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Disentangling the effects of solar radiation, wrack macroalgae and beach macrofauna on associated bacterial assemblages

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ABSTRACT

Wrack detritus plays a significant role in shaping community dynamics and food-webs on sandy beaches. Macroalgae is the most abundant beach wrack, and it is broken down by the combination of environmental processes, macrofauna grazing, and microbial degradation before returning to the sea as nutrients. The role of solar radiation, algal species and beach macrofauna as ecological drivers for bacterial assemblages associated to wrack was investigated by experimental manipulation of *Laminaria ochroleuca* and *Sargassum muticum*. We examined the effects of changes in solar radiation on wrack-associated bacterial assemblages by using cut-off filters: PAR + UVA + UVB (280–700 nm; PAB), PAR + UVA (320–700 nm; PA), PAR (400–700 nm; P), and a control with no filter (C). Results showed that moderate changes in UVR are capable to promote substantial differences on bacterial assemblages so that wrack patches exposed to full sunlight treatments (C and PAB) showed more similar assemblages among them than compared to patches exposed to treatments that blocked part of the solar radiation (P and PA). Our findings also suggested that specific algal nutrient quality-related variables (i.e. nitrogen, C:N ratio and phlorotannins) are main determinants of bacterial dynamics on wrack deposits. We showed a positive relationship between beach macrofauna, especially the most abundant and active wrack-users, the amphipod *Talitrus saltator* and the coleopteran *Phaleria cadaverina*, and both bacterial abundance and richness. Moderate variations in natural solar radiation and shifts in the algal species entering beach ecosystems can modify the role of wrack in the energy-flow of nearshore environments with unknown ecological implications for coastal ecosystems.

1. Introduction

Sandy beaches are ubiquitous ecosystems mostly appreciated for providing valuable recreational and economical services to society. Sandy beaches also comprise an important part of any coastal region and harbour a range of often under-appreciated biodiversity commonly subjected to strong variations in the rates of waves, tides, sun exposure and nutrients (McLachlan and Brown, 2006). Simultaneously, allochthonous subsidies of organic material, also known as wrack, play a critical role in shaping community dynamics on beaches with profound implications on coastal food-web dynamics and nearshore ecosystem functioning (e.g. Dugan et al., 2003, 2011; Marczak et al., 2007; Lastra et al., 2008; Spiller et al., 2010).

The lack of *in situ* beach primary production means that beach communities are almost entirely dependent on the accumulation of allochthonous organic debris; i.e., macroalgal wrack, dead animals, and/or dissolved and particulate organics flushed into the sand by waves and tides (Colombini and Chelazzi, 2003). These communities play a key role in the decomposition and transformation of the organic matter accumulated in sandy beaches (Orr et al., 2005; Lastra et al., 2008; Dugan et al., 2011). Once wrack is cast ashore it undergoes physical processes that allow algal loss, including breakdown via drying–rewetting cycles through solar radiation or morning dew, sedimentation, leaching, and eventually fragmentation, decomposition and remineralisation by bacteria, meiofauna and grazers (see Orr et al., 2005). Bacteria colonize wrack deposits releasing dissolved and particulate organic matter into the sediments. Also, a diverse assemblage of meio- and macrofauna rapidly colonizes wrack and strongly influences the microbial community (e.g. Koop and Griffiths, 1982; Griffiths et al., 1983; Inglis et al., 1989). Thus, scavengers, such as amphipods, isopods and insects feed directly upon the macrophytes or other wrack-dependent

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organisms, and their activities release particulates, leachates, and faecal pellets, which stimulate the growth of bacteria and other invertebrates (Koop and Griffiths, 1982).

Detrital processing by beach organisms plays a key role in coastal nutrient cycling (Colombini and Chelazzi, 2003; McLahlan and Brown, 2006). Previous studies on the biodegradation of beach wrack showed that the role of invertebrates is largely variable, with measured consumptions ranging from 5 to 75% of the biomass of detrital wrack in different beach systems (e.g. Koop et al., 1982; Griffiths et al., 1983; Lastra et al., 2008). Similar studies showed that microorganisms and leaching play a more significant role than macrofauna in the breakdown of wrack and in the ecological functioning of this ecosystem, accounting for as much as 87% of the annual beach production (e.g. Koop and Griffiths, 1982; Koop et al., 1982; Inglis, 1989). In this process, fragments and mineralized wrack components are transported to the nearshore environment, the atmosphere or stored within the beach (Koop and Griffiths, 1982; Koop et al., 1982; McLachlan, 1985; Dugan et al., 2011). Therefore, microorganisms serve as a natural biofilter that mineralizes organic material, providing essential nutrient recycling in nearshore environments, maintaining coastal ecosystem health.

