and  $^{15}\text{N}$ : $^{14}\text{N}$ ) (**paper IV**). Particulate organic matter (POM) was collected from the water column (within the first metre), and filtered in the laboratory. Sedimentary organic matter (SOM) was sampled by collecting the first centimetres of sediment. *Ulva* was hand-collected from the water column. Macrofauna was sampled using cores, forks and by sieving ~50 litres of sediments (1mm mesh-size). Meiofauna (mainly nematodes and copepods, Carriço et al. 2013) was sampled using cores and by scraping the uppermost layer of the sediment (ca. 1.5cm), and was later sieved in the laboratory. Flatfish and epibenthic crustaceans were caught using a beach trawl and a push net (8mm mesh size each).

All samples were brought back to the laboratory for conservation. Sediments collected for SOM were re-suspended in filtered Milli-Q water using an ultrasonic bath. Seawater collected for POM was pre-filtered using a net (90  $\mu\text{m}$ ) to remove large detritus (i.e. pieces of macroalgae). Both the supernatant and the pre-sieved seawater were then sieved on pre-combusted (450°C for 5h) GF/F filters (3 filters per type of sample, per sampling occasion) and quickly acidified. *Ulva* thalli were cleaned of from any epiphytes and rinsed with Milli-Q water. All fauna collected were sorted in the laboratory and kept frozen (-20°C) until preparation for analyses. Fauna was identified to the lowest possible taxonomic level and measured (total length or width of first setigers for polychaetes). Samples consisted of muscle tissue of large species (fish, bivalves, echinoderms, some polychaetes) or of pooled individuals (5-300 individuals, in order to reach the minimum weight needed for isotope analyses) for the smallest spe-

cies. When pooling was required, gut content was carefully removed by dissection. Species containing calcium carbonate, e.g. ophiuroids and cumaceans, were split into two subsamples: one was acidified (10% HCl) for  $\delta^{13}\text{C}$  analysis, the other subsample not acidified and used for  $\delta^{15}\text{N}$  analysis. All samples were rinsed using Milli-Q water, oven-dried (48h at 60°C) and ground into fine powder using a ball mill (fauna, macroalgae) or gently scraped using a scalpel (POM and SOM collected on filters). Part of the powder (400 $\mu\text{g}$ ), or the fragments (1mg), was then packed into 5  $\times$  8mm ultra-clean tin capsules.

#### *Environmental variables*

At each fauna sampling site, a single sediment core (in the intertidal) or grab (in the subtidal) was extracted to obtain grain size distribution and organic matter characteristics. Grain size was assessed by dry sieving, using a series of sieves (from 63 $\mu\text{m}$  to 10,000 $\mu\text{m}$ ). Median grain size was equal to the second quartile (Q50) of the sediment grain size value. The Sorting index (also called Sorting) was calculated based on the first and the third quartiles of the sediment grain size ratio ( $\sqrt{Q25/Q75}$ , where Q25 and Q75 denote the first and third quartiles, respectively). Total organic matter content was assessed by weighted loss after ignition at 450°C for 5h.

For the intertidal sites, *Ulva* biomass data was collected from the Algae Study and Valorisation Centre (CEVA, [www.ceva.fr/fre](http://www.ceva.fr/fre)) an institute in charge of estimation of green tides amplitude through monthly aerial surveys (for estimation of surface covered by algae) and field sampling (for conversion to biomass). At subtidal sites, *Ulva* biomass was assessed on board the sampling vessel by weighting algae collected in beam trawls (each one covering an area of 1000m<sup>2</sup>). Intertidal seawater temperature (hereafter 'SWT') and salinity, as well as dissolved oxygen content (**paper III**) were measured on each sampling occasion using an YSI-OMS v2 probe. Larger scale (**paper I**) or subtidal (**paper II**) monthly to 5 days' mean values of SWT, salinity, as well as phytoplankton concentrations (**paper III**) were extracted from datasets provided by the PREVIMER system ([www.previmer.org](http://www.previmer.org)) and data used for analyses were obtained by averaging the values of 5 days before each sampling occasion for both variables.

### 3.4. Stable isotope analyses

Stable isotopes are emerging as one of the most common tools used to infer feeding relationships among organisms within a system and the energy flow through food webs. Stable isotopes of a chemical element differ by their neutron number, which influences the element's mass. Depending on their mass, stable isotopes of an element are magnetically separated by mass spectrometry in order to determine a stable isotope ratio. Stable isotope ratios (heavy [<sup>H</sup>] / light [<sup>L</sup>] isotopes) are expressed related to an internationally accepted standard, in the delta unit notation ( $\delta$ ) in per mil (‰) following the formula:

$$\delta^H X (\text{‰}) = [(\delta^H X_{\text{sample}} / \delta^L X_{\text{sample}}) / (\delta^H X_{\text{standard}} / \delta^L X_{\text{standard}}) - 1] \times 10^3.$$

Among all the macroelements required for life, two elements are most commonly employed in a food web context: nitrogen (N) and carbon (C) (Layman et al. 2012). The standard ratios used for the measure of  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  are the Vienna Pee Dee Belemnite and  $\text{N}_2$  in air, respectively. Samples prepared through this thesis were sent to the isotope spectrometry platform (LIENSs laboratory, University of La Rochelle, France). Analytical precision based on isotope values of the acetanilide (Thermo Scientific) used to estimate C and N content for each sample series was  $<0.1\text{‰}$  both for carbon and nitrogen.

Different primary producers (e.g. C3 vs. C4 plants, pelagic vs. benthic production) vary significantly in their  $\delta^{13}\text{C}$  values, and consumers of respective primary producers mirror values of the resources as  $\delta^{13}\text{C}$  is largely conserved through trophic transfer (Post 2002, Bearhop et al. 2004). Consequently,  $\delta^{13}\text{C}$  enables identification of dietary carbon sources. Complementary to this,  $\delta^{15}\text{N}$  can be used to estimate trophic position as it shows a stepwise enrichment with trophic transfer (Post, 2002).

Assessments of community trophic structure and dynamics can be conducted through the examination of the relative positioning of consumers and resources in bivariate stable isotope space ( $\delta^{13}\text{C}$  -  $\delta^{15}\text{N}$ ; Layman et al. 2012). The relative positioning of individuals, populations, and communities in bivariate isotope space represent occupancy of isotopic niche space (i.e. a concept that encompasses information on environmental

as well as bionomic dimensions of ecological niche space, after Newsome et al. 2007, Nordström 2009). Several metrics for this 'isotopic niche' have been developed, enabling comparisons of e.g. trophic similarity (potential separation in isotopic niche location, and overlap of niches), niche width or trophic diversity (isotopic niche size) among communities or within assemblages over time (Turner et al. 2010, Jackson et al. 2011, Layman et al. 2012). Also, recently developed isotopic indices weighted with species biomass (Rigolet et al. 2015) allow a multifaceted (richness, evenness, and divergence) quantification of functional trophic diversity and a better characterisation of the structure of energy accumulation in food webs (e.g. Grall et al. 2006). Using the isotopic niche concept and indices constructed from it, it is possible to identify changes in fundamental food web attributes following anthropogenic disturbances, such as shifts in major trophic pathways (visualized using biomass-weighted isotope signatures) or in niche width.

### 3.5. Data analyses

Univariate parametric or non-parametric approaches (analysis of variance, as well as Friedman, Chi<sup>2</sup>, Kruskal-Wallis, Wilcoxon-Mann-Whitney, and t-test) were used to test for differences between, as well as independent and interactive factor effects on, primary community variables (univariate response variables) and environmental variables (papers I, III and IV, Table 2). Before performing statistical tests on these univariate characteristics of faunal diversity and environment, all biotic and abiotic variables were checked for normality (graphically, and using Agostino and Shapiro-Wilk tests), and forth-root, log, or arcsine transformed when necessary.

When testing for differences in community structure between sites, and over time, multivariate approaches (MANOVA, PERMANOVA, distance-based Moran's Eigenvector Maps [dbMEMs] in variation partitioning) were used after testing for homogeneity of variance when necessary (Papers I-III, Table 2). While MANOVA and PERMANOVA are considered classical approaches in the study of variation within multi

Table 2. Summary of hypotheses tested, the temporal and spatial extent, and the analytical methods used in the four field studies. Additional details are found in respective paper (I-IV). *Résumé des hypothèses testées, de l'étendue spatiale et temporelle, et des méthodes analytiques employées dans chacune des quatre études réalisées. Ces éléments sont détaillés dans les quatre études présentées dans cette thèse (articles I-IV).*

	Paper I	Paper II	Paper III	Paper IV
<b>H<sub>0</sub></b>	Winter sandy beach zoobenthic community structure (i) is not driven by the presence of green tides in spring, and (ii) respond similarly to anthropogenic stress, regardless the type of SB (exposed vs. semi-exposed)	Macroalgal mats, affect equally benthic communities depending on (i) the faunal group (infauna vs. flatfish), and (ii) the habitat (intertidal vs. subtidal)	Variation in macrofaunal benthic structure is independent on (i) location at small spatial scale, (ii) time/month of the year, and (iii) presence of <i>Ulva</i> spp. mats	<i>Ulva</i> stranding on normally unvegetated sandy beaches do not change (i) basal resource isotope signature, nor (ii) species-specific diets, neither (iii) structure and functioning of community-wide trophic web
<b>Response variables</b>	<b>Univ.:</b> S, A, H', D; <b>Multiv.:</b> species abundance	<b>Univ.:</b> relative species abundance <b>Multiv.:</b> species abundance	<b>Univ.:</b> S, A, H', D <b>Multiv.:</b> species abundance, species biomass	<b>Univ.:</b> $\delta^{13}\text{C}$ , $\delta^{15}\text{N}$ <b>Multiv.:</b> IS ( $\delta^{13}\text{C} * \delta^{15}\text{N}$ ), IS * Biomass
<b>Explanatory variables</b>	Coverage by <i>Ulva</i> , occurrence of GT, organic matter, median, sorting, beach index, gravel, sand, mud, SWT, salinity, air temp., wind speed, wind direction, rainfall, temporal MEMs, spatial MEMs	<i>Ulva</i> biomass, organic matter, median, sorting, salinity, SWT, temporal MEMs	<i>Ulva</i> biomass, Chl-a, organic matter, median, sorting, wave height, slope, salinity, SWT, dissolved oxygen, location along beach, temporal MEMs	<i>Ulva</i> biomass
<b>Spatial scale (extent)</b>	Regional (thousands of kilometres)	Local - Vertical (hundreds of meters, from low-intertidal to shallow subtidal)	Local (meters to kilometres)	Local (meters)
<b>Temporal scale (duration, frequency)</b>	Multi-years (7y, yearly)	In a span of a year (10mo, seasonally)	In a span of a year (10mo, monthly)	In a span of a year (7mo, seasonally)
<b>Factors</b>	Two factors: "Type" & "GT"		Two factors: "Beach" & "Sampling occasion"	Two factors: "Season" & "Green tides"
<b>Data analyses</b>	<b>Univ.:</b> Two-way ANOVA, t-test, Wilcoxon-Mann-Whitney <b>Multiv.:</b> Two-way PERMANOVA, dbMEMs in varpart, RDA	<b>Univ.:</b> $\text{Chi}^2$ -test <b>Multiv.:</b> dbMEMs in varpart, RDA	<b>Univ.:</b> Kruskal-Wallis test, Friedman test, Two-way ANOVA, stepwise regression models <b>Multiv.:</b> MANOVA, dbMEMs in varpart, RDA	<b>Univ.:</b> Two-way ANOVA, Wilcoxon tests <b>Multiv.:</b> SIBER, Linear models, RPP

Univ. = univariate/*univariées*; Multiv. = multivariate/*multivariées*; S = species richness/*richesse spécifique*; A = abundance/*abondance*; B = biomass/*biomasse*; H' = Shannon index/*indice de diversité de Shannon*; D = Simpson index/*indice de diversité de Simpson*; IS = isotopic signature/*signature isotopique*; GT = green tides/*marées vertes*; temp. = temperature/*température*; Chl-a = phytoplankton concentration/*concentration en phytoplancton*; median = median grain size/*grain médian*; SWT = seawater temperature/*température de l'eau de mer*; sorting = sorting index/*indice de tri*; y = years/*années*; mo = months/*mois*; dbMEMs = Distance-based Moran's Eigenvector Maps/*cartes de vecteurs propres de Moran basées sur la distance*; MEMs = Moran's Eigenvector Maps/*cartes de vecteurs propres de Moran*; varpart = variation partitioning/*partitionnement de variance*; RDA = Redundancy analysis/*analyse de redondance*; SIBER = Stable Isotope Bayesian Ellipses/*ellipses bayésiennes basées sur des signatures isotopiques*; RPP = Residual Permutation Procedure/*procédure de permutation des résidus*.

-variate datasets, the combination of dbMEMs and variation partitioning is yet emerging (Legendre & Gauthier 2014). This rather novel approach enables the disentangling of effects of several sets of explanatory variables, such as environmental, including *Ulva* mats, temporal and spatial variables.

Both univariate and multivariate statistical analyses were complemented with rarefaction curves (sample-based RC) and ordination analyses (principal coordinate analysis, redundancy analysis) in order to visualize spatial and temporal patterns within benthic communities.

When exploring the underlying processes explaining the effects of *Ulva* on the some aspects of dynamic system functioning through the study of food webs, a Bayesian approach (SIBER; Jackson et al., 2011) coupled with linear models and a residual permutation procedure (Turner et al. 2010) were used (paper IV). In addition, in order to evaluate the effects of an abundant additional food source in the form of *Ulva* on the trophic functioning of highly dynamic systems, (i) patterns of biomass were estimated, and (ii) indices recently developed to measure structural- and functional diversity (see section 3.4) in a  $\delta$ -space (Layman et al. 2007, Rigolet et al. 2015) were calculated.

All analyses conducted in this thesis (papers I-IV) were performed within the R environment (R Development Core Team, 2013), using the *BiodiversityR* (Kindt & Coe 2005), *FD* (Laliberté et al. 2014), *packfor* (Dray et al. 2013), *PCNM* (Legendre et al. 2013), and *SIAR* (Parnell & Jackson 2013) packages.

## 4. Results and discussion

In this thesis, I assessed the influence of GT (together with other environmental variables known to structure sandy beach communities; Defeo & McLachlan 2005, Ramos et al. 2009) on benthic community structural and functional dynamics (papers I-IV). Investigating benthic community structure across large spatial and temporal scale, paper I revealed a significant general regional response of macrotidal sandy beach fauna to the presence of GT. Further exploring faunal responses to *Ulva* accumulations across two habitats and faunal groups, as well as across a vertical scale, I found differential responses in term of intensity

(papers I and II). Based on these findings, I identified intertidal zoobenthic invertebrates inhabiting exposed SBs as the most impacted entity by GT. Focussing on this ecological compartment, I have revealed the subtle but highly significant influence of GT on benthic communities, on both univariate and multivariate assemblage characteristics along a gradient of *Ulva* coverage (paper III). Exploring the processes explaining these shifts through the study of trophic structure and functioning, I found changes induced by the presence of high biomasses of *Ulva* on primary producer level, and revealed consequent propagation of effects up through the food web (paper IV). The induced changes affected the overall consumer assemblages and altered SB trophic functioning. These results are presented and discussed below.

### 4.1. Long-lasting eutrophication effects over large scales

By investigating SB benthic assemblage responses to GT across large spatial and temporal scales, which implies a great variability of biotic and abiotic conditions, I found significant effects of the occurrence and spread of *Ulva* accumulation on several univariate community variables (abundance and species richness) of benthic fauna (paper I, Table 3).

**Table 3.** Results of 2-way ANOVAs of macrofauna abundance of the thirteen sandy beaches sampled yearly from 2007 to 2013 (part of the table 3 presented in paper I). Total number of observations was 273. Significant values at  $p \leq 0.05$  are shown in bold; \*  $p \leq 0.05$ , \*\*\*  $p \leq 0.001$ . *Résultats des analyses de variances à deux facteurs basées sur les données d'abondance de macrofaune échantillonnée à treize plages entre 2007 et 2013 (correspondant à une partie des résultats présentés dans le tableau 3 de l'article I). Le nombre total d'observations est de 273. Les valeurs significatives à  $p \leq 0,05$  apparaissent en gras ; \*  $p \leq 0,05$ , \*\*\*  $p \leq 0,001$ .*

	df	MS	F	p	
<b>Log(A)</b>					
Type	1	167.51	178.94	<2.10 <sup>-16</sup>	***
GT	1	4.53	4.84	<b>2.87.10<sup>-2</sup></b>	*
Type * GT	1	0.8	0.86	3.55.10 <sup>-1</sup>	
Res.	269	0.94			
<b>S</b>					
Type	1	10.62	348.56	<2.10 <sup>-16</sup>	***
GT	1	698	22.89	<b>2.83.10<sup>-16</sup></b>	***
Type * GT	1	108	3.56	6.10 <sup>-2</sup>	
Res.	269	30			

This study also demonstrates that eutrophication by green tides significantly modifies the structure of SB communities (with differences in

terms of multivariate dispersion between faunal assemblages in pristine and impacted sites). These shifts were mainly explained by a decrease in abundance of bivalve molluscs and some polychaete species (most notably *Euclymene oerstedii*, *Lanice conchilega*, and *Notomastus latericeus*), as well as by increases in other species such as the polychaete annelid *Owenia fusiformis* and the ophiuroid *Acrocnida cf. spatulispina* abundance. More generally, and in a biological/functional trait perspective, **paper I** suggests that, where *Ulva* blooms occur in dynamic systems, herbivorous and suspension-feeding invertebrates are favoured, whereas sub-surface deposit feeders and large species appear to be negatively affected by the presence of GT. The present results are generally consistent with previous studies assessing the responses of macrofauna to eutrophication by macroalgal accumulations (e.g. Hull 1987, Norkko & Bonsdorff 1996a).

More importantly, given the time lag between the *Ulva* blooms, and the sampling of fauna (in early Spring, ca. 6 months after blooms), I revealed the long-lasting and conservative nature of these responses (**paper I**). The study represents the first *in situ* non-manipulative study of the effects of green tides at large spatial and temporal scales. Consequently, the results presented in this study are novel, and since a great variability (a total of 819 diversity samples were examined and were representative of 13 beaches, over 7 years, and across 2730 km of coastline) was encompassed by the study, the generality of these findings is fundamentally enhanced (Hewitt et al. 2007).

## 4.2. Differential responses of sandy beach communities to green tides

The **papers I and II** report the effects of GT on benthic community structure and diversity across different (i) type of beaches (clean homogeneous vs. muddy heterogeneous sands, i.e. exposed vs. semi-exposed), (ii) depth (intertidal vs. subtidal), and (iii) biotic compartments (infauna vs. flatfish). In general, green tides significantly impact SB benthic communities (**papers I and II**), but in terms of intensity, there were (for certain variables) differential responses between exposed and semi-exposed beaches, as well as between habitats at exposed sites, and between faunal groups in the intertidal areas of these sites (FIG. 8).

### Differential influence of exposure

Two sandy habitats exist among the 13 sandy beaches included in **paper I**: exposed sandy beaches, which are composed of clean homogeneous sands, and semi-exposed sandy beaches that are made of heterogeneous muddy sands. Analysing the effects of the eutrophication by macroalgae on SB fauna depending on exposure (exposed vs. semi exposed), I found that the abundance and biomass of fauna at both type of sites were significantly influenced by GT. However, sandy beach diversity indices ( $H'$  and  $D$ ) were significantly changed by *Ulva* accumulation at exposed sandy shores, only (FIG. 7). The differential response, with more pronounced effects of GT at exposed sandy sites compared to semi-exposed ones, was consistent when considering multivariate variables

	Res. $\Delta$	Eff.		Res. $\Delta$	Eff.		Res. $\Delta$	Eff.
Exp.	H', D, Str.	+++	Inter.	Str.	+++	Zoo.	Str.	+++
Semi exp.	Str.	+	Sub.	Str.	+	Fl. fish	Str., Ar.	+

FIG. 7. Interlinked tables recapitulating the main results of **papers I and II**, and thus showing the intensity (slight: +; very clear: +++) of the response of benthic communities to the presence of green tides. Exp. = exposed SBs made of clean well-sorted sands; Semi exp. = semi-exposed SBs made of heterogeneous muddy sands; Inter. = intertidal; Sub. = subtidal; Zoo. = zoobenthos; Fl. Fish = flat fish; Eff = global effects; Res.  $\Delta$  = response variables; S = species richness;  $H'$  = Shannon index;  $D$  = Simpson index; Str. = multivariate community structure; Ar = relative abundance. The color codes are the same than the ones used in FIG. 3. *Tables liées récapitulant les résultats majeurs des articles I et II, et montrant l'intensité des réponses des communautés benthiques à la présence des marées vertes (légère: +; marquée: +++)*. Exp. = plages exposées composées de sables propres et bien triés; Semi exp. = plages semi-exposées composées de sables envasés hétérogènes; Inter. = intertidal; Sub. = subtidal; Eff. = effet global; Res.  $\Delta$  = variables réponses; S = richesse spécifiques;  $H'$  = indice de diversité de Shannon;  $D$  = indice de diversité de Simpson; Str. = structure multivariée de la communauté; Ar = abondance relative. Le code couleur utilise est le même que celui employé pour la figure 3.

(cf. Table 4 and FIG. 6 in **paper I**). Unconstrained exposed sandy ecosystems are resilient systems (Schlacher et al. 2007), but human modification of the coast (through e.g. coastal development, Davis 2015) may affect their flexibility. The present findings add to the list of human-induced threats affecting sandy beach ecosystem resilience. One explanation perhaps lies in the fact that exposed macrotidal sandy beach fauna is adapted to withstand great “natural” variation within usually unvegetated systems, but is less able to tolerate overlapping additional stress of anthropogenic origin. Conversely, semi-exposed macrotidal SBs receive significant amounts of organic material (e.g. in the form of seaweed wrack subsidies, particulate matter sedimentation) on a more regular basis, and the distinct fauna inhabiting these systems is potentially adapted to face *Ulva* accumulations. A study conducted within similar macrotidal environments, but investigating sheltered beach fauna responses to eutrophication also highlighted very few effects of ephemeral mats on sandy beach fauna (Ouisse et al. 2011), which in a general manner contradicts findings made within non- or micro-tidal systems (e.g. Norkko & Bonsdorff 1996a). My results suggest that eutrophication by green tides is an important factor stressing and structuring zoobenthos living at macrotidal sandy beaches that are usually uncovered by vegetation (exposed SBs), while sites more susceptible to accumulate organic matter (semi-exposed SBs) harbour a fauna that is probably less affected by additional organic material.

#### *Decreasing impacts of the accumulation of *Ulva* with increasing depth*

While structurally and functionally interrelated (McLachlan & Brown 2006), intertidal and subtidal sands are both under human-induced stress in the form of green tides (Merceron & Morand 2004). Specifically focussing on exposed sandy shores (FIG. 7), I analysed the influence of GT on the variation in benthic fauna living inshore (at low-intertidal) and nearshore (at shallow subtidal) (**paper II**). This study demonstrated that GT significantly influence the multivariate structure of benthic community at intertidal sites, while only few effects were found at subtidal sites (cf. FIG. 4, 8 in **paper II**). Similar to the harshness contrast existing between exposed and semi-

exposed shores, intertidal and subtidal open sandy areas do not face the same environmental forcing (cf. FIG. 3 in **paper II**). Intertidal sandy beach fauna withstands harsher conditions than subtidal benthic assemblages, and the addition of high biomasses of green opportunistic macroalgae (*Ulva* spp.) may act as the last straw stress. In addition, the intrinsic nature of algal mats differs from intertidal to subtidal with algae floating above the seafloor nearshore (Merceron & Morand 2004) and stranding on sand within inshore areas (Charlier et al. 2007). The fact that GT are in direct physical contact with - and even enter (*pers. obs.*) - sands, may induce transient anoxic conditions and increasing pore water sulphide concentrations (e.g. Green & Fong 2016) and most likely lead to increases in temperatures underneath stranded *Ulva* mats. Findings in **paper II** highlight the greater vulnerability of intertidal open macrotidal SB benthic community compared to subtidal sandy benthic assemblages.

#### *Two biotic compartments with contrasting responses to green tides*

To detect potential different responses of two related biotic compartments (macroinfauna and flatfish) where GT develop, I simultaneously studied invertebrate and fish communities over the span of a year (**paper II**). I observed significant differences between pristine and impacted sites for both macroinvertebrate (*Ulva* variables significantly explaining 30% of the variation in zoobenthos) and flatfish ( $\chi^2=51.6$ ,  $N=317$ ,  $df=3$ ,  $p=3.6 \cdot 10^{-11}$ ) assemblages. For example, relative abundance of some species of limited commercial interest (e.g. *Pegusa lascaris*) was higher than the abundance of species of high commercial value (e.g. *Scophthalmus maximus*) at sites impacted by green tides. The multidimensional analyses revealed clear structural shifts in macro-invertebrate community where green tides occur, while only slight changes occurred in flatfish assemblages looking at community-level responses (cf. FIG. 5, 7 in **paper II**, FIG. 7). The greater influence of the accumulation of *Ulva* on infauna may be explained by species-specific life history traits. Flatfish are more mobile than infauna, and may more successfully escape transient hypoxia induced by the presence of *Ulva* mats (Baden et al. 1990). Differential shifts at community level revealed by **paper**

II contrast with results from studies conducted within more sheltered or non- and micro-tidal systems (Pihl et al. 2005).

The findings of papers I and II thus underline above all the vulnerability of macroinvertebrate communities inhabiting open macrotidal sandy beaches (Type I SBs) to human-induced stress in the form of GT. Hence, the two following sections (papers III and IV) do focus on this specific ecosystem and aim to explore small spatial and temporal scale patterns and underlying processes and mechanisms explaining the shifts observed at large horizontal and temporal scales.

#### 4.3. Green tides impact variability of zoobenthos at small scales

Considering intertidal invertebrate communities living in clean, homogeneously sorted sands, I investigated small spatial and temporal scale structural patterns along a gradient of green tides (defined based on the distribution of *Ulva* biomass along the shore; from ‘no GT’ to ‘homogeneous cover of *Ulva*’) (paper III). The analysis of the 261 biodiversity samples together with environmental variables including *Ulva*-related variables show that patterns and differences in macrofaunal community structure comparing three beaches along a gradient of green tides arose specifically from *Ulva* accumulation on the sandy shores, rather than from other environmental variables (paper III). Indeed, with the exception of the presence of *Ulva* mats, the other environmental variables (cf. Table 1 in paper III) were not significantly different among the three beaches or over time. More precisely, I demonstrated that species richness (S) was influenced by the presence of GT, with the lowest found at the SB with a homogeneous coverage of *Ulva*, and a higher S (compared to pristine site) found at the SB where a gradient in *Ulva* stranding occurred (cf. FIG. 4 in paper III). This pattern was close to the pattern that would have been expected from the benthic successional paradigm on the effects of increasing organic-matter input on benthic fauna communities (Pearson & Rosenberg 1978), although distinct. For example, I did not find a complete replacement of SB species by some other where GT occurred, neither the typical bell curve for species richness along the stress-gradient, which suggests the existence of a parallel paradigm associated to

dynamic marine sedimentary systems. I also found significant shifts in variation in multivariate community characteristics, as for example shown through an overall decrease in beta-diversity (*i.e.* the total variance of a community matrix, *sensu* Legendre & De Cáceres 2013) from the pristine site (No GT) to the SB that was homogeneously covered by *Ulva* (Hom. GT; FIG. 8), with a significant difference in beta-diversity found between No GT and Hom. GT ( $W = 54$ , corrected  $p = 0.021$ ). These changes in univariate and multivariate faunal characteristics along a gradient in GT were accompanied by a decrease in the explanatory power of spatial variables (with a complete lack of significant spatial patterns where *Ulva* homogeneously cover sand) and a shift from physical to biological variables (including *Ulva*) explaining most of faunal variation from pristine to fully impacted site (cf. Table 2, Figure 8 in paper III). These results suggest that the presence of high biomasses of *Ulva* stimulates biological interactions and processes (such as competition, predation, reproduction and recruitment), which induces changes in community composition among sites impacted by GT, and may ultimately

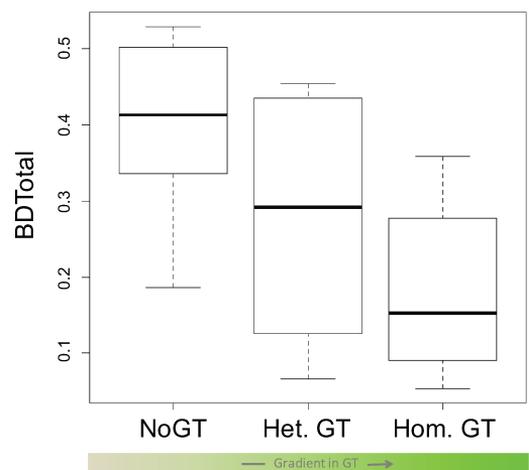
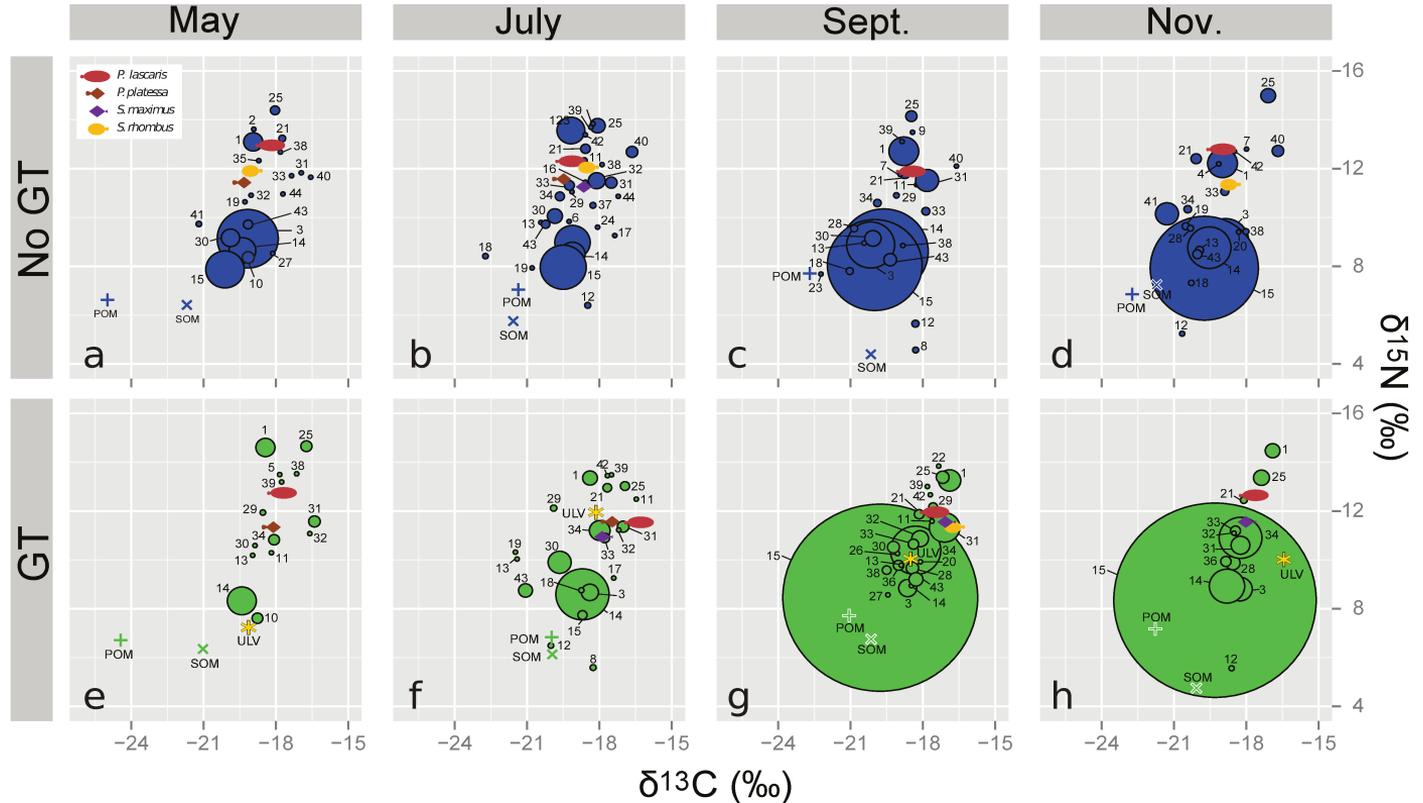


FIG. 8. Total  $\beta$ -diversity (BDTotal) across space and time at three sandy beaches; one never has green tides (NoGT), another is heterogeneously covered by GT (Het. GT), and the third one is homogeneously covered by *Ulva* (Hom. GT). Box plots show the median (line in box), the first and the third quartiles (hinges), and the most extreme data points which are 1.5 times the interquartile range from the box (whiskers) (paper III). Diversité bêta totale (BDTotal) dans le temps et l'espace pour trois plages de sable fin ; l'une d'elles n'est jamais impactée par les marées vertes (NoGT), une autre est couverte par les ulves de manière hétérogène (Het. GT), et la dernière est couverte par les ulves de manière homogène (Hom. GT). Les boîtes à moustache représentent la médiane, les premiers et troisièmes quartiles, ainsi que les valeurs extrêmes (résultats extrait de l'article III).

