

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

N. QUILLIEN^{1,2,3}, M. C. NORDSTRÖM², H. LE BRIS⁴, E. BONSDORFF² AND J. GRALL³

¹Laboratoire des Sciences de l'Environnement Marin, Institut Universitaire Européen de la Mer, Université de Bretagne Occidentale, Plouzané, France, ²Abo Akademi University, Environmental and Marine Biology, Turku, Finland, ³Observatoire Marin, Institut Universitaire Européen de la Mer, Plouzané, France, ⁴ESE, Ecology and Ecosystem Health, Agrocampus Ouest, INRA, Rennes, France

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

Keywords: benthic infauna, flatfish, inshore, nearshore, sandy sediments, *Ulva*, eutrophication, space-time analysis

Submitted 21 February 2016; accepted 21 December 2016; first published online 25 January 2017

INTRODUCTION

Coastal areas are dominated by marine sediments, which are more or less well sorted depending on wave action and the influence of currents. From pelites to pebbles, but generally sand, sediments accumulate along the coast to form beaches that extend from terrestrial systems (dunes) to depths where the wave action on the seafloor ceases (Short & Jackson, 2013). These systems harbour a highly diverse biota and are very productive (Costanza *et al.*, 1997; Barbier *et al.*, 2011). In particular, sandy beaches provide ecological functions that are not achieved by any other ecosystem on earth (McLachlan & Brown, 2006). For instance, both intertidal and subtidal sands provide essential foraging and nesting habitats for many adapted invertebrate and vertebrate organisms (benthic macrofauna, meiofauna, fishes, turtles and shorebirds) (Schlacher *et al.*, 2008; Defeo *et al.*, 2009). In addition, sandy systems play a key role in maintaining coastal fisheries and providing reproduction and nursery areas for commercially valuable species (Gibson, 1994; McLachlan &

Brown, 2006), such as bivalve molluscs of the genus *Donax* and, in their juvenile form, several flatfish species (e.g. *Scophthalmus* spp. (Linnaeus, 1758), *Pleuronectes platessa* (Linnaeus, 1758)).

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

Corresponding author:
N. Quillien
Email: nolwenn.quillien@gmail.com

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

Such macroalgal accumulations greatly affect sheltered and non- or microtidal sediment invertebrate as well as flatfish communities (Baden *et al.*, 1990; Norkko & Bonsdorff, 1996; Pihl *et al.*, 2005). For example, on the microtidal Swedish Skagerrak coast, the recruitment of the young of *P. platessa* may be reduced by 40% due to the presence of opportunistic macroalgal mats (Pihl *et al.*, 2005). Conversely, within the same study area, Baden *et al.* (1990), have not found negative effects of eutrophication on flatfish recruitment, but on macrofauna, with widespread mortality of bivalves. More subtle changes have been highlighted within open, and macrotidal sandy beaches (Quillien *et al.*, 2015a; Le Luherne *et al.*, 2016), although the effects of macroalgal blooms within such dynamic systems have not been fully understood yet. In particular, the influence of accumulation of opportunistic macroalgae on function of nursery area for flatfish harbouring

by open sandy beaches is in its early stages (Le Luherne *et al.*, 2016), and the impact of algal blooms within dynamic subtidal systems has not been comprehended yet, although algal blooms are found from the inshore to the subtidal.

In the present study, we investigated possible shifts in intertidal and subtidal benthic communities induced by the presence of *Ulva* mats, using open sandy systems located in Brittany, France, as a study case. The study region is locally heavily affected by green tides (Ménésguen & Piriou, 1995). There, *Ulva* blooms occur both at intertidal and subtidal sites (Merceron & Morand, 2004). Therefore, the aim of the present study was more particularly to assess the effects of drifting and stranding opportunistic macroalgae on sandy bottom benthic communities, namely macrozoobenthos (infauna) and juvenile flatfish (epifauna) in the span of a year. We set out to assess functional facets (i.e. diversity, community structure and nursery area) of sandy bottoms over time (four seasons over 1 year), and from intertidal habitats (low shore at spring tide) to directly connected subtidal areas (5 m depth), combining traditional multivariate methods and novel approaches. Following this approach, we explored simultaneous variations in macrofaunal and flatfish communities by testing the following hypotheses: environmental factors, and especially macroalgal mats, differentially affect benthic communities depending on (i) the biological compartment (macrozoobenthos vs flatfishes), and (ii) the habitat (intertidal vs subtidal).

MATERIALS AND METHODS

Study system

On the highly indented western coast of Brittany (France), fine sediments accumulate to form large subtidal sandy beds and kilometre-long sandy beaches. Within this region, our study was conducted in the Bay of Douarnenez, and the Crozon peninsula (48.2°N 4.4°W, and 48.2°N 4.6°W, respectively), which are both known as important nurseries for flatfish (Quiniou, 1986). Four sites were selected for the study (Figure 1): two intertidal sandy beaches, one which does not harbour green tides (Inter-NoGT), and one that is annually covered by *Ulva* (Inter-GT); as well as two subtidal sandy beds adjacent to the beaches: one which never harbours macroalgal mats (Sub-NoGT), and another which is annually impacted by green tides (Sub-GT). The two intertidal sites were selected based on a previous study (Quillien *et al.*, 2015a), as the endpoints of a gradient of eutrophication (from no GT to high biomass of *Ulva*). The two subtidal sites were chosen as extensions of the intertidal sites, but at 5-metre depth, following the vertical slope/gradient. The impacted and control sites are located in the same water body and share the same characteristics (Quillien *et al.*, 2015a), which enable the comparison of the sites impacted or not by green tides. In addition, the studied sites were selected among a greater range of localities where the effects of green tides on intertidal macrobenthic communities have been previously highlighted (Quillien *et al.*, 2015a, b).

The intertidal sites show large areas (up to 500 m from shore during spring tides) that are uncovered at low tide. A mean breaking wave height of 1.4 ± 0.5 m and a mean tidal regime of 6.5 m (Quillien *et al.*, 2015a) characterize these ultra-dissipative sandy beaches (Masselink & Short, 1993).

