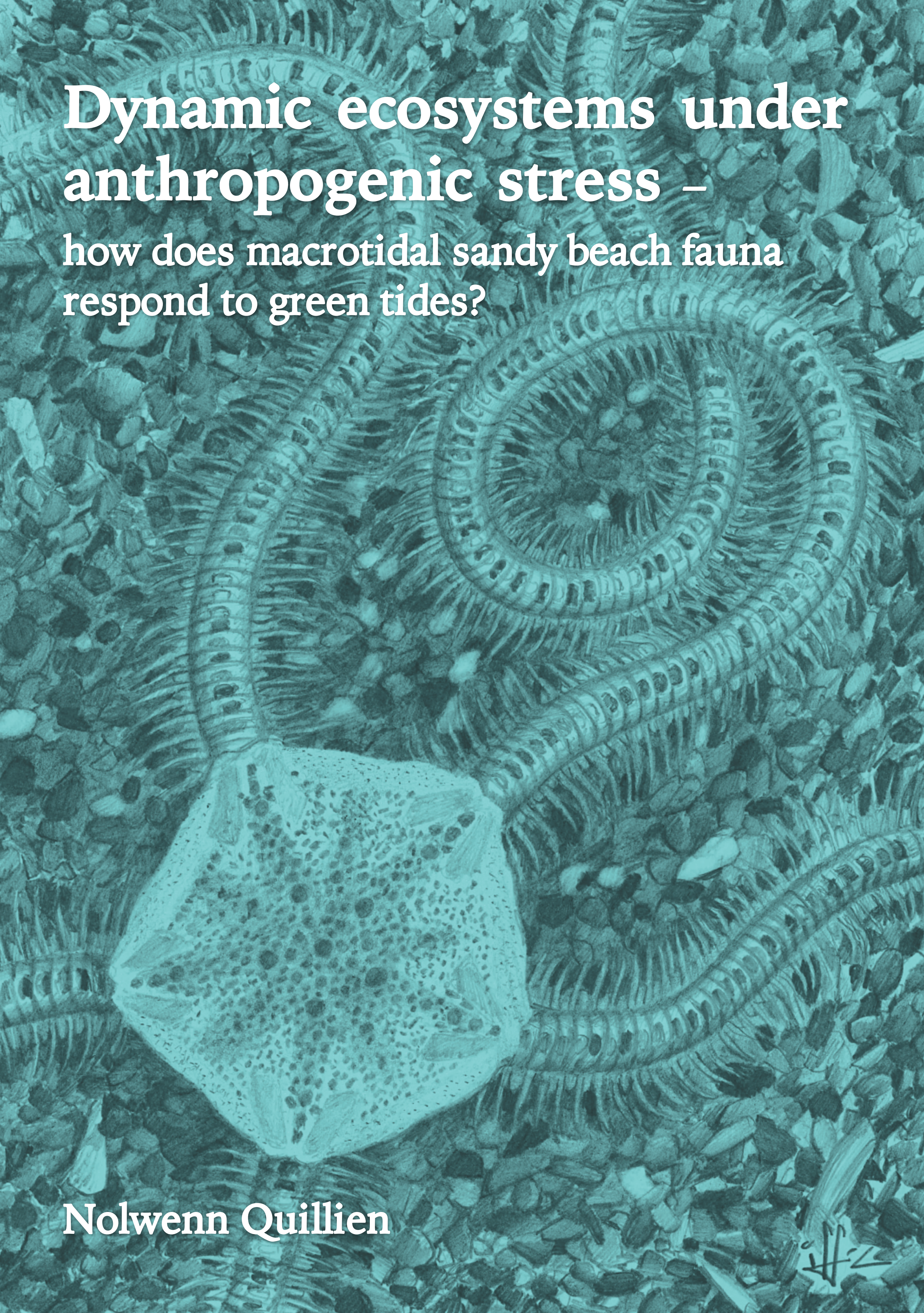

Dynamic ecosystems under anthropogenic stress –

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 av världens isfria kustlinje. Det ökade trycket av mänsklig påverkan hotar dessa system, och t.ex. massutveckling av opportunistiska makroalger (huvudsakligen Chlorophyta, s.k. *makroalgblomning*), till följd av kustvattnens övergödning, väcker oro. Effekterna av makroalgblomningar har tidigare utvärderats i system som är mer skyddade, eller saknar tidvatten. Om mer dynamiska ekosystems, 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 makroalgblomningar 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 makroalgblomning, över hundratals kilometer och över en sjuårsperiod; jag lyfter fram den starkare responsen hos zoobentos i exponerade sandstrandsområden 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 evertebratsamhällen i tidvattenszonen, i förhållande till evertebratsamhällen som lever under tidvattennivån, såväl som plattfisksamhällen.