1: *Acrocnida brachiata*; 2: *Amphiporus langiaegeminus*; 3: *Angulus tenuis*; 4: Aphroditidae; 5: *Arenicola marina*; 6: Aricidae; 7: *Balanoglossus arnoglossus*; 8: *Bathyporeia pelagica*; 9: *Cerebratulus roseus*; 10: Copepoda; 11: *Crangon crangon*; 12: *Cumopsis* spp.; 13: *Diogenes pugilator*; 14: *Donax trunculus*; 15: *Donax vittatus*; 16: *Echinocardium cordatum*; 17: *Ensis siliqua*; 18: *Eocuma dollfusi*; 19: *Eurydice pulchra*; 20: *Euspira* spp.; 21: *Glycera convoluta*; 22: Gobiidae; 23: *Idotea baltica*; 24: *Idotea pelagica*; 25: *Lineus acutifrons*; 26: *Liocarcinus holsatus*; 27: *Mactra stultorum*; 28: *Magelona filiformis*; 29: Mysida; 30: Nematoda; 31: *Nephtys assimilis*; 32: *Nephtys hombergii*; 33: *Nephtys cirrosa* (juveniles); 34: *Owenia fusiformis*; 35: *Phyllodoce mucosa*; 36: Planaria; 37: *Pontocrates arenarius*; 38: *Portunus latipes*; 39: *Scoletoma impatiens*; 40: *Sigalion mathildae*; 41: *Spiophanes bombyx*; 42: *Trachinus draco*; 43: *Urothoe poseidonis*; 44: *Venus gallina*.



**FIG. 9.** Stable isotope bi-plots showing benthic consumers' (denoted by the numbers) isotope signatures weighted by biomass (ash-free dry weight per square meter) (filled circles), juvenile flatfishes' isotope signatures (denoted by fish symbols), and source isotope signatures (POM [plus sign], SOM [cross], and *Ulva* spp. [yellow star]) at the pristine sandy beach (blue, upper panels) and the sandy beach impacted by green tides (green, lower panels) over time: May (a, e), July (b, f), September (c, g) and November 2012 (d, h). Each benthic consumer species is denoted by a number (see the list in the right corner of the figure). *Graphique représentant la signature isotopique des consommateurs benthiques (les espèces sont repérés par les numéros) pondérée par leur biomasse respective (poids sec sans cendre/m<sup>2</sup>) (cercles), celle des juvéniles de poissons plats (représentés par des poissons symbolisés) et celle des sources (POM : +, SOM : x; Ulva spp. : astérisque jaune) obtenues à partir d'organismes échantillonnés sur la plage non impactée par les marées vertes (en bleu) et à la station eutrophisée (en vert) à différentes dates : mai (a, e), juillet (b, f), septembre (c, g) et novembre (d, h). Les numéros désignent les espèces incluses dans l'analyse (voir la liste à droite de la figure).*

homogenized the spatial structure of dynamic assemblages.

This hypothesis is supported by variation in species specific dominance patterns with increasing algal cover (cf. Figure 10 in **paper III**). In particular, the densities of *Donax trunculus* (a species of commercial importance; Augris et al. 2005, McLachlan & Brown 2006) and *Spiophanes bombyx* (a species considered as key prey for flatfish; Speybroeck et al. 2007) were lower where green tides occurred. Potential impacts of GT on essential ecosystem-functions are thus likely to occur. No widespread mortality was observed through the study, while within less dynamic ecosystems it has been recognized that accumulation of opportunistic macroalgae has strong negative effects on sedentary infauna (Raffaelli et al. 1998, Grall & Chauvaud 2002, Korpinen & Bonsdorff 2015). The subtle responses of open macrotidal SB fauna to GT would likely not have been revealed if it were not for the combination of fine spatial-temporal scale monitoring with novel statistical approaches (dbMEMs in variation partitioning; Borcard & Legendre 1994, Dray et al. 2006, Legendre & Gauthier 2014). Findings from **paper III**, which highlight a decrease in structural univariate- and multivariate community metrics as well as explanatory variable number along a gradient in GT, 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). The biotic homogenization may be explained by changed species interactions and processes induced by the presence of green tides. More explicit hypotheses specifically investigating shifts in highly dynamic ecosystem functioning could be tested using appropriate tools, such as stable isotope analysis that has proven to be an accurate method when aiming at investigating trophic interactions and inferring carbon transfer through food webs (e.g. Grall et al. 2006, Nordström 2009).

#### 4.4. Stranding *Ulva* directly and indirectly alter trophic functioning

When weighting the mean isotope signature of every consumer in pristine and impacted SB food web by their respective mean biomass per square metre, major trophic pathways were visually identified (FIG. 9). Two different pictures emerged,

revealing a significant influence of GT on SB trophic functioning dynamics. At the pristine site (No GT), the consumers constituting most of the benthic biomass (89.8 to 97.1% of the total biomass) on all sampling occasions were the ophiuroid *Acrocynida brachiata*, the bivalves *Angulus tenuis*, *Donax trunculus* and *Donax vittatus*, the amphipod *Urothoe poseidonis*, the polychaete *Glycera convoluta*, as well as the nemertean *Lineus acutifrons* (FIG. 9a, b, c, d). In the green-tide SB community, the brittle star *A. brachiata*, the nemertean *L. acutifrons* and the polychaetes *Owenia fusiformis* and *Nephtys assimilis* made up 4.5 to 35.5% of total biomass considering all sampling dates. The bivalve *D. trunculus* represented the largest biomass (60.3 and 67.6%) in May and July, while *D. vittatus* constituted most of the total biomass (90.3 and 91.9%) in September and November (FIG. 9e, f, g, h). The energetic set up of the web, in terms of distribution of biomass, changed markedly over time where green tides occurred while it remains roughly the same at pristine site. When the bloom of *Ulva* was decaying (November), the combination of consumer biomass and isotope signature showed that most of the biomass (up to 95%) is channelled into the bivalve (deposit feeding) primary consumer compartment, made up by *D. trunculus*, *D. vittatus* and *A. tenuis*, at pristine site, yet essentially formed by *D. vittatus* at impacted SB. A food web structure and functioning that are changed may induce key ecological features to be lost in the case of additional disturbances (de Ruiter et al. 2005).

The dynamic depiction of species-specific isotope signatures at SB impacted by green tides also highlights the simplification of the whole food web structure, with a practically linear arrangement of food web components in November (i.e. after the strong *Ulva* biomass season, while algae have started to decay), suggesting a single trophic pathway (FIG. 9). This contrasts with the pristine SB picture where benthic organisms seem to consume a greater spectrum of food sources, as shown through the depiction of several trophic pathways. Interestingly, this finding contradicts the idea that addition of organic material in the form of macroalgae and plants inherently diversifies baselines within a system, and concurrently diversifies energy pathways within food webs (McClelland & Valiela 1998, Schaal et al. 2008,

Layman et al. 2012). On the contrary, the findings from **paper IV** support the hypothesis of simplification of macrotidal beach trophic webs where an opportunistic basal resource develops to become dominant.

Such changes in the whole SB community trophic structure and functioning were explained by direct and indirect effects of high biomasses of *Ulva* on consumers' and primary producers' isotope signature. Indeed, I found that the presence of green tides significantly affected baseline (other than *Ulva*, i.e. particulate organic matter [POM] and sedimentary organic matter [SOM]) isotope signatures. Despite the inherent great variability in stable isotope signatures of primary producers and basal resources (Rolff 2000), I found that POM and SOM were respectively more  $^{13}\text{C}$ - and  $^{15}\text{N}$ - enriched where GT occurred compared to pristine SB (cf. Figure 2 and Table 1 in **paper IV**). The shift observed in POM isotope signature is most likely due to high uptake of  $^{12}\text{C}$  carbon through high photosynthetic rates of *Ulva* (Johnson et al. 1974, Van Alstyne et al. 2015) causing remaining  $\text{CO}_2$  to become enriched in  $^{13}\text{C}$ , and leading to progressive  $^{13}\text{C}$  enrichment of phytoplankton (Rolff 2000). An increase in  $\delta^{13}\text{C}$  of dissolved inorganic carbon in the presence of *Ulva* was experimentally verified in our study, supporting this assumption (**paper IV**). The increase in  $\delta^{15}\text{N}$  of SOM occurred during autumn (September and November), which temporally matched the decay of *Ulva*; the senescence process may gradually change the composition of sediments and their isotope signature through bacterial activity, release of organic molecules and integration of

micro- or macro-debris in the detritus pool (Lahaye & Robic 2007, Schaal et al. 2008, Dubois et al. 2012). The direction of the shift observed in basal resource isotope signature in presence of *Ulva* was consistent over time, and more importantly, was persistent and traceable across higher trophic levels. Assessing changes in mean isotope signature of three consumers (*Donax vittatus*, *Owenia fusiformis*, and *Acrocnida brachiata*) of different trophic levels (primary and secondary consumers), I found that the mean location in stable isotope space of each consumer differed significantly in the presence of green tides ( $p < 0.002$  for every species): individuals sampled where GT occurred showed heavier  $\delta^{13}\text{C}$  than ones from pristine site. This shift was more or less pronounced depending on the species, although in the same direction for all of them (cf. Figure 3 in **paper IV**). These findings revealed direct (through ingestion of wave smashed *Ulva*, e.g. *O. fusiformis*; Phillips Dales 1957) and indirect (through ingestion of modified organic matter, e.g. *D. vittatus*) influence of *Ulva* on macroinvertebrate trophic niches. The influence of high biomasses of *Ulva* would presumably occur on all species, and may induced consequent changes in species interactions, ultimately influencing the general community structure and functioning (de Ruiter et al. 2005). In addition, the higher  $\delta^{13}\text{C}$  observed at the whole community scale where green tides occurred (FIG. 9, and cf. Figure 4 in **paper IV**) contrasts with previous studies conducted in sheltered and non-tidal systems highlighting an increase in  $\delta^{15}\text{N}$  within eutrophied food webs (McClelland et al. 1997, Carlier et al. 2008).



## 5. Conclusions

### 5.1. Key findings

Overall, this thesis demonstrates that strongly dynamic ecosystems, which are often considered to be highly resilient, may be altered by anthropogenically-induced stress and that identifiable effects of such particular pressure remains for months in their community structure and/or functioning (papers I-IV). The approach used in this work, combining several study scales and analytical tools, was crucial to inferring changes in so variable environments.

Despite great variability in space and time (at scales from meters to thousands of kilometres, and from months to years), this thesis shows the significant influence of eutrophication-induced accumulation of green opportunistic algae (*Ulva* spp.) on macrotidal sandy beach benthic community structure (papers I and III). In this work, I have demonstrated that intertidal macrobenthic communities inhabiting exposed SBs are the assemblages that are most affected by the presence of GT (papers I and II). The investigation of responses of this specific compartment at small spatial and temporal scales along a gradient of green tides revealed a homogenization of the community structure (affecting alpha and beta diversity), and shifts in the drivers of variation (spatial and environmental variables) with increasing coverage by *Ulva* (paper III, FIG. 10). These patterns, although close to the patterns that arose from the benthic “classical” successional paradigm (Pearson & Rosenberg 1978), are distinct (*i.e.* no complete shift in species composition along succession stages occurred) suggesting the existence of an alternative model to, or at the least a declension of, Pearson and Rosenberg paradigm that could be associated to highly dynamic marine sedimentary systems.

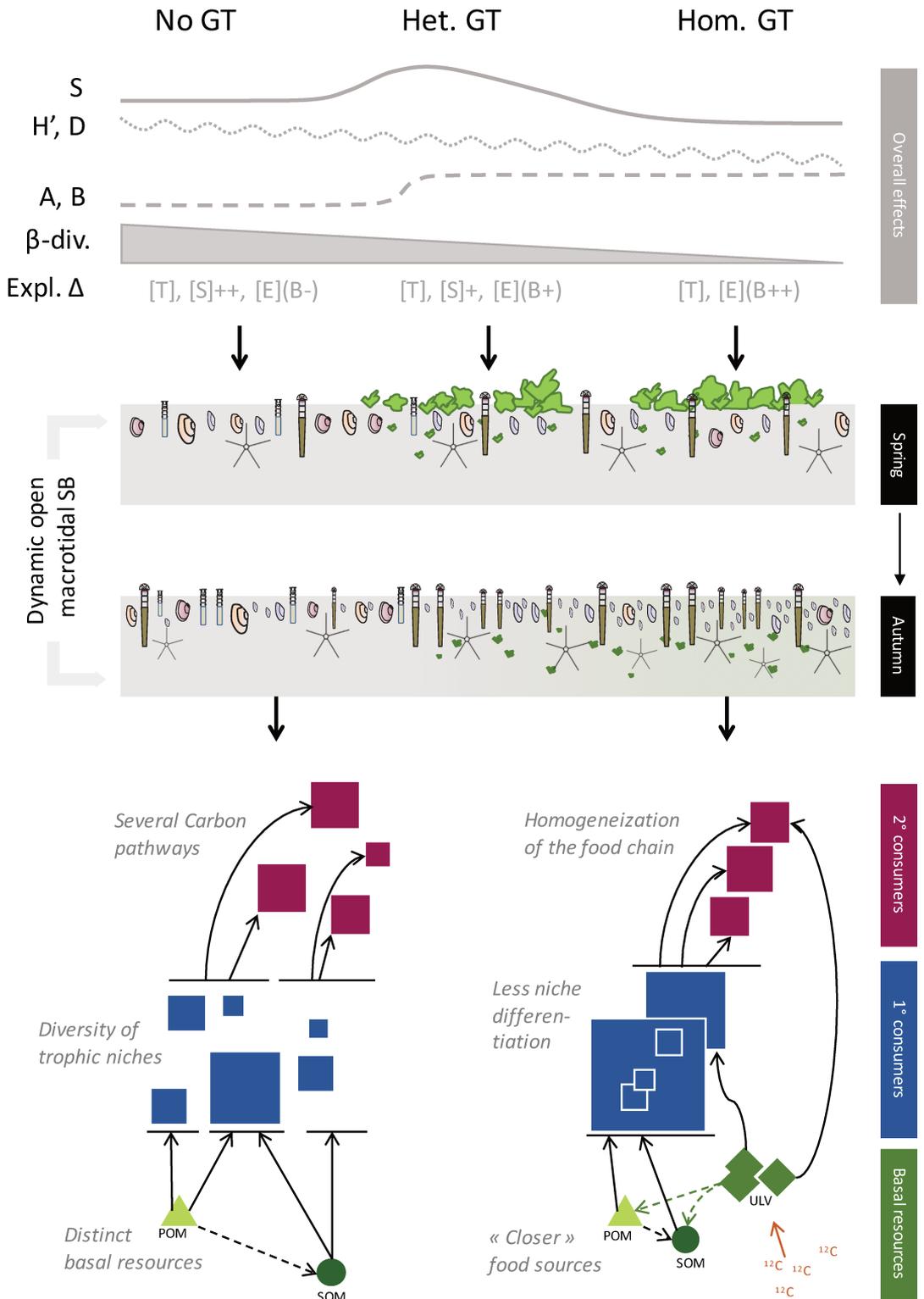
This thesis also highlights consistent consequential changes for the functioning of sandy beach ecosystem. Indeed, an accumulation of high biomasses of *Ulva* modifies the trophic structure of SB systems, through direct and indirect influence of GT at several trophic levels (from basal resources to predators) and ultimately induce a shift from multiple to single carbon pathway(s), highlighted by an alignment of the impacted food web components (paper IV, FIG.

10). The simplification of a highly dynamic system food web, together with its community structure homogenization, resulting from the occurrence of a stress *per se*, underlines the vulnerability of such systems to human-induced stress.

### 5.2. Implications and future directions

Ecologists study benthic communities since they “represent the best response data available to answer questions about species–environment relationships” (Legendre & Gauthier 2014), and more specifically because they accurately mirror human-induced disturbances (Pearson & Rosenberg 1978). To explore disturbance effects on ecosystem functioning, *in situ* investigations of benthic fauna responses often go beyond controlled and manipulative studies, which entail important limitations when trying to understand ecosystem-scale responses to perturbations. However, the use of *in situ* designs imposes dealing with a great challenge in community ecology: the need to disentangle signs of stress *per se* from the

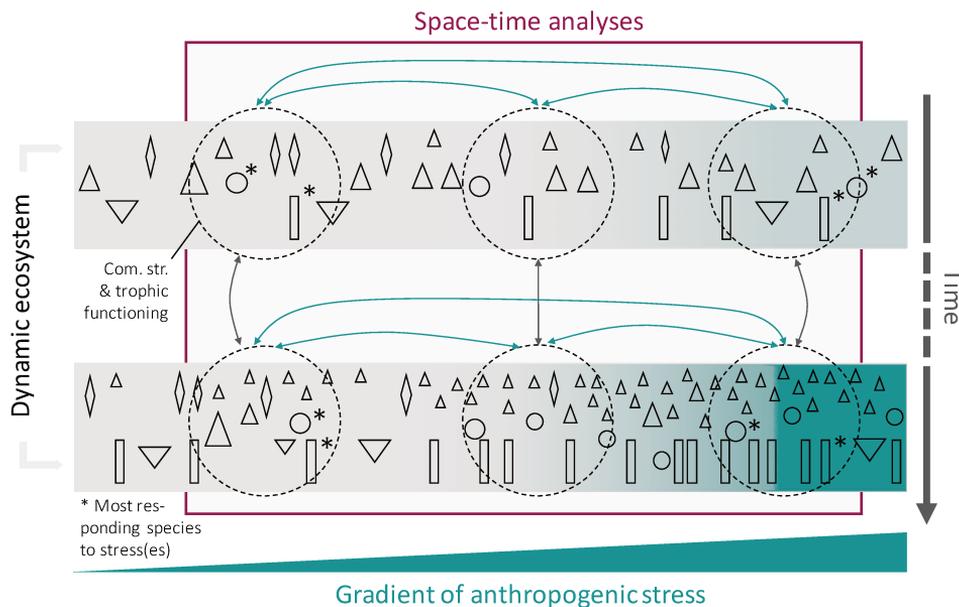
>> FIG. 10. Conceptual model of the effects of green tides on community- and trophic- structure and functioning of open macrotidal sandy beaches. The upper part of this scheme represents univariate and multivariate macrobenthic community characteristic variation along a gradient of green tides; the middle part represents the drift in dynamic ecosystem structure along the eutrophication gradient and over time; the lower part represents simplified pristine and impacted food web and highlights a shift from plural to single carbon pathway(s), modification of feeding inter-specific (each species is denoted by a square, which size is correlated to the species biomass) relationships (solid arrows), contributions/influences of primary producers to sedimentary organic matter pool/on particulate organic matter pool (dashed arrows) and high uptakes of <sup>13</sup>C (orange arrow) in the presence of high biomasses of *Ulva*. GT = green tides; Env. var. = environmental variables; +: 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 content. *Modèle conceptuel des effets des marées vertes sur la structure et le fonctionnement de la communauté et du réseau trophique des plages de sable fin macrotidales. La partie supérieure du schéma représente les variations des caractéristiques univariées et multivariées de la faune le long d'un gradient de marées vertes ; la partie centrale représente la dérive observée en terme de structure des communautés le long du gradient d'eutrophication et dans le temps ; la partie inférieure de ce modèle montre une schématisation du réseau trophique d'une plage impactée ou non par les marées vertes et met en exergue une simplification des voies de transfert du carbone, une modification des relations trophiques (flèches pleines) entre les organismes (représentés par des carrés, dont la taille est corrélée à la biomasse de chacune des espèces), la contribution/l'influence des producteurs primaires au pool de matière sédimentée/sur la matière organique particulaire et l'utilisation massive d'atome de carbone léger (flèche orange) en présence d'ulves . GT = marées vertes ; Env. Var. = variables environnementales ; + = stimulation ; - = inhibition ; SWT = température de l'eau de mer ; S = richesse spécifique ; H et D = indices de diversité de Shannon et Simpson, respectivement ; A et B = abondance et biomasse ; Waves = hauteur de houle ; Sal. = salinité ; Org. = taux de matière organique. Modèle conceptuel illustrant les effets directs et indirects de la présence de fortes biomasses d'ulves sur la structure et le fonctionnement trophiques des plages de sable fin macrotidales.*



variation observed in zoobenthos resulting from interspecific biotic interactions and “natural” abiotic conditions (*i.e.* conditions that are not induced by anthropogenic perturbations). This challenge is even greater within dynamic ecosystems, and considering marine coastal systems, results in an “estuarine or sandy beach quality paradox” (Elliott & Quintino 2007, Daief et al. 2014). The findings in this thesis provide a framework for coupling classical and novel community- and trophic-based approaches to determine the responses of highly dynamic systems to anthropogenically induced disturbances (FIG. 11). Such an approach, revealing subtle, but highly significant, shifts from pristine to impacted states (papers I-IV), is most likely to be preferable in the study of dynamic systems under eutrophication stress than most of the widely used biotic indices.

As an example, I have calculated the AMBI (AZTI Marine Biotic index, Borja et al. 2000)

values for the 3 beaches included in **paper III** and this index gives rise to the opposite conclusion, with the pristine SB being disturbed ( $AMBI_{No\_GT} = 1.54$ ), and the two impacted sites being undisturbed ( $AMBI_{Het\_GT} = 0.52$ ,  $AMBI_{Hom\_GT} = 0.44$ ). These conflicting values underline the importance of the approach used in this thesis as a step towards the development of methods based on *in situ* studies that combine the investigation of benthic community responses along stress and temporal gradients with specifically developed analytical methods that precisely detect direct or indirect human-induced changes in dynamic ecosystem structure and functioning (FIG. 11). Although this thesis assesses some facets of functioning in highly dynamic systems (**paper IV**), further evaluation of the relationship linking organisms and ecosystem functioning would strengthen the methodological framework suggested here. A recent study has shown that the evaluation of underlying functional identity (*i.e.* the quantitative



**FIG. 11.** Illustration of a framework coupling a sampling inferring community and trophic structure (dashed line circles) along gradient of stress (turquoise stretched triangle) and over time (grey bold arrow) with space-time analyses (bordeaux frame) to depict dynamic ecosystem drifts under anthropogenic stress. Arrows linking samplings denote their inter-comparisons along the stress gradient and over time through the use of analytical approaches able to test space-time interactions in repeated ecological survey data. The use of stable isotope analyses is suggested here as it has proven to be a good proxy of dynamic ecosystem drifts in this thesis (**paper IV**). Using the latter tool, special focus on some species which respond markedly to green tides (in terms of abundance, biomass or trophic niche; denoted by asterisks) is worth considering. Com. str. = community structure. *Cadre conceptuel alliant un échantillonnage visant à caractériser la structure de la communauté et du réseau trophique (cercles pointillés) le long d'un gradient de stress d'origine anthropique (triangle turquoise allongé horizontalement) au cours du temps (flèche grise verticale) avec des analyses spatio-temporelles (cadre bordeaux) adaptées à la caractérisation d'une dérive potentielle d'un écosystème soumis à une pression d'origine anthropique. Les flèches reliant les échantillonnages entre eux désignent les comparaisons inter sites le long du gradient de stress (flèches bleu turquoise) et dans le temps (flèches grises) à l'aide de méthodes analytiques adaptées au test de l'interaction espace-temps basé sur un échantillonnage répété dans le temps. L'utilisation des isotopes stables s'est révélée pertinente pour la détection des dérives d'un écosystème dynamique (article IV). Plus particulièrement, l'analyse de la signature isotopique d'espèce particulièrement affectée par le stress (en termes d'abondance, de biomasse ou de niche trophique; indiquées par des astérisques) peut être utile. Com. str. = structure des communautés.*

measure of qualitative functions of ecosystems) focussed on two functional aspects (including one that was linked to trophic relationships), is an accurate proxy for ecosystem performance and sheds light on underlying system functional expressions (Weigel et al. 2016). The study of trophic relationships, which *e.g.* provides information on energy transfer through an ecosystem (as shown in **paper IV** through the use of stable isotope analyses), combined with trait-based analyses (see for example Törnroos & Bonsdorff 2012) for evaluation of other functional aspects, would probably ensure a better assessment of ecosystem functioning. In addition, the investigation of the responses of other group of organisms, such as meiofauna and microbial communities, which play key roles in ecosystems (through trophic interactions, and processes of recycling nutrients for example) and exhibit a high turnover that implies quick responses to changes, would increase our understanding of the functioning of these systems under anthropogenic influence.

As this thesis highlights shifts in carbon transfer throughout subsets of SB food webs (**paper IV**), the repercussions of different anthropogenic stresses on higher trophic levels (*e.g.* shorebirds, fish, geese) would need to be investigated (*e.g.* Dugan et al. 2008), which is a real challenge on a fishery perspective as well as on a conservation level. Also, a better assessment of effects of stress on physicochemical characteristics of dynamic systems at finer scale (*e.g.* at low tide: what fine

scale processes occur underneath a dense mat of *Ulva*?) would help exploring and finding potential other processes responsible of shifts.

Our comprehension of responses of beach systems to anthropogenically induced disturbance is *hitherto* restricted to specific pressure assessment (**paper I-IV**, see also *e.g.* Reyes-Martínez et al. 2014), although multiple stressors have been studied in other dynamic systems (*e.g.* Hewitt et al. 2003, Christensen et al. 2006, Thrush et al. 2008). However, as shown on the map in **FIG. 3**, human-induced stresses often appear simultaneously. In case a system with simplified trophic structure and functioning further changes (*i.e.* the overlap of additional anthropogenically induced stress(es), such as increasing temperatures and rainfall, because of climate change), these systems are expected to be more susceptible to collapse (de Ruiter et al. 2005). Continuing with the eutrophication example, inferring changes occurring in SB systems where *e.g.* green macroalgal and toxic microalgal blooms co-occur, would increase our understanding of the responses of dynamic ecosystems facing multi-pressures, and thus contribute to elucidate a current fundamental issue in a global change context (Duarte 2014). The use of extensive datasets obtained through long-term monitoring surveys of biogeographical areas (such as the REBENT-programme in Brittany) together with quantitative evaluation of stress(es) intensity (*e.g.* the CEVA estimations of *Ulva* coverage and biomass) can also aid in achieving this goal.

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# Original publications (I-IV)



# Paper I



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



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### ABSTRACT

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 tidal 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, coastal 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

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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  $\beta$ -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  $\approx$  180  $\mu$ m), 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  $\approx$  380  $\mu$ m) 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.

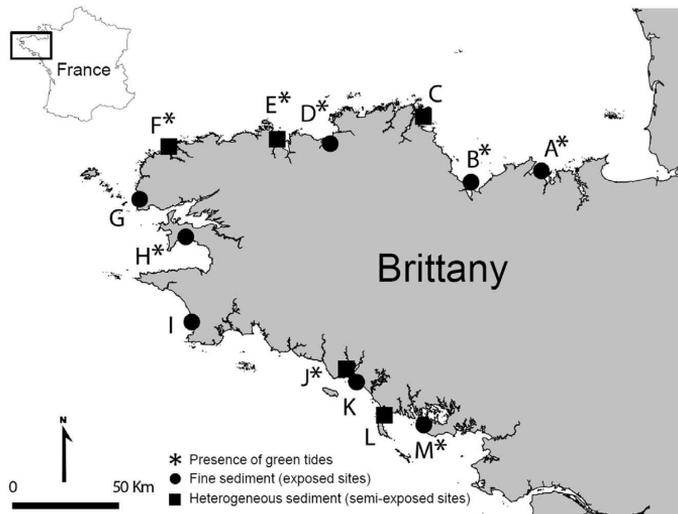
The ultimate aim of the present study was to examine whether responses of macrotidal ecosystems were attributable to occurrence of *Ulva* spp. To reach this objective, we analysed the effects of temporal, spatial and environmental variables, and specifically eutrophication in the form of green tides, 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).

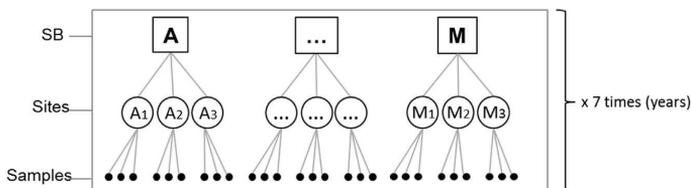
2.2. Sampling design

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<sup>2</sup>, 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<sup>2</sup>. 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<sub>1</sub> = one opposite end of beach A, A<sub>2</sub> = middle of beach A, A<sub>3</sub> = 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  $\mu\text{m}$  grain size fraction) and dry-sieving, using a series of 14 sieves from 63  $\mu\text{m}$  to 10,000  $\mu\text{m}$ . 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  $\mu\text{m}$  to 2 mm, and mud includes sediment exhibiting grain sizes smaller than 63  $\mu\text{m}$  (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 ( $\log_{10}[\text{sand.tide}/\text{slope}]$ , 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](http://www.previmer.org)) using the PyPredator software (i.e. Python Previmmer 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 PERMANOVA (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 Geoportal 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<sub>A</sub>) to south-west (SB<sub>M</sub>), 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<sub>C</sub>, SB<sub>G</sub>, SB<sub>I</sub>, SB<sub>K</sub>, and SB<sub>L</sub>, 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  $\mu\text{m}$  and from 1.7 to 3.3 at SBs of Type I, and from 300 to 560  $\mu\text{m}$  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  $\times$  GT), on multivariate responses of macrofaunal 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<sub>A</sub> to SB<sub>M</sub>), 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) <sup>a</sup>	W (m) <sup>b</sup>	S (ha) <sup>c</sup>	Spring tide (m)	Slope (%)
Saint-Cast	A <sup>d</sup>	I	48.63	-2.25	1.7	2410	403	13.2	0.5
Saint-Brieuc	B <sup>d</sup>	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 <sup>d</sup>	I	48.68	-3.60	3.0	1536	457	10.05	0.7
Callot	E <sup>d</sup>	II	48.68	-3.93	4.9	760	372	9.7	1.4
Sainte-Marguerite	F <sup>d</sup>	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 <sup>d</sup>	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
Gävres	J <sup>d</sup>	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
Plouhamel	L	II	47.56	-3.12	3.2	1025	324	5.7	0.6
Kerjouanno	M <sup>d</sup>	I	47.53	-2.87	1.9	149	28	5.1	3.7

<sup>a</sup> Length of beach.

<sup>b</sup> Width of beach.

<sup>c</sup> Surface of beach.

<sup>d</sup> Presence of green tides.