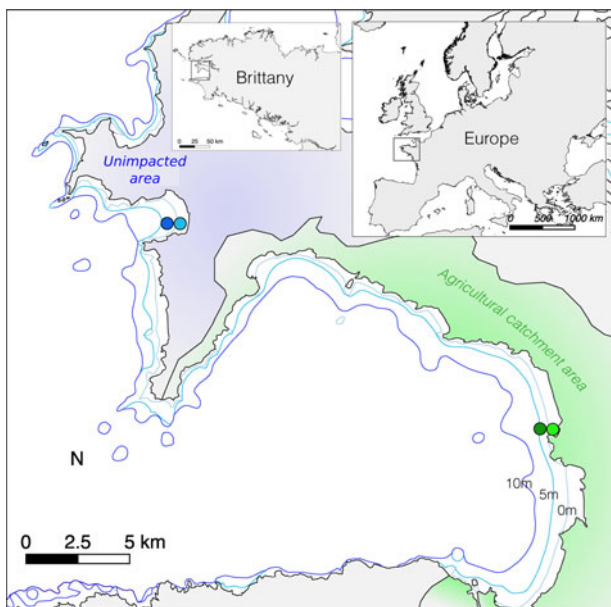


Figure 1. Location (Brittany, north-western Europe) of the four study sites (circles) at the low-intertidal (light colours) and at the shallow subtidal (dark colours) of the two studied sandy sediment areas [colour online]. Blue lines along coastline represent isobaths (0, 5 and 10 m). The sites impacted by green tides are denoted by green circles and are located downstream of an agricultural catchment area (area filled with shades of green). The blue circles denote the sites that are never affected by accumulation of *Ulva* (un-impacted area denoted by the area filled with shades of blue).

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

Sampling

To assess macrofaunal and flatfish variability following a vertical scale, sampling was conducted at low intertidal (spring low tide) and at 5 m depth at the two study areas (Inter-NoGT = 48°14.682'N 4°32.908'W, Inter-GT = 48°10.22'N 4°17.775'W, Sub-NoGT = 48°14.641'N 4°33.615'W,

Sub-GT = 48°10.216'N 4°18.074'W). To evaluate temporal variability of benthic communities, the four sites were sampled from February to December 2013. Temporal variability was assessed at five and four dates in the intertidal and the subtidal, respectively, and more precisely in early spring (February/March), spring (May), summer (June/July), autumn (September) and early winter (November/December) (Figure 3).

Macrofauna (>1 mm) was collected using a tube corer (surface = 0.03 m²) at the intertidal sites, and using a Smith-grab (surface = 0.1 m²) in the subtidal. Samples from both the intertidal and subtidal were sieved through mesh bags (1 mm mesh size) to separate the fauna from the finer part of sediment. At each sampling site, three (core) and five (grab) replicate samples were taken randomly within an area of a few m². Faunal samples were preserved in 4% buffered formalin for later sorting in the lab where macrofaunal invertebrates were identified to the lowest possible taxonomic level with the aid of a binocular magnifier, and counted.

At intertidal sites, flatfishes were sampled using a beach trawl (5 m wide, 0.3 m high, with an 8 mm stretched mesh net in the cod-end), which is a net towed at 50 cm water depth by two people who maintain its lateral spread (Quiniou, 1986). Beach trawls were carried out during the day at rising tides (i.e. at flooding tide), at least once along 80–260 m long latitudinal transects (sampled surface: 400–1300 m²). The length of the trawl was variable to ensure the haul's catchability and avoiding clogging of the trawl. At subtidal sites, a beam trawl (2 m wide, 0.5 m high, with a 4 mm

A Eutrophied state in winter



B Eutrophied state in summer

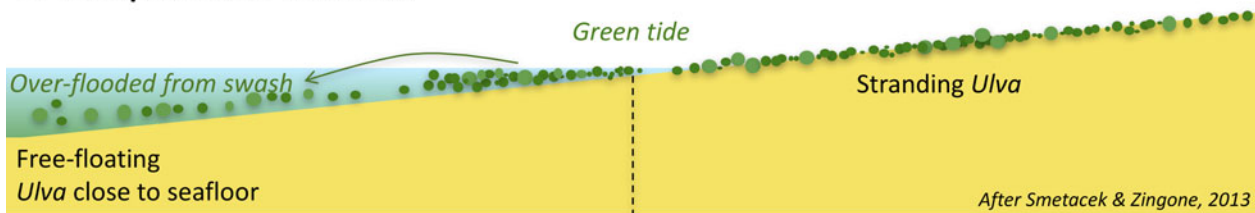


Figure 2. Schematic illustration of the distribution of green tides occurring at two contrasted seasons: (A) eutrophied state in winter, and (B) eutrophied state in summer. Arrows denote algal material in motion.

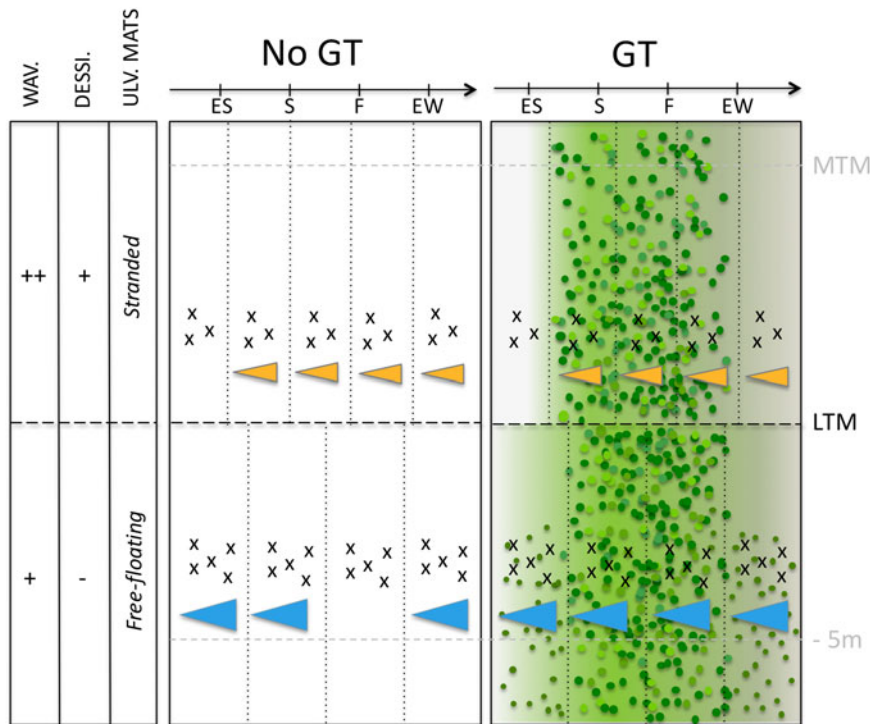


Figure 3. Sampling design over time (from early spring (ES), to early winter = (EW); S, summer; F, autumn), showing the four sites (Intertidal – No GT, Intertidal – GT, Subtidal – No GT, Subtidal – GT), core and grab samples (black crosses), beach and beam trawling (triangles) and three environmental variables (WAV., waves; DESSI., desiccation; GT, green tide). ULV. MATS, *Ulva* mats; MTM, middle tidal mark; LTM, low tidal mark; 5 m = 5 m depth.

stretched mesh net in the cod-end) was used from a vessel to sample the benthic ichthyofauna. Beam trawls were carried out during the day, at neap tide, along 500 m transects (sampled surface: 1000 m²), at least twice at each site within the subtidal zone. The flatfish were sorted, identified and measured (total length) on board and released immediately after the investigations. For each species, individuals were classified into age groups based on their size and on peer-reviewed literature and research-reports on flatfish growth (including Deniel, 1973; Gibson & Ezzi, 1980; Nottage & Perkins, 1983).