Med fokus på småskaliga variationer i de mest utsatta samhällena (nämligen, bentiska evertebrater i tidvattenszonen), påvisar denna avhandling en minskning av beta-diversitet längs en övergödningsgradient i form av makroalgblomning, liksom den ökade betydelsen av biologiska variabler för den ekologiska variabiliteten hos bentiska makroevertebrat sandstrandssamhällen. För att illustrera den underliggande processen som förklarar de observerade strukturella förändringarna där det skett makroalgblomning, 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 δ^{13}C, inte i δ^{15}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: Makroalgblomning – *Ulva* spp. – Övergödning – Dynamiska ekosystem – Sandstränder – Tidvatten – Zoobentos – Plattfisk – Samhällsstruktur – Födovävar – Trofisk funktion – Stabila isotoper δ^{13}C och δ^{15}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 $\delta^{13}C$, not in $\delta^{15}N$) 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 $\delta^{13}C$ and $\delta^{15}N$ - 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 (médiolittoral 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 médiolittoral 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 ß 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 a 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 δ^{13}C et δ^{15}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:

	Paper I	Paper II	Paper III	Paper IV
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

* plus summer students and colleagues/volunteers.

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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 resettle 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 < 4m) and macrotidal (TA ≥ 4m) 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).

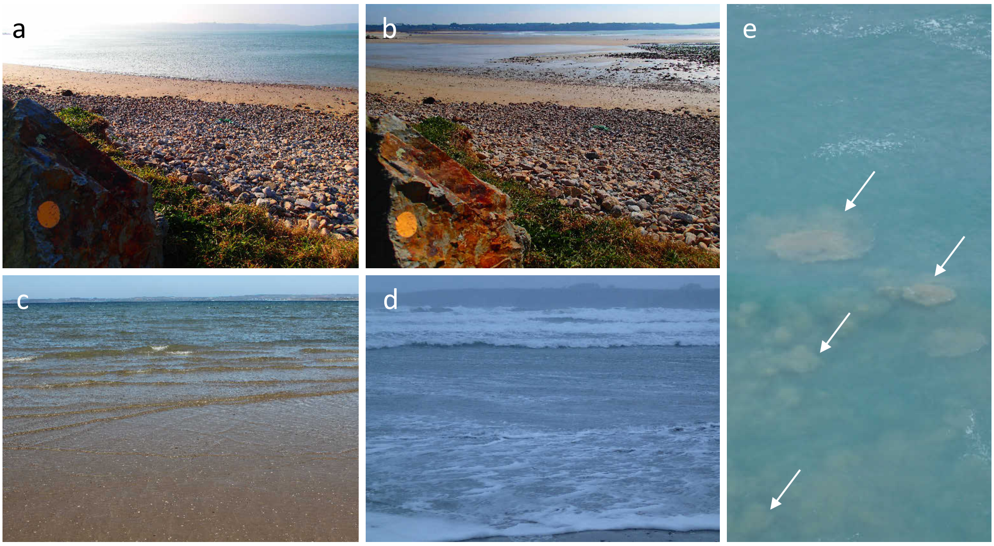


FIG. 1. Photographs of the Anse of Dinan (Brittany, France) showing variation in energy within a macrotidal sandy beach; a) high tide, b) low tide, c) low wave action, d) high wave energy, e) resuspension of particles after a wave has broken, the arrows denote some sedimentary whirls. Pictures: N.Q. *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 physicochemical 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