**Table 2**

Environmental characteristics of the thirteen sandy beaches (from SB<sub>A</sub> to SB<sub>M</sub>) 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	Gävres	Erdeven	Plouharnel	Kerjouanno
	Beach code	A <sup>i</sup>	B <sup>j</sup>	C	D <sup>j</sup>	E <sup>j</sup>	F <sup>j</sup>	G	H <sup>j</sup>	I	J <sup>j</sup>	K	L	M <sup>j</sup>
	Beach type	I	I	II	I	II	II	I	I	I	II	I	II	I
<i>Biological var.</i>	GT occurrence <sup>a</sup>	7	19	0	20	18	18	0	4	0	5	0	0	2
	Ulva coverage <sup>b</sup>	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 <sup>c,d</sup> (%)	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
<i>Sediment var.</i>	Median <sup>e</sup> (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 <sup>c</sup>	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 <sup>c</sup>	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 <sup>f</sup> (%)	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 <sup>f</sup> (%)	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
<i>Marine var.</i>	Mud <sup>f</sup> (%)	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
	SWT <sup>g</sup> (°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 <sup>h</sup> (‰)	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
<i>Terrestrial var.</i>	Air Temp. <sup>g</sup> (°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 <sup>i</sup> (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 <sup>i</sup> (1/10 m/s)													
	Wind dir. <sup>h</sup> (/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 <sup>j</sup> (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	

<sup>a</sup> Count over 21 flight overs (3 per year from 2007 to 2013).

<sup>b</sup> Mean estimation of GT coverage of the measured values from 2007 to 2013 (CEVA).

<sup>c</sup> Mean ± SD of the measured values from 2007 to 2013.

<sup>d</sup> OMC = Organic Matter Content.

<sup>e</sup> Mean ± SD of the measured values between January and March from 2007 to 2013.

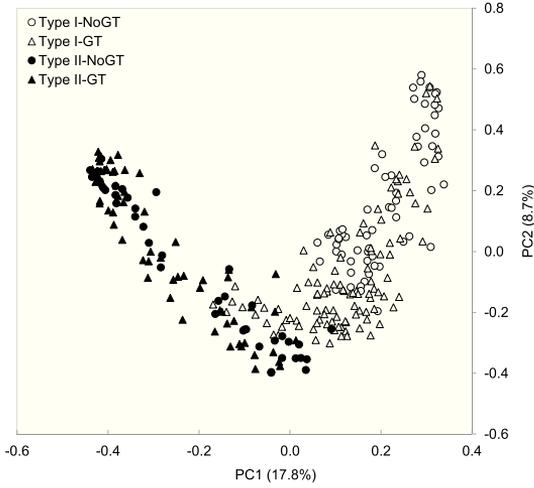
<sup>f</sup> SWT = Sea Water Temperature.

<sup>g</sup> Temp. = temperature.

<sup>h</sup> Dir. = direction.

<sup>i</sup> Mean ± SD of sums of rainfall felt between January and March from 2007 to 2013.

<sup>j</sup> 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.

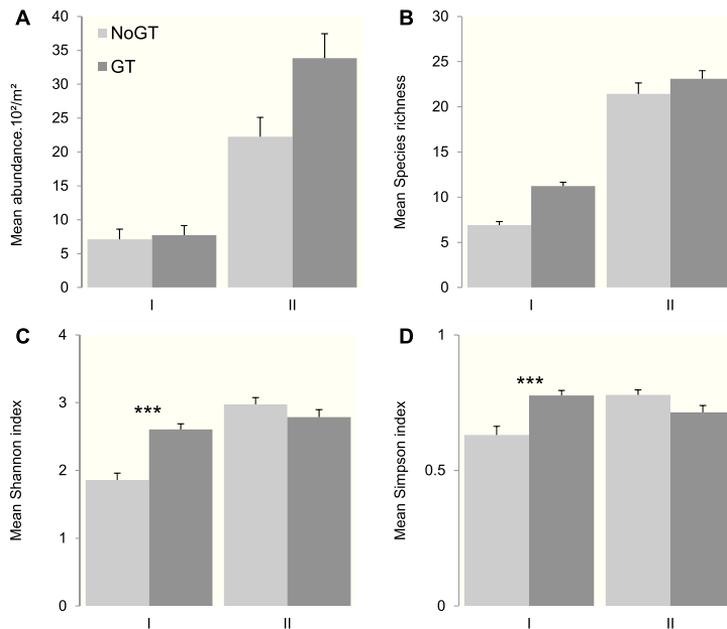
without green tides). The Type I sandy beach community was dominated by the suspension-feeding bivalve *D. vittatus* (Table 5), which contribution to the total abundance by almost 50% in beaches where no green tides occurred. However, the relative abundance of *D. vittatus* did not exceed 26% at sandy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

**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  $p \leq 0.05$  are shown in bold; \* $p \leq 0.05$ , \*\*\* $p \leq 0.001$ .

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

tides. Other species were also negatively affected by green tides at sandy beaches of Type I, namely the selective surface-feeder *Spio-phanes 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: \* $p \leq 0.05$ , \*\*\* $p \leq 0.001$ .

**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	<b><math>1.10^{-4}</math> ***</b>
GT	1	3.48	5.73	<b><math>1.10^{-4}</math> ***</b>
Type* GT	1	3.20	5.27	<b><math>1.10^{-4}</math> ***</b>
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 oerstedii*, *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

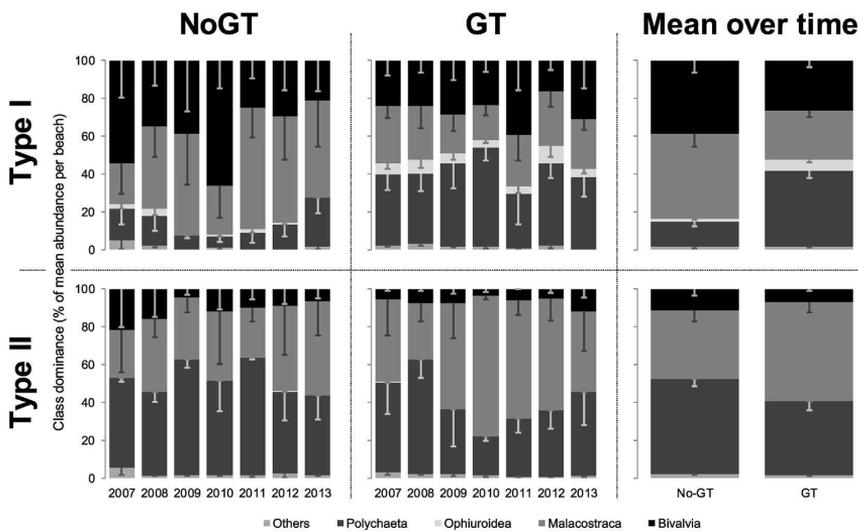
environmental variables as well as spatial and temporal variables in the context of this large scale study, we partitioned the variance of macrofauna in the two habitats with respect to environment (variables not related to GT), presence of *Ulva* mats (*Ulva* occurrence and coverage), spatial and temporal 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						
<i>Ampharete</i> sp.	Annelida polychaeta	–	–	–	0.9	D	SF, SPF	T	~20	Ovi	
<i>Aonides oxycephala</i>		–	0.0	0.1	1.7	D	SuF, SPF	T	81	Ovi	
<i>Cauterella alata</i>		–	–	0.3	0.7	D	SuF, SPF	T	12	Ovi	
<i>Chaetozona gibber</i>		–	1.6	0.3	0.5	D	SuF, SPF	T	20	Ovi	
<i>Euclimene oerstedii</i>		–	0.2	7.8	1.9	D	SuF	T	100	Ovi	
<i>Glycera triadactyla</i>		–	0.8	0.2	0.3	Ca	SPF	B, (S)	50	Ovi	
<i>Lanice conchilega</i>		–	0.5	3.9	0.9	D	SF, SPF	T	300	Ovi	
<i>Leiochone leiopygos</i>		–	1.6	1.7	1.4	D	SuF	T	200	Ovi	
<i>Macroclymene santandarensis</i>		–	0.0	1.4	0.7	D	SuF	T	150	Ovi	
<i>Magelona filiformis</i>		0.5	1.6	0.1	–	D	SuF, SPF	B	80	Ovi	
<i>Marphysa bellii</i>		–	0.0	0.2	0.5	Ca	SPF	B	200	Ovi (Ovo)	
<i>Nephtys cirrosa</i>		3.1	3.2	1.6	0.2	Ca, Sc	SPF	B, C, (S)	100	Ovi	
<i>Nephtys hombergii</i>		0.1	0.7	0.7	0.7	Ca, Sc	SPF	B, C, (S)	200	Ovi	
<i>Notomastus latericeus</i>		–	1.7	13.8	9.1	D	SuF	B	300	F, Ovi	
<i>Oligochaeta</i> spp./ <i>Oligochaeta</i> spp.		0.0	0.1	–	0.6	D	SuF	B	–	F, Ovi	
<i>Owenia fusiformis</i>		0.2	8.0	0.4	0.0	D	SuF, SF, SPF	T	100	Ovi	
<i>Paradoneis</i> sp2/ <i>Paradoneis</i> sp2		–	–	1.9	0.1	D	SPF	B	15	Ovi	
<i>Phyllodoce mucosa</i>		0.2	0.1	0.1	0.6	Ca	SPF	B, C, (S)	100	Ovi	
<i>Poecilochaetus serpens</i>		–	–	1.2	0.1	D	SF, SuF, SPF	T	55	Ovi	
<i>Scoloplos armiger</i>		0.2	0.6	3.8	3.9	D	SSF	B, C	120	Ovo	
<i>Sigalion mathildae</i>		0.4	2.1	0.0	–	Ca	SPF	B, C, (S)	150	Ovi	
<i>Spio</i> spp./ <i>Spio</i> spp.		0.1	0.4	1.8	1.0	D	SPF	B	~150	F, Ovi	
<i>Spiophanes bombyx</i>		3.9	0.4	0.1	0.0	D	SuF, SPF	T	60	Ovi	
<i>Ampelisca brevicornis</i>		Arthropoda Malacostraca	0.0	–	0.5	0.7	D	SF	T	12	Ovo
<i>Apeudopsis latreillii</i>			0.0	–	36.1	49.2	D, H	SPF	S, (C)	7	Ovo
<i>Bathyporeia elegans</i>			2.7	0.4	–	0.1	D, H $\mu$	SPF	B	6	Ovo
<i>Bathyporeia pelagica</i>			4.1	1.2	0.2	0.1	D, H $\mu$	SPF	B, (nS)	8	Ovo
<i>Corophium arenarium</i>	–		–	0.0	8.1	D, H	SuF, SF, SPF	B, C	7	Ovo	
<i>Cumopsis</i> spp.	6.3		0.4	0.2	0.0	D	SSF, SPF	B (nS)	~6	Ovo	
<i>Diogenes pugilator</i>	0.6		1.6	0.0	–	Ca	SPF	C, (B)	20	Ovo	
<i>Eurydice affinis</i>	9.0		0.3	–	–	Ca	SPF	S, B, (nS)	7	Ovo	
<i>Leptocheirus hirsutimanus</i>	–		0.4	0.8	0.1	H $\mu$	SF	T	8	Ovo	
<i>Leucothoe incisa</i>	–		0.6	0.4	0.3	D	SuF, SPF	B, C	7	Ovo	
<i>Siphonocetes kroyeranus</i>	–		6.9	0.6	0.8	D, H $\mu$	SuF, SPF	T, C	5	Ovo	
<i>Synchelidium maculatum</i>	3.8		0.2	–	–	Ca	SPF	B	5	Ovo	
<i>Urothoe poseidonis</i>	0.1		3.4	1.6	1.0	H $\mu$	SSF	B (nS)	6	Ovo	
<i>Urothoe pulchella</i>	0.6		5.9	3.3	1.2	H $\mu$	SSF	B (nS)	5	Ovo	
<i>Acrocnida</i> cf. <i>spatulispina</i>	1.0		5.5	0.0	–	O, (Ca)	SPF	B	12*	Ovi	
<i>Cerastoderma edule</i>	Mollusca bivalvia		–	1.2	0.6	0.6	H $\mu$	SF	B	20	Ovi
<i>Donax trunculus</i>			6.2	2.2	–	–	D, H $\mu$	SF, SPF, (SuF)	D, C, B	45	Ovi
<i>Donax vittatus</i>			48.4	25.8	0.0	–	D, H $\mu$	SF, SPF, (SuF)	D, C, B	38	Ovi
<i>Kurtiella bidentata</i>			0.3	4.2	0.1	1.0	D, H $\mu$	SF, SuF	C, B	6	Ovi
<i>Loripes lacteus</i>			–	0.0	3.0	1.6	Sy, D	SF, Sy	B	22	Ovi
<i>Lucinoma borealis</i>			–	0.0	0.3	0.9	Sy, D	SF, Sy	B	39	Ovi
<i>Tellina tenuis</i>			2.4	7.5	0.6	0.2	D, H $\mu$	SuF, SPF	B	20	Ovi
<i>Nassarius reticulatus</i>			0.0	0.3	0.7	0.3	Sc	SPF	C	30	Ovi

Feeding habit: Ca = Carnivore; D = Detritivore; H = Herbivore; H $\mu$  = 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.

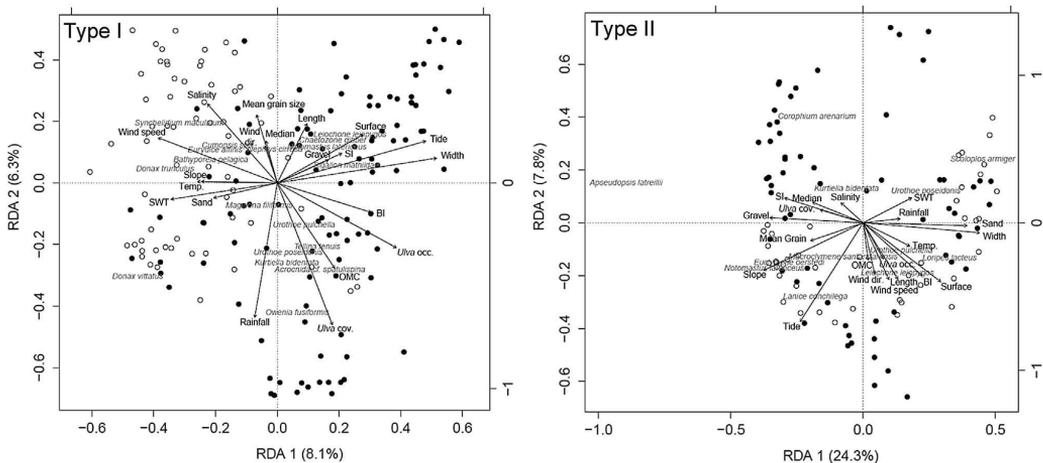
Reproduction development: F = Fragmentation; Ovi = Oviparous; Ovo = Ovoviviparous.

(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 (biophysical 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, Ménéguen & 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 macroalgal 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 macroalgal 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 atidal 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-Courtet 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 from 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. *spatulispira* 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). *Apsseudopsis 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 benefit 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 oerstedii* 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 Carrico 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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*The following data supplement accompanies the article*

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

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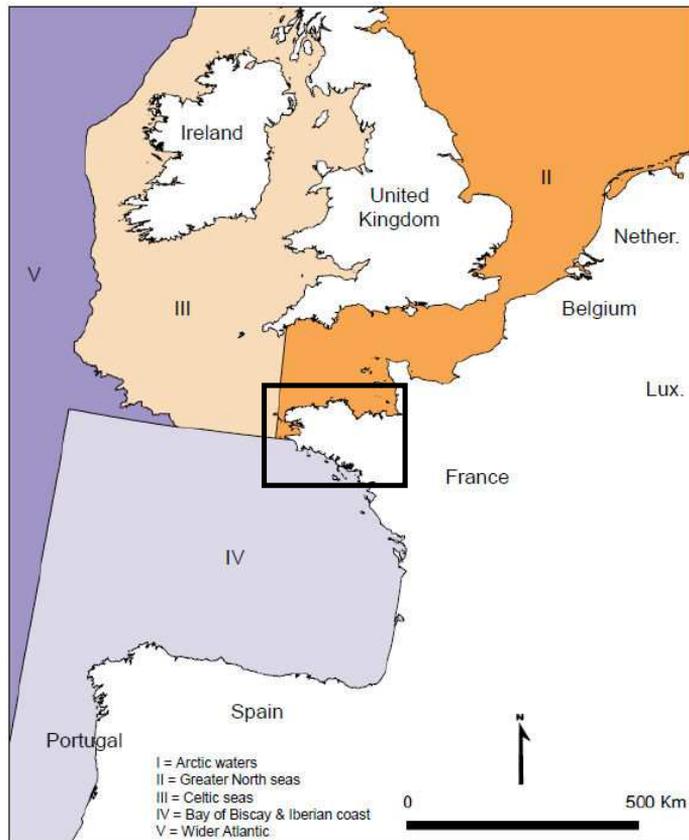
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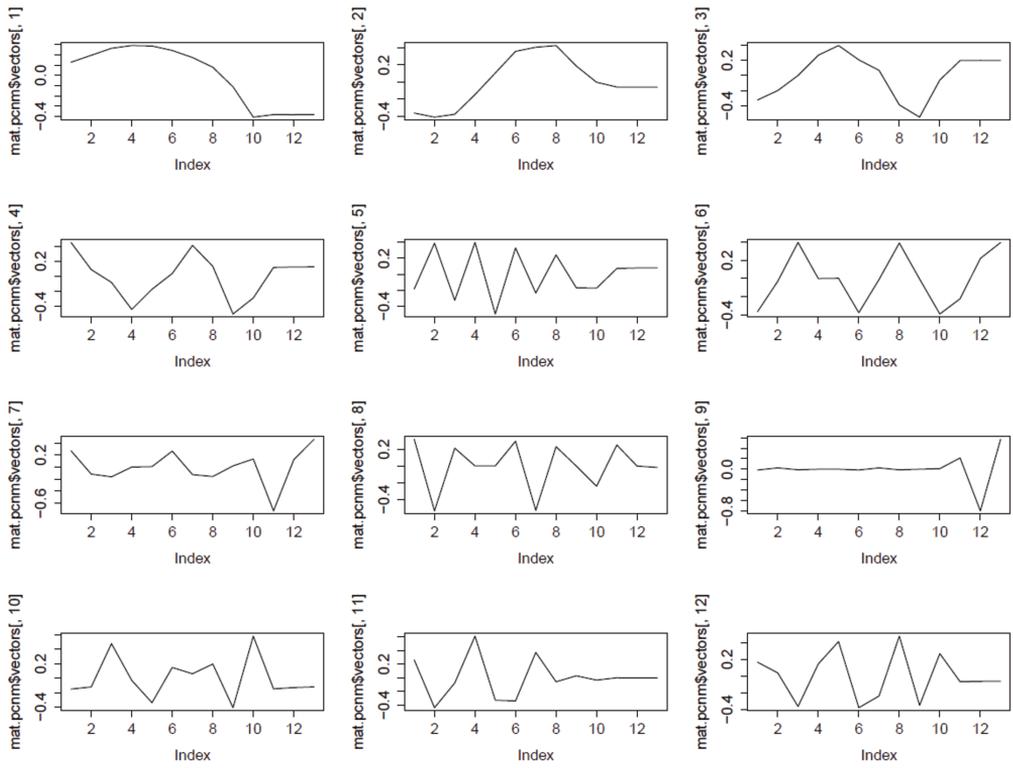
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**Supplement.** Additional information on spatial & temporal MEMs, and results of normality tests.

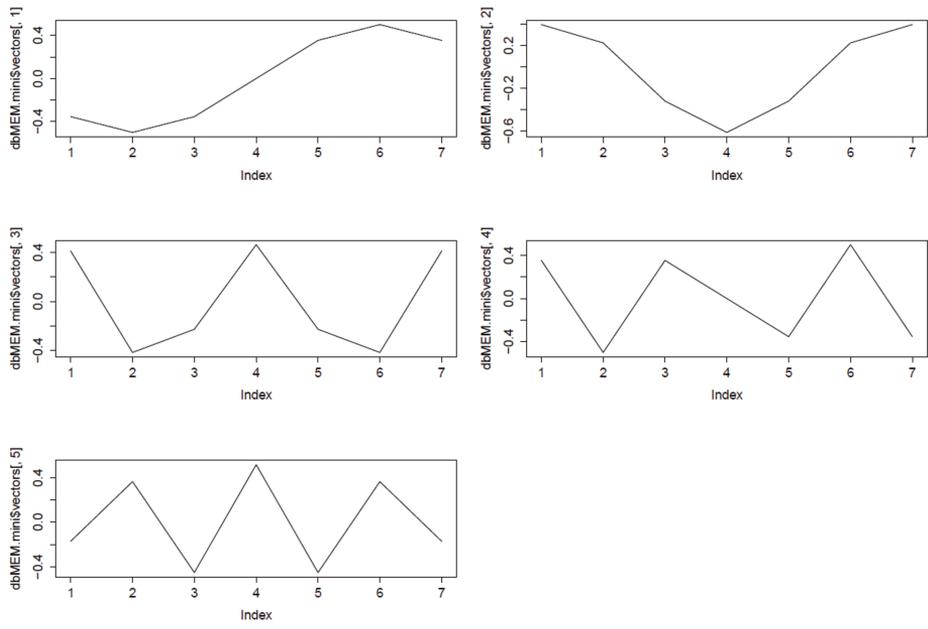
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**Supplement 1.** Brittany (encompassed by the black box) is a marine biogeographical transition zone between two marine regions *sensu* the OSPAR commission: the separation between region IV (southern Brittany) and region II (northern Brittany) is mainly linked to hydrodynamics alternating vs. vortex/gyre currents).



**Supplement 2.** All dbMEMs (individual curves above) eigenfunctions generated based on distance matrix obtained by measuring distances between sandy beaches along the coasts of Brittany.



**Supplement 3.** All dbMEMs (individual curves above) eigenfunctions generated based on the number of sampling occasions and the number of years between sampling occasions.

Univariate variables within types				
	Test	df	W/t	p
<b>Type I (NoGT vs. GT)</b>				
H	W		1566.5	$1.18 \cdot 10^{-8}$ ***
D	W		2035.5	$3.10 \cdot 10^{-5}$ ***
<b>Type II (NoGT vs. GT)</b>				
H	t	101.55	1.23	$2.23 \cdot 10^{-1}$ ns
D	W		1484	$2.94 \cdot 10^{-1}$ ns

**Supplement 4.** Results of the tests (t = Student; W = Wilcoxon-Mann-Whitney test) performing within each Type of SB<sub>s</sub> (I or II) to compare mean univariate variables when *U/va* mats are washed ashore or not (GT or NoGT respectively). These tests were performed when significant interaction of factors GT and Type was found after performing two-way ANOVAs. With H = Shannon index, D = Simpson index.



# Paper II

# Green tides on inter- and subtidal sandy shores: differential impacts on infauna and flatfish.

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## Abstract

Beach ecosystems extend from dune to offshore areas along most of the coasts, and provide essential services that are not provided by any other ecosystem. Indeed, sandy systems contain unique biodiversity and supply nursery- and foraging areas for numerous commercially important marine species, such as flatfish. However, these systems are threatened by increasing anthropogenic pressure. Green tides (GT, i.e. accumulations of green opportunistic macroalgae) are a major human-induced threat to marine ecosystems, from inshore to nearshore. Such eutrophication process greatly affects both benthic invertebrate communities and flatfish communities, within sheltered and non- or microtidal systems. However, the responses of dynamic open macrotidal sandy systems to eutrophication in the form of macroalgal mats remain to be fully understood. In particular, understanding the effects of GT on two connected biological compartments (infauna and flatfish) within two connected habitats (intertidal and subtidal) is crucial. Here, we set out to assess the influence of several environmental variables, including *Ulva* biomass, on the variability in infauna and flatfish communities in both the intertidal and the subtidal at four sites impacted or not by GT. In total, 110 biodiversity samples were analysed with classic and novel analytical approaches. Our results demonstrate that the presence of GT specifically impact intertidal macroinvertebrate communities. However, small effects of GT on subtidal infauna communities, as well as on species-specific flatfish at both intertidal and subtidal, were still detectable. Our findings underline the vulnerability of highly dynamic ecosystems exposed to anthropogenic stress, in particular intertidal sandy shores.

## Keywords

Benthic infauna – Flatfish – Inshore – Nearshore – Sandy sediments – *Ulva* – Eutrophication – Space-time analysis.

## Introduction

Marine sediments constitute the second most common habitat on earth (Gray & Elliott, 2009). This habitat also dominates coastal areas, where sediments are more or less sorted depending on

wave action and the influence of currents. From pelites to pebbles, but generally sand, marine sediments accumulate along the coast to form beaches that extend from terrestrial systems (dunes) until depths where the wave action on bottom ceases (Short & Jackson, 2013). These systems harbour a highly diverse biota and are very productive systems (Costanza *et al.*, 1997; Barbier *et al.*, 2011). In particular, sandy beaches provide ecological functions that are not achieved by any other ecosystem on earth (McLachlan & Brown, 2006). For instance, both intertidal and subtidal sands provide essential foraging and nesting habitats for many adapted invertebrate and vertebrate organisms (benthic macrofauna, meiofauna, fishes, turtles and shorebirds) (Schlacher *et al.*, 2008; Defeo *et al.*, 2009). In addition, sandy systems play a key role in maintaining coastal fisheries and providing reproduction and nursery areas for commercially valuable species (Gibson, 1994; McLachlan & Brown, 2006), such as bivalve molluscs of the genus *Donax* and, in their juvenile form, several flatfish species (e.g. *Scophthalmus* spp. (Linnaeus, 1758), *Pleuronectes platessa* (Linnaeus, 1758)).

Considering simultaneously both intertidal and subtidal sands in the study of coastal ecosystem functioning is important. Indeed, inshore and nearshore sandy systems exchange material (i.e. sand grains and organic debris) with each other in response to seasonal coastal processes (Aubrey, 1979), which structurally link the two habitats. Intertidal and subtidal biological compartments are also linked in different ways; through daily tidal (Gibson, 2003) and seasonal migrations (Gillanders *et al.*, 2003), as well as movements induced by foraging and/or competitive behaviours. However, intertidal and subtidal sands differ in some other ways, and for example nearshore sediments are not subject to desiccation stress, and they are less affected by wave action compared to swash-zone/intertidal systems (McLachlan & Brown, 2006). In instances where these two adjacent, although distinct, habitats experience the same stress from anthropogenic origin, one can ask if intertidal and subtidal sand communities would respond the same, or rather differently to the accumulation of high biomass of opportunistic green algae (i.e. green tides formed by *Ulva* spp. (Linnaeus, 1753))?

Today, 60% of the world's population is living within coastal areas, and particularly at the vicinity of sandy coasts, as they are prime sites for human recreation (Schlacher *et al.*, 2008); making sandy coastal systems highly vulnerable to anthropogenic pressure. Among the human-induced threats to coastal ecosystems, the escalating nutrient enrichment of coastal waters leading to the eutrophication of marine systems (Cloern, 2001), is of major concern. One direct symptom of eutrophication is the massive development of opportunistic macroalgae (Schramm, 1999; Korpinen & Bonsdorff, 2015), which form large mats of stranding or drifting algae along beaches or in shallow bays (Grall & Chauvaud, 2002). These blooms occur both within intertidal and subtidal systems, stranding on shore, or floating over the sediments, respectively (Pihl *et al.*, 1999; Merceron & Morand, 2004; Charlier *et al.*, 2007); and this phenomenon is increasing in frequency and intensity worldwide (Ye *et al.*, 2011).

Such macroalgal accumulations greatly affect sheltered and non- or microtidal sediment invertebrate-, as well as flatfish- communities (Baden *et al.*, 1990; Norkko & Bonsdorff, 1996; Pihl *et al.*, 2005). For example, on the microtidal Swedish Skagerrak coast, the recruitment of young of the year *P. platessa* may be reduced by 40% due to the presence of opportunistic macroalgal mats (Pihl *et al.*, 2005). Conversely, within the same study area, Baden *et al.* (1990), have not found negative effects of eutrophication on flatfish recruitment, but on macrofauna, with wide-spread mortality of bivalves. More subtle changes have been highlighted within open, and macrotidal sandy beaches (Quillien *et al.*, 2015a), although the effects of macroalgal blooms within such dynamic systems have not been fully understood yet. In particular, the influence of accumulation of opportunistic macroalgae on flatfish nursery communities occurring within open sandy beaches has not yet been fully understood, nor has the impact of algal blooms within dynamic subtidal systems, although algal blooms are found from the inshore to the subtidal.

In the present study, we investigated possible shifts in intertidal and subtidal benthic communities induced by the presence of *Ulva* mats, using open sandy systems located in Brittany, France, as a study case. The study region is locally heavily affected by green tides (Ménèsquen & Piriou,

1995), and for example, fifty-one sandy sites were affected by accumulations of *Ulva* in 2013 (CGDD, 2014). There, *Ulva* blooms occur both at intertidal and subtidal sites (Merceron & Morand, 2004). More particularly, the aim of the present study was to assess the effects of drifting and stranding opportunistic macroalgae on sandy bottom benthic communities, namely macrozoobenthos (infauna) and juvenile flatfish (epifauna). We set out to assess functional facets (i.e. diversity, community structure and nursery area) of sandy bottoms over time (4 seasons over one year), and from intertidal habitats (low shore at spring tide) to directly connected subtidal areas (5m depth), combining traditional multivariate methods and novel approaches. Following this approach, we explored simultaneous variations in macrofaunal and flatfish communities by testing the following hypotheses: environmental factors, and especially macroalgal mats, differentially affect benthic communities depending on (i) the biological compartment (macrozoobenthos vs. flatfishes), and (ii) the habitat (intertidal vs. subtidal).

## Materials and methods

### Study system

On the highly indented western coast of Brittany (France), fine sediments accumulate to form large subtidal sandy beds and kilometre long sandy beaches. Within this region, our study was conducted in the Bay of Douarnenez, and the Crozon peninsula (48.2°N, -4.4°W, and 48.2°N, -4.6°W, respectively), which are both known as important nurseries for flatfish (Quiniou, 1986). Four sites were selected for the study (Figure 1): two intertidal sandy beaches, one which does not harbour green tides (Inter-NoGT), and one that is annually covered by *Ulva* (Inter-GT); as well as two subtidal sandy beds adjacent to the beaches; one which never harbours macroalgal mats (Sub-NoGT), and an other which is annually impacted by green tides (Sub-GT). The two intertidal sites were selected based on a previous study (Quillien *et al.*, 2015a), as the endpoints of a gradient of eutrophication (from no GT to high biomass of *Ulva*). The two subtidal sites were chosen as extensions of the intertidal sites, but at 5-meter depth, following the vertical slope/gradient. The intertidal sites show large areas (up to 500 m from shore during

spring tides) that are uncovered at low tide (mean tidal regime = 6.5 m). A lower shore with a slope of 1.5% characterizes them, and since the tidal regime is macrotidal, these beaches are defined as dissipative (Short, 1996). The beaches are 2.3 and 2.8 km long, respectively. The anthropogenic impacts on Inter-NoGT and Sub-NoGT are negligible. Indeed, a wetland area located just behind the beach filters water inputs from land, and the urbanization there is limited (Figure 1). In contrast, the Inter-GT beach is located below a large agricultural catchment area and has experienced yearly *Ulva* bloom events since the early 1980s (Ménesguen & Piriou, 1995; Charlier *et al.*, 2007). The subtidal zone is also affected by these accumulations of green macroalgae. Merceron and Morand (2004) have shown the presence of a deep subtidal stock of free-floating *Ulva* beyond the surf-zone, at depths reaching 15 m. Both intertidal and subtidal drifting *Ulva* mats are variable in space and time, and exchange material between each other (Figure 2). In winter, small pieces of *Ulva* stay in the subtidal zone, and this small amount of material is likely to seed the intertidal zone in spring (Figure 2a). Later in the season, the subtidal stock could be supplied, at least partially, by the intertidal (Figure 2b; Merceron and Morand, 2004).

### Sampling

To assess macrofaunal and flatfish variability following a vertical scale, sampling was conducted at low intertidal (spring low tide) and at 5 m depth at the 2 study areas (Inter-NoGT = 48° 14.682'N, 4° 32.908'W, Inter-GT = 48° 10.22'N, 4° 17.775'W, Sub-NoGT = 48°14.641'N, 4°33,615'W, Sub-GT = 48°10.216'N, 4°18.074'W). To evaluate temporal variability of benthic communities, the 4 sites were sampled from February to December 2013. Temporal variability was assessed at 5 and 4 dates in the intertidal and the subtidal, respectively, and more precisely in early spring (February/March), spring (May), summer (June/July), fall (September), and early winter (November/December) (Figure 3).