For both macrofauna and flatfish, species nomenclature follows the ‘World Register of Marine Species’ (www.marine-species.org/). The abundance of zoobenthos was converted to units per m² for comparison across zones. For each haul, flatfish apparent abundance standardized per surface unit (1000 m²) was assessed considering the number of flatfish caught and the surface covered (haul length × trawl opening). In addition to the quantitative dataset, global information on biological traits was linked to each dominant species. Information about the feeding ecology, mobility, size, and reproduction for the dominant species was thus gathered from peer-reviewed literature and publicly available databases such as MarLIN/BIOTIC and EOL/polytraits (*sensu* Törnroos & Bonsdorff, 2012).

At each site where fauna was sampled, a single sediment core (in the intertidal) or grab (in the subtidal) was extracted to obtain grain size distribution and total organic matter content over time. Grain sizes were assessed by dry sieving, using a series of 16 sieves (from 63 to 10 000 µm). Median grain size was equal to the second quartile (Q₅₀) of the sediment grain size value. Sorting was calculated based on the first and the third quartiles of the sediment grain size ratio ($\sqrt{Q_{25}/Q_{75}}$, where Q₂₅ and Q₇₅ denote first and third quartile, respectively). Total organic matter content was assessed by weighted loss of sediments (no removal of carbonates) after

ignition at 450°C for 5 h. For the intertidal sites, *Ulva* biomass data were estimated by CEVA (www.ceva.fr/fre) through monthly aerial surveys (for estimation of surface covered by algae) and field sampling (for conversion to biomass). At subtidal sites, *Ulva* biomass was assessed on board by weighing algae collected in beam trawls (each one covering an area of 1000 m²). Intertidal seawater temperature (hereafter ‘SWT’) and salinity were measured on each sampling occasion using a YSI-OMS v2 probe. Subtidal SWT and salinity were extracted from datasets provided by the PREVIMER system (www.previmer.org) and data used for analyses were obtained by averaging the values for both variables of five days before each sampling occasion.

Community data analysis

Multivariate analyses were performed to evaluate the differences between intertidal and subtidal communities, as well as their respective responses to the presence of green tides. For all multivariate analyses, faunal data (both zoobenthos and flatfish data) were first transformed using the Hellinger transformation, which is recommended for analysis of species abundance data since it does not give high weights to rare species (Legendre & Gallagher, 2001). Redundancy analyses (RDA) were performed to visualize patterns in the distribution of assemblages of macrofauna and flatfish in space and time within each habitat; with or without green tides (i.e. Inter-NoGT, Inter-GT, Sub-NoGT, Sub-GT), and to determine which environmental variables constrain the variation of benthic communities in this setting.

Temporal (seasonal sampling from February to December 2013) variation of each of the age-grouped flatfish species represented at intertidal and subtidal zones, with or without GT (Inter-NoGT, Inter-GT, Sub-NoGT, Sub-GT) was

assessed to extricate diversity trends. In order to compare assemblages between control and impacted sites, chi-squared tests were performed based on pooled (all dates together for each habitat; data from September were not used for subtidal to ensure a balanced design) flatfish data. In order to disentangle the effects of *Ulva* mats, time and habitat (inter- or subtidal) on the assemblages of macrofauna, two recently developed methods were combined: distance-based Moran's eigenvector maps (dbMEM, Dray *et al.*, 2006; Legendre & Gauthier, 2014) were used in variation partitioning (Borcard & Legendre, 1994). First, dbMEM eigenfunctions were generated based on the number of sampling occasions (4–5 seasons). The generated dbMEM eigenfunctions were used as temporal variables (here called MEMs). The location along the vertical gradient (i.e. from inter- to subtidal) was used as a spatial variable and was coded by Helmert contrasts (Legendre & Anderson, 1999). The variation of the multivariate responses was then first partitioned with respect to three groups of explanatory variables: *Ulva* (variables related to the occurrence and biomass of GT), space (the factors encoded by Helmert contrasts) and time (the MEMs). Variation of macrofaunal multivariate responses was also partitioned separately for each habitat, and thus with respect to two groups of explanatory variables (*Ulva* and time) at intertidal and subtidal. Each fraction of variation, i.e. the explanatory power of each set of the explanatory variables, was tested using multiple linear regressions (Legendre & Legendre, 2012).

All analyses were conducted within the R environment (R Development Core Team, 2013) and relied on the vegan (Oksanen *et al.*, 2011), and PCNM (Legendre *et al.*, 2012) packages.

RESULTS

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

Setting the scene: environmental and faunal characterization

On average, environmental characteristics were similar between sites within the same habitat (Table 1). However,

the total organic matter content tended to be higher at un-impacted sites (1.4–1.7%; at intertidal and subtidal sites, respectively) than at impacted sites (1.1–1.4%, idem), as observed also in a previous study (Quillien *et al.*, 2015a). The environment, both at intertidal and subtidal sites, is fully marine (salinity range: 33.6–35.6 psu). Intertidal sites displayed higher mean seawater temperatures (+1°C), sediment sorting (+0.2 μm) and median grain size (+40–50 μm) compared with subtidal sites. Also, the variability of environmental values was higher for intertidal compared with subtidal. This pattern was even more pronounced for sediment variables (sorting and median grain size), suggesting a lower influence of hydrodynamics in the subtidal domain.

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

Over the 4 sites sampled through the study, i.e. among the 70 macrofaunal- and the 40 flatfish samples, 119 macrofauna and six flatfish species were found between February and December 2013 (Table 2). Thirty infaunal species were found at both intertidal and subtidal sites, and 18 were found only at intertidal sites, while 71 occurred only within the subtidal area. Thirty-one and 72 infauna species were sampled at the un-impacted inter- and sub-tidal sites, respectively. Where green tides occurred, 39 and 79 species were found in the intertidal and subtidal, respectively. Also, flatfish species numbers were equally distributed among intertidal and subtidal sites, impacted or not by green tides, with 2 species only found at intertidal sites (*Pleuronectes platessa* (Linnaeus, 1758) which vernacular name is plaice, and *Scophthalmus maximus* (Linnaeus, 1758) the turbot), two species only found at subtidal sites (*Buglossidium luteum* (Risso, 1810) also named solenette, and *Arnoglossus laterna* (Walbaum, 1792) the scald fish), as well as two species shared between the two habitats (*Pegusa lascaris* (Risso,

Table 1. Environmental characterization of the four sites (Intertidal – No GT, Intertidal – GT, Subtidal – No GT, Subtidal – GT) sampled seasonally from February to December 2013. SWT, Seawater temperature; Sorting = sorting index calculated based on first and third quartile ratio.