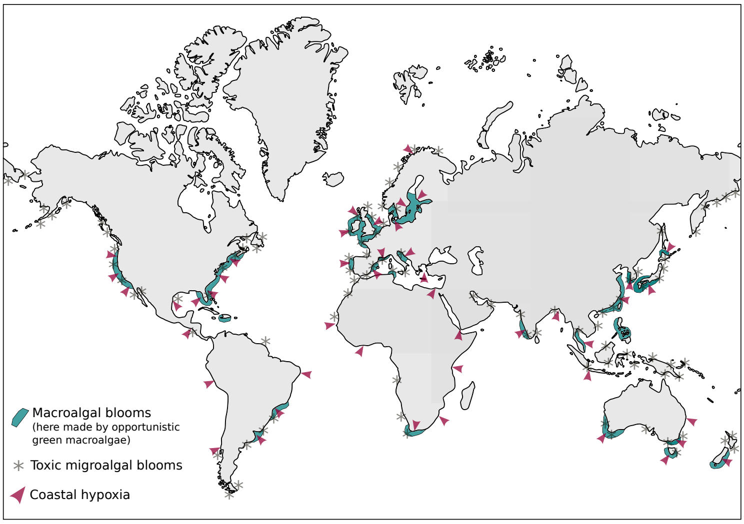


FIG. 2. Worldwide blooms formed by green macroalgae (*i.e.* green tides), toxic microalgal blooms, and coastal hypoxia distribution during the past three decades; information shown here is the combination of several maps presented in the following publications: in Anderson et al. (2015), Ye et al. (2011), 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}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 community 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).

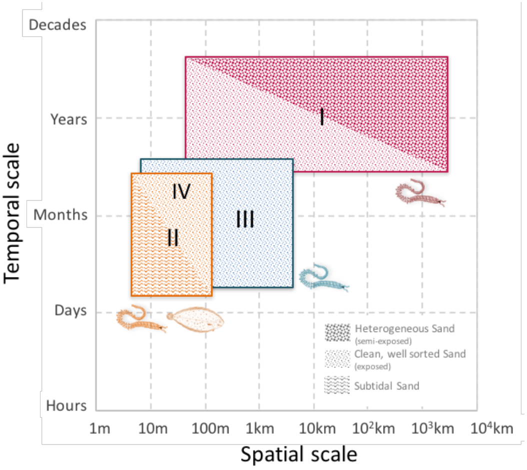


FIG. 4. Spatial and temporal scales covered by the specific papers presented in this thesis (**I-IV**). The colours of boxes refer to those used in the conceptual diagram illustrated in FIG. 5, except for paper **II**. The illustrations denote the communities studied in each paper: macroinfauna and flatfish (**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 poisons 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).

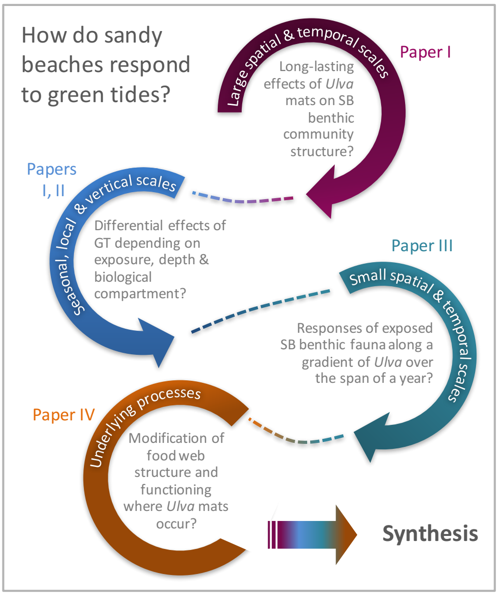


FIG. 5. Conceptual diagram showing the main questions addressed in the four papers (I-IV), as well as the logical links between each study, which build up upon each other at several scales. *Diagramme conceptuel montrant les principales questions traitées dans les articles I-IV, et illustrant la logique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