Macrofauna (>1 mm) was collected using a tube corer (surface = 0.03 m<sup>2</sup>) at the intertidal sites, and using a Smith-grab (surface = 0.1 m<sup>2</sup>) in the subtidal. Samples from both the intertidal and subtidal were sieved through mesh bags (1

mm mesh size) to separate the fauna from the finer part of sediment. At each sampling site, 3 (core) and 5 (grab) replicate samples were taken randomly within an area of a few m<sup>2</sup>. Faunal samples were preserved in 4% buffered formalin for later sorting in the lab where macrofaunal invertebrates were identified to the lowest possible taxonomic level with the aid of a binocular magnifier, and counted.

Flatfishes were sampled using a beach trawl (5 m wide, 0.3 m high, with an 8 mm stretched mesh net in the cod-end) in the intertidal, and using a beam trawl (2 m wide, 0.5 m high, with a 4 mm stretched mesh net in the cod-end) in the subtidal. At intertidal sampling sites, beach trawls were carried out during the day at rising tides, at least once along 80 to 260 m long latitudinal transects (sampled surface: 400 to 1300 m<sup>2</sup>). Beam trawls were carried out during the day, at neap tide, along 500m transects (sampled surface: 1000 m<sup>2</sup>), at least twice at each site within the subtidal zone. The flatfish were sorted, identified and measured (total length) on board and released immediately after the investigations. For each species, individuals were classified into age groups based on their size and on peer-reviewed literature and research-reports on flatfish growth (including Deniel, 1973; Gibson & Ezzi, 1980; Nottage & Perkins, 1983).

For both macrofauna and flatfish, species nomenclature follows the 'World Register of Marine Species' ([www.marinespecies.org/](http://www.marinespecies.org/)). The abundance of zoobenthos was converted to units per m<sup>2</sup> for comparison across zones. For each haul, flatfish apparent abundance standardised per surface unit (1000m<sup>2</sup>) was assessed considering the number of flatfish caught and the surface covered (haul length \* trawl opening). 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 and Bonsdorff, 2012).

At each site where fauna was sampled, a single sediment core (in the intertidal) or grab (in the subtidal) was extracted to obtain grain size distribution and total organic matter content over time. Grain sizes were assessed by dry sieving, using a series of 16 sieves (from 63 to 10 000 µm). Medi-

an grain size was equal to the second quartile (Q50) of the sediment grain size value. Sorting was calculated based on the first and the third quartiles of the sediment grain size ratio ( $\sqrt{Q25/Q75}$ , where Q25 and Q75 denote first and third quartile, respectively). Total organic matter content was assessed by weighted loss after ignition at 450°C for 5 h. For the intertidal sites, *Ulva* biomass data was estimated by CEVA ([www.ceva.fr/fre](http://www.ceva.fr/fre)) through monthly aerial surveys (for estimation of surface covered by algae) and field sampling (for conversion to biomass). At subtidal sites, *Ulva* biomass was assessed on board by weighting algae collected in beam trawls (each one covering an area of 1000 m<sup>2</sup>). Intertidal seawater temperature (hereafter ‘SWT’) and salinity were measured on each sampling occasion using an YSI-OMS v2 probe. Subtidal SWT and salinity were extracted from datasets provided by the PREVIMER system ([www.previmer.org](http://www.previmer.org)) and data used for analyses were obtained by averaging the values for both variables of 5 days before each sampling occasion.

### Community data analysis

Multivariate analyses were performed to evaluate the differences between intertidal and subtidal communities, as well as their respective responses to the presence of green tides. For all multivariate analyses, faunal data (both zoobenthos and flatfish 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 & Gallagher, 2001). Redundancy analyses (RDA) were performed to visualize patterns in the distribution of assemblages of macrofauna and flatfish in space and time within each habitat; with or without green tides (i.e. Inter-NoGT, Inter-GT, Sub-NoGT, Sub-GT), and to determine which environmental variables constrain the variation of benthic communities in this setting.

Temporal (seasonal sampling from February to December 2013) variation of each of the age-grouped flatfish species represented at intertidal and subtidal zones, with or without GT (Inter-NoGT, Inter-GT, Sub-NoGT, Sub-GT) was assessed to extricate diversity trends. In order to compare assemblages between pristine and impacted sites, chi-squared tests were performed

based on pooled (all dates together for each habitat; data from September were not used for subtidal to ensure a balanced design) flatfish data. In order to disentangle the effects of *Ulva* mats, time, and habitat (inter- or subtidal), on the assemblages of macrofauna, two recently developed methods were combined: distance-based Moran’s eigenvector maps (dbMEM, 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 (4 to 5 seasons). The generated dbMEM eigenfunctions were used as temporal variables (here called MEMs). The location along the vertical gradient (i.e. from inter- to subtidal) was used as a spatial variable and was coded by Helmert contrasts (Legendre & Anderson, 1999). The variation of the multivariate responses was then first partitioned with respect to 3 groups of explanatory variables: *Ulva* (variables related to the occurrence and biomass of GT), space (the factors encoded by Helmert contrasts) and time (the MEMs). Variation of macrofaunal multivariate responses was also partitioned separately for each habitat, and thus with respect to 2 groups of explanatory variables (*Ulva* and time) at intertidal and subtidal. Each fraction of variation, i.e. the explanatory power of each set of the explanatory variables, was tested using multiple linear regressions (Legendre & Legendre, 2012).

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

## Results

We found a clear separation between intertidal and subtidal benthic communities, as well as changes induced by the presence of green tides. The responses of benthic organisms to the occurrence of macroalgal mats were different depending on the habitat (intertidal vs. subtidal) and on the benthic compartment (macroinfauna vs. flatfish). The environmental context assessed in the analyses underlined these changes.

### Setting the scene: environmental and faunal characterisation

On average, environmental characteristics were similar between sites within the same habitat (Table 1). However, the total organic matter content tended to be higher at un-impacted sites (1.4–1.7%; at intertidal and subtidal sites, respectively) than at impacted site (1.1–1.4%, *idem*). The environment, both at intertidal and subtidal sites, is fully marine (salinity range: 33.6 – 35.6 psu). Intertidal sites displayed higher mean seawater temperatures (+1°C), sediment sorting (+0.2µm) and median grain size (+40–50µm) compared to subtidal sites. Also, the variability of environmental values was higher for intertidal compared to subtidal. This pattern was even more pronounced for sediment variables (sorting and median grain size), suggesting a lower influence of hydrodynamics in the subtidal domain.

No green macroalgal mat was reported for sites Inter-NoGT and Sub-NoGT, while mean *Ulva* biomass estimated (based on available data) at Inter-GT and Sub-GT sites was 155 and 10 g/m<sup>2</sup> (fresh weight), respectively (Table 1). *Ulva* biomass was variable in space, with higher biomass in the intertidal compared to subtidal, as well as over time (Figure 4). At the intertidal site, a green algae bloom started in May 2013, with a peak in late summer (August, Figure 4a). This setting contrasted with a previous bloom occurring in 2012 within the same study area, which formed in late March (Quillien *et al.*, 2015a). At the impacted subtidal site, the presence of green algal material occurred from March to December (Figure 4b), and algal material most likely remain without temporal disconnection within this habitat. The link between intertidal and subtidal algal stocks is thus maintained spatially and temporally (Figure 2, 4).

Over the 4 sites sampled through the study, i.e. among the 70 macrofaunal- and the 40 flatfish samples, 119 macrofauna and 6 flatfish species were found between February and December 2013 (Table 2). Thirty infaunal species were found at both intertidal and subtidal sites, and 18 were found only at intertidal sites, while 71 occurred only within the subtidal area. Thirty-one and 72 infauna species were sampled at the un-impacted inter- and sub-tidal sites, respectively. Where green tides occurred, 39 and 79 species were

found in the intertidal and subtidal, respectively. Also, flatfish species numbers were equally distributed among intertidal and subtidal sites, impacted or not by green tides, with 2 species only found at intertidal sites (Plaice *Pleuronectes platessa*, and Turbot *Scophthalmus maximus* (Linnaeus, 1758)), 2 species only found at subtidal sites (Solenette *Buglossidium luteum* (Risso, 1810), and Scald fish *Arnoglossus laterna* (Walbaum, 1792)), as well as 2 species shared between the two habitats (Sand sole *Pegusa lascaris*, and Brill *Scophthalmus rhombus* (Linnaeus, 1758)).

The 47 infaunal species presented in Table 2, which mainly belong to crustaceans, polychaetes, and molluscs, made up most (>90% at each site) of the total abundance observed for macrofauna at each of the 4 sites. Intertidal areas were mainly dominated by the bivalves *Donax trunculus* (Linnaeus, 1758) and *Donax vittatus* (da Costa, 1778), the cumacean *Cumopsis fagei* (Băcescu, 1956) and *Cumopsis longipes* (Dohrn, 1869), the amphipod *Bathyporeia pelagica* (Bate, 1856), and the polychaetes *Owenia fusiformis* (Delle Chiaje, 1844) and *Nephtys cirrosa* (Ehlers, 1868) (Table 2). Subtidal sites were mainly dominated by the bivalve *D. vittatus*, the polychaetes *Sigalion mathildae* (Audouin & Milne Edwards in Cuvier, 1830) (juveniles), *Nephtys hombergii* (Savigny in Lamarck, 1818), and *Paradoneis armata* (Glémarec, 1966), as well as the cumacean *Iphinoe trispinosa* (Goodsir, 1843) and the amphipod *Bathyporeia sarsi* (Watkin, 1938).

### Spatial-temporal shifts/patterns in infaunal communities

The relative abundances of infaunal species shifted in the presence of green tides, such as the polychaete *Spiophanes bombyx* (Claparède, 1870), the bivalve *D. trunculus*, and the amphipod *Urothoe poseidonis* (Reibish, 1905), whose relative abundance was lower at the impacted intertidal site. On the other hand, the relative abundances of the ophiuroid *Acrocnida cf. spatulispina* (Stöhr & Muths, 2010) and the polychaete *Magelona mirabilis* (Johnston, 1865) were higher where green tides occurred. At the subtidal site where green tides occurred, the relative abundances of the species *Diogenes pugilator* (Roux, 1829) (carnivorous Anomuran), *Acrocnida brachiata* (Montagu, 1804) (omnivorous Ophiuroid), *Atylus swammerdami* (Milne Edwards, 1830) (omnivorous Amphipod),

and *M. mirabilis* (detritivorous Polychaete) were high. Three of the most dominant species (*D. vittatus*, *S. mathildae*, and *N. hombergii*) occurred in low relative abundances at the impacted subtidal site (Table 2).

Accounting for time and space, the correlation triplot of redundancy analysis of macrofaunal data from all 4 sites constrained by environmental variables (Figure 5) revealed 3 groups of data: a diagonal on the left contained the subtidal samples (both with and without green tides), a dense and small cloud on the top-right contained the Inter-No GT samples, and an almost vertical diagonal on the bottom-right contained the inter-GT samples (Figure 5a). The separation of the subtidal from the intertidal data points is associated with the explanatory variables ‘sorting’ and ‘salinity’, while the separation of the two intertidal dot clouds from each other is associated with the explanatory variable ‘macroalgal mat’ and ‘total organic matter content’ (Figure 5a, b). There was no clear separation of the two subtidal sites from each other. On the other hand, both subtidal and intertidal zoobenthic communities exhibited clear seasonal patterns (Figure 5c). Subtidal infaunal assemblages, irrespective of being sampled at sites with or without *Ulva* accumulations, showed similar temporal paths, albeit with slight shifts between Sub-NoGT and Sub-GT at each season. In contrast, intertidal zoobenthic assemblages displayed different temporal paths, with seasonal development of fauna taking opposite directions when *Ulva* is present (Figure 5c).

The proportion of the variation of infauna at the 4 sites is largely explained by *Ulva* variables (13.6%), the location of site (intertidal vs. subtidal, with 13.2%), and the temporal variables (6.6%) (Table 3). Taking into account ‘pure’ explanatory variables, the occurrence and biomass of *Ulva* explain again the largest part of the variation of infauna (12.3%), while spatial and temporal variables explain 10.8 and 9.2% of the total variation of infauna, respectively. Considering intertidal sites, pure *Ulva* and temporal variables explain 30 and 11% of the variation of infauna, respectively (Figure 6a). The explanatory power of *Ulva* was relatively low at subtidal sites (11%) (Figure 6b), with temporal variables explaining a larger part of the total variation of infauna (21%). These results corroborate the hypothesis that *Ulva* plays a major role in driving variation of infauna

between impacted and pristine intertidal sites, while its explanatory power was less pronounced considering subtidal sites harbouring or not green tides.

#### Variation in space and time of flatfish communities

The correlation triplot of redundancy analysis based on age-grouped flatfish community data sampled at the 4-study sites (Inter-NoGT, Inter-GT, Sub-NoGT, Sub-GT) (Figure 7) revealed two distinguished groups of data containing subtidal (on the right) and intertidal samples (on the left) (Figure 7a). The separation of the dot clouds was associated with the environmental variables ‘sorting’ and ‘median’ (Figure 7b). No distinction depending on the presence of green tides was shown, as dots within each habitat-specific dot-cloud were close to each other, and showed similar temporal paths (Figure 7c).

Although no clear shift between flatfish communities was shown through the redundancy analysis, the relative abundance of age-grouped flatfish varied depending on the habitat and the site (Table 2). At intertidal sites, the juveniles (young of the year) of turbot dominated the flatfish community at Inter-NoGT (39.3%), while sand sole dominated the sandy beach where green tides occurred (31.2%), leading to significant differences between these two sites ( $\chi^2=51.6$ ,  $N=317$ ,  $df=3$ ,  $p=3.6 \cdot 10^{-11}$ ). Adults (i.e. individuals that have reached maturity size) of solenettes dominated both the un-impacted subtidal site (27.0%), and the Sub-GT site (36.8%). Even without accounting for age groups, the flatfish community sampled at the two subtidal sites was significantly different ( $\chi^2=18.3$ ,  $N=174$ ,  $df=2$ ,  $p=0.0001$ ) from each other. In addition, flatfish assemblages depending on age group and site varied over time (Figure 8). The most notable difference in the intertidal flatfish community within the study time frame was the dominance of *P. platessa* in July at Inter-GT, which contrasted with the dominance of *S. maximus* at impacted intertidal site. Also, *Pegusa lascaris* (Risso, 1810) largely dominated the flatfish community in autumn and early winter at impacted site (Inter-GT), while this pattern was less pronounced at un-impacted intertidal site. At the subtidal impacted site (Sub-GT), *B. luteum* largely dominated the flatfish community to the detriment of the sand

sole (especially for young classes) and the scald fish. Also, at both intertidal and subtidal sites, the relative abundance of young of the year sand soles and solenettes was greater at *Ulva*-impacted sites.

## Discussion

Benthic communities inhabiting sandy sediments have been studied either in the intertidal (e.g. Barboza & Defeo, 2015; Defeo & McLachlan, 2005; Degraer *et al.*, 1999) or in the subtidal (Morin *et al.*, 1985; Rakocinski *et al.*, 1993) zones, but seldom assessed considering the inshore and the nearshore conjointly (Knott *et al.*, 1983), even though these two habitats are closely linked. Likewise, *in situ* investigation of variation within both infaunal and flatfish communities simultaneously is not common (with the exception of studying specific fish feeding habits; see for example Aarnio & Mattila, 2000; Kostecki *et al.*, 2012). In addition, the effects of green macroalgal mats in high-energy environments are not yet fully understood (but see Quillien *et al.*, 2015a, 2015b), and have not been investigated considering both infauna and flatfish along a gradient from inshore to nearshore shallow habitats. By simultaneously considering seasonal variation of infauna- and flatfish assemblages over the span of a year, both at intertidal and subtidal sites impacted or not impacted by green tides, our integrated study highlighted a distinctness between low-shore and nearshore communities, and revealed differential responses of the benthic compartments and of the habitats to the accumulation of *Ulva*. Interestingly, intertidal infauna respond more markedly to the presence of algal mats, compared to subtidal benthic invertebrate assemblages, while flatfish communities showed minor/secondary species-specific responses to the occurrence of GT.

### Two habitats that differ in community structure...

The investigation of sandy sediment zoobenthic and flatfish community variation at intertidal (low shore at spring tide) and shallow subtidal (nearshore at 5 m depth) sites revealed a clear separation between the two habitats in terms of community structure (as shown in Figure 5a, 6a, and Table 2). The infaunal assemblage consisted of about 30 species in the intertidal, and more

than twice that, 72 species, in subtidal pristine sands. The increase in species richness of sandy sediment infauna with depth may be linked to the gradient from relatively harsh to benign conditions when going from the low intertidal to the subtidal zone, as suggested by Rakocinski *et al.* (1993). The grain size measured at our study sites decreased from the intertidal to the subtidal, supporting a shift in hydrodynamic conditions, and ultimately in benthic species assemblages, between the two habitats (McLachlan, 1996). In addition to exposure to wave action, also heat and desiccation stresses are exerted on intertidal habitats. Some species, which are not able to withstand these stresses for long periods (McLachlan & Brown, 2006), are more likely to occur in subtidal sands. In our study, 50 species were exclusive to nearshore, subtidal sands, notably the molluscs *Macra stultorum* (Linnaeus, 1758), *Tellina fabula* (Gmelin, 1791) and *Lunatia alderi* (Forbes, 1838), as well as the amphipod *Hippomedon denticulatus* (Bate, 1857), polychaetes of the genus *Phyllodoce* (Browne, 1789) and the echinoderms *A. brachiata* and *Echinocardium cordatum* (Pennant, 1777). Fewer species are able to endure the harsh conditions occurring in intertidal systems (i.e. instability of sandy substratum, desiccation on rocky shores, and heavy wave action) (See for example Knott *et al.*, 1983; Scrosati *et al.*, 2011). We found twelve species that only occurred within intertidal pristine sands, such as the two bivalve molluscs *D. trunculus* and *Tellina tenuis* (da Costa, 1778), the echinoderm *A. cf. spatulispina* and the cumacean *Cumopsis longipes*. These species have adapted to life in high-energy systems, i.e. sandy beaches, being both rapid and strong enough in order to income wave and swash (McLachlan & Brown, 2006). For example, *D. trunculus* has a large and powerful foot that makes it able to quickly re-settle in the sediment to regain its position after being swept by waves (De la Huz *et al.*, 2002; McLachlan & Brown, 2006). The observed shift in infaunal community with depth is concordant with faunal zonation in macrozoobenthos within soft sediments (Glémarec, 1973) and sandy sediments in particular (Dahl, 1952; Knott *et al.*, 1983), and is in accordance with the findings of Guillou (1980) made within the same habitats and study area.

In contrast to the patterns for macrofauna, the species richness for flatfish measured in this study

was similar both in intertidal and subtidal sandy bottoms, although the composition of the flatfish assemblages differed significantly between low- and near-shore habitats. Within the intertidal zone, the flatfish community consisted mainly of sand sole, plaice, turbot and brill, and the subtidal flatfish community was formed by scaldfishes, solenettes, brills and sand soles. These findings are in general accordance with other studies conducted within the same systems, but decades ago (Quiniou, 1986). Also, both assemblages were dominated by juveniles, highlighting the role of open sandy coasts as flatfish nursery areas, which has often been disregarded in comparison to estuaries, seagrass meadows, and other sheltered habitats (Beck *et al.*, 2001; McLachlan & Brown, 2006).

Our study also revealed temporal shifts within sandy sediment intertidal and subtidal benthic communities (Figure 5, 6 and 7). Temporal variations were mainly due to changes in the relative abundance (recruitment) of the bivalve *D. vittatus*, which is a dominant and structuring species in these systems (Guillou, 1980; Quillien *et al.*, 2015a), and of the polychaete *Sigalion mathildae*. These changes in temporal variation of infauna communities are consistent with the findings of Leber (1982) and Degraer *et al.* (1999) made within comparable environments. In parallel, we detected seasonal trends within flatfish communities, mainly linked to the settlement of young-of-the-year individuals (i.e. *Pleuronectes platessa* in July, as well as *Pegusa lascaris* and *Buglossidium luteum* in autumn), in line with patterns reported for similar environments (Quiniou, 1986); thus confirming the role as nursery area for flatfish at sandy beaches (McLachlan and Brown, 2006).

#### ... but that are functionally connected

The results of the present study confirm that a clear distinction exists between low-shore and nearshore benthic communities, both for infauna and flatfish, although there are linkages between the two habitats. The relatively large proportion (>20%) of shared species between low intertidal and shallow subtidal habitats highlights the relationships between these two communities. More specifically, some dominant species in terms of abundance are living in both systems (Table 2).

For example, *Donax vittatus* was the dominant species both at intertidal and subtidal sites.

The relationships between inter- and subtidal benthic communities mainly depend on migrations in relation to species-specific life cycles (reproduction, feeding), behaviours (predator avoidance), or interactions (competition) (see for review: Gillanders *et al.*, 2003). The links between the two zones may be exemplified by both fish and invertebrate seasonal migrations, which are common within the studied systems (Leber, 1982b; Dorel *et al.*, 1991). Continuing with the *Donax vittatus* example, young-of-the-year individuals of this bivalve species occur both in the intertidal and in the subtidal, but adults mainly occur within the subtidal (Guillou, 1980). Also, the polychaete *Sigalion mathildae* occurs in its adult form within intertidal sands, while only juveniles were found at the subtidal habitat. Regarding flatfish, *Pegusa lascaris* recruits occurred within the intertidal sandy beach, while older age-class individuals of this species were distributed along an increasing depth gradient depending on their age. This pattern is common in Soleidae and other flatfish species such as *Pleuronectes platessa* (Lockwood, 1974; Dorel *et al.*, 1991). On an annual scale, seasonal migrations between intertidal and subtidal sands occur; for instance the young solenettes living at intertidal sites in summer, migrate to greater depths in winter, but come back to the intertidal area the next spring (Figure 8; Quiniou, 1986). Both inshore and nearshore sandy bottoms are used by the some identical species depending on the time of the year, which strengthens the links between the two habitats.

Low intertidal and shallow subtidal sandy systems show connections, but also differences in terms of diversity and community structure; thus, one can ask if these systems respond similarly, or rather differently, to the presence of opportunistic macroalgae accumulating within these two habitats.

#### Differential influence of GT depending on elevation and biological compartment

We analysed the variation of infaunal benthic invertebrate and flatfish communities living at sandy sites with respect to the presence and the intensity (biomass) of green tides. This was done simultaneously with other environmental varia-

bles (grain size, sorting, sea water temperature, salinity, organic matter content), which are known to structure marine sediment benthic communities (Defeo & McLachlan, 2005; Ramos *et al.*, 2009). Our analyses demonstrated that the influence of *Ulva* accumulation was significant on benthic infaunal communities (Figure 5, 6). Indeed, not accounting for time, *Ulva*-related variables explained 30% of the total variation in macrobenthic infauna (Figure 6a). These results complement a previous study conducted within the same system (open macrotidal sandy beaches), which highlights shifts in intertidal benthic invertebrate communities along a gradient of eutrophication by green macroalgae (Quillien *et al.*, 2015a).

Contrastingly to the patterns for the infauna, the influence of algal mats was less pronounced for flatfish communities (Figure 7). The greater influence of the accumulation of *Ulva* on infauna compared to flatfish communities may be explained by species life-history traits. Indeed, flatfish are highly mobile compared to benthic invertebrates (Table 2), and may escape transient decrease in dissolved oxygen content induced by the presence of *Ulva* mats (Baden *et al.*, 1990). However, our study revealed that relative abundance of young-of-the-year sand soles and solenettes was higher at sites harbouring *Ulva*-mats compared to pristine sites (Figure 8). Contrasts were also found considering other flatfish species: young plaice dominated the impacted site, while turbot dominated pristine site. Because our fish sampling design did not encompass a high number of samples, these results must be considered cautiously, and would need to be strengthened by broader studies. Still, these results contrast with findings from studies conducted in non-tidal and/or more sheltered systems (e.g. Pihl *et al.*, 2005). In our case, the presence of drifting macroalgal material may increase the complexity of bare sediments (Norkko *et al.*, 2000), without inducing long-lasting hypoxia because of hydrodynamics and tidal currents, which may improve the settlement of flatfish larvae, thus increasing population size (Gibson, 1994).

Our study also demonstrates a greater influence of the presence of green tides on the intertidal invertebrate community compared to subtidal benthic assemblages. Intertidal sandy

beach benthic species withstand harsher conditions than subtidal zoobenthic assemblages, and the addition of high biomasses of green opportunistic macroalgae (*Ulva* spp.) may act as the last straw stress. Also, this finding may be linked to the intrinsic structure of algal mats, which differs between the intertidal and the subtidal (Figure 2). At five meters depth, subtidal *Ulva* stocks are often arranged in strips a few decimetres wide and float above the seafloor (Merceron & Morand, 2004). While at low tide in intertidal sandy areas, algal mats strand on shore, with *Ulva* thalli being in direct contact with the sediment (Charlier *et al.*, 2007). In addition, a noticeable amount of *Ulva* thallus pieces were found relatively deep in the intertidal sands, but were not observed within subtidal sediments. In addition, *Ulva* biomasses estimated inshore were greater than in subtidal areas (Figure 4), although these values were probably under-estimated due to possible reflux from trawl, and were not directly comparable due to the use of different estimation methods for the two habitats. Since the subtidal *Ulva* stock, with lower biomass than in the intertidal, was close to - but somehow disconnected from - the seafloor, macroalgal mats would most likely not have impacted nearshore sandy benthic communities. However, the intensity of green tides (both at intertidal and subtidal area) is highly variable depending on the year, mainly because of weather conditions and nutrient loads (CEVA pers. comm.), and thus may have different impacts within open sandy systems depending on the amount of *Ulva* stranding or floating.

## Conclusions

The present study proves that within usually unvegetated dynamic systems, infauna inhabiting low-intertidal sandy shores is more affected by the presence of high biomass of opportunistic macroalgae than shallow nearshore subtidal macro-invertebrates and flatfish communities. This is supported by shifts between intertidal pristine and impacted macrobenthic community structure, whereas subtidal infauna, as well as inshore and nearshore flatfish are less affected by the presence of *Ulva* blooms when looking at community-level responses. This study underlines the importance of monitoring intertidal systems stressed by anthropogenic activities, as they may help to give

early warning of potential overall shift within dynamic marine systems from inshore to near-shore.

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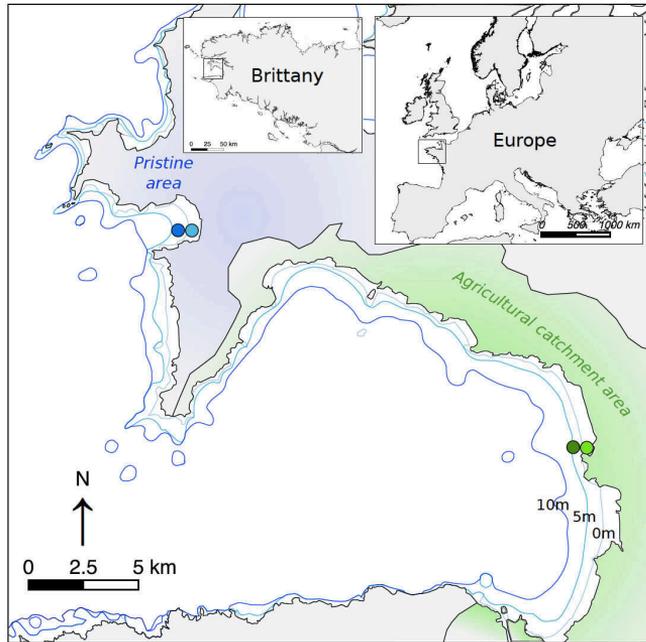
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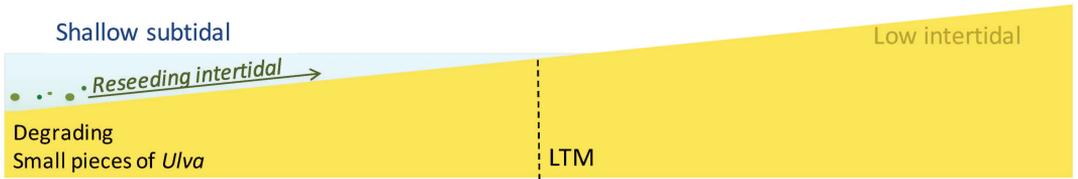
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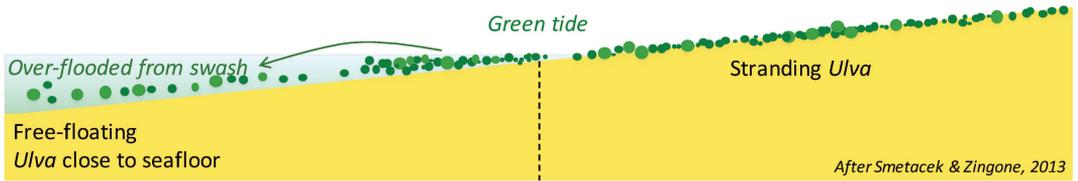


**FIG. 1.** Location (Brittany, Northwestern Europe) of the 4 study sites (circles) at the low-intertidal (light colours) and at the shallow subtidal (dark colours) of the two studied sandy sediment areas. Blue lines along coastline represent isobaths (0, 5, and 10m). The sites impacted by green tides are denoted by green circles and are located downstream of an agricultural catchment area. The blue circles denote the sites that are never affected by accumulation of *Ulva*.

**a. Eutrophied state in winter**



**b. Eutrophied state in summer**



**FIG. 2.** Schematic illustration of the distribution of green tides occurring at two contrasted seasons. Arrows denoted algal material in motion.

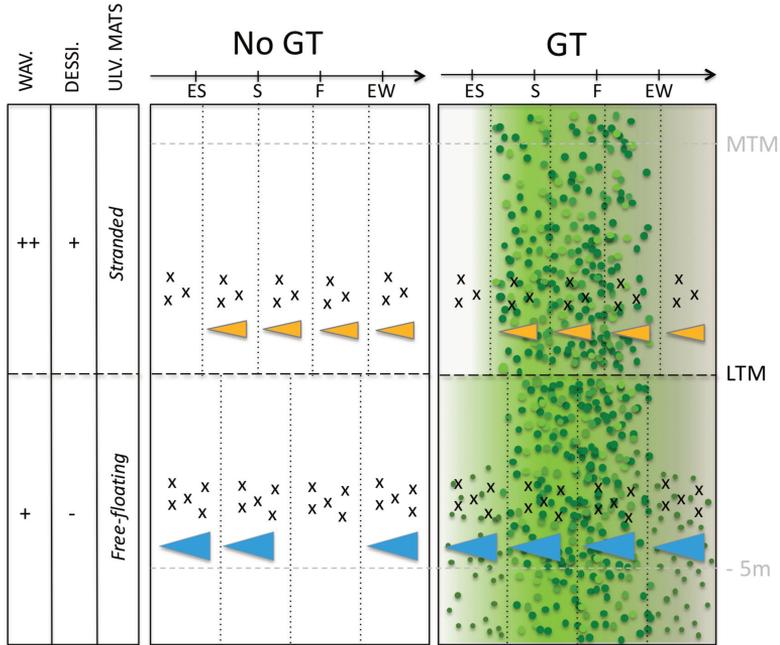


FIG. 3. Sampling design over time (from Early Spring = ES, to Early Winter = EW; S = Summer, F = Fall), showing the 4 sites (Intertidal - NoGT, Intertidal - GT, Subtidal - NoGT, Subtidal - GT), core and grab samples (black crosses), beach and beam trawling (triangles), and three environmental variables (WAV. = Waves, DESSI. = Desiccation, GT = Green Tides). MTM = middle tidal mark, LTM = low tidal, and -5m = 5m depth.

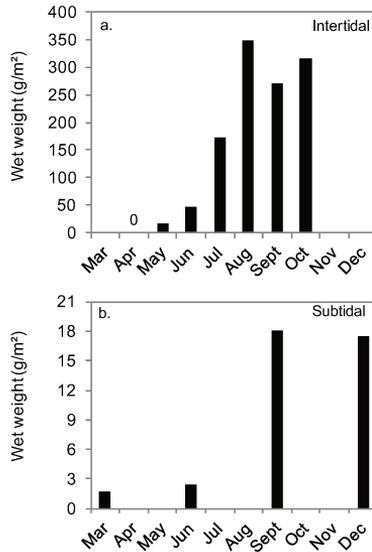


FIG. 4. Monthly biomass of stranded *Ulva* through the year 2013 estimated within the intertidal (source: CEVA) and the subtidal (source: this study). Note that the scales are not the same on the two plots.