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

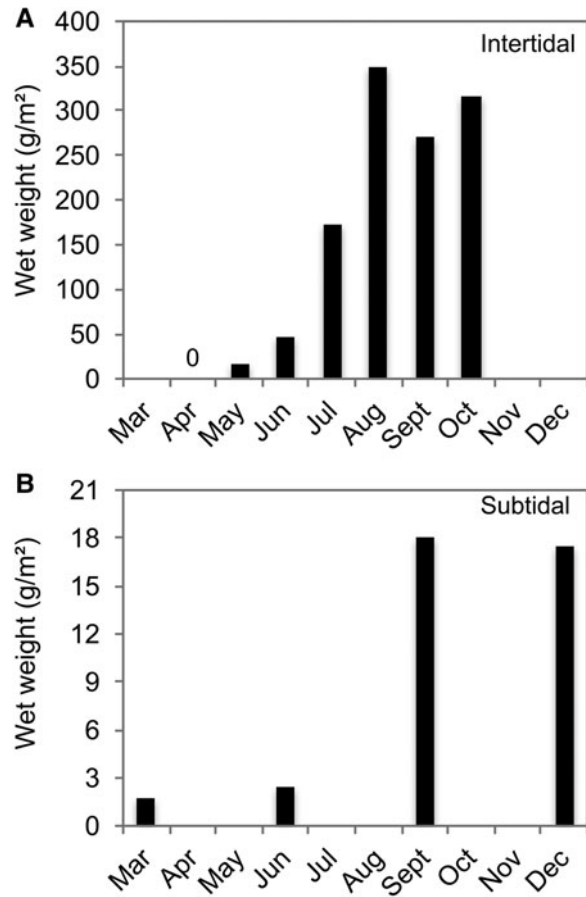


Figure 4. Monthly biomass of stranded *Ulva* through the year 2013 at intertidal (A; source: CEVA) and subtidal (B; source: this study) impacted sites. Note that the scales are not the same on the two plots.

1810) which common name is sand sole, and *Scophthalmus rhombus* (Linnaeus, 1758) the brill).

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

Spatial-temporal shifts/patterns in infaunal communities

The relative abundances of infaunal species shifted in the presence of green tides, such as the polychaete *Spiophanes bombyx* (Claparède, 1870), the bivalve *D. trunculus*, and the amphipod *Urothoe poseidonis* (Reibish, 1905), whose relative abundance was lower at the impacted intertidal site. On the other hand,

the relative abundances of the ophiuroid *Acrocrida cf. spatulispina* (Stöhr & Muths, 2010) and the polychaete *Magelona mirabilis* (Johnston, 1865) were higher where green tides occurred. At the subtidal site where green tides occurred, the relative abundances of the species *Diogenes pugilator* (Roux, 1829) (carnivorous Anomuran), *Acrocrida brachiata* (Montagu, 1804) (omnivorous Ophiuroid), *Atylus swammerdami* (Milne Edwards, 1830) (omnivorous Amphipod), and *M. mirabilis* (detritivorous Polychaete) were high. Three of the most dominant species (*D. vittatus*, *S. mathildae*, and *N. hombergii*) occurred in low relative abundances at the impacted subtidal site (Table 2).

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

The proportion of the variation of infauna at the four sites is largely explained by *Ulva* variables (13.6%), the location of site (intertidal vs subtidal, with 13.2%), and the temporal variables (6.6%) (Table 3). Taking into account 'pure' explanatory variables, the occurrence and biomass of *Ulva* explain again the largest part of the variation of infauna (12.3%), while spatial and temporal variables explain 10.8 and 9.2% of the total variation of infauna, respectively. Considering intertidal sites, pure *Ulva* and temporal variables explain 30 and 11% of the variation of infauna, respectively (Figure 6A). The explanatory power of *Ulva* was relatively low at subtidal sites (11%) (Figure 6B), with temporal variables explaining a larger part of the total variation of infauna (21%). These results corroborate the hypothesis that *Ulva* plays a major role in driving variation of infauna between impacted and control intertidal sites, while its explanatory power was less pronounced considering subtidal sites harbouring or not green tides.

Variation in space and time of flatfish communities

The correlation triplot of redundancy analysis based on age-grouped flatfish community data sampled at the four study sites (Inter-NoGT, Inter-GT, Sub-NoGT, Sub-GT) (Figure 7) revealed two distinguished groups of data containing subtidal (on the right) and intertidal samples (on the left) (Figure 7A). The separation of the dot clouds was associated with the environmental variables 'sorting' and 'median'

Table 2. Per cent dominance in terms of abundance for the major species (threshold = 90% for zoobenthos, 100% for flatfish) living at intertidal and subtidal sandy bottoms harbouring or not harbouring green tides (GT or no-GT). Numbers in bold show contributions that are higher than 1%. Numbers in italics refer to values that are not relative abundance values. Taxonomic group and selected biological traits (feeding habit, feeding strategy, mobility, maximal size and reproduction/development) are given for each species. Traits data collected from MarLIN, EOL, polytraits and BIOTIC databases, and personal observations. For fish species, age groups have been based on individual sizes and peer literature and research reports on flatfish growth.