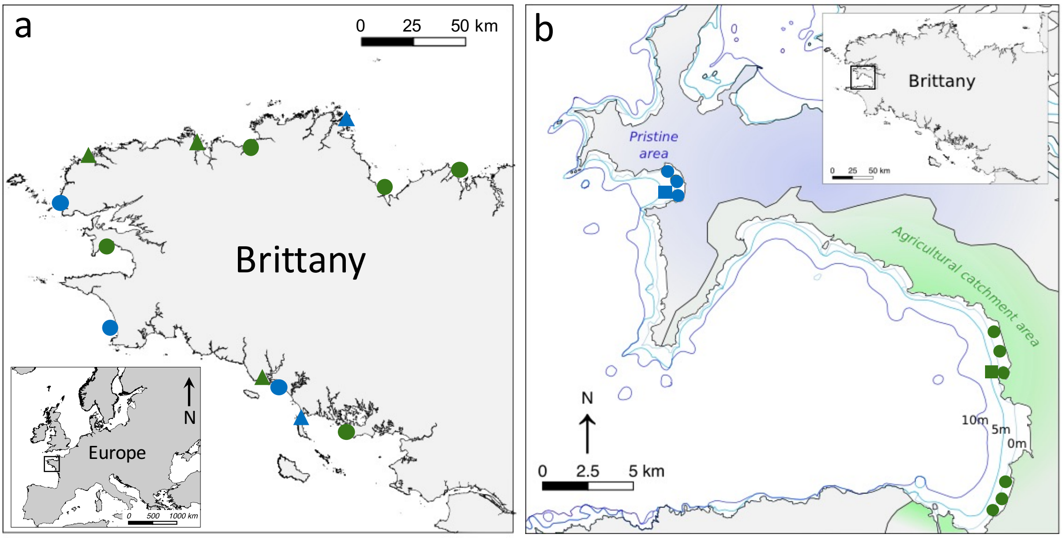


FIG. 6. Location in Brittany (NW France) of the 24 exposed (circles/squares) and semi-exposed (triangles) sandy sites sampled in this thesis (**papers I-IV**); at low-intertidal (circles) and at shallow subtidal (squares) sites impacted (green) or not (blue) by green tides. (a) Location in Brittany of 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 symbolises 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) (Ménesguen & 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 encompasses 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^2, 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^2), and five replicate samples were randomly taken at each site within an area of a few m^2.

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^2. 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^2). Beam trawls were carried out during the day, at neap tide, along 500m transects (sampled surface: 1000m^2)

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}C:^{12}C and ^{15}N:^{14}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 µm) 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 species. 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 $\delta^{13}C$ analysis, the other subsample not acidified and used for $\delta^{15}N$ 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 (400µg), or the fragments (1mg), was then packed into 5 × 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 63µm to 10,000µm). 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) 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^2). 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) 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 [^{H}] / light [^{L}] isotopes) are expressed related to an internationally accepted standard, in the delta unit notation (δ) in per mil (‰) following the formula:

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

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 $\delta^{13}C$ and $\delta^{15}N$ are the Vienna Pee Dee Belemnite and 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‰ both for carbon and nitrogen.

Different primary producers (*e.g.* C3 *vs.* C4 plants, pelagic *vs.* benthic production) vary significantly in their $\delta^{13}C$ values, and consumers of respective primary producers mirror values of the resources as $\delta^{13}C$ is largely conserved through trophic transfer (Post 2002, Bearhop et al. 2004). Consequently, $\delta^{13}C$ enables identification of dietary carbon sources. Complementary to this, $\delta^{15}N$ 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 ($\delta^{13}C$ - $\delta^{15}N$; 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, eveness, 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^{2}, 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
H$_0$	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 *Ulva* spp. mats	*Ulva* 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
Response variables	**Univ.:** S, A, H', D; **Multiv.:** species abundance	**Univ.:** relative species abundance **Multiv.:** species abundance	**Univ.:** S, A, H', D **Multiv.:** species abundance, species biomass	**Univ.:** δ^{13}C, δ^{15}N **Multiv.:** IS (δ^{13}C * δ^{15}N), IS * Biomass
Explanatory variables	**Coverage by *Ulva*, 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	***Ulva* biomass**, organic matter, median, sorting, salinity, SWT, temporal MEMs	***Ulva* biomass**, Chl-a, organic matter, median, sorting, wave height, slope, salinity, SWT, dissolved oxygen, location along beach, temporal MEMs	***Ulva* biomass**
Spatial scale (extent)	**Regional** (thousands of kilometres)	**Local - Vertical** (hundreds of meters, from low-intertidal to shallow subtidal)	**Local** (meters to kilometres)	**Local** (meters)
Temporal scale (duration, frequency)	**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)
Factors	**Two factors:** "Type" & "GT"		**Two factors:** "Beach" & "Sampling occasion"	**Two factors:** "Season" & "Green tides"
Data analyses	**Univ.:** Two-way ANOVA, t-test, Wilcoxon-Mann-Whitney **Multiv.:** Two-way PERMANOVA, dbMEMs in varpart, RDA	**Univ.:** Khi^2-test **Multiv.:** dbMEMs in varpart, RDA	**Univ.:** Kruskal-Wallis test, Friedman test, Two-way ANOVA, stepwise regression models **Multiv.:** MANOVA, dbMEMs in varpart, RDA	**Univ.:** Two-way ANOVA, Wilcoxon tests **Multiv.:** 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 δ-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≤0,05 apparaissent en gras ; * p≤0,05, *** p≤0,001.*

