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

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ABSTRACT

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

1. Introduction

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

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

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

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

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

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

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

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

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

2. Material and methods

2.1. Study area

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

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