Species	Taxonomic group	Abundance dominance (%)				Functional characteristics					
		Intertidal		Subtidal		Feeding habit	Feeding strategy	Mobility	Maximal size (mm)	Development mechanism	
		No GT	GT	No GT	GT						
<i>Glycera convoluta</i>	Annelida polychaeta	0.2	1.5	1.9	1.2	Ca	SPF	B, (S)	50	Ovi	
<i>Magelona mirabilis</i>		–	3.8	2.4	5.9	D	SuF, SPF	B	80	Ovi	
<i>Nephtys assimilis</i>		0.2	0.1	0.2	0.4	Ca, Sc	SPF	B, C, (S)	115	Ovi	
<i>Nephtys cirrosa</i>		1.2	2.0	1.6	0.7	Ca, Sc	SPF	B, C, (S)	100	Ovi	
<i>Nephtys hombergii</i>		0.2	1.5	6.4	2.2	Ca, Sc	SPF	B, C, (S)	200	Ovi	
<i>Orbinia latreilli</i>		–	0.3	0.8	–	D	SSF	B	400	Ovi	
<i>Owenia fusiformis</i>		1.5	3.1	1.7	1.1	D	SuF, SF, SPF	T	100	Ovi	
<i>Paradoneis armata</i>		–	–	3.7	6.6	D	SSF	B, C, (S)	30	Ovi	
<i>Piromis eruca</i>		–	–	–	1.4	D	SSF	B	60	Ovi	
<i>Scolecopsis cf. mesnili</i>		0.3	0.4	2.5	1.8	D, (Ca), (Hμ)	SSF, (SPF)	B	20	Ovi	
<i>Scoloplos armiger</i>		–	–	0.3	1.7	D	SSF	B, C	120	Ovi	
<i>Sigalion mathildae</i>		0.3	0.3	8.0	4.2	Ca	SPF	B, C, (S)	150	Ovi	
<i>Spiophanes bombyx</i>		9.4	0.1	1.5	0.8	D	SuF, SPF	T	60	Ovi	
<i>Ampelisca sarsi</i>		Arthropoda malacostraca	–	–	2.1	–	D	SuF, SSF	T	8	Ovo
<i>Atylus falcatus</i>			–	–	–	1.1	O	SPF	C, S	7	Ovo
<i>Atylus swamerdami</i>			–	0.3	0.2	3.2	O	SPF	C, S	10	Ovo
<i>Bathyporeia guillamsoniana</i>			0.3	1.4	1.3	0.8	D	SSF, SuF	B, S	10	Ovo
<i>Bathyporeia pelagica</i>	2.1		2.3	–	–	D, Hμ	SPF	B, (nS)	8	Ovo	
<i>Bathyporeia sarsi</i>	–		4.2	2.6	4.7	D	SSF, SuF	B	8	Ovo	
<i>Cumopsis fagei</i>	4.5		3.8	2.4	0.4	D	SSF, SPF	B, (nS)	6	Ovo	
<i>Cumopsis longipes</i>	1.7		2.0	–	–	D	SSF, SPF	B, (nS)	6	Ovo	
<i>Diogenes pugilator</i>	–		–	0.5	13.5	Ca	SPF	C, (B)	20	Ovo	
<i>Hippomedon denticulatus</i>	–		–	0.7	1.5	D, H	SSF	B	14	Ovo	
<i>Idotea pelagica</i>	0.3		0.1	0.1	0.6	O, (H)	S, C	SuF	20	Ovo	
<i>Iphinoe trispinosa</i>	0.2		0.3	4.8	6.1	D	SSF, SuF	B, S	10	Ovo	
<i>Mysida</i>	–		–	2.6	1.7	D, Ca	SuF, SSF	S, C, B	20	Ovo	
<i>Perrierella audouiniana</i>	0.2		–	0.1	0.9	Ca	SPF	S, C	4	Ovo	
<i>Pontocrates arenarius</i>	1.7		0.4	–	0.1	D	SSF	B, C	7	Ovo	
<i>Portunus latipes</i>	0.3		0.4	–	–	O, Sc	SSF, SuF	B, C	27	Ovo	
<i>Urothoe poseidonis</i>	–		18.7	0.5	0.8	Hμ	SSF	B, (nS)	6	Ovo	
<i>Urothoe pulchella</i>	–	–	1.5	–	Hμ	SSF	B, (nS)	5.0	Ovo		
<i>Acrocynida brachiata</i>	Echinodermata echinoidea	–	–	0.9	2.3	O, (Ca)	SPF	B	12*	Ovi	
<i>Acrocynida cf. spatulispina</i>		0.2	9.8	–	–	O, (Ca)	SPF	B	12*	Ovi	
<i>Echinocardium cordatum</i>		–	–	0.5	0.7	D	SuF, SSF	B	100	Ovi	
<i>Donax trunculus</i>	Mollusca bivalvia	6.3	1.8	–	–	D, Hμ	SF, SPF, (SuF)	D, C, B	45	Ovi	
<i>Donax vittatus</i>		65.0	36.2	27.9	10.5	D, Hμ	SF, SPF, (SuF)	D, C, B	38	Ovi	

Continued

Table 2. Continued

Species	Taxonomic group	Abundance dominance (%)				Functional characteristics				
		Intertidal		Subtidal		Feeding habit	Feeding strategy	Mobility	Maximal size (mm)	Development mechanism
		No GT	GT	No GT	GT					
<i>Mactra stultorum</i>		–	–	1.9	4.8	D, Hμ	SuF	B	5	Ovi
<i>Pharus legumen</i>		–	–	0.7	1.7	D, Hμ	SF	B	130	Ovi
<i>Tellina fabula</i>		–	–	2.5	1.5	D, Hμ	SuF	B	20	Ovi
<i>Tellina tenuis</i>		0.7	2.2	–	–	D, Hμ	SuF, SPF	B	20	Ovi
<i>Euspira nitida</i>	Mollusca gastropoda	–	0.1	0.6	0.3	Ca	SSF	B, C	16	Ovi
<i>Nassarius reticulatus</i>		–	–	0.7	1.0	Sc	SPF	C	30	Ovi
<i>Philine aperta</i>		–	–	0.9	0.5	Ca, Sc	SPF	C	100	Ovi
<i>Nemerta</i> sp.2	Nemertea	0.2	–	1.5	0.2	Ca	SPF	T	?	Ovi, F
<i>Lineus acutifrons</i>	Nemertea anopla	1.3	0.7	3.4	1.8	Ca	SPF	B	?	Ovi, F
<i>Tubulanus polymorphus</i>	Nemertea palaeonemertea	0.2	0.1	0.7	1.0	Ca	SPF	B, (T)	750	Ovi, F
<i>Platyhelminth</i>	Platyhelminthes	–	0.4	0.3	0.2	Ca	SPF	B, (S)	?	Ovo
Number of total taxa		31	39	72	79					
Total abundance (m2) (SD)		236.3 (152.0)	145.0 (63.7)	24.5 (10.3)	29.4 (8.5)					
Sampling method		Core	Core	Grab	Grab					
<i>Arnoglossus laterna</i> (3+)	Chordata actinopteri	–	–	20.0	6.6	Ca	SPF	S	130	Ovi
<i>Buglossidium luteum</i> (0)		–	–	6.0	14.2	Ca	SPF	S	50	Ovi
<i>Buglossidium luteum</i> (1)		–	–	2.0	17.9	Ca	SPF	S	60	Ovi
<i>Buglossidium luteum</i> (2)		–	–	11.0	9.4	Ca	SPF	S	60	Ovi
<i>Buglossidium luteum</i> (3+)		–	–	27.0	36.8	Ca	SPF	S	130	Ovi
<i>Pegusa lascaris</i> (0)		24.5	31.2	13.0	8.5	Ca	SPF	S	60	Ovi
<i>Pegusa lascaris</i> (0+)		16.3	17.3	6.0	0.0	Ca	SPF	S	110	Ovi
<i>Pegusa lascaris</i> (1)		2.5	4.4	8.0	0.0	Ca	SPF	S	160	Ovi
<i>Pegusa lascaris</i> (2)		0.0	0.5	5.0	3.8	Ca	SPF	S	220	Ovi
<i>Pegusa lascaris</i> (3+)		–	–	2.0	1.9	Ca	SPF	S	320	Ovi
<i>Pleuronectes platessa</i> (0)		6.6	26.0	–	–	Ca, Sc	SPF	S	90	Ovi
<i>Scophthalmus maximus</i> (0)		39.3	9.5	–	–	Ca	SPF	S	70	Ovi
<i>Scophthalmus maximus</i> (1)		2.3	0.9	–	–	Ca	SPF	S	140	Ovi
<i>Scophthalmus rhombus</i> (0)		7.2	8.4	–	–	Ca	SPF	S	60	Ovi
<i>Scophthalmus rhombus</i> (0+)		1.4	1.9	–	–	Ca	SPF	S	80	Ovi
<i>Scophthalmus rhombus</i> (1)		–	–	–	0.9	Ca	SPF	S	150	Ovi
Number of total taxa		4	4	3	4					
Mean apparent abundance (103 m2) (SD)		22.4 (17.5)	22.1 (10.2)	7.3 (2.5)	8.8 (6.3)					
Sampling method		Beach	Beach	Beam	Beam					