	df	MS	F	p	
Log(A)					
Type	1	167.51	178.94	**$<2.10^{-16}$**	***
GT	1	4.53	4.84	**$2.87.10^{-2}$**	*
Type * GT	1	0.8	0.86	$3.55.10^{-1}$	
Res.	269	0.94			
S					
Type	1	10.62	348.56	**$<2.10^{-16}$**	***
GT	1	698	22.89	**$2.83.10^{-16}$**	***
Type * GT	1	108	3.56	6.10^{-2}	
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 subsurface 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).

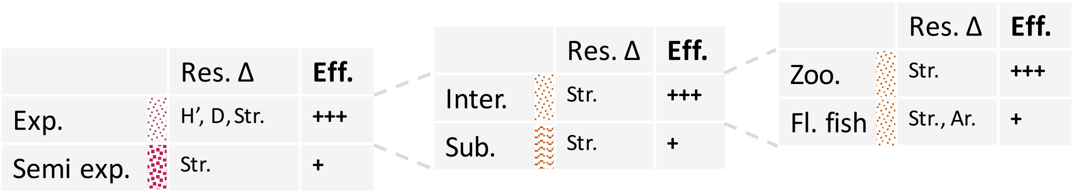
More importantly, given the time lag between the *Ulva* blooms, and the sampling of fauna (in early Spring, *ca.* 6 months after blooms), I revealed the long-lasting and conservative nature of these responses (**paper I**). The study represents the first *in situ* non-manipulative study of the effects 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. Δ	Eff.
Exp.	H', D, Str.	+++
Semi exp.	Str.	+

	Res. Δ	Eff.
Inter.	Str.	+++
Sub.	Str.	+

	Res. Δ	Eff.
Zoo.	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. Δ = 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 presence des marées vertes (légère : + ; marquée : +++). Exp. = plages exposées composes de sables propres et bien triés ; Semi exp. = plages semi-exposées composes de sables envasés hétérogènes ; Inter. = intertidal ; Sub. = subtidal ; Eff. = effet global ; Res. Δ = 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 (χ^2=51.6, N=317, df=3, p=3.6.10^{-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

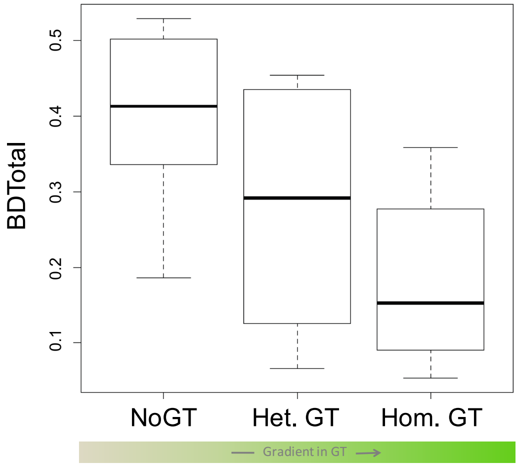


FIG. 8. Total β-diversity (BDTotal) across space and time at three sandy beaches; one never has green tides (NoGT), another is heterogeneously covered by GT (Het. GT), and the third one is homogeneously covered by *Ulva* (Hom. GT). Box plots show the median (line in box), the first and the third quartiles (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 arnoglosus*; 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: *Portumnus latipes*; 39: *Scoletoma impatiens*; 40: *Sigalion mathildae*; 41: *Spiophanes bombyx*; 42: *Trachinus draco*; 43: *Urothoe poseidonis*; 44: *Venus gallina*.