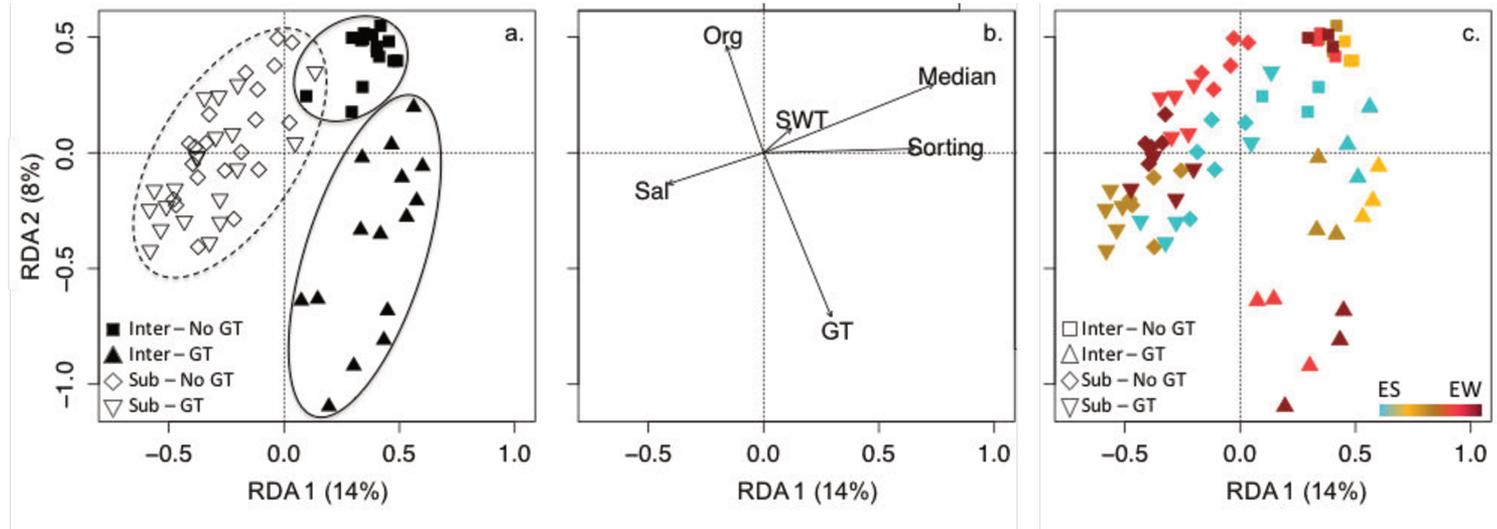
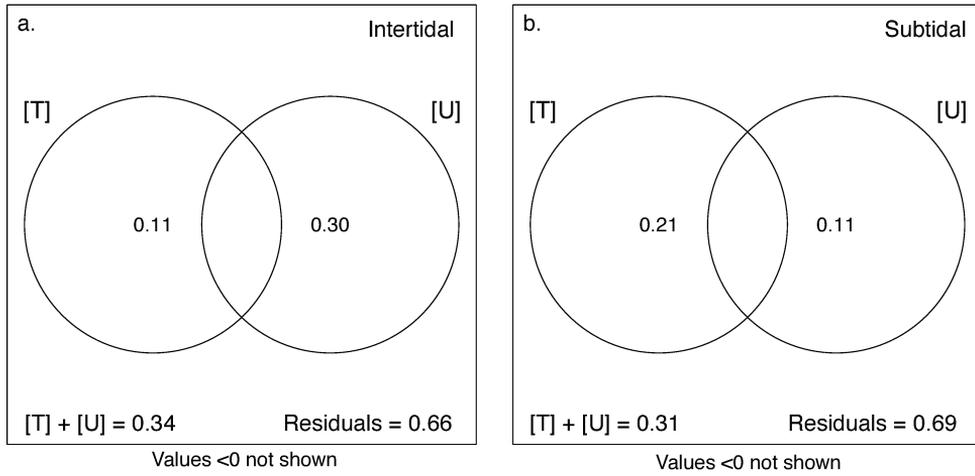
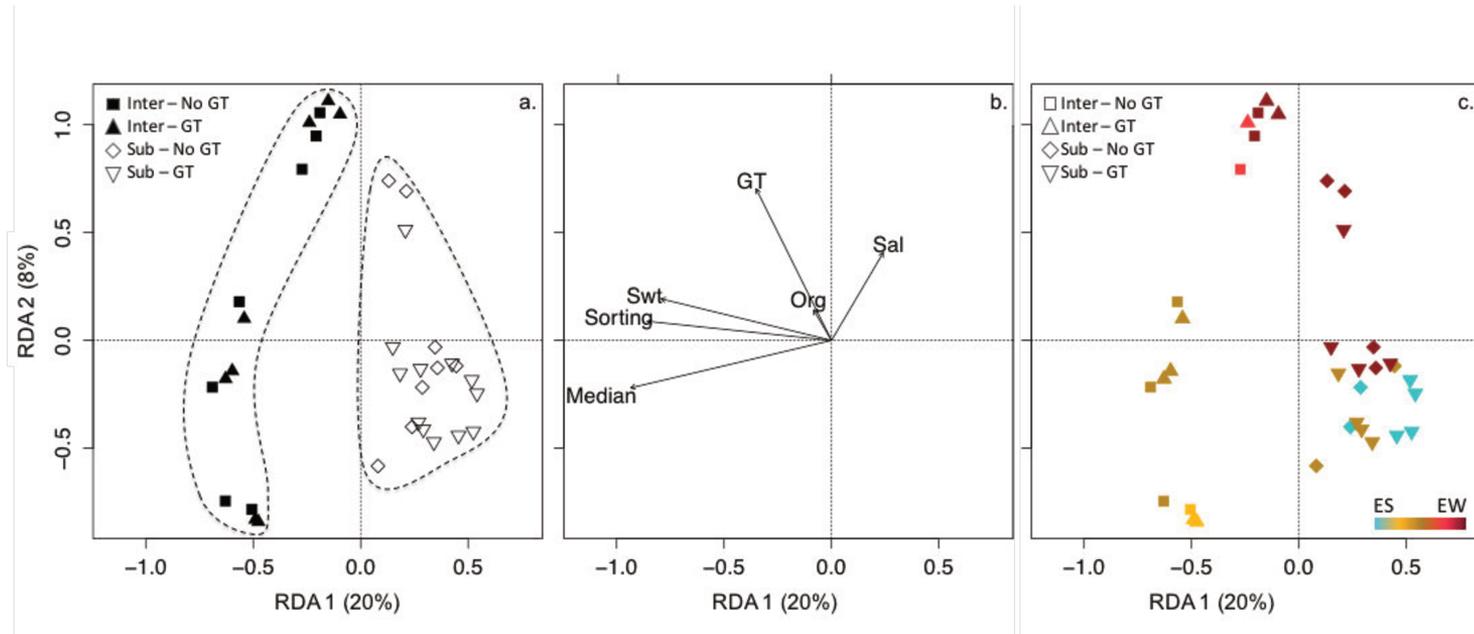


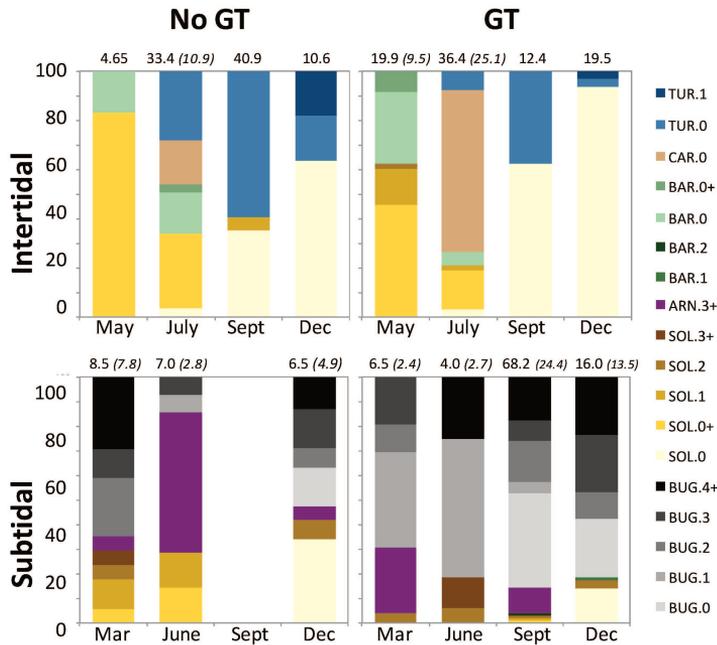
FIG. 5. RDA correlation triplots (scaling 2) of macrofaunal community data (abundance) and explanatory variables of the 4 sites together: Inter - NoGT (squares), Inter - GT (triangles), Sub - NoGT (diamonds), Sub - Gt (reversed triangles); highlighting differences between habitats (a), environmental drivers (b), and seasonal patterns (c). GT = *Ulva* biomass, Sal = Salinity, Org = organic matter content, SWT = Sea-water temperature.



**FIG. 6.** Venn diagrams illustrating the result of variance partitioning of the macrofauna time series at Inter - NoGT, Inter - GT, Sub - NoGT, Sub - GT with respect to the presence of *Ulva* mats (GT/NoGT), spatial (intertidal/subtidal), and temporal (distance-based Moran's eigenvector maps [dbMEMs]) explanatory variables. Variation explained is expressed as a percentage (%) based on adjusted R<sup>2</sup>. [T]: temporal variables, [S]: spatial location across the shore, [U]: environmental variables, Residuals: unexplained variation



**FIG. 7.** RDA correlation triplots (scaling 2) of age-grouped flatfish community data (apparent abundance) and explanatory variables of the 4 sites together: Inter - NoGT (squares), Inter - GT (triangles), Sub - NoGT (diamonds), Sub - Gt (reversed triangles); highlighting differences between habitats (a), environmental drivers (b), and seasonal patterns (c). GT = *Ulva* biomass, Sal = Salinity, Org = organic matter content, SWT = Seawater temperature.



**FIG. 8.** Relative abundance of flatfish depending on their age-group at sandy bottoms within the intertidal (top panels) and the subtidal (low panels), harbouring green tides (right panels) or not (left panels). Numbers on top of bars show mean apparent abundance, with standard deviation in italics and between brackets. TUR = *Scophthalmus maximus*, CAR = *Pleuronectes platessa*, BAR = *Scophthalmus rhombus*, ARN = *Arnoglossus laterna*, SOL = *Pegusa lascaris*, BUG = *Buglossidium luteum*.

**TABLE 1.** Environmental characterization of the 4 sites (Intertidal – NoGT, Intertidal – GT, Subtidal – NoGT, Subtidal – GT) sampled seasonally from February to December 2013. SWT = Seawater temperature, Sorting = sorting index calculated based on first and third quartile ratio.

	Intertidal						Subtidal					
	No GT			GT			No GT			GT		
	Mean	Max.	Min.	Mean	Max.	Min.	Mean	Max.	Min.	Mean	Max.	Min.
SWT (°C)	14.4	20.0	9.5	14.6	21.2	9.0	13.0	17.0	9.5	13.4	18.1	9.5
Salinity (psu)	34.9	35.6	33.6	34.8	35.6	33.8	35.3	35.4	35.1	35.3	35.4	35.0
Agal mat biomass (g/m <sup>2</sup> ; wet weight)	0	0	0	155.3	315.0	0.0	0	0	0	9.9	18.1	1.7
Sorting	1.7	2.1	1.5	1.8	2.0	1.6	1.5	1.6	1.4	1.5	1.6	1.3
Median grain size (µm)	179.8	200.2	160.6	180.5	251.7	140.4	142.8	145.5	141.3	132.5	138.1	118.1
Organic content (%)	1.5	1.6	1.4	1.2	1.4	1.1	1.5	1.7	1.4	1.3	1.3	1.2

**TABLE 2.** Percent dominance in terms of abundance for the major species (threshold = 90% for zoobenthos, 100% for flatfish) living at intertidal and subtidal sandy bottoms harbouring or not green tides (GT or no-GT). Bold face type numbers show contributions that are higher than 1%. Italic numbers refer to values that are not relative abundance values. 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. For fish species, age groups have been based on individual sizes and peer literature and research reports on flatfish growth.

Species	Taxonomic group	Abundance dominance (%)				Functional characteristics				
		Intertidal		Subtidal		Feeding habit	Feeding strategy	Mobility	Maximal size (mm)	Development mechanism
		No GT	GT	No GT	GT					
<i>Glycera convoluta</i>	Annelida polychaeta	0.2	<b>1.5</b>	<b>1.9</b>	<b>1.2</b>	Ca	SPF	B, (S)	50	Ovi
<i>Magelona mirabilis</i>		-	<b>3.8</b>	<b>2.4</b>	<b>5.9</b>	D	SuF, SPF	B	80	Ovi
<i>Nephtys assimilis</i>		0.2	0.1	0.2	0.4	Ca, Sc	SPF	B, C, (S)	115	Ovi
<i>Nephtys cirrosa</i>		<b>1.2</b>	<b>2.0</b>	<b>1.6</b>	0.7	Ca, Sc	SPF	B, C, (S)	100	Ovi
<i>Nephtys hombergii</i>		0.2	<b>1.5</b>	<b>6.4</b>	<b>2.2</b>	Ca, Sc	SPF	B, C, (S)	200	Ovi
<i>Orbinia latreilli</i>		-	0.3	0.8	-	D	SSF	B	400	Ovi
<i>Owenia fusiformis</i>		<b>1.5</b>	<b>3.1</b>	<b>1.7</b>	<b>1.1</b>	D	SuF, SF, SPF	T	100	Ovi
<i>Paradoneis armata</i>		-	-	<b>3.7</b>	<b>6.6</b>	D	SSF	B, C, (S)	30	Ovi
<i>Piromis eruca</i>		-	-	-	<b>1.4</b>	D	SSF	B	60	Ovi
<i>Scolecopsis cf mesnilli</i>		0.3	0.4	<b>2.5</b>	<b>1.8</b>	D, (Ca), (Hj)	SSF, (SPF)	B	20	Ovi
<i>Scoloplos armiger</i>		-	-	0.3	<b>1.7</b>	D	SSF	B, C	120	Ovi
<i>Sigalion mathildae</i>		0.3	0.3	<b>8.0</b>	<b>4.2</b>	Ca	SPF	B, C, (S)	150	Ovi
<i>Spiophanes bombyx</i>		<b>9.4</b>	0.1	<b>1.5</b>	0.8	D	SuF, SPF	T	60	Ovi
<i>Ampeleis sarsi</i>	Arthropoda malacostraca	-	-	<b>2.1</b>	-	D	SuF, SSF	T	8	Ovi
<i>Atylus falcatius</i>		-	-	-	<b>1.1</b>	O	SPF	C, S	7	Ovo
<i>Atylus swamerdami</i>		-	0.3	0.2	<b>3.2</b>	O	SPF	C, S	10	Ovo
<i>Bathyporeia guillamsoniana</i>		0.3	<b>1.4</b>	<b>1.3</b>	0.8	D	SSF, SuF	B, S	10	Ovo
<i>Bathyporeia pelagica</i>		<b>2.1</b>	<b>2.3</b>	-	-	D, Hj	SPF	B, (nS)	8	Ovo
<i>Bathyporeia sarsi</i>		-	<b>4.2</b>	<b>2.6</b>	<b>4.7</b>	D	SSF, SuF	B	8	Ovo
<i>Cumopsis fagei</i>		<b>4.5</b>	<b>3.8</b>	<b>2.4</b>	0.4	D	SSF, SPF	B, (nS)	6	Ovo
<i>Cumopsis longipes</i>		<b>1.7</b>	<b>2.0</b>	-	-	D	SSF, SPF	B, (nS)	6	Ovo
<i>Diogenes pugilator</i>		-	-	0.5	<b>13.5</b>	Ca	SPF	C, (B)	20	Ovo
<i>Hippomedon denticulatus</i>		-	-	0.7	<b>1.5</b>	D, H	SSF	B	14	Ovo
<i>Idotea pelagica</i>		0.3	0.1	0.1	0.6	O, (H)	S, C	SuF	20	Ovo
<i>Iphinoe trispinosa</i>		0.2	0.3	<b>4.8</b>	<b>6.1</b>	D	SSF, SuF	B, S	10	Ovo
<i>Mysida</i>		-	-	<b>2.6</b>	<b>1.7</b>	D, Ca	SuF, SSF	S, C, B	20	Ovo
<i>Perrierella audouiniana</i>		0.2	-	0.1	0.9	Ca	SPF	S, C	4	Ovo
<i>Pontocrates arenarius</i>		<b>1.7</b>	0.4	-	0.1	D	SSF	B, C	7	Ovo
<i>Portunus latipes</i>		0.3	0.4	-	-	O, Sc	SSF, SuF	B, C	27	Ovo
<i>Urothoe poseidonis</i>		-	<b>18.7</b>	0.5	0.8	Hj	SSF	B, (nS)	6	Ovo
<i>Urothoe pulchella</i>		-	-	<b>1.5</b>	-	Hj	SSF	B, (nS)	5.0	Ovo
<i>Acrocnida brachiata</i>	Echinodermata echinoidea	-	-	0.9	<b>2.3</b>	O, (Ca)	SPF	B	12*	Ovi
<i>Acrocnida cf. spatulispina</i>		0.2	<b>9.8</b>	-	-	O, (Ca)	SPF	B	12*	Ovi
<i>Echinocardium cordatum</i>		-	-	0.5	0.7	D	SuF, SSF	B	100	Ovi
<i>Donax trunculus</i>	Mollusca bivalvia	<b>6.3</b>	<b>1.8</b>	-	-	D, Hj	SF, SPF, (SuF)D, C, B	45	Ovi	
<i>Donax vittatus</i>		<b>65.0</b>	<b>36.2</b>	<b>27.9</b>	<b>10.5</b>	D, Hj	SF, SPF, (SuF)D, C, B	38	Ovi	
<i>Macra stultorum</i>		-	-	<b>1.9</b>	<b>4.8</b>	D, Hj	SuF	B	5	Ovi
<i>Pharus legumen</i>		-	-	0.7	<b>1.7</b>	D, Hj	SF	B	130	Ovi
<i>Tellina fabula</i>		-	-	<b>2.5</b>	<b>1.5</b>	D, Hj	SuF	B	20	Ovi
<i>Tellina tenuis</i>		0.7	<b>2.2</b>	-	-	D, Hj	SuF, SPF	B	20	Ovi
<i>Euspira nitida</i>	Mollusca gastropoda	-	0.1	0.6	0.3	Ca	SSF	B, C	16	Ovi
<i>Nassarius reticulatus</i>		-	-	0.7	1.0	Sc	SPF	C	30	Ovi
<i>Philine aperta</i>		-	-	0.9	0.5	Ca, Sc	SPF	C	100	Ovi
<i>Nemerta sp.2</i>	Nemertea	0.2	-	<b>1.5</b>	0.2	Ca	SPF	T	?	Ovi, F
<i>Lineus acutifrons</i>	Nemertea anopla	<b>1.3</b>	0.7	<b>3.4</b>	<b>1.8</b>	Ca	SPF	B	?	Ovi, F
<i>Tubularius polymorphus</i>	Nemertea palaeonemertea	0.2	0.1	0.7	1.0	Ca	SPF	B, (T)	750	Ovi, F
<i>Platyhelminth</i>	Platyhelminthes	-	0.4	0.3	0.2	Ca	SPF	B, (S)	?	Ovo
Number of total taxa		31	39	72	79					
Total abundance ( $\bar{n}$ ) (sd)		236.3 (152.0)	145.0 (63.7)	24.5 (10.3)	29.4 (8.5)					
Sampling method		Core	Core	Grab	Grab					
<i>Arnoglossus lateralis</i> (3+)	Chordata actinopteri	-	-	<b>20.0</b>	<b>6.6</b>	Ca	SPF	S	130	Ovi
<i>Buglossidium luteum</i> (0)		-	-	<b>6.0</b>	<b>14.2</b>	Ca	SPF	S	50	Ovi
<i>Buglossidium luteum</i> (1)		-	-	<b>2.0</b>	<b>17.9</b>	Ca	SPF	S	60	Ovi
<i>Buglossidium luteum</i> (2)		-	-	<b>11.0</b>	<b>9.4</b>	Ca	SPF	S	60	Ovi
<i>Buglossidium luteum</i> (3+)		-	-	<b>27.0</b>	<b>36.8</b>	Ca	SPF	S	130	Ovi
<i>Pegusa lascaris</i> (0)		<b>24.5</b>	<b>31.2</b>	<b>13.0</b>	<b>8.5</b>	Ca	SPF	S	60	Ovi
<i>Pegusa lascaris</i> (+)		<b>16.3</b>	<b>17.3</b>	<b>6.0</b>	0.0	Ca	SPF	S	110	Ovi
<i>Pegusa lascaris</i> (s)		<b>2.5</b>	<b>4.4</b>	<b>8.0</b>	0.0	Ca	SPF	S	160	Ovi
<i>Pegusa lascaris</i> (s)		0.0	0.5	<b>5.0</b>	<b>3.8</b>	Ca	SPF	S	220	Ovi
<i>Pegusa lascaris</i> (s+)		-	-	<b>2.0</b>	<b>1.9</b>	Ca	SPF	S	320	Ovi
<i>Pleuronectes platessa</i> (0)		<b>6.6</b>	<b>26.0</b>	-	-	Ca, Sc	SPF	S	90	Ovi
<i>Scophthalmus maximus</i> (0)		<b>39.3</b>	<b>9.5</b>	-	-	Ca	SPF	S	70	Ovi
<i>Scophthalmus maximus</i> (s)		<b>2.3</b>	0.9	-	-	Ca	SPF	S	140	Ovi
<i>Scophthalmus rhombus</i> (0)		<b>7.2</b>	<b>8.4</b>	-	-	Ca	SPF	S	60	Ovi
<i>Scophthalmus rhombus</i> (0+)		<b>1.4</b>	<b>1.9</b>	-	-	Ca	SPF	S	80	Ovi
<i>Scophthalmus rhombus</i> (s)		-	-	-	0.9	Ca	SPF	S	150	Ovi
Number of total taxa		4	4	3	4					
Mean apparent abundance ( $\bar{1}\bar{n}^2$ ) (sd)		22.4 (17.5)	22.1 (10.2)	7.3 (2.5)	8.8 (6.3)					
Sampling method		Beach	Beach	Beach	Beach					

Feeding habit: Ca = Carnivore; D = Detritivore; H = Herbivore; Hj = 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 = Oviviparous.

**TABLE 3.** Variance partitioning of the macrofauna time series at both intertidal and subtidal sites with respect to temporal (distance-based Moran's eigenvector maps [dbMEMs]), *Ulva* (occurrence and biomass), and spatial (location across shore encoded by Helmert contrasts) explanatory variables. Variation explained is expressed as percentage (%) based on adjusted R<sup>2</sup>. The significance of the fraction of interest is denoted by stars; \*\*\* denote p<0.001. [T] = temporal variables, [U] = *Ulva* variables, [S] = spatial variables, Unexpl. = unexplained variation.

Variable	Df	Adj R <sup>2</sup> (%)	Sign.
[T + U + S]	6	32.8	***
[T]	3	6.6	***
[U]	2	13.6	***
[S]	1	13.2	***
[T   (U + S)]	3	9.2	***
[U   (T + S)]	2	12.3	***
[S   (U + T)]	1	10.8	***
Unexpl.		67.2	

A horizontal band of a photograph showing fossilized fern fronds. The fronds are dark green to black, showing the characteristic segmented structure of fern leaves. They are set against a lighter, textured rock matrix. The text 'Paper III' is overlaid in white on the right side of this band.

# Paper III

# 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  $\beta$ -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 ·  $\beta$ -diversity

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## 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  $\beta$ -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

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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 (Ménèsquen & 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<sub>A</sub>) (Fig. 1a), one that harbours spatially heterogeneous green tides (SB<sub>B</sub>), and a third one (SB<sub>C</sub>) that receives green tides homogeneously along the entire shore (Fig. 1b). Thus, the 3

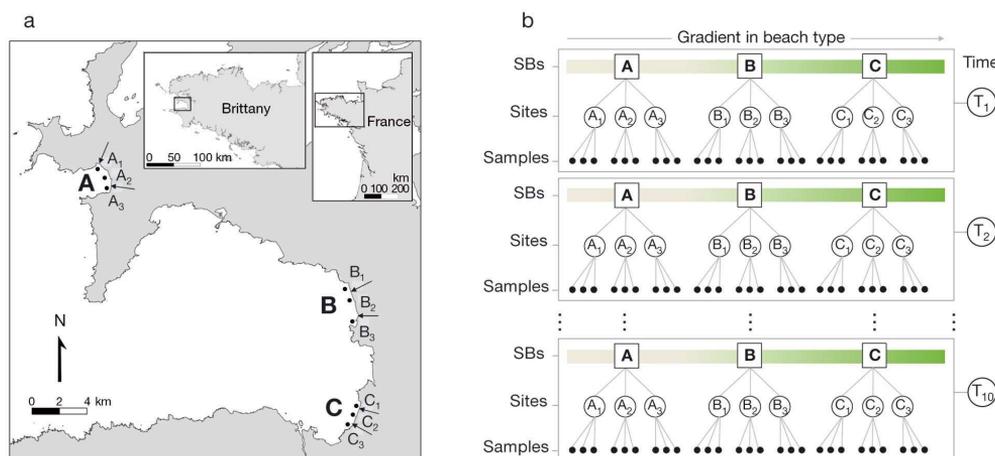


Fig. 2. (a) Location (Brittany, France) of the 3 sandy beaches (SBs: A, B and C), the 9 sampling sites (black filled circles) where 3 replicates were sampled monthly and the coastal rivers' mouths (arrows). (b) Sampling design, repeated in time (10 dates: T<sub>1</sub>, T<sub>2</sub>, ... T<sub>10</sub>) showing the 3 SBs (A, B and C), the corresponding sampling sites (A<sub>1</sub>, A<sub>2</sub>, A<sub>3</sub>, B<sub>1</sub>, B<sub>2</sub>, B<sub>3</sub>, C<sub>1</sub>, C<sub>2</sub>, C<sub>3</sub>) 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 =  $6.5 \pm 0.5$  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<sub>A</sub> 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<sub>B</sub> and SB<sub>C</sub> 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<sub>1</sub> = 48° 15.206' N, 4° 33.298' W; A<sub>2</sub> = 48° 15.003' N, 4° 33.051' W; A<sub>3</sub> = 48° 14.109' N, 4° 32.545' W; B<sub>1</sub> = 48° 11.355' N, 4° 18.202' W; B<sub>2</sub> = 48° 11.193' N, 4° 18.149' W; B<sub>3</sub> = 48° 10.132' N, 4° 17.465' W; C<sub>1</sub> = 48° 06.585' N, 4° 17.050' W; C<sub>2</sub> = 48° 06.367' N, 4° 17.145' W; C<sub>3</sub> = 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  $900 \pm 200$  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<sub>C</sub> 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<sup>2</sup>, 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<sub>1</sub>, A<sub>2</sub>, 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/](http://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<sup>2</sup>. 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<sub>1,2,3</sub>; B<sub>1,2,3</sub>; C<sub>1,2,3</sub>), 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](http://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](http://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](http://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  $\alpha$ -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](http://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  $\beta$ -diversity (BDTotal) is defined as the total variance of a community matrix (*sensu* Legendre & De Cáceres 2013). BDTotal was computed for each of the 3 sites within each sandy beach

(SB<sub>A</sub>, SB<sub>B</sub>, and SB<sub>C</sub>) 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  $\beta$ -diversity, BDTotal values were correlated (Kendall rank correlation) with the sum of *Ulva* coverage at each beach. To test if the different regimes of macroalgal accumulations could be linked to overall  $\beta$ -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<sub>A</sub>, SB<sub>B</sub>, and SB<sub>C</sub> 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<sub>A, B, C</sub>) 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<sub>A</sub>, while the mean biomass of fresh green macroalgae mats was estimated at approximately 720 and 340 t stranded along SB<sub>B</sub> and SB<sub>C</sub>, respectively. Particularly large standard deviations were found for *Ulva* biomass (Table 1) due to the temporal variability of stranded macroalgae, which annually occurs in spring and summer. Considering the 3 sampling sites along the shore of SB<sub>B</sub> and SB<sub>C</sub>, *Ulva* biomass washed ashore was variable both in time (Fig. 3a,c) and space (Fig. 3b,d). Macroalgal biomass measured on SB<sub>B</sub> showed a gradient from Site B<sub>1</sub> to Site B<sub>3</sub> with a maximum in June,

Table 1. Environmental characterization of the 3 beaches (SB<sub>A</sub>, SB<sub>B</sub>, and SB<sub>C</sub>) 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 ( $p \leq 0.05$ ); 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 <sub>A</sub>		SB <sub>B</sub>		SB <sub>C</sub>		Sources	Test	Effect
		Mean	SD	Mean	SD	Mean	SD			
<i>Ulva</i> biomass (10 <sup>3</sup> 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 <i>a</i> (µg l <sup>-1</sup> )	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<sub>C</sub> 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 12781 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<sub>1</sub> and B<sub>2</sub> ( $S = 32$  and  $33$  respectively). Sites A<sub>1</sub>, A<sub>2</sub>, A<sub>3</sub>, and B<sub>3</sub> exhibited similar values (26, 27, 28, and 28, respectively). Species richness estimated for sites sampled on SB<sub>C</sub> 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-

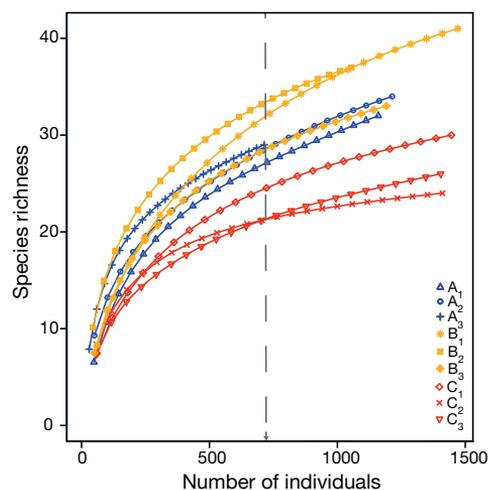


Fig. 4. Sample-based rarefaction curves for the 3 SBs (A, B and C) and each site. The dashed grey vertical arrow indicates the chosen number of individuals for comparison between sites ( $n = 720$ )

mass) varied only slightly at SB<sub>A</sub>, while it showed evident seasonal variability at SB<sub>B</sub> and SB<sub>C</sub> (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<sub>B</sub> and SB<sub>C</sub> 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

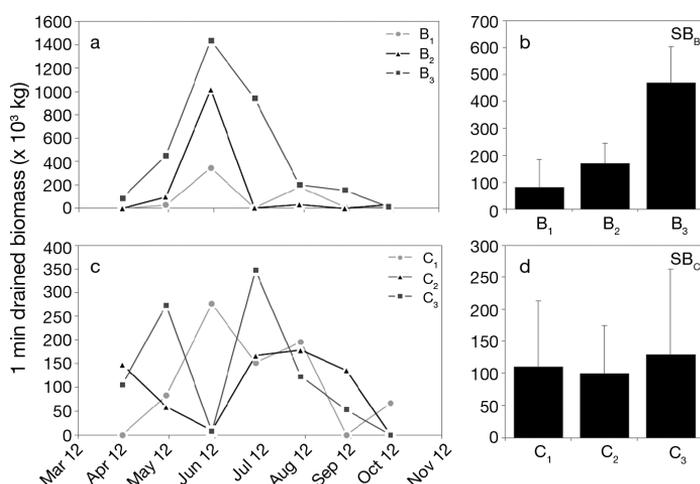


Fig. 3. Monthly biomass of stranded *Ulva* throughout the year 2012 estimated at (a) SB<sub>B</sub> and (c) SB<sub>C</sub> and yearly mean ( $\pm$  SD) at (b) SB<sub>B</sub> and (d) SB<sub>C</sub>. Note that the scales are not the same on all plots

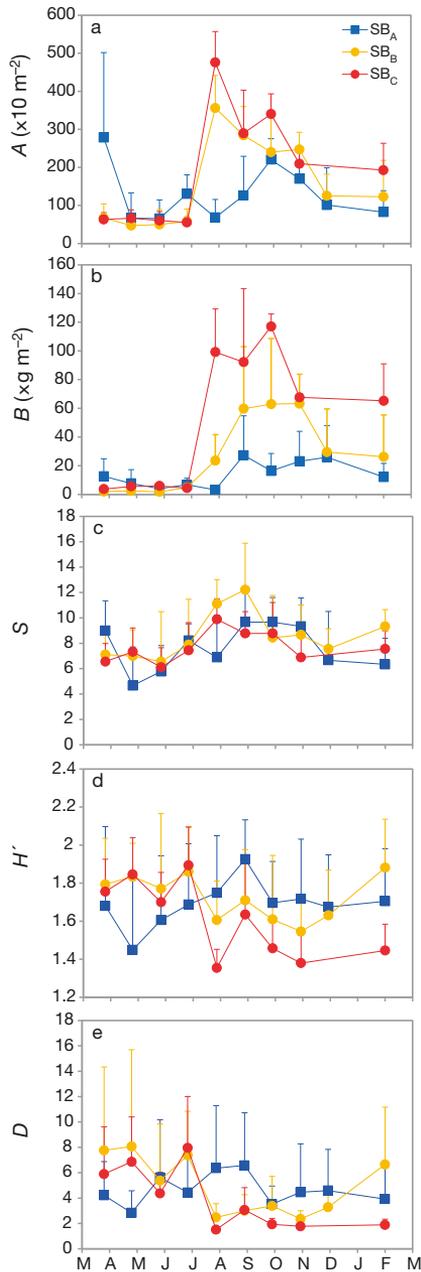


Fig. 5. Mean ( $\pm$ SD) abundance (A), biomass (B), species richness (S), numerical equivalents of Shannon's entropy  $\exp(H')$  and Simpson's  $(1/D)$  indices (after Jost 2006) from April 2012 to February 2013 at the 3 beaches (SB<sub>A</sub>, SB<sub>B</sub> and SB<sub>C</sub>)

the variation observed in univariate responses of the 3 beaches considered in this study, especially for SB<sub>C</sub> (Table 2).