Feeding habit: Ca, Carnivore; D, Detritivore; H, Herbivore; Hμ, Micro-Herbivore; O, Omnivore; Sc, Scavenger; Sy, Symbiosis.

Feeding strategy: SF, Suspension feeder; SPF, Selective particle feeder; SSF, Sub-surface feeder; SuF, Surface feeder; Sy, Symbiosis.

Mobility: B, Burrower; C, Crawler; D, Drifter; nS, night Swimmer; S, Swimmer; T, Tube dweller.

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

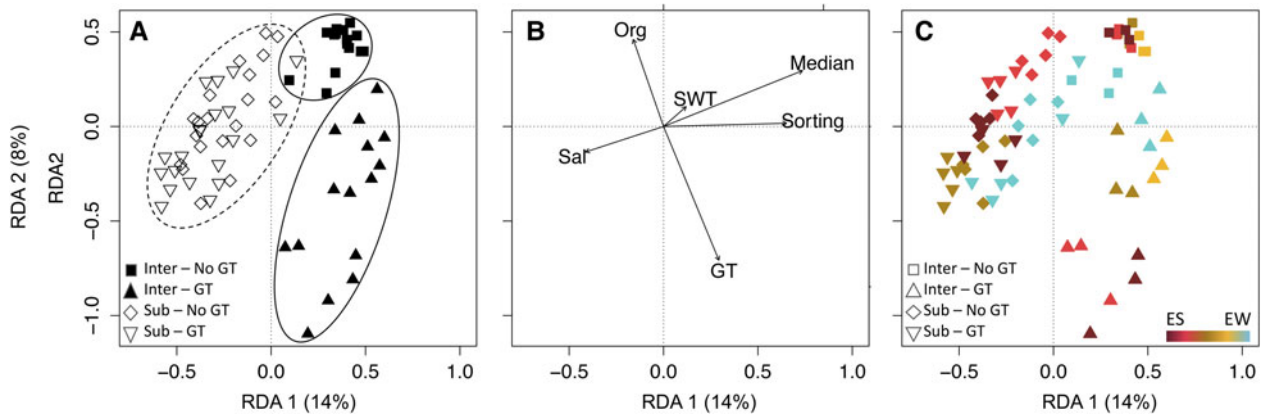


Figure 5. RDA correlation triplots (scaling 2) of macrofaunal community data (abundance) and explanatory variables of the four sites together: Inter – NoGT (squares), Inter – GT (triangles), Sub – NoGT (diamonds), Sub – Gt (reversed triangles); highlighting differences between habitats (A), environmental drivers (B) and seasonal patterns (C). GT, *Ulva* biomass; Sal, Salinity; Org, organic matter content, SWT, Seawater temperature.

(Figure 7B). No distinction depending on the presence of green tides was shown, as dots within each habitat-specific dot-cloud were close to each other, and showed similar temporal paths (Figure 7C).

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

early winter at impacted site (Inter-GT), while this pattern was less pronounced at un-impacted intertidal site. At the subtidal impacted site (Sub-GT), *B. luteum* largely dominated the flatfish community to the detriment of the sand sole (especially for young classes) and the scald fish. Also, at both intertidal and subtidal sites, the relative abundance of young of the year sand soles and solenettes was greater at *Ulva*-impacted sites.

DISCUSSION

Benthic communities inhabiting sandy sediments have been studied either in the intertidal (e.g. Degraer *et al.*, 1999; Defeo & McLachlan, 2005; Barboza & Defeo, 2015) or in the subtidal (Morin *et al.*, 1985; Rakocinski *et al.*, 1993) zones, but seldom assessed considering the inshore and the nearshore conjointly (Knott *et al.*, 1983), even though these two habitats are closely linked. Likewise, *in situ* investigation of variation within both infaunal and flatfish communities simultaneously is not common (with the exception of studying specific fish feeding habits; see for example Aarnio & Mattila, 2000; Kostecki *et al.*, 2012). In addition, the effects of green macroalgal mats on dynamic ecosystems are not yet fully understood (but see Quillien *et al.*, 2015a, b; Le Luherne *et al.*, 2016), and have not been investigated considering both infauna and flatfish along a gradient from inshore to nearshore shallow habitats. By simultaneously considering seasonal variation of infauna and flatfish assemblages over the span of a year, both at intertidal and subtidal sites impacted or not impacted by green tides, our integrated study highlighted a distinctness between low-shore and nearshore communities, and revealed differential responses of the benthic compartments and of the habitats to the accumulation of *Ulva*. Interestingly, intertidal infauna respond more markedly to the presence of algal mats, compared with subtidal benthic invertebrate assemblages, while flatfish communities showed minor/secondary species-specific responses to the occurrence of GT.

Two habitats that differ in community structure . . .