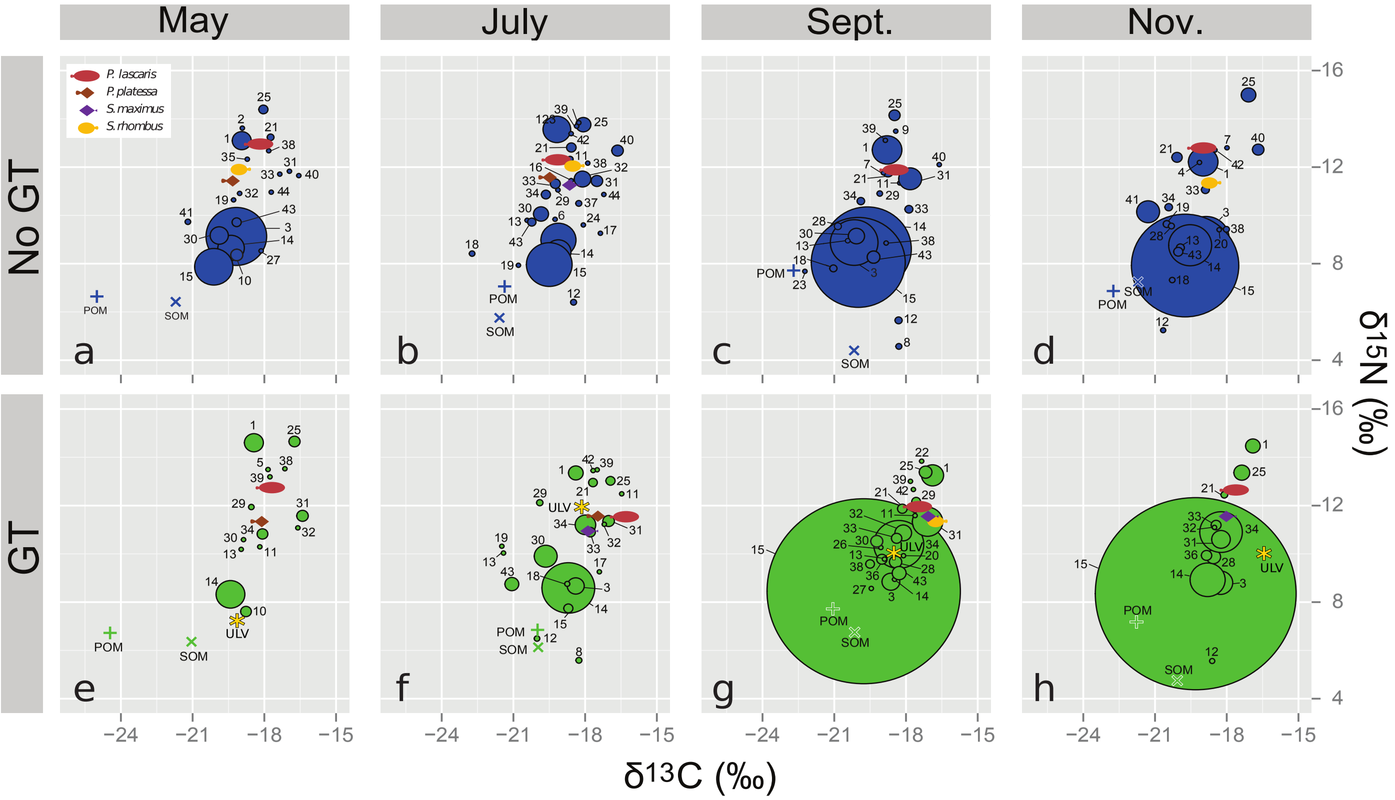


FIG. 9. Stable isotope bi-plots showing benthic consumers' (denoted by the numbers) isotope signatures weighted by biomass (ash-free dry weight per square meter) (filled circles), juvenile flatfishes' isotope signatures (denoted by fish symbols), and source isotope signatures (POM [plus sign], SOM [cross], 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/m²) (cercles), celle des juvéniles de poisons plats (représentés par des poisons symbolises) et celle des sources (POM : +, SOM : ×; 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 were 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 *Acrocnida brachiata*, the bivalves *Angulus tenuis*, *Donax trunculus* and *Donax vittatus*, the amphipod *Urothoe poseidonis*, the polychaete *Glycera convoluta*, as well as the nermetean *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}C- and ^{15}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}C carbon through high photosynthetic rates of *Ulva* (Johnson et al. 1974, Van Alstyne et al. 2015) causing remaining CO_2 to become enriched in ^{13}C, and leading to progressive ^{13}C enrichment of phytoplankton (Rolff 2000). An increase in $\delta^{13}C$ of dissolved inorganic carbon in the presence of *Ulva* was experimentally verified in our study, supporting this assumption (**paper IV**). The increase in $\delta^{15}N$ 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 $\delta^{13}C$ 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 $\delta^{13}C$ 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 $\delta^{15}N$ 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.