Considering the variables separately, temporal, spatial, and environmental variables explained univariate community variables for SB<sub>A</sub> and SB<sub>B</sub> 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<sub>B</sub> than in SB<sub>A</sub>, and significant models explained less variation. More remarkably, spatial variables did not significantly explain any variation observed in univariate responses for SB<sub>C</sub>, 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<sub>A</sub>. SB<sub>B</sub> 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<sub>C</sub>, 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<sub>B</sub> and SB<sub>C</sub>), *Donax vittatus* largely contributed to the total biomass, while *D. trunculus* and *Angulus tenuis* were under-represented, opposite to SB<sub>A</sub>. 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. *Lumbrineris* 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<sub>A</sub>, SB<sub>B</sub>, and SB<sub>C</sub>). Variation explained is expressed as a percentage (%) based on adjusted R<sup>2</sup>. [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 <sub>A</sub>					SB <sub>B</sub>					SB <sub>C</sub>				
	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   (S + E)]	31	10	17	0	14	6	3	10	0	0	13	9	2	16	21
[S   (T + E)]	0	7	8	21	0	0	1	12	18	0	0	0	0	0	4
[E   (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<sub>A</sub>, SB<sub>B</sub>, and SB<sub>C</sub>) 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
<b>SB<sub>A</sub></b>	<b>Adj R<sup>2</sup>:</b>		14.2	35.9	7.0	1.6	13.0
SWT (°C)	P						
Salinity (psu)	P	**	**	**			
Dissolved O <sub>2</sub> (%)	<b>P/B</b>	**					***
<i>Ulva</i> biomass (t)	B						
Mean wave height (m)	<b>P</b>	**	**	*			
Sorting index (unitless)	P						
Slope (%)	<b>P</b>	*	***				
Organic matter (%)	B				*		
Phytoplankton (µg l <sup>-1</sup> )	B		***				
Median (µm)	P						
<b>SB<sub>B</sub></b>	<b>Adj R<sup>2</sup>:</b>		59.7	59.9	11.3	11.1	14.0
SWT (°C)	<b>P</b>	***	***				
Salinity (psu)	P						
Dissolved O <sub>2</sub> (%)	<b>P/B</b>	***	***				
<i>Ulva</i> biomass (t)	<b>B</b>	**	**	**	*	**	
Mean wave height (m)	P	***					
Sorting index (unitless)	P						
Slope (%)	<b>P</b>		***		*	**	
Organic matter (%)	<b>B</b>				**	*	
Phytoplankton (µg l <sup>-1</sup> )	<b>B</b>	***	***	**			
Median (µm)	P						
<b>SB<sub>C</sub></b>	<b>Adj R<sup>2</sup>:</b>		66.9	72.0	30.8	36.3	33.5
SWT (°C)	<b>P</b>	***	***	***			
Salinity (psu)	P	***	***	***			
Dissolved O <sub>2</sub> (%)	<b>P/B</b>	***	***	***			
<i>Ulva</i> biomass (t)	<b>B</b>	*	*		**	*	
Mean wave height (m)	<b>P</b>	***	***	***	**	**	
Sorting index (unitless)	P						
Slope (%)	P						
Organic matter (%)	<b>B</b>				**	***	***
Phytoplankton (µg l <sup>-1</sup> )	<b>B</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<sub>A</sub> (no green tide present during any of the sampling times) and SB<sub>C</sub> (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<sub>B</sub>, with a local persistent gradient in *Ulva* coverage along the shore, had an intermediate BDTotal value and exhibited a greater dispersion than SB<sub>A</sub> and SB<sub>C</sub> (Fig. 6). SB<sub>B</sub> did not significantly differ from SB<sub>A</sub> ( $W = 46, corrected p = 0.321$ ) or SB<sub>C</sub> ( $W = 45, corrected p = 0.321$ ).

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<sub>A</sub> 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<sub>B</sub> and SB<sub>C</sub> (Fig. 7B,C) with a shift in benthic community composition over time and a spatial structuring for SB<sub>B</sub> macrofauna communities. No discernible spatial patterns appeared at SB<sub>C</sub>.

Table 4. Percentage dominance in terms of biomass for the major species (threshold = 99.9%) living in the sampled sites (A<sub>1</sub>, A<sub>2</sub>, A<sub>3</sub>, B<sub>1</sub>, B<sub>2</sub>, B<sub>3</sub>, C<sub>1</sub>, C<sub>2</sub>, and C<sub>3</sub>). **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; SF: suspension 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); <sup>a</sup>diameter of central disc; <sup>b</sup>length of carapace

Species	Taxonomic group	Biomass dominance (%)									Cohorts (pers. obs.)	Functional characteristics			
		A <sub>1</sub>	A <sub>2</sub>	A <sub>3</sub>	B <sub>1</sub>	B <sub>2</sub>	B <sub>3</sub>	C <sub>1</sub>	C <sub>2</sub>	C <sub>3</sub>		Feeding strategy	Mobility	Max. size	Rep./dev.
<i>Donax vittatus</i>	Mollusca: Bivalvia	<b>24.73</b>	<b>46.83</b>	<b>35.94</b>	<b>85.88</b>	<b>65.68</b>	<b>90.42</b>	<b>85.64</b>	<b>83.69</b>	<b>87.22</b>	Ad., Juv.	SF	D, C, B	38	BS/Pel.
<i>Donax trunculus</i>	Mollusca: Bivalvia	<b>9.14</b>	<b>19.12</b>	<b>39.79</b>	<b>2.79</b>	<b>10.98</b>	<b>4.32</b>	<b>10.41</b>	<b>10.17</b>	<b>4.06</b>	Ad.	SF	D, C, B	45	BS/Pel.
<i>Angulus tenuis</i>	Mollusca: Bivalvia	<b>36.07</b>	<b>27.14</b>	<b>5.60</b>	<b>2.17</b>	<b>3.77</b>	<b>0.75</b>	<b>2.19</b>	<b>3.49</b>	<b>5.05</b>	Ad., Juv.	SDF	B	20	BS/Pel.
<i>Acrocnida brachiata</i>	Echinodermata: Ophiurida	<b>4.38</b>	<b>3.39</b>	<b>6.74</b>	0.58	<b>4.74</b>	<b>1.30</b>	0.53	0.32	0.41	Ad., Juv.	SDF, P	B	12 <sup>a</sup>	BS/Pel.
<i>Spiophanes bombyx</i>	Annelida: Polychaeta	<b>12.60</b>	<b>0.91</b>	<b>4.82</b>	0.03	0.01	0.01	0.20	0.02	0.01	Ad.	SDF	T	60	BS/Pel.
<i>Owenia fusiformis</i>	Annelida: Polychaeta	0.69	0.02	0.08	<b>5.82</b>	<b>7.10</b>	<b>1.40</b>	0.18	<b>0.74</b>	<b>1.62</b>	Ad., Juv.	SDF, SF	T	100	BS/Pel.
<i>Nephtys assimilis</i>	Annelida: Polychaeta	<b>2.81</b>	<b>0.77</b>	<b>3.09</b>	<b>0.79</b>	<b>2.71</b>	0.60	0.19	<b>0.72</b>	0.61	Ad., Juv.	P	B, C (S)	115	BS/Pel.
<i>Nephtys hombergii</i>	Annelida: Polychaeta	<b>5.03</b>	0.30	–	0.28	–	–	0.15	–	0.15	Ad.	P	B, C (S)	200	BS/Pel.
<i>Urothoe poseidonis</i>	Arthropoda: Malacostraca	0.35	0.52	0.03	0.26	<b>1.01</b>	0.36	0.16	0.33	0.27	Ad.	SSDF	B (nS)	6	Ov./BE
<i>Nemertea sp.</i>	Nemertea	<b>1.31</b>	0.09	0.69	0.31	0.43	0.11	0.13	0.10	0.06	–	P	B	–	Cut.
<i>Lineus acutifrons</i>	Nemertea: Anopla	<b>0.90</b>	0.44	0.69	0.20	0.49	0.16	0.04	0.04	–	Ad., s-Ad.	P	B	250	Cut.
<i>Glycera tridactyla</i>	Annelida: Polychaeta	<b>0.84</b>	0.11	0.50	0.04	0.23	0.05	0.02	0.06	0.02	Ad., Juv.	P	B (S)	50	BS/Pel.
<i>Sigalion mathildae</i>	Annelida: Polychaeta	0.42	–	0.41	0.18	0.57	–	–	–	0.05	Ad., s-Ad.	P	B, C (S)	150	BS/Pel.
<i>Nephtys cirrosa</i>	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.
<i>Magelona filiformis</i>	Annelida: Polychaeta	0.13	0.00	0.02	0.18	<b>0.77</b>	0.13	0.01	0.05	0.06	Ad.	SDF	B	80	BS/Pel.
<i>Lumbrineris sp.</i>	Annelida: Polychaeta	–	–	–	–	0.48	0.16	–	0.13	0.25	Ad.	P	B	150	Ov./BE
<i>Diogenes pugilator</i>	Arthropoda: Malacostraca	0.20	0.02	0.49	0.09	0.05	0.08	–	–	–	Ad., Juv.	P	C (B)	7.5 <sup>b</sup>	Ov.
<i>Bathyporeia pelagica</i>	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
<i>Scolecopsis cantabra</i>	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.
<i>Eocuma dollfusi</i>	Arthropoda: Malacostraca	0.05	0.02	0.14	–	0.01	0.00	0.00	–	–	Ad.	SDF, SSDF	B (nS)	15	Ov./BE
<i>Cumopsis fagei</i>	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<sub>A</sub> to SB<sub>C</sub> (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<sub>A</sub> to SB<sub>C</sub> (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<sub>A</sub> to SB<sub>C</sub> (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<sub>A</sub> and SB<sub>B</sub>, while the location along the shore does not explain macrofauna community structure observed at SB<sub>C</sub>, 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<sub>A</sub> sites; and 2 diagonals in the centre and in the lower part of the diagram were formed by SB<sub>C</sub> and SB<sub>B</sub> 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*.

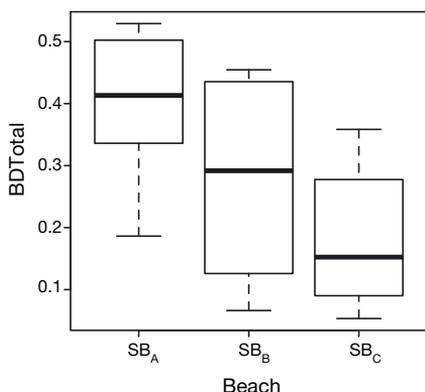


Fig. 6. Total  $\beta$ -diversity (BDTotal) across space and time at the 3 beaches (SB<sub>A</sub>, SB<sub>B</sub> and SB<sub>C</sub>). Box plots show the median (line in box), the first and third quartiles (hinges), and the most extreme data points which are 1.5 times the interquartile range from the 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<sub>A</sub> (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).

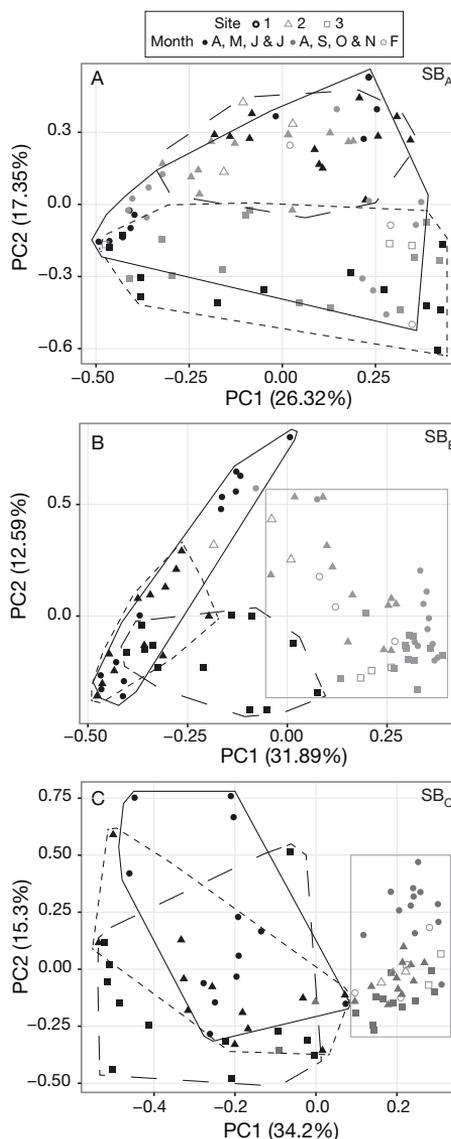


Fig. 7. Principal component analysis (PCA) distance biplots (i.e. scaling 1) of Sites 1 (circles), 2 (triangles), and 3 (squares), based on Hellinger-transformed abundance of benthic community sampled at SB<sub>A</sub>, SB<sub>B</sub>, and SB<sub>C</sub> from April 2012 to February 2013 (excluding December 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])

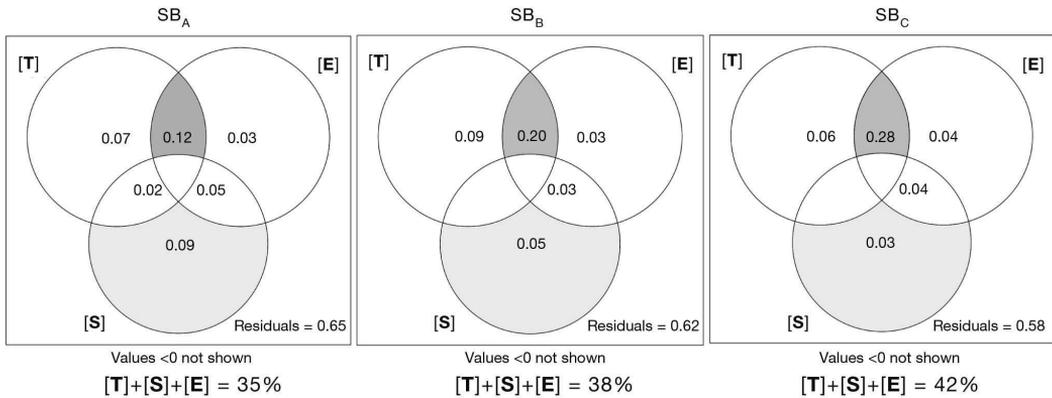


Fig. 8. Venn diagrams illustrating the result of variance partitioning of the macrofauna time series at  $SB_A$ ,  $SB_B$ , and  $SB_C$  with respect to environmental (physical and biological variables), spatial (location along shore), and temporal (distance-based Moran's eigenvector maps [dbMEMs]) explanatory 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

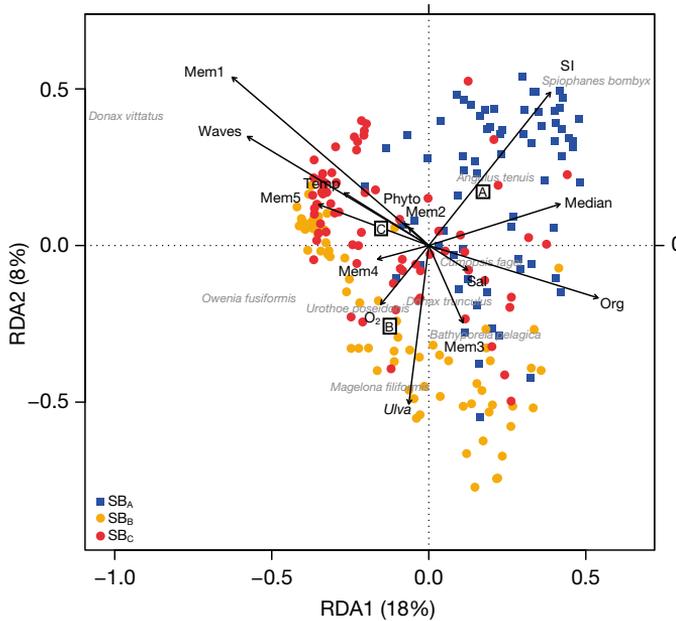


Fig. 9. RDA correlation triplot (scaling 2) of macrofaunal communities data and all explanatory variables (environmental, spatial, and temporal) of the 3 sandy beaches together: A (blue), B (orange), and C (red). Org: total organic matter; Sal: salinity;  $O_2$ : dissolved oxygen; Temp: temperature; 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; Memx: temporal variable x generated dbMEM eigenfunctions, x: centroid for SBs

Variance 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.

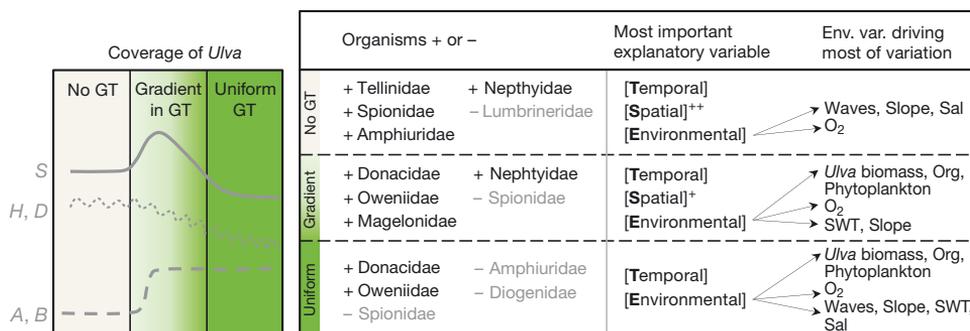


Fig. 10. Conceptual model of the effects of green tides on macrobenthic characteristics of sandy beaches. GT: green tide; Env.: environmental; var.: variable; +: stimulated; -: stifled; SWT: seawater temperature; S: species richness; H', D: Shannon and Simpson indices; A, B: abundance and biomass; Waves: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

Also, temporal variables influenced abundance, biomass, and species richness at SB<sub>A</sub>. 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 dif-

fered among the 3 SBs due to temporal variations (see Fig. S5 in the Supplement at [www.int-res.com/articles/suppl/m522p097\\_supp.pdf](http://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<sub>B</sub> and SB<sub>C</sub> 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 (Ménésguen & Piriou 1995).

In the present study, the rarefied richness differed among beaches. The beach where a gradient in *Ulva* stranding occurred (SB<sub>B</sub>) exhibited higher rarefied species richness than was found at SB<sub>A</sub> which did not harbour green macroalgal blooms. Where *Ulva* mats occurred homogeneously along the shore (SB<sub>C</sub>), 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 ( $\sim 1.5 \text{ kg m}^{-2}$ , 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  $\beta$ -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<sub>C</sub>), 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<sub>B</sub> and SB<sub>C</sub>, 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<sup>-2</sup> at SB<sub>C</sub> (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<sup>-2</sup> 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 (Guilou 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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*The following data supplement accompanies the article*

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

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**Supplement.** Additional information regarding MEMs, variation partitioning, variation of univariate variables and organic matter content at each site per beach.

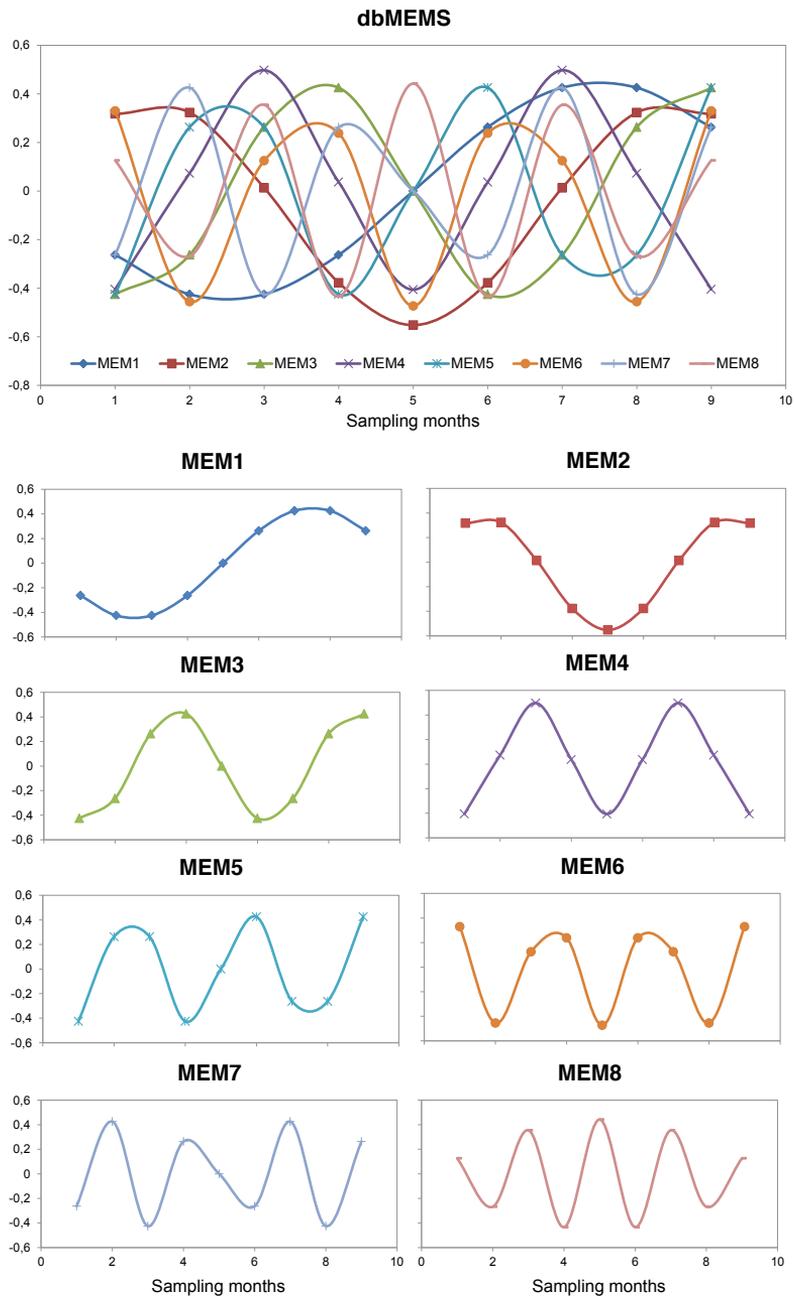


Fig. S1. All dbMEMS (upper panel) and decomposed dbMEMS (individual curves below) eigenfunctions generated based on the number of sampling occasions and the number of days between sampling occasions.

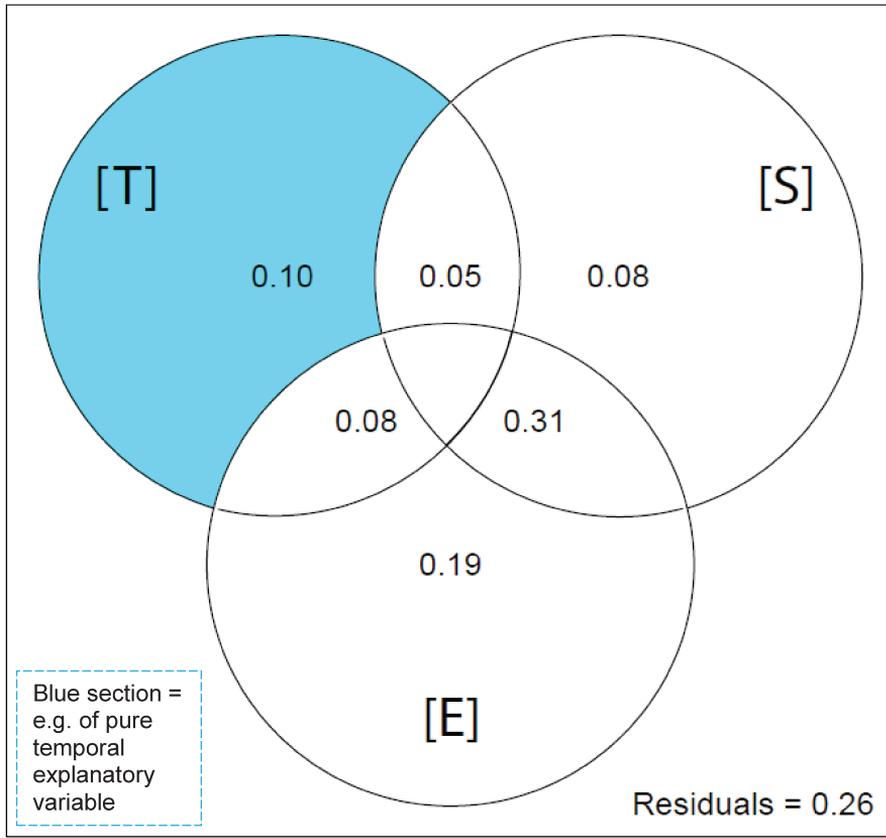


Fig S2. Venn diagram illustrating the result of variation partitioning of the biomass time series at SBA with respect to environmental ([E]), spatial ([S]) and MEM ([T]) explanatory variables. The fractions of variation displayed in the diagram are computed from adjusted  $r^2$ . Circles are not drawn to scale.

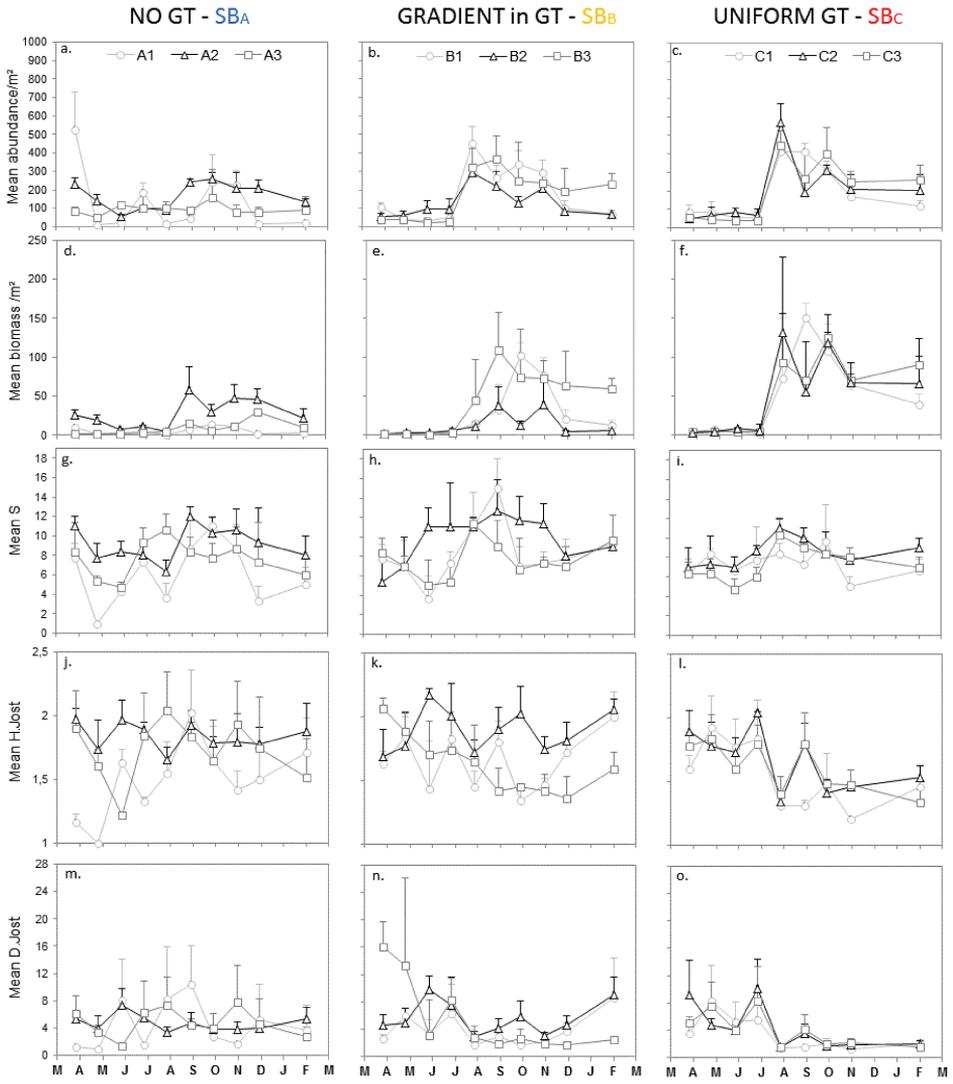


Fig S3. Mean (+ sd) abundance, biomass, species richness, numbers equivalent Shannon's entropy and Simpson's index (after Jost 2006) in the period April 2012 to February 2013 at each site for the three beaches (SB<sub>A</sub>, SB<sub>B</sub>, SB<sub>C</sub>). GT = Green tides.