The investigation of sandy sediment zoobenthic and flatfish community variation at intertidal (low shore at spring tide)

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

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

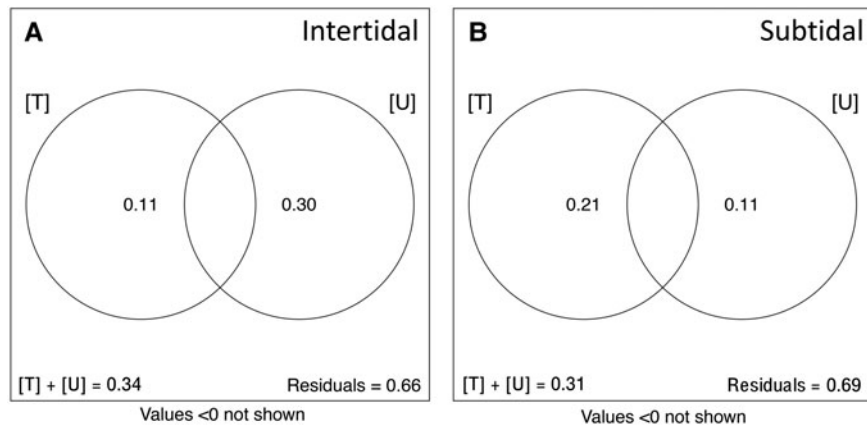


Figure 6. Venn diagrams illustrating the result of variance partitioning of the macrofauna time series at intertidal (A) and subtidal (B) sites with respect to the presence of *Ulva* mats (GT/No GT), and temporal (distance-based Moran's eigenvector maps [dbMEMs]) explanatory variables. Variation explained is expressed as a percentage (%) based on adjusted R^2 . T, temporal variables; U, environmental variables; Residuals: unexplained variation.

and shallow subtidal (nearshore at 5 m depth) sites revealed a clear separation between the two habitats in terms of community structure (as shown in Figures 5A & 6A, and Table 2). The infaunal assemblage consisted of about 30 species in the intertidal, and more than twice that, 72 species, in subtidal un-impacted sands. The increase in species richness of sandy sediment infauna with depth may be linked to the gradient from relatively harsh to benign conditions when going from the low intertidal to the subtidal zone, as suggested by Rakocinski *et al.* (1993). The grain size measured at our study sites decreased from the intertidal to the subtidal, supporting a shift in hydrodynamic conditions, and ultimately in benthic species assemblages, between the two habitats (McLachlan, 1996). In addition to exposure to wave action, also heat and desiccation stresses are exerted on intertidal habitats. Some species, which are not able to withstand these stresses for long periods (McLachlan & Brown, 2006), are more likely to occur in subtidal sands. In our study, 50 species were exclusive to nearshore, subtidal sands, notably the molluscs *Macra stultorum* (Linnaeus, 1758), *Tellina fabula* (Gmelin, 1791) and *Lunatia alderi* (Forbes, 1838), as well as the amphipod *Hippomedon denticulatus* (Bate, 1857),

polychaetes of the genus *Phyllodoce* (Browne, 1789) and the echinoderms *A. brachiata* and *Echinocardium cordatum* (Pennant, 1777). Fewer species are able to endure the harsh conditions occurring in intertidal systems (i.e. instability of sandy substratum, desiccation on rocky shores, and heavy wave action) (see for example Knott *et al.*, 1983; Scrosati *et al.*, 2011). We found 12 species that only occurred within intertidal un-impacted sands, such as the two bivalve molluscs *D. trunculus* and *Tellina tenuis* (da Costa, 1778), the echinoderm *A. cf. spatulispina* and the cumacean *Cumopsis longipes*. These species are adapted to life in dynamic ecosystems, i.e. sandy beaches, being both rapid and strong enough in order to cope with wave and swash (McLachlan & Brown, 2006). For example, *D. trunculus* has a large and powerful foot that makes it able to quickly re-settle in the sediment to regain its position after being swept by waves (De la Huz *et al.*, 2002; McLachlan & Brown, 2006). The observed shift in infaunal community with depth is concordant with faunal zonation in macrozoobenthos within soft sediments (Glémarec, 1973) and sandy sediments in particular (Dahl, 1952; Knott *et al.*, 1983), and is in accordance with the findings of Guillou (1980) made within the same habitats and study area.

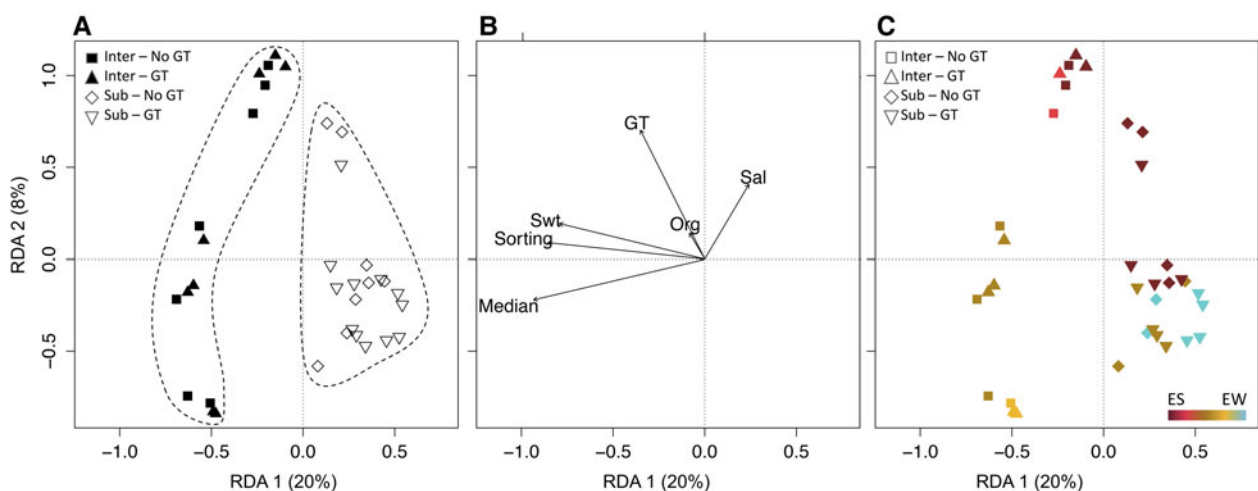


Figure 7. RDA correlation triplots (scaling 2) of age-grouped flatfish community data (apparent abundance) and explanatory variables of the four sites together: Inter - NoGT (squares), Inter - GT (triangles), Sub - NoGT (diamonds), Sub - GT (reversed triangles); highlighting differences between habitats (A), environmental drivers (B) and seasonal patterns (C). GT, *Ulva* biomass; Sal, Salinity; Org, organic matter content; SWT, seawater temperature.