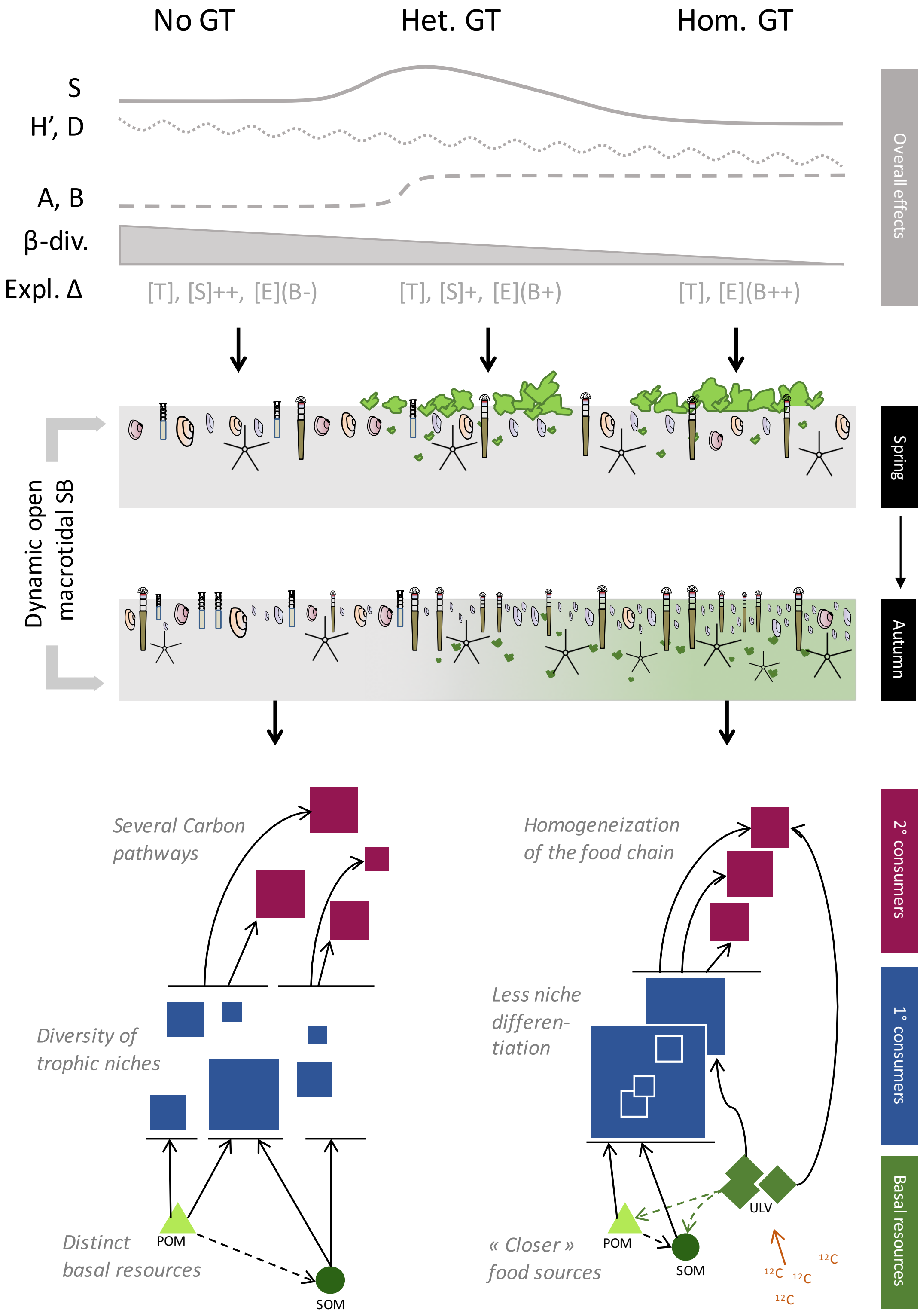
Despite great variability in space and time (at scales from meters to thousands of kilometres, and from months to years), this thesis shows the significant influence of eutrophication-induced accumulation of green opportunistic algae (*Ulva* spp.) on macrotidal sandy beach benthic community structure (**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 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 ^{12}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'eutrophisation 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.*