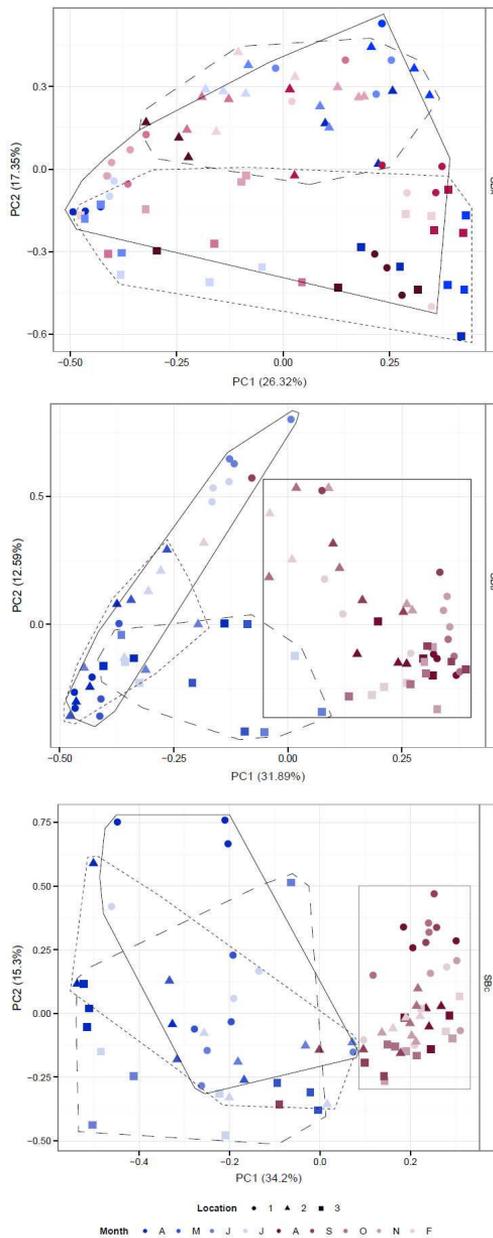


Fig S4. Principal component analysis (PCA) plots (scaling 1) of sites 1 (circles), 2 (triangles), and 3 (squares), based on Hellinger transformed abundance of benthic community sampled at SB<sub>A</sub>, SB<sub>B</sub> and SB<sub>C</sub> from April 2012 to February 2013 (excluding December 2012 for balanced design) with superimposed indicative clusters for spatial (continuous [sites 1], loose-dotted line [sites 2] or stippled-line [sites 3] polygons) and/or temporal structuring (grey boxes for autumn/winter dots, highlighting the difference to spring/summer dots).

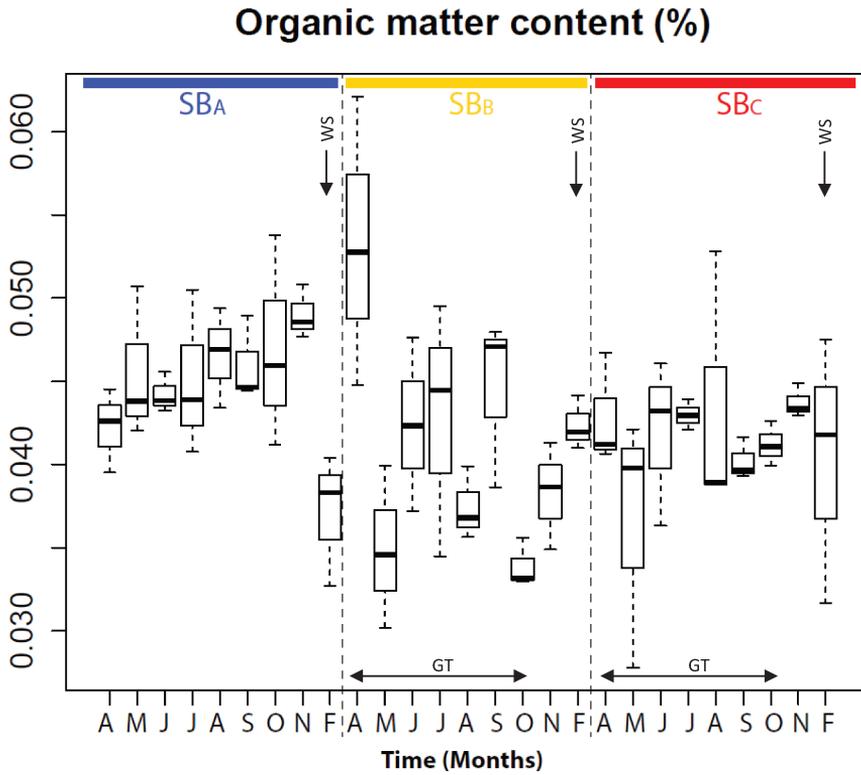


Fig S5. Boxplots of organic matter content time series at each SBs, WS = winter storm, GT = presence of stranded *Ulva* onshore. A clear seasonal variation with increasing of organic matter content until winter storms was observed at SB<sub>A</sub> while highly variable organic matter contents in time were measured at SBB and SBC, both harbouring green tides.



# Paper IV



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## Journal of Experimental Marine Biology and Ecology

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# Opportunistic basal resource simplifies food web structure and functioning of a highly dynamic marine environment



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## ABSTRACT

Carbon flow through ecosystems is determined by the nature, availability and incorporation of basal resources (BRs) to higher trophic levels of food webs. The occurrence of abundant supplementary BR often diversifies trophic niches within food webs. Blooms of opportunistic macroalgae, which may act as additional BRs, have increased in intensity, and are expected to amplify further because of global change. Understanding the effects of high biomasses of opportunistic BRs on the functioning of naturally unvegetated coastal ecosystems is thus crucial. We set out to assess whether and how green algae (opportunistic BR) modifies macrotidal sandy beach trophic structure and functioning. We also investigated whether these effects propagate up through the web, looking at different scales and trophic levels (i.e. primary producers, specific primary consumers, and the general higher-consumer assemblage). To achieve these objectives, we used a high-resolution field sampling (over 1200 individual stable isotope-, and 180 biodiversity samples) at pristine and macroalgal-bloom-affected macrotidal sandy beaches, together with recent and novel analytical approaches (biomass-weighted isotope signatures, Isotopic Functional Indices). We found that the opportunistic BR, both directly and indirectly affects the entire beach food web across several trophic levels, by inducing shifts in trophic interactions. Overall, we found that the dominance of a BR in the form of opportunistic algae simplifies the entire food web over time. Our findings challenge the paradigm that addition of BR inherently diversifies trophic interactions within an ecosystem, and have implications for the interpretation of shifts in dynamic system food webs and eutrophicated environments.

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## 1. Introduction

Within ecosystems, basal resource composition and availability to consumers determine carbon flow (Fisher and Likens, 1973; Pingram et al., 2012). Changes in primary producer assemblages, such as those resulting from plant invasion, habitat fragmentation, or conversely habitat restoration, modify trophic interactions and affect carbon pathways within food webs (Layman et al., 2007; Nordström et al., 2015). The addition of organic material, in the form of macroalgae and plants, within naturally sparsely vegetated systems, may diversify energy pathways within food webs (Hyndes and Lavery, 2005; Layman et al., 2012). For instance, in created salt marshes in the Venice Lagoon, a successional establishment of vascular plants induced local feeding processes in the benthic macroinvertebrate assemblage, resulting in a diversity of distinct, habitat-specific trophic niches for the consumer (Nordström et al., 2015). Conversely, removal of basal resources through anthropogenic activities induces a loss of carbon pathways, and concurrently a

simplification of the trophic network (McClelland and Valiela, 1998). As an example, studying fragmentation in mangrove habitats and tidal creeks, Layman et al. (2007) found that the food web was constrained to a single basal resource pool (microalgal mats) in fragmented systems, and that carbon passed through fewer intermediate consumers compared to unfragmented systems. Such a homogenization of trophic pathways, shown by a narrowing of the predator stable isotope niche, resulted in simplification of the entire food web (Layman et al., 2007). In instances where processes of anthropogenic disturbance also include establishment of additional basal resources, one can ask if the food web structure and functioning of these systems would diversify, or whether they would become simplified.

A major and worldwide human-induced pollution threat is the escalating nutrient enrichment of coastal waters, which drives the eutrophication of marine systems (Cloern, 2001). One direct symptom of eutrophication is the massive development of fine and fragile opportunistic macroalgae (Cloern, 2001; Korpinen and Bonsdorff, 2015; Schramm, 1999), which are easily detached and transported by coastal currents to form large mats of drifting algae along beaches or in shallow bays (Grall and Chauvaud, 2002). When free-living algal mats mainly consist of Chlorophyta, they are called green tides (GT). Such notable green algal blooms are increasing in

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frequency and intensity worldwide (Liu et al., 2013; Ye et al., 2011), and in Brittany, France, GT affect more than fifty sandy beaches spread over thousands of kilometres of coastline (CGDD, 2014; Charlier et al., 2007; Quillien et al., 2015b). Such macroalgal accumulations modify several compartments of the soft-sediment ecosystems: biochemistry of the water column (for example through high uptake of carbon during photosynthesis; Van Alstyne et al., 2015), primary producers, and primary & secondary consumers, in terms of diversity and community structure, both in micro- and non-tidal systems (see Arroyo and Bonsdorff, 2015; Grall and Chauvaud, 2002; Raffaelli et al., 1998 for reviews), as well as within highly dynamic macrotidal systems (Quillien et al., 2015a). In comparison, few studies have investigated the effects of opportunistic macroalgal blooms on community-wide food web structure and species-specific trophic relationships, and most of them have taken place within sheltered system (e.g. Ouisse et al., 2011), non- or micro-tidal systems (e.g. Carlier et al., 2008), or have been addressed by experimental studies (e.g. Nordström and Booth, 2007), which infers some constraints when trying to appreciate ecosystem scale responses. Even fewer studies – to our knowledge none – have investigated the effects of the accumulation of opportunistic macroalgae on macrotidal and open system food webs following *in situ* approaches.

A central aspect in ecology is to understand ecosystem functioning and responses to environmental and anthropogenic pressures, to enable prediction of functional shifts under environmental perturbations (Borja, 2014; Hooper et al., 2005). Assessment of the functioning of systems relies on community ecology through investigation of species richness and community composition (Hooper et al., 2005, and references therein), which has, more recently, been expanded to include biological traits of the species (e.g. Törnroos and Bonsdorff, 2012). In the field of ecosystem ecology, fluxes of energy and matter through ecosystems are used to elucidate ecosystem functioning (Lindeman, 1942). However, a discrepancy exists between these two main approaches (Thompson et al., 2012). A way to combine community and ecosystem ecology is to quantitatively study food web dynamics within a system (Thompson et al., 2012; Woodward, 2009). The study of trophic webs over time and space, tracking changes in species biomass, provides opportunity to investigate energy pathways based on the structure and dynamics of species' feeding relationships.

Assessments of community trophic structure and dynamics can be conducted through examination of the relative positioning of consumers and resources in bivariate stable isotope space ( $\delta^{13}\text{C}$ – $\delta^{15}\text{N}$ , Layman et al., 2012). The relative positioning of individuals, populations, and communities in bivariate isotope space represents occupancy of isotopic niche space. Several metrics for this 'isotopic niche' have been developed, enabling comparisons of e.g. trophic similarity (potential separation in isotopic niche location, and overlap of niches), niche width or trophic diversity (isotopic niche width/size) among communities or within assemblages over time (Jackson et al., 2011; Layman et al., 2012; Turner et al., 2010). Also, newly developed isotopic functional indices weighted with species biomass (IFI, Rigolet et al., 2015), based on functional indices developed by Villéger et al. (2008), allow a multifaceted (richness, evenness, and divergence) quantification of functional/trophic diversity and a better characterization of the structure of energy accumulation in food webs (e.g. Grall et al., 2006). Using the isotopic niche concept and indices constructed from it, it is possible to identify changes in fundamental food web attributes following anthropogenic or natural disturbances, such as shifts in major trophic pathways (visualized using biomass-weighted isotope signatures) or in niche width.

In order to elucidate the impact of an additional basal resource, present due to anthropogenic disturbance, on food web structure and functioning, we focus here on a naturally unvegetated ecosystem, such as open macrotidal sandy beaches. Sandy beaches (SBs) are well represented coastal habitats as they cover two thirds of the world's ice-free coastline (Bascos, 1980). These highly dynamic

systems harbour a diverse and specialized fauna (McLachlan and Brown, 2006) and provide essential functions and services (filtration of large volumes for both saline and fresh water, provision of nursery and feeding habitats for species of commercial importance, protein supply through coastal fisheries) (Schlacher et al., 2008). However, SBs are severely affected by multiple threats, including blooms of opportunistic macroalgae (Defeo et al., 2009; Quillien et al., 2015a), yet still overlooked in stable-isotope based studies that focus on the influence of stranded algae on SB community-wide trophic structure and dynamics (but see Ouisse et al., 2011). Here, using recent and novel approaches and metrics for measuring community-wide and species-specific isotopic niches, we investigated potential alteration in coastal community trophic structure and functioning caused by the presence of an additional opportunistic food source (*i.e.* *Ulva* spp., hereafter *Ulva*) over time (4 seasons), using macrotidal sandy beaches located in Brittany (France) as a case study system. We explored potential indirect and direct influences of green tides on SB consumer communities by testing two main hypotheses: First, that the presence of free-living *Ulva* mats on the low shore of normally unvegetated sandy beaches modifies the isotope signature of trophic baselines, *i.e.* the two main food sources within unvegetated systems: suspended particulate organic matter (POM) and sedimentary organic matter (SOM). Second, that the presence of *Ulva* influences species-specific diets in the benthic consumer community. Also, our study aims to assess the knock-on effects of indirect and direct changes induced by high biomasses of free-living green algae on the structure and the functioning of community-wide trophic network. More specifically, this work was designed to answer one overarching question: are macrotidal sandy beach (SB) trophic networks diversified by the addition of an opportunistic basal resource within the system?

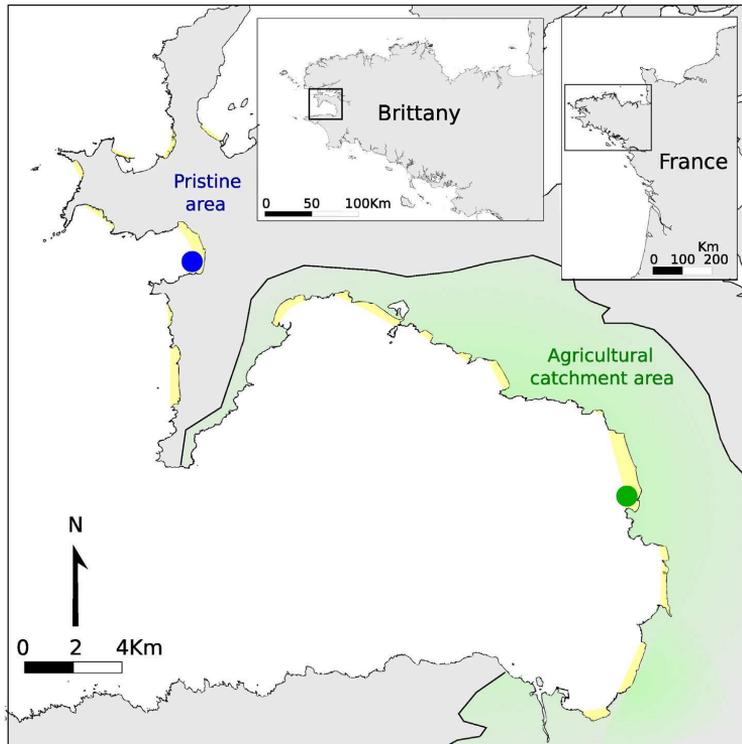
## 2. Material and methods

### 2.1. Study system

The Bay of Douarnenez (Brittany, France) is an open and a macrotidal system where sediments accumulate to form several kilometres long SBs. Two dissipative beaches (Short, 1996), which share the same characteristics and surrounding water body (Quillien et al., 2015a), were selected for this study (Fig. 1). Almost 3 km long, these two SBs show large areas that are bared up to 500 m at low tide during spring tides (mean tidal regime = 6.5 m). Since the tidal regime is macrotidal ( $\geq 4$  m, Allaby, 2010) and because these beaches are open to the west, they are highly dynamic systems exposed to strong waves and currents (Augris et al., 2005), which are similar in terms of direction and strength for both beaches. The only distinction between the two sites is the presence of green tides as the result of local eutrophication of coastal waters at one of the beaches. One SB never has green tides because a wetland area located behind the beach filters continental water input, and urbanization in the catchment area is limited. Conversely, the other beach, which is located downstream of an agricultural catchment area (Fig. 1), has experienced annual *Ulva* bloom events (from spring to autumn) since the early 1980's (Charlier et al., 2007; Ménesguen and Piriou, 1995).

### 2.2. Sampling

To assess temporal variability of sediment-dwelling macrofauna and nematode communities in terms of abundance and biomass, sampling was conducted seasonally (May, July, September and November 2012) during low tide (swash-zone) at the two SBs. Macrofauna (larger than 1 mm) was sampled using a tube-corer (sampled surface = 300 cm<sup>2</sup>), and samples were sieved through mesh bags (1 mm mesh size) to separate the fauna from the sediment. The sampling was conducted monthly at three sandy beaches (Quillien et al., 2015a), although here we have made use of the abundance and biomass data collected at



**Fig. 1.** Location (Brittany, France) of the 2 study sites (circles) at the south of the two studied sandy beaches. Yellow areas along coastline represent sandy beaches within the study area. The site impacted by green tides is denoted by the green circle and is located downstream of an agricultural catchment area. A blue circle denotes the site that is never affected by accumulation of *Ulva*. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

two of those three, only at four times, in order to proceed to isotope weighting procedures (see *Data analyses* section below). Thus at both studied beaches, nine replicate samples were randomly taken at each sampling occasion (for methodological details, see Quillien et al., 2015a). Macrofaunal samples were preserved in 4% buffered formalin for later sorting in the laboratory where macrofauna was identified to the lowest possible taxonomic level with the aid of a binocular magnifier, counted and weighted. Species nomenclature follows the “World Register of Marine Species” (<http://www.marinespecies.org/>). Biomass of each taxa was measured by weight loss after combustion at 450 °C for 4 h (ash-free dry weight). Abundance and biomass were converted to units per m<sup>2</sup>. Meiofauna (animals smaller than 1 mm in length) was sampled using a tube-corer (sampled surface = 60 cm<sup>2</sup>), and freeze-preserved (−20 °C). Three replicates were taken at each beach at each sampling occasion. Meiofauna samples were first sifted through 1 mm mesh sieve (to remove macrofauna), undersize fraction was then sifted through 40 μm mesh sieve to get a sample composed of units whose size was between 40 and 1000 μm. Centrifugation was then applied to the samples (flotation method with Ludox, Nichols, 1979) in order to separate fauna from the sediment. The extracted meiofauna was fixed with 4% buffered formalin and stained with Rose Bengal (0.5 g L<sup>−1</sup>). Meiofauna was sorted using a Delfuss cuvette and a binocular magnifier. Nematodes were counted and measured (body length [L] and width [W]) with the aid of a stereomicroscope. Nematode biomass was calculated from the biovolume, which was estimated from all individuals per replicate using the Andrassy formula ( $V = L \cdot W^2 \cdot 0.063 \cdot 10^{-5}$ , expressed in μm<sup>3</sup>, (Andrassy, 1956). *Ulva* biomass stranded at each SB was estimated by CEVA (<http://www.ceva.fr/fre>)

through monthly aerial surveys (for estimating of surface covered by mats) and field sampling (for conversion into biomass).

### 2.3. Stable isotope analyses

At each sampling date, the low-shore community trophic structure of the two macrotidal SBs was assessed by sampling biota for stable isotope analyses (<sup>13</sup>C:<sup>12</sup>C and <sup>15</sup>N:<sup>14</sup>N). δ<sup>13</sup>C enables identification of dietary carbon sources. Indeed, different primary producers (e.g. C3 vs. C4 plants, pelagic vs. benthic production) vary significantly in their δ<sup>13</sup>C values (<sup>13</sup>C:<sup>12</sup>C expressed relative to a standard), and consumers of respective primary producers mirror values of the resources as δ<sup>13</sup>C is largely conserved through trophic transfer (Bearhop et al., 2004; Post, 2002). Complementary to this, δ<sup>15</sup>N (<sup>15</sup>N:<sup>14</sup>N expressed relative to a standard) can be used to estimate trophic position as it shows a step-wise enrichment with trophic transfer (Hussey et al., 2014; Post, 2002). Particulate organic matter (POM) was collected from the water column (within the first metre) in polyethylene tanks, and filtered in the laboratory. Sedimentary organic matter (SOM) was sampled using a scraper to collect the first centimetres of sediment. Drifting *Ulva* was hand-collected from the water column at the impacted beach. Macrofauna was sampled using cores, forks and by sieving ~50 L of sediments (1 mm mesh-size). Meiofauna (mainly nematodes, Carriço et al., 2013) was sampled using cores and by scraping the uppermost layer of the sediment (ca. 1.5 cm), and was later sieved back in the laboratory. Flatfish and epibenthic crustaceans were caught using a beach trawl and a push net (8 mm mesh size each).

All samples were brought back to the laboratory for conservation. Sediments collected for SOM were re-suspended in filtered Milli-Q water using an ultrasonic bath. The supernatant was then filtered on pre-combusted (450 °C for 5 h) GF/F filters, six filters were taken at each sampling occasion, at each beach. Three filters were acidified (10% HCl), and the other three were not.  $\delta^{13}\text{C}$  from acidified and  $\delta^{15}\text{N}$  from untreated subsamples were later combined to obtain valid (*i.e.* undisturbed by calcium carbonate residues, neither by acidification) isotope signatures. Seawater collected for POM was pre-filtered using a net (90  $\mu\text{m}$ ) to remove large detritus (*i.e.* pieces of macroalgae), then sieved on pre-combusted GF/F filters and quickly acidified. *Ulva* thalli were cleaned from any epiphytes and rinsed with Milli-Q water. All fauna collected were sorted in the laboratory and kept frozen ( $-20\text{ }^\circ\text{C}$ ) until prepared for analyses. Fauna was identified to the lowest possible taxonomic level and measured (total length, or width of first setigers for polychaetes). Samples consisted of muscle tissue of large species (fish, bivalves, echinoderms, some polychaetes), or of pooled individuals (5–300 individuals, in order to reach the minimum weight needed for isotope analyses) for the smallest species. When pooling was required, gut contents were carefully removed by dissection. Species containing calcium carbonate, *e.g.* ophiuroids and cumaceans, were split into two subsamples: one was acidified (10% HCl) for  $\delta^{13}\text{C}$  analysis, the other subsample was not acidified and was used for  $\delta^{15}\text{N}$  analysis. All samples were rinsed using Milli-Q water, oven-dried (48 h at 60 °C) and ground into fine powder using a ball mill (fauna, macroalgae) or gently scrapped using a scalpel (POM and SOM collected on filters). Part of the powder (400  $\mu\text{g}$ ), or the fragments (1 mg), was then packed into  $5 \times 8$  mm ultra-clean tin capsules and sent to the isotope spectrometry platform (LIENSs laboratory, University of La Rochelle, France). Samples were analysed using an elemental analyser (Flash EA 1112) coupled to an isotope ratio mass spectrometer (Delta V Advantage with a ConFlo IV interface). Results are expressed in the  $\delta$  unit notation as deviations from standards (Vienna Pee Dee Belemnite for  $\delta^{13}\text{C}$  and  $\text{N}_2$  in air for  $\delta^{15}\text{N}$ ) following the formula:  $\delta^{13}\text{C}$  or  $\delta^{15}\text{N} = [(R_{\text{sample}}/R_{\text{standard}}) - 1] \times 10^3$ , where R is  $^{13}\text{C}/^{12}\text{C}$  or  $^{15}\text{N}/^{14}\text{N}$ . Reference gas calibration was done using reference materials (USGS-24, IAEA-CH6, IAEA-600 for carbon; IAEA-N1, IAEA-N2, IAEA-N3, IAEA-600 for nitrogen). Analytical precision based on isotope values of the acetanilide (Thermo Scientific) used to estimate C and N content for each sample series was  $<0.1\%$  both for carbon and nitrogen.

Separately, an experiment designed to assess the influence of *Ulva* mats on the isotope signature of dissolved inorganic carbon (DIC) *in vitro*, during respiration (night) and photosynthesis-dominated (day) times, was run in the laboratory. In a climatic room (17 °C), six large round-bottom flasks (2 L) filled with filtered seawater (5  $\mu\text{m}$ ) were placed on a rotating surface (regular movement). The round-bottom flasks received the same light amount (verification measures taken using a light-metre; in addition, the position of the round-bottom flasks was randomly shifted at each sampling occasion). Three of the bottles contained freshly collected *Ulva* thalli (20 g), while the three others acted as controls and only contained filtered seawater. Every two hours for twenty-six hours, water samples from the flasks were sampled for determination of  $\delta^{13}\text{C}$  DIC by gently over-filling headspace vials (12 mL) with water. Vials were rinsed with sample water three times before sampling. A volume of 2 mL of a saturated  $\text{HgCl}_2$  solution, which is a chemical inhibitor against oxidation forms, was added and the vials were capped and stored at room temperature until analysis. Dissolved oxygen, temperature and pH were measured using multi-parameter probes. In addition, relative growth rate of *Ulva* thalli was evaluated by weighting fresh algae before starting the experiment and two days after the end of the experiment, in order to check for possible degradation. Samples (only one replicate for each treatment analysed – with and without *Ulva*, respectively) for isotope analyses of DIC were sent to the Department of Analytical Chemistry (ANCh),

Vrije Universiteit, Brussel, Belgium for carbon stable isotope analyses. Samples were analysed following the method described by Gillikin & Bouillon (2007), and using the elemental analyser Flash 1112 Series EA, coupled via a ConFlo III to a ThermoFinnigan Delta p XL continuous flow (CF)-IRMS.

#### 2.4. Data analyses

In order to test if the presence of an abundant additional food source (*Ulva* mats) induces changes in isotope signatures of naturally unvegetated SB basal resources (POM and SOM), and to test if the effect of green tides differs depending on the sampling time (interaction of both factors 'Season' and 'GT'), two-way ANOVAs were used.

To evaluate effects of *Ulva* accumulations on community trophic structure and dynamics of sandy beaches, we tested for changes in isotopic niche attributes for 'shared' (*i.e.* common to the two SBs) consumers between beaches over time. We applied quantitative metrics using a Bayesian approach (Jackson et al., 2011) to estimate the amount of  $\delta$ -space filled by the community at the two beaches. The assemblage overlap was assessed based on standard ellipse areas corrected for small sample sizes (SEAc) using the SIBER metrics (Jackson et al., 2011). Comparing the two SB ellipses over time, we expressed per cent overlap in relation to the surface of the smallest ellipse. In addition, we assessed differences in community and species-specific position within  $\delta$ -space (centroid location), trophic diversity (distance to centroid) and trophic redundancy (nearest neighbour distance) using nested linear models and a residual permutation procedure (Euclidean distance, 9999 permutations) (Turner et al., 2010).

Also, to determine the influence of an abundant additional food source on the trophic functioning of highly dynamic systems, we assessed patterns of biomass. We weighted the isotope signature of every species that was part of the SB food webs using values of biomass per square metre (individual ash-free dry weight  $\times$  abundance per square metre) within the two beaches and over time to identify changing pathways of trophic transfer. We visualized this by setting the area of circles to reflect the biomass of each species. In order to identify possible differences in the structure and functioning of the two systems, of which one harbours an additional food source, we used indices recently developed to measure three independent facets of functional diversity: functional richness (amount of functional space filled by the community), functional evenness (regularity of abundance/biomass distribution in the functional space), and functional divergence (location of abundance/biomass at the borders vs. close to the centre of gravity) (Villéger et al., 2008) in  $\delta$ -space, as proposed by Rigolet et al. (2015). Statistical differences between the isotopic structural (MDC = mean distance to centroid, MNN = mean distance to nearest neighbour), and functional indices (IFRiC = isotopic functional richness, IFVe = isotopic functional evenness, IFDiv = isotopic functional divergence) were tested using Bayesian methods (Turner et al., 2010), and Wilcoxon tests (as data did not fill all conditions required for parametric tests), respectively.

All analyses were performed within the R environment (R Development Core Team, 2013), using the FD (Laliberté et al., 2014) and SIAR (Parnell and Jackson, 2013) packages, as well as R scripts made available by A. L. Jackson and T. F. Turner (<http://www.tcd.ie/Zoology/research/research/theoretical/Rpodcasts.php> and <http://www.esapubs.org/archive/ecol/E091/157/suppl-1.htm>, respectively).

### 3. Results

We found changes induced by the presence of green tides on primary producer level and consequent propagation of effects up through the web. Indeed, looking at species-specific responses, we found significant shifts in species diets, directionally consistent with changes seen at basal resource level. We also showed that the induced changes, both at primary producer and primary consumer levels, affect the overall

higher-level consumer assemblages, altering the entire food web structure, and ultimately its functioning.

### 3.1. Baselines of SB food webs: temporal variation and influence of GT

Temporal patterns were revealed for both basal resources within sandy beaches (i.e. POM and SOM). Also, the presence of green tides significantly affected baseline isotope signatures. Isotopic signatures of organic matter sources (POM, SOM and *Ulva*) showed wide ranges of stable isotope composition, with mean  $\delta^{13}\text{C}$  values ranging from  $-25.1 \pm 0.5\%$  for particulate organic matter sampled in May at pristine SB, to  $-16.7 \pm 0.3\%$  for *Ulva* sampled in November at impacted SB; and with mean  $\delta^{15}\text{N}$  values ranging from  $5.0 \pm 0.1\%$  for sedimentary organic matter sampled in September at pristine SB, to  $11.9 \pm 2.5\%$  for *Ulva* sampled in July at the impacted SB (Fig. 2). Values of  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  of sources varied over the production season. The POM showed significant temporal variability both in  $\delta^{13}\text{C}$  and in  $\delta^{15}\text{N}$  within the two sites, while an effect of 'Time' was significant only for  $\delta^{15}\text{N}$  of SOM (Fig. 2, Table 1). Different green tide effects for POM ( $\delta^{13}\text{C}$ ) and SOM ( $\delta^{15}\text{N}$ ) were highlighted by the analysis. Particulate organic matter was significantly more  $^{13}\text{C}$ -enriched where green tides occur than on the pristine SB, while there was no significant influence of GT on nitrogen isotopic signature of POM (Fig. 2, Table 1). Conversely,  $\delta^{15}\text{N}$  of sedimentary organic matter was significantly affected by the presence of GT and varied over time, which was not the case considering  $\delta^{13}\text{C}$  (Table 1).

Possible indirect effects of high biomasses of *Ulva* on the isotope composition of organic matter sources, through the modification of dissolved inorganic carbon (DIC) isotope signature, was tested in the laboratory (data not shown). The  $\delta^{13}\text{C}$  of DIC in the control flask remained stable for the whole experiment (night and day) with a mean value of  $-1.1 \pm 0.5\%$ . Conversely, in the flask where *Ulva* were floating,  $\delta^{13}\text{C}_{\text{DIC}}$  decreased from 0.8 to  $-3.6\%$  during night and increased by more than 8‰ to reach 4.6‰ when light became available. High growth rates of *Ulva* thalli were measured during the time of experiment

**Table 1**

Results of 2-way ANOVAs testing the effects of time (factor 'Month') and the presence of green tides (factor 'GT'), and the interaction of both factors (Month  $\times$  GT), on isotope signature of potential food sources (SOM and POM) sampled from May to November 2012 at two macrotidal sandy beaches. Total number of stable isotope signatures was 48.

Treatment	df	MS	F	p-value	
<i>Particulate organic matter</i>					
$\delta^{13}\text{C}$					
GT	1	8.66	14.76	<b>1.44.10<sup>-3</sup></b>	**
Month	3	17.3	29.52	<b>9.32.10<sup>-7</sup></b>	***
GT $\times$ Month	3	0.38	0.64	0.59	
Res.	16	0.59			
$\delta^{15}\text{N}$					
GT	1	0.08	0.26	0.61	
Month	3	1.32	4.37	<b>0.02</b>	*
GT $\times$ Month	3	0.10	0.33	0.80	
Res.	16	0.30			
<i>Sedimentary organic matter</i>					
$\delta^{13}\text{C}$					
GT	1	0.22	0.82	0.38	
Month	3	0.36	1.36	0.29	
GT $\times$ Month	3	0.41	1.55	0.24	
Res.	16	0.27			
$\delta^{15}\text{N}$					
GT	1	1.14	4.75	<b>0.04</b>	*
Month	3	1.03	4.31	<b>0.02</b>	*
GT $\times$ Month	3	0.32	1.34	0.29	
Res.	16	0.24			

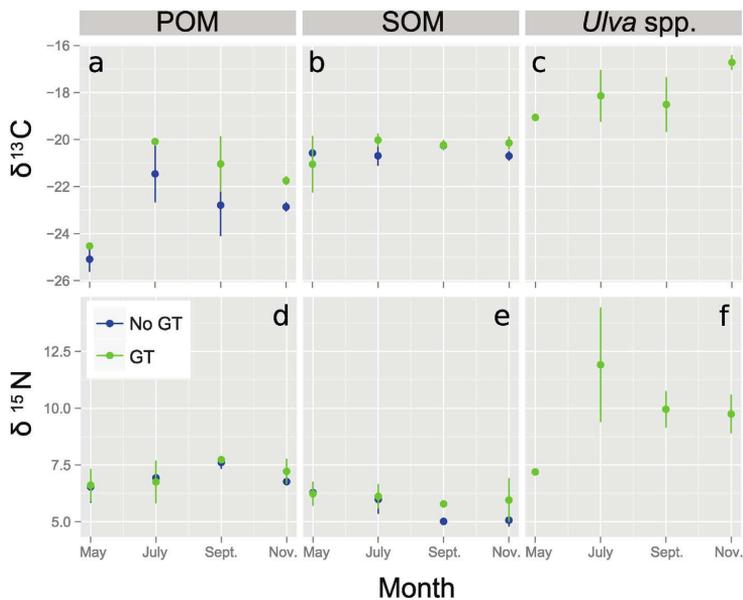
Significant values at  $p \leq 0.05$  are shown in bold.