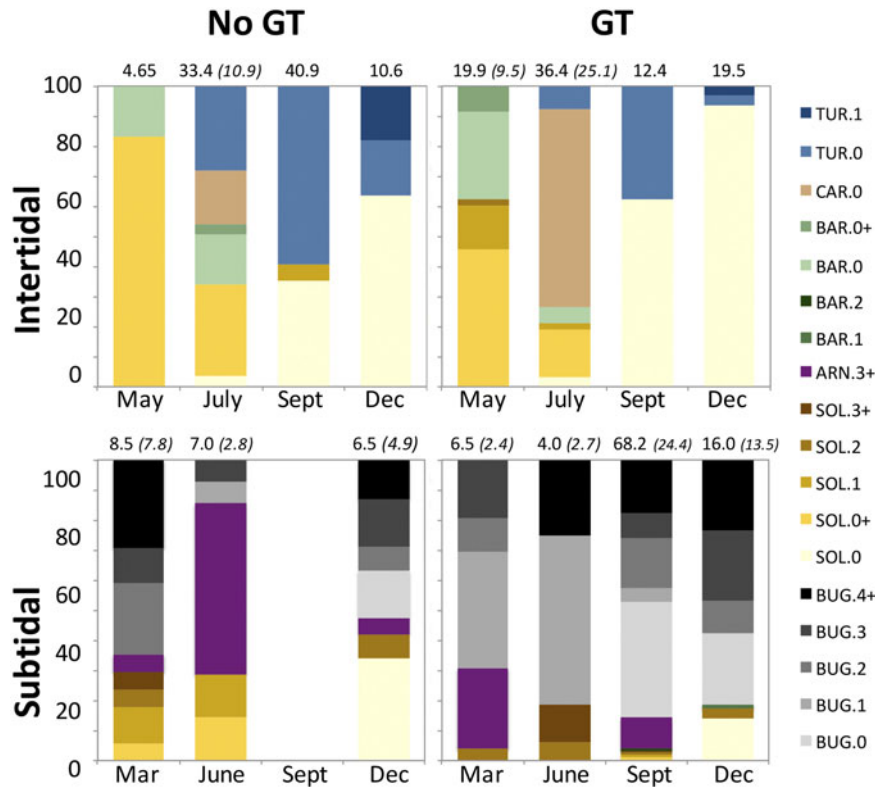


Figure 8. Relative abundance of flatfish depending on their age-group at sandy bottoms within the intertidal (top panels) and the subtidal (low panels), harbouring green tides (right panels) or not (left panels). Numbers on top of bars show mean apparent abundance, with standard deviation in italics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

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

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

role as nursery area for flatfish at sandy beaches (McLachlan & Brown, 2006).

... but that are functionally connected

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

The relationships between inter- and subtidal benthic communities mainly depend on migrations in relation to species-specific life cycles (reproduction, feeding), behaviours (predator avoidance) or interactions (competition) (see for review: Gillanders *et al.*, 2003). The links between the two zones may be exemplified by both fish and invertebrate seasonal migrations, which are common within the studied systems (Leber, 1982b; Dorel *et al.*, 1991). Continuing with the *Donax vittatus* example, young-of-the-year individuals of this bivalve species occur both in the intertidal and in the subtidal, but adults mainly occur within the subtidal (Guillou, 1980). Also, the polychaete *Sigalion mathildae* occurs in its adult form within intertidal sands, while only juveniles were found at the subtidal habitat. Regarding flatfish, *Pegusa lascaris* recruits occurred within the intertidal sandy beach, while older age-class individuals of this species were

distributed along an increasing depth gradient depending on their age. This pattern is common in Soleidae and other flatfish species such as *Pleuronectes platessa* (Lockwood, 1974; Dorel *et al.*, 1991). On an annual scale, seasonal migrations between intertidal and subtidal sands occur; for instance the young solenettes living at intertidal sites in summer, migrate to greater depths in winter, but come back to the intertidal area the next spring (Figure 8; Quiniou, 1986). Both inshore and nearshore sandy bottoms are used by some identical species depending on the time of the year, which strengthens the links between the two habitats.

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

Differential influence of GT depending on elevation and biological compartment

Based on the study of the temporal shifts in macrofaunal and ichthyofaunal communities sampled at our two representative sites (Quillien *et al.*, 2015a), our analyses demonstrated that the influence of *Ulva* accumulation was significant on benthic infaunal communities (Figures 5 & 6). Indeed, not accounting for time, *Ulva*-related variables explained 30% of the total variation in macrobenthic infauna (Figure 6A). These results complement a previous study conducted within the same system (open macrotidal sandy beaches), which highlights shifts in intertidal benthic invertebrate communities along a gradient of eutrophication by green macroalgae (Quillien *et al.*, 2015a).

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

Our study also suggests a greater influence of the presence of green tides on the intertidal invertebrate community compared with subtidal benthic assemblages. Intertidal sandy beach benthic species withstand harsher conditions than subtidal zoobenthic assemblages, and the addition of high biomasses of green opportunistic macroalgae (*Ulva* spp.) may act as the ultimate stressor. Also, this finding may be linked to the intrinsic structure of algal mats, which differs between the intertidal and the subtidal (Figure 2). At five metres depth, subtidal *Ulva* stocks are often arranged in strips a few decimetres wide and float above the seafloor (Merceron & Morand, 2004). While at low tide in intertidal sandy areas, algal mats strand on shore, with *Ulva* thalli being in direct contact with the sediment (Charlier *et al.*, 2007). In addition, a noticeable amount of *Ulva* thallus pieces was found relatively deep in the intertidal sands, but were not observed within subtidal sediments. In addition, *Ulva* biomasses estimated inshore were greater than in subtidal areas (Figure 4), although these values were probably underestimated due to possible reflux from trawl, and were not directly comparable due to the use of different estimation methods for the two habitats. Since the subtidal *Ulva* stock, with lower biomass than in the intertidal, was close to – but somehow disconnected from – the seafloor, macroalgal mats would most likely not have impacted nearshore sandy benthic communities. However, the intensity of green tides (both at intertidal and subtidal area) is highly variable depending on the year, mainly because of weather conditions and nutrient loads (CEVA personal communication), and thus may have different impacts on macroinfauna or the ichthyofauna within open sandy systems depending on the amount of *Ulva* stranding or floating, as shown by Le Luherne *et al.* (2016).

ACKNOWLEDGEMENTS

We gratefully thank the able assistance of V. Le Garrec, C. Jouan, M. Maguer, S. Laurand, G. Schaal and numerous volunteers in the field. We are very grateful to the crew of the oceanographic research vessel *Albert Lucas* for their assistance on board for subtidal sampling. We thank V. Le Garrec for assistance with species identification. We acknowledge L. Quiniou (UBO) and O. Gallet (Parc Naturel Marin d'Iroise) for providing useful advice on beach trawling. We are also grateful to S. Ballu (CEVA), who provided *Ulva* biomass data.

FINANCIAL SUPPORT

This study was supported by the national interdisciplinary Ecosphère Continentale et Côtière EC2CO-INSU 'MAVERIQ', the Région Bretagne, the Université de Bretagne Occidentale, and Åbo Akademi University. This study was conducted as part of the PhD thesis of N. Quillien for Université de Bretagne Occidentale and Åbo Akademi University. E. Bonsdorff and M. C. Nordström were funded through the Åbo Akademi University Endowment.

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Correspondence should be addressed to:

N. Quillien

Laboratoire des Sciences de l'Environnement Marin, Institut Universitaire Européen de la Mer, Université de Bretagne Occidentale, Plouzané, France

email: nolwenn.quillien@gmail.com