No GT
Het. GT
Hom. GT
S
H', D
A, B
β-div.
Expl. Δ
[T], [S]++, [E](B-)
[T], [S]+, [E](B+)
[T], [E](B++)
Overall effects
Dynamic open macrotidal SB
Spring
Autumn
Several Carbon pathways
Diversity of trophic niches
Distinct basal resources
POM
SOM
Homogeneization of the food chain
Less niche differen-tiation
« Closer » food sources
ULV
^{12}C
^{12}C
^{12}C
^{12}C
2° consumers
1° consumers
Basal resources

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 ($\text{AMBI}_{\text{No GT}} = 1.54$), and the two impacted sites being undisturbed ($\text{AMBI}_{\text{Het. GT}} = 0.52$, $\text{AMBI}_{\text{Hom. GT}} = 0.44$). 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

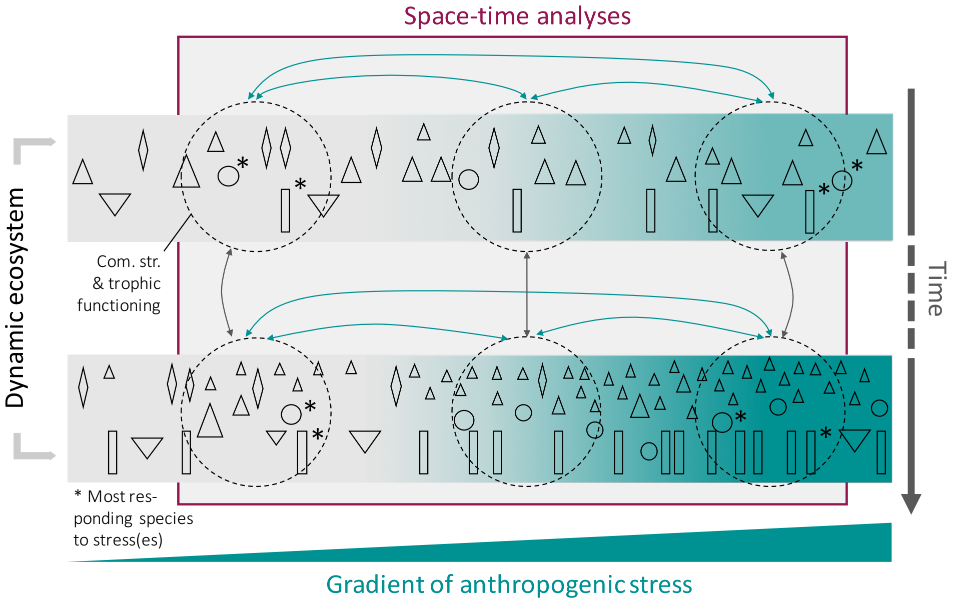


FIG. 11. Illustration of a framework coupling a sampling inferring community and trophic structure (dashed line circles) along gradient of stress (turquoise stretched triangle) and over time (grey bold arrow) with space-time analyses (bordeaux frame) to depict dynamic ecosystem drifts under anthropogenic 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 needed 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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Dynamic ecosystems under anthropogenic stress –

how does sandy beach macrofauna respond to green tides?

Mass-development of opportunistic macroalgae, resulting from the eutrophication of coastal waters, is increasing in frequency and intensity worldwide. The modifications induced by accumulations of these algae have long been evaluated within sheltered and non-tidal ecosystems. Little is known, however, about the responses to such stress of more dynamic ecosystems such as open sandy beaches, although they cover most of the world's ice-free coastline. This thesis aims at assessing the effects of high biomasses of opportunistic algae on the structure and the functioning of normally unvegetated and highly variable environments. Analysing temporal dynamics (from decadal to seasonal) of macrotidal sandy beach benthic communities (from zoobenthos to flatfish) and food webs (from species-specific trophic relationships to community-wide carbon transfer) at different spatial scales (horizontal: from regional to local, and vertical: from intertidal to subtidal), this thesis assesses multi-scale responses of highly dynamic system to accumulations of opportunistic green macroalgae (*Ulva* spp). Eventually, this work presents a framework coupling field investigations with analytical approaches to describe shifts in highly variable ecosystems under human-induced stress.

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