\*  $p \leq 0.05$ .

\*\*  $p \leq 0.01$ .

\*\*\*  $p \leq 0.001$ .

(9.85  $\pm$  2% increase in biomass), suggesting that no significant degradation occurred. Consequently, the results of the experiment indicate that the presence of *Ulva*, at least at small scales, changes values of  $\delta^{13}\text{C}_{\text{DIC}}$ , creating a potential for knock-on effects influencing the  $\delta^{13}\text{C}$  of other basal resources.



**Fig. 2.** Mean ( $\pm$ SD) isotope signatures ( $\delta^{13}\text{C}$  [upper panels] and  $\delta^{15}\text{N}$  [lower panels]) of particulate organic matter (POM, a, d), sedimentary organic matter (SOM, b, e), and the green macroalgae *Ulva* spp. (c, f) sampled in May, July, September and November at pristine (blue) and impacted (green) sandy beaches. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

### 3.2. Shifts in species-specific diets in the presence of GT

Changes in food web structure and functioning were also analysed at species level, assessing changes in mean isotope signature ( $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$ , mean  $\pm$  SD) for different size classes (small, medium, large) of three consumers of different trophic levels (primary and secondary consumers). The three species are also among the six most dominant species in terms of biomass, within this system (Quillien et al., 2015a). In total, 80 *Donax vittatus*, 65 *Owenia fusiformis*, and 18 *Acrocnida brachiata*, sampled in autumn were included in this analysis. The specific pattern of trophic niches depended on the species and on the beach where they were sampled (Fig. 3). The mean location in stable isotope space (i.e. all size classes pooled) of each primary consumer differed significantly from conspecifics in the presence of green tides ( $p = 0.002$ , 0.0001, and 0.001, for *D. vittatus*, *O. fusiformis*, and *A. brachiata*, respectively). These differences were due to the changing  $\delta^{13}\text{C}$  of all three species sampled where green tides occurred (Fig. 3). Across size classes, the stable isotope signature of consumers got heavier. Isotopic space occupied by small, medium and large *D. vittatus* at both SBs (with and without green tides) overlapped (Fig. 3a), although medium and large individuals showed higher  $\delta^{13}\text{C}$  at SB where green tides occur. Carbon signatures of individuals of *O. fusiformis* differed markedly between the two SBs (GT/no-GT) with no overlap in  $\delta$ -space (Fig. 3b). The isotope signature of *O. fusiformis* sampled where green tides occurred showed considerably heavier  $\delta^{13}\text{C}$  than individuals from pristine SB. There were large shifts in  $\delta^{13}\text{C}$  between individuals of the ophiuroid *A. brachiata* that were sampled at pristine vs. GT-impacted SBs. From primary consumers (*D. vittatus*) to top-consumers (*A. brachiata*), the  $\delta^{13}\text{C}$  values of organisms sampled at SB impacted by green tides were higher compared to  $\delta^{13}\text{C}$  of organisms at the pristine site.

The location of the Donacidae in  $\delta$ -space is right above both SOM and POM signatures. Within the pristine environment, trophic linkages between POM and small *O. fusiformis*, and between SOM and medium individuals of this species are apparent (Fig. 3c). Where detached green macroalgae occurred, *O. fusiformis* isotope signatures occurred above and close to SOM and *Ulva* locations (Fig. 3b), while the ophiuroid *A. brachiata* was positioned above the others in  $\delta$ -space.

### 3.3. Dynamic community-wide isotopic niche changes induced by GT

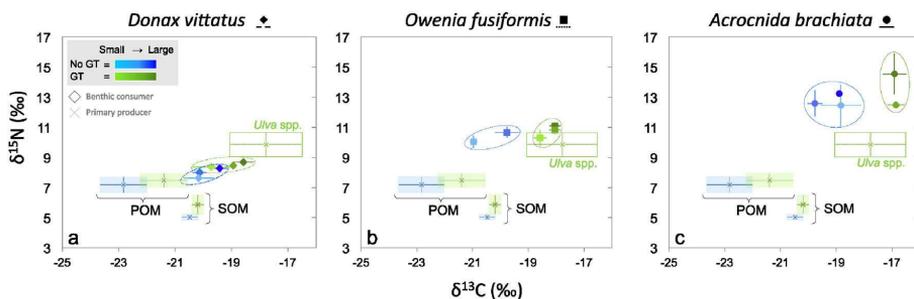
Among the sixty-seven species in the low-shore SB zoobenthic communities of the study area (Quillien et al., 2015a), forty-three species of benthic invertebrates (accounting for 99% of the total biomass), four species of flatfish, two species of demersal fish, and one meiofaunal

compartment (nematodes), were sampled and analysed for isotopic composition (1144 individual stable isotope samples).

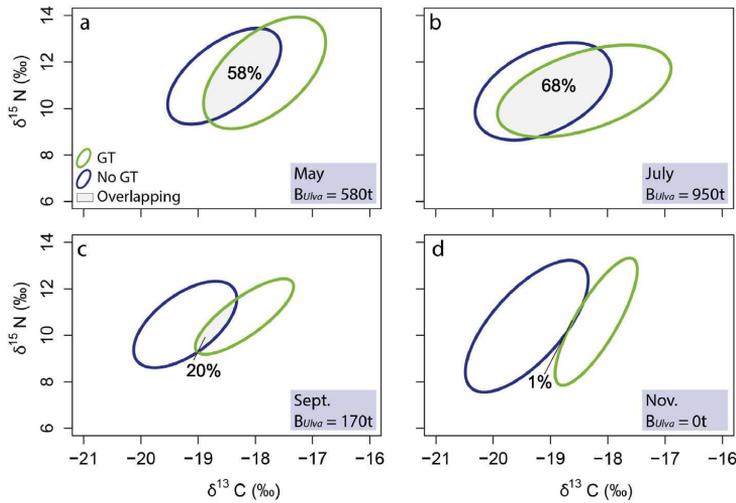
The isotopic niches of benthic assemblages (benthic consumers shared by both SBs), estimated as SEAc (Fig. 4), consistently overlapped in May and July (58% and 68% niche overlap, respectively) showing a high similarity in  $\delta$ -space of communities sampled at sites with and without green tides (Fig. 4a, b). The overlap of the two sandy beaches ellipses decreased in September (20%) and was almost non-existent (<1%) in November, indicating a progressive shift in isotopic niche space between the two beaches over time during the season (Fig. 4c, d). The mean location of the consumers differed significantly between the two beaches in September and November ( $p < 0.001$  at both dates), but not in May and July ( $p = 0.18$  and  $p = 0.13$ , respectively). In addition, the size of community isotopic niches at SB where green tides occur was smaller than of SEAc calculated for pristine SB assemblages (in September and November) (Fig. 4c, d; probabilities that SEAc for impacted beach is smaller than SEAc for pristine beach are 0.85 and 0.81, respectively). Also, significant differences in mean distance to centroid (MDC) and mean distance to nearest neighbour (MNN) between the two SBs were found in September (Table 2), confirming greater occupancy of isotopic niche space, as well as highlighting sparser species packing in that niche space, for the consumer assemblage at the pristine SB at that time.

### 3.4. Seasonal influence of GT on trophic functioning

By weighting the mean isotope signature of every taxon in the food web (food sources, primary and secondary consumers, except flatfish) by their respective mean biomass per square metre, major trophic pathways were visually identified. Two different pictures emerged, revealing an influence by GT on SB dynamics (Fig. 5). The ophiuroid *A. brachiata*, the bivalves *Angulus tenuis*, *Donax trunculus* and *D. vittatus*, the amphipod *Urothoe poseidonis*, the polychaete *Glycera convoluta*, as well as the nemertean *Lineus acutifrons* constituted most of the benthic biomass (89.8 to 97.1% of the total biomass) in the pristine community on all sampling occasions (Fig. 5a, b, c, d). In the green-tide SB community, the brittle star *A. brachiata*, the nemertean *L. acutifrons* and the polychaetes *O. fusiformis* and *Nephtys assimilis* made up 4.5 to 35.5% of total biomass considering all sampling dates. The bivalve *D. trunculus* represented the largest biomass (60.3 and 67.6%) in May and July, while *D. vittatus* constituted most of the total biomass (90.3 and 91.9%) in September and November (Fig. 5e, f, g, h). The combination of consumer biomass and isotope signature showed that most of the biomass (up to 95%) is channelled into the bivalve primary consumer



**Fig. 3.** Stable isotope bi-plots illustrating species-specific size-related isotopic niches of three primary consumers in autumn at sandy beaches impacted (green) and not impacted (blue) by green tides. *Donax vittatus* values are denoted by filled squares, light colour squares refer to small individuals ( $L_1 = 7$ –15 mm) less than one year old, mid-colour squares refer to medium individuals ( $L_1 = 16$ –22 mm) that were one year old, and dark colour squares refer to large individuals ( $L_1 = 23$ –30 mm) that were two years old. *Owenia fusiformis* values were denoted by filled diamonds, light colour diamond-shapes refer to small individuals (width of second setiger [ $W$ ] = 0.25–1 mm) that were juveniles, mid-colour diamond-shapes refer to medium-sized individuals ( $W = 1.5$ –2 mm), and dark-colour diamond-shapes refer to large adult individuals ( $W = 2.5$ –4 mm). *Acrocnida brachiata* values are denoted by filled circles, light colour (blue or green) circles refer to small individuals (disc diameter [ $L_1$ ] = 7–9 mm) one to two years old, mid-colour circles refer to medium individuals ( $L_1 = 10$ –11 mm) two to three years old, and dark colour circles refer to large individuals ( $L_1 = 12$ –13 mm) three to four years old. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)



**Fig. 4.** Standard ellipses (SEAC) illustrating the isotopic niches of shared species between communities at sandy beaches harbouring green tides (green ellipses) or not harbouring green tides (blue ellipses) over time: a) May, b) July, c) September, and d) November 2012. Biomass of *Ulva* spp. stranded on the impacted beach is reported in grey boxes. Overlap between species is expressed as per cent. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

compartment, made up by *D. trunculus*, *D. vittatus* and *A. tenuis*, both in pristine and impacted SBs. In addition, positioning of flatfishes in this  $\delta$ -space revealed that juveniles of *Pegusa lacaris*, *Pleuronectes platessa*, *Schophthalmus maximus* and *S. rhombus* were found lower in the web compared to other predators such as the nemerteans *L. acutifrons* and *Cerebratulus roseus*, the polychaetes *Scoletoma impatiens* and *G. convoluta*, and the brittle star *A. brachiata* (Fig. 5).

Also, the isotopic functional indices (IFI) were used to depict and quantify functional characteristics of the food webs (Rigolet et al., 2015). IFI calculated for the two food webs across seasons based on mean isotope signatures of consumers (Table 2) indicated no significant changes between the two communities in trophic structure and functioning in May and July. Conversely, the mean distance to the centroid and the mean nearest neighbour, as well as the functional divergence showed significant differences between the two food webs in September, indicating a shift in trophic structure. In November, significant differences between the two isotopic niches were expressed within two facets of functional diversity: the functional richness and the functional divergence (Table 2). The functional richness index (IFRic), which represents the amount of isotopic space filled by the community, was significantly lower for the assemblage where GT occurred ( $p = 0.02$ ). The functional divergence, which helps to quantify whether higher biomasses are close to the borders (i.e. distant to the centre of gravity) of the trophic niche (IFDiv), was significantly greater ( $p = 0.0004$ ) at SB where GT occurred, indicating that biomass was more distant to the centre of gravity there than at pristine beach. Finally, a

progressive alignment of isotope signatures of species composing the food web at the sandy beach where green tides occur over time was also clear (Fig. 5e-h).

#### 4. Discussion

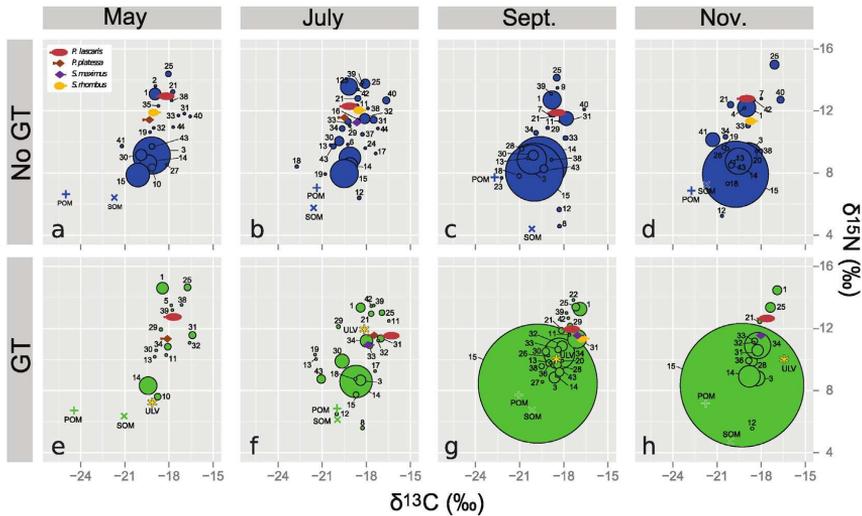
Whereas high biomasses of opportunistic macroalgae resulting from eutrophication of coastal waters have well documented effects on faunal biodiversity, such as species richness and community composition (see Arroyo and Bonsdorff, in press; Lyons et al., 2014, for reviews), changes in the trophic structure, and the subsequent energy flow through faunal communities, are seldom assessed simultaneously (Ouisse et al., 2011). Here we go further by analysing an extensive data set collected through high-resolution field sampling to study the effects of green tides on the dynamic trophic structure and functioning of the intertidal (low shore) sandy beach ecosystem. This study complements the work on community structure in Quillien et al. (2015a) by assessing trophic functioning, and evaluating part of the data on community structure specifically in a trophic context. The two SB communities studied were located within the same water body, and were comparable except for the presence of green tides due to local eutrophication on one of the beaches (Quillien et al., 2015a), which allowed direct comparison using stable isotopes. In addition, the findings presented in this study are consistent with the patterns (in diversity and species assemblages) significantly explained by the presence of high biomass of *Ulva*, found at larger spatial and temporal scales (Quillien et al., 2015a, 2015b), making the two

**Table 2**

Isotopic structural and functional indices (MDC = mean distance to centroid, MNN = mean distance to nearest neighbour, IFRic = isotopic functional richness, IFEve = isotopic functional evenness, IFDiv = isotopic functional divergence) calculated at the two sandy beaches (with and without green tides, GT and No GT, respectively).

Metric/Index	May			July			Sept.			Nov.		
	No GT	GT	p									
MDC	2.03	1.97	<b>0.91</b>	2.17	2.35	<b>0.64</b>	2.20	1.40	<b>0.04</b>	2.16	1.88	<b>0.64</b>
MNN	0.85	1.33	0.25	0.81	0.96	0.52	0.80	0.45	<b>0.01</b>	0.94	0.82	0.66
IFRic	1.32	0.96	<b>0.29</b>	3.03	2.90	<b>0.60</b>	4.53	3.67	<b>0.08</b>	3.40	1.57	<b>0.02</b>
IFEve	0.50	0.68	<b>0.08</b>	0.40	0.46	<b>0.49</b>	0.30	0.49	<b>0.08</b>	0.30	0.38	<b>0.44</b>
IFDiv	0.66	0.83	<b>0.11</b>	0.72	0.55	<b>0.09</b>	0.62	0.87	<b>0.05</b>	0.63	0.97	<b>&lt;0.001</b>

Significant differences ( $p \leq 0.05$ ; Wilcoxon tests) between indices at beach 'No GT' and beach 'GT' are shown in bold.



**Fig. 5.** Stable isotope bi-plots showing benthic consumers' isotope signatures weighted by biomass per square metre (filled circles), juvenile flatfishes' isotope signatures (denoted by fish symbols), and source isotope signatures (POM [plus sign], SOM [cross], and *Ulva* spp. [yellow star]) at the pristine sandy beach (blue, upper panels) and the sandy beach impacted by green tides (green, lower panels) over time; May (a, e), July (b, f), September (c, g) and November 2012 (d, h). Each benthic consumer species is denoted by a number: 1 = *Acrocrania brachiata*; 2 = *Amphiporus langiaegeminus*; 3 = *Angulus tenuis*; 4 = Aphroditidae; 5 = *Arenicola marina*; 6 = Aricidae; 7 = *Balanoglossus armoglossus*; 8 = *Bathyporeia pelagica*; 9 = *Cerebratulus roseus*; 10 = Copepoda; 11 = *Crangon crangon*; 12 = *Cumopsis* spp.; 13 = *Diogenes pugilator*; 14 = *Donax trunculus*; 15 = *Donax vittatus*; 16 = *Echinocardium cordatum*; 17 = *Ensis siliqua*; 18 = *Eocuma dollfusi*; 19 = *Eurydice pulchra*; 20 = *Euspira* spp.; 21 = *Glycera convoluta*; 22 = Gobiidae; 23 = *Idotea baltica*; 24 = *Idotea pelagica*; 25 = *Lineus acutifrons*; 26 = *Liocarcinus holstius*; 27 = *Macra stultorum*; 28 = *Magelona filiformis*; 29 = *Mysida*; 30 = Nematoda; 31 = *Nephtys assimilis*; 32 = *Nephtys hombergii*; 33 = *Nephtys cirrosa* (juveniles); 34 = *Owenia fusiformis*; 35 = *Phyllodoce mucosa*; 36 = Planaria; 37 = *Pontocrates arenarius*; 38 = *Portunus latipes*; 39 = *Scoletoma impatiens*; 40 = *Sigalion mathildae*; 41 = *Spiophanes bombyx*; 42 = *Trachinus draco*; 43 = *Urothoe poseidonis*; 44 = *Venus gallina*. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

study sites highly representative. Our study on the effects of an abundant additional food resource, in the form of opportunistic green macroalgae (*Ulva*), on whole-community trophic structure and functioning revealed a progressive simplification of the food web over time, with a narrowing of energy flows. Driving this simplification is both indirect and direct effects of green tides at several trophic levels within macrotidal SB systems, i.e. baselines (particulate and sedimentary organic matter), primary consumers, and secondary consumers. Below, we discuss them in detail.

#### 4.1. High-biomasses of *Ulva* affect food web natural baselines

The isotope signatures of food sources, both particulate and sedimentary organic matter (POM and SOM, respectively), were significantly affected by the presence of green tides, thus supporting our Hypothesis 1. Despite the inherent great variability in stable isotope signatures of primary producers and basal resources (Rolff, 2000), we found a shift at sites where *Ulva* occurred. The direction of this shift was consistent over time (Fig. 2), and, most importantly, was persistent and traceable across higher trophic levels, also considering the community-wide trophic structure (see Sections 4.2. and 4.4. below). More precisely, we have found that the presence of large amounts of *Ulva* influenced  $\delta^{13}\text{C}$  of POM, which was higher than the  $\delta^{13}\text{C}$  of POM sampled at the pristine SB. High photosynthetic rates measured for *Ulva* (Johnson et al., 1974) lead to high uptake of carbon in the form of both  $\text{CO}_2$  and  $\text{HCO}_3^-$  during the day (Van Alstyne et al., 2015). Selective assimilation of  $^{12}\text{C}$  causes remaining  $\text{CO}_2$  to become enriched in  $^{13}\text{C}$ , leading to progressive  $^{13}\text{C}$  enrichment of phytoplankton (Rolff, 2000). An increase in  $\delta^{13}\text{C}$  of DIC in the presence of *Ulva* was experimentally verified in our study, supporting this assumption. Furthermore, we found that the presence of green tides affects  $\delta^{15}\text{N}$  of SOM, which was higher where *Ulva* accumulates compared to sediments in a pristine environment. This significant shift occurs during autumn (September and November), which corresponds to a period of

senescence and decomposition of mats in temperate systems (Arroyo and Bonsdorff, in press). Algal decomposition is more rapid close to the sediment than in the water column, due to the high metabolic activity occurring close to the sediment (Salvo and Bonsdorff, 2004). Decaying macroalgae enter the detritus pool in the form of micro- or macro-detritus, thus gradually changing the composition of sediments and their isotope signature (Dubois et al., 2012). During senescence, bacterial activity stimulates organic matter recycling in sediments, which is known to cause a  $\delta^{15}\text{N}$  enrichment of SOM (as discussed in Iken et al., 2001; Schaal et al., 2008). Also during macroalgal decay, organic molecules (e.g. polysaccharides that make up around 50% of dry *Ulva* spp., Lahaye and Robic, 2007) are released or broken down, and enter the sediment, thus affecting its composition. The release of biomolecules during senescence of macroalgal mats also probably affects the isotope signature of POM, although this was not evident in our study. Indeed, particles released in the water column after *Ulva* degradation can be quickly diluted by tidal currents, mitigating isotopic effects in POM. Furthermore, the isotope composition of POM is well known to be highly variable in marine systems (Lorrain et al., 2002). Our study also revealed seasonal variation of the isotope signature of basal resources occurring at both sandy beaches. Variation over time may be explained by several known causes of isotopic fluctuations (Rolff, 2000).

#### 4.2. Species-specific diet modifications where green tides occur

Our hypothesis regarding the influence of green tides on species-specific diets was also verified, and the present study revealed direct and indirect influence of *Ulva* accumulation on macroinvertebrate trophic/isotopic niches. Three species from three different trophic levels of the low-shore SB food web, also dominant in terms of biomass within the benthic community, i.e. *D. vittatus*, *O. fusiformis*, and *A. brachiata*,

were selected to test this hypothesis. The isotope signatures obtained within this study are in line with those measured in sandy systems within the same broad geographic area (e.g. Bodin et al., 2008; Colombini et al., 2011; Rigolet et al., 2014). Across size classes, the stable isotope signature of consumers got heavier, indicating either a diet shift or a metabolic accumulation of  $\delta^{15}\text{N}$  and  $\delta^{13}\text{C}$ . Comparison between consumers found at the two beaches showed species-specific and marked responses to the presence of green tides, which contradicts findings made for similar beaches in the same ecoregion (Ouisse et al., 2011).

Also, the direction of change within the species-specific trophic niches at sites with *Ulva* ( $\delta^{13}\text{C}$  of organisms sampled at beach where green tides occurred was higher than  $\delta^{13}\text{C}$  of organisms sampled at pristine site) is consistent with the findings at the primary producer level. As the  $\delta^{15}\text{N}$  of *Ulva* isotope signature was more than 1‰ above the Donacidae signature, we suggest that this bivalve is not directly influenced by the presence of the green algae. Instead, our study confirms that *D. vittatus*, no matter its size, feeds on both SOM and POM, and that its position in the trophic web is indirectly driven by the presence of *Ulva* through the ingestion of isotopically modified organic matter. On the other hand, the present study highlights a direct way in which *Ulva* enters SB food webs. As isotope signatures of *O. fusiformis* are significantly different between the two beaches, and as it was similar to the *Ulva* isotopic composition, we hypothesize that this polychaete feeds directly on green macroalgae. This scenario is plausible since *O. fusiformis* feeds in two distinct ways, either by removing small suspended particles from the water column in a ciliary manner, or by taking up much larger particles with its labial palps (Phillips Dales, 1957), which could be a way to ingest wave-smashed *Ulva*. In addition, we found green algae fragments in the stomach content of *O. fusiformis* sampled at the impacted SB. Our study also highlights another possible way of direct integration of the green algae within low-shore sandy beach food webs through the feeding activity of *A. brachiata*. This ophiuroid takes on suspension feeding posture and likely feeds on macrodetritus, including dead animals (such as parts of *Liocarcinus* sp., pers. obs.) and algae, which are abundant in the form of *Ulva* within the impacted site. Ingestion of pieces of *Ulva* thalli and other organisms with modified isotope signature would thus explain the significant differences between *A. brachiata* isotope signatures between the two sites (impacted or not by green tides).

#### 4.3. Macrotidal sandy beach food web structure and functioning

Our study also revealed the trophic structure, and ultimately some aspects of the functioning of benthic food web of low shore macrotidal SBs (i.e. energy flow through the intertidal community). At the pristine sandy beach, the whole isotopic niche was wide and several potential energy pathways emerged from the different bivariate plots (Fig. 4, 5). Biomass-weighted isotope signatures, within the isotopic space, visualize the diversity of energy pathways, which suggests that the pristine SB consumers feed on different food sources available over time. Approaches combining isotope signature with biomass distribution within benthic communities are rare in the literature (Grall et al., 2006; Rigolet et al., 2015). Using this approach, our study revealed that most of the biomass within SB food web is concentrated in the bivalve primary consumer compartment, made up by *D. trunculus*, *D. vittatus*, and *A. tenuis*, which are known to be suspension and deposit feeders (Levinton, 1971). This denotes the importance of both particulate and sedimentary organic matter as food sources for consumers in the macrotidal SB benthic community, and challenges the findings made for other dissipative beaches, where only POM was considered as the major trophic contributor to the food web (Bergamino et al., 2011). Hydrodynamics (macro-tides, waves) occurring within the studied systems could explain these contrasted findings: wave action re-works sediment, and in turn sedimentary organic matter is re-suspended within the water/sediment interface (as discussed in Schaal et al., 2008).

#### 4.4. Structural and functional trophic shifts occur where opportunistic algae develop

We also hypothesized that the presence of large amounts of detached *Ulva* on low shore of macrotidal SBs would modify the structure and the functioning of the trophic network. The significant shift in trophic structure and differences revealed by isotopic functional indices (Fig. 4; Table 2) support this hypothesis. We found a significant separation between pristine and impacted whole-community trophic niches as green tides decayed. This shift in  $\delta$ -space may be linked to the input of *Ulva* that significantly affects isotope signature of baselines (Fig. 2; Table 1), and may also constitute a direct energy source for consumers (Section 4.2.; Fig. 3), as observed in non-tidal systems (Nordström et al., 2006). This finding is supported by the coinciding direction of changes occurring at primary producer and consumer levels where green tides occurred.

The progressive change in food web structure over time logically suggests a lag in the response of benthic consumers to the addition of another basal resource within high-energy systems, i.e. low-shore macrotidal SBs. The separation of trophic niches between the two beaches was accompanied by a narrowing of the community-wide occupancy of  $\delta$ -space where green tides occurred, suggesting a simplification of the food web where *Ulva* accumulate. The dynamic depiction of species-specific isotope signatures at SB impacted by green tides (Fig. 5) also highlights the simplification of the whole food web structure. Indeed, we saw a practically linear arrangement of food web components in November, suggesting a single trophic pathway. This contrasts with the pristine SB picture where benthic organisms consume different food sources available over time, as shown through the depiction of several trophic pathways. Interestingly, this finding contradicts the fact that addition of organic material in the form of macroalgae and plants inherently diversifies baselines within a system, and concurrently diversifies energy pathways within food webs (Hyndes and Lavery, 2005; Layman et al., 2012; Schaal et al., 2008). On the contrary, our findings support the hypothesis of simplification of macrotidal beach trophic webs where an opportunistic basal resource develops to become dominant. Also, interestingly, higher  $\delta^{13}\text{C}$  was observed at the whole community scale where green tides occurred. Such changes in the whole SB community trophic structure are explained by direct and indirect species-specific responses, as elucidated above. These findings contrast with previous studies conducted in sheltered and non-tidal systems highlighting an increase in  $\delta^{15}\text{N}$  within eutrophicated food webs (Carlier et al., 2008; McClelland et al., 1997); enrichment of heavy nitrogen throughout whole food webs has been proposed as a eutrophication indicator, providing a detectable signal in biota of sheltered systems before eutrophication leads to major structural and functional changes in benthic communities (Carlier et al., 2008). Our findings might have some implication for the development of markers of eutrophication within highly dynamic ecosystems. Overall, this study has implications for the interpretation of shifts in food webs of general interest in ecology. Indeed, while to date effects of climate change on trophic networks have mainly been investigated within microcosms (O'Connor et al., 2009; Petchey et al., 1999), investigating complex responses generated in entire food webs in natural systems is crucial. This would improve the understanding of functional shifts within ecosystems under multiple stressors in a global change context. Furthermore, our study challenges an ecological paradigm (i.e. the addition of basal resource diversifies food-web structure), which has been demonstrated in several other ecosystems, including terrestrial systems (see for example Djigal et al., 2012).

Trophic functioning was also modified over time, as illustrated by contrasting energy pathways and biomass dominance between beaches impacted or not impacted by green tides (Fig. 5). The shift in SB food web functioning was progressive and significant during autumn, as the communities differed in two components of isotopic functional diversity at that time (Table 2). In addition, biomass distribution did not

follow the same pathway depending on beaches (impacted vs. non-impacted). Although macrobenthic assemblages were similar in terms of taxon identity, biomass patterns were dominated by different groups of species depending on beaches. Quillien et al. (2015a) documented that the presence of detached macroalgae on macrotidal SB shores stimulates the recruitment of some dominant species, and represses the abundance of other species assuming key roles for the functioning of these highly dynamic ecosystems. Modification of community composition and development of fauna (abundance, biomass) alter trophic interactions in the food web by changing prey availability and affecting predation rates (Norkko and Bonsdorff, 1996; Raffaelli et al., 1998), which could explain the structural and functional shifts we found. Top-down control could explain the pattern found in our study as it has been shown that foraging efficiency of juvenile flatfish is affected by the presence of drifting macroalgae (Aarnio and Mattila, 2000; Nordström and Booth, 2007). Juveniles of flatfishes were positioned in the middle of macrotidal SB  $\delta$ -space: stomach content analyses revealed that they mainly feed on deposit-feeding crustaceans (cumaceans and gammarids), and on suspension/deposit-feeding bivalves (Fabvre, pers. comm.). This finding also suggests a certain trophic plasticity of some of the macrotidal SB consumers when organic material in the form of macroalgae is added to the system, which is in line with conclusions made by Nordström et al. (2006) highlighting the large potential of macroinvertebrates to process/feed on opportunistic filamentous annual macroalgal material.

## 5. Conclusion

The addition of an opportunistic basal resource in the form of macroalgae within a naturally unvegetated and dynamic aquatic ecosystem induces an overall simplification of community-wide food web structure and functioning. This finding contrasts with other systems (including terrestrial), where the addition of new basal resource diversifies food webs, and thus challenges an essential ecological paradigm. This conclusion is supported by:

1. Differences in other basal resources (*i.e.* particulate and sedimentary organic matter) isotope signature over time and between beaches,
2. Species-specific responses highlighting direct (*i.e.* assimilation of additional basal resource [*Ulva* spp.]) and indirect (*i.e.* assimilation of modified particulate and sedimentary organic matter, respectively) effects of additional opportunistic basal resource on the sandy beach consumer community diet,
3. Community-wide shift in  $\delta^{13}\text{C}$  over time, progressively splitting up into two distinct isotopic niches (*i.e.* no green tide vs. green tides), with a linear arrangement of trophic web components indicating a single carbon pathway where *Ulva* mats strand on shore.

Shifts observed in trophic structure and functioning within the studied system may affect higher trophic levels, *i.e.* top predators (shorebirds, geese, fish) of ecological and commercial significance, for which SB are crucial foraging areas (McLachlan and Brown, 2006; Schlacher et al., 2008). The observed and projected impacts of additional opportunistic basal resources on high-energy system trophic webs structure and functioning would thus make ecosystems at risk in a global change context (*i.e.*, potentially less robust to probable future changes induced by interactive effects of multiple stressors, both natural and anthropogenic).

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