The number of microorganisms on a beach depends on many environmental factors, although the most important one is the supply and content of organic matter (Nair and Bharathi, 1980; Novitsky and MacSween, 1989). Large standing stocks of sedimentary bacteria are expected under wrack deposits even if the initial agents of biodegradation are macroinvertebrates. Bacteria can show preferences for different algal species with specific physical and biochemical traits in a similar way as beach macrofauna does (Duarte et al., 2011; Rodil et al., 2015a,b). However, although microorganisms play a critical ecological role on the biodegradation of wrack within beach ecosystems, there is limited knowledge of the microbial function linked to wrack (e.g. Koop and Griffiths, 1982; Inglis, 1989; Colombini and Chelazzi, 2003).

Over the next decades, climate change is expected to increase the exposure of marine organisms to damaging UV wavelengths (Andrady et al., 2010). In temperate latitudes, the amount of UVR reaching Earth's ecosystems has not been stable over the past years due to anthropogenic-related changes in cloudiness and aerosol concentrations, causing what is known as the “global dimming and brightening effect” (*sensu* Wild, 2009). This effect is hold responsible for promoting detrimental variations in the UV levels in mid-latitude regions with implications for climate change and far-reaching ecological consequences (Wild, 2009; Mateos et al., 2013) that can affect beach communities (Rodil et al., 2015a,b). Several studies focused on the role of solar radiation (UVR) on marine bacteria have provided evidence that UVR-alteration, particularly UVB (280–320 nm), has significant negative effects on productivity, activity and abundance of bacterial cells (e.g. Pérez and Sommaruga, 2007; Manrique et al., 2012). It has also been demonstrated that shifts in the natural levels of UVR have direct effects on macrophytes with consequences on consumers (e.g. Swanson and Fox, 2007; Rodil et al., 2015a,b). Microbial communities in sandy beach sediments are organized in response to their requirements for chemical and light needs (Bühring et al., 2014). Therefore, UVR-induced changes in wrack biochemical traits (i.e. nutrients, pigments or phlorotannins) and effects on associated macrofauna might influence microbial responses with consequences on wrack degradation process and fate. To our knowledge this is the first beach study regarding the effects of UVR on wrack-associated bacterial assemblages.

We performed a wrack experimental manipulation by using two different species of brown macroalgae: the native *Laminaria ochroleuca* Bachelot de la Pylaie, 1824, and the non-indigenous *Sargassum muticum* (Yendo) Fensholt, 1955. We manipulated the ambient solar radiation using cut-off filters to simulate a moderate change in UVB, and we tested the responses of the associated bacterial assemblages. This work was nested within a larger experiment that tested the joint effects of wrack identity and solar radiation on macrofauna assemblages (Rodil et al., 2015b). The aim is to determine whether two different algal species with inherent biochemical composition and typical beach macrofauna can promote different microbial responses when combined with different UVR treatments. Recently, it was suggested that beach grazers, such as talitridae sand-hoppers, might obtain their food source indirectly from wrack via bacterial communities that are specific to different types of imported material (Porri et al., 2011). Therefore, we take the opportunity to evaluate the top-down impact of macroinvertebrates on bacterial assemblages colonizing wrack in a sandy beach.

2. Methods

2.1. Study site and experimental design

This study was based on a subset of treatments that were part of a larger experiment that examined the role of wrack as beach macrofauna shelter, and aimed at determining how different UVR treatments affected the algal biochemical composition of two macroalgal species, and the consequent effects on associated macrofauna (Rodil et al., 2015b). Brown canopy-forming macroalgae *L. ochroleuca* and *S. muticum* are abundant species frequently found stranded on beaches from the Atlantic coasts of the Iberian Peninsula. We performed the experiment in Ladeira beach (Corrubedo Natural Park), an exposed sandy beach from NW Spain (42° 34′ 36″ N; 9° 3′ 20″ W, NW Spain), where wrack is abundant and diverse (see Rodil et al., 2015b).

The day before starting the experiment, we collected by hand fresh amounts of *L. ochroleuca* and *S. muticum* from nearby rocky areas, taken to the laboratory, washed, and separated in wrack patches of similar weight (~1.0 ± 0.2 kg wet weight, 16 patches per species). At the field (20 September 2013), 4-replicated squared-patches (20 × 20 cm) per algal species and UVR-treatment (i.e., a total of 32 experimental wrack patches) were placed at the northern part of the beach between the highest mark of the drift line and the toe of the dunes parallel to the shoreline. Each patch was placed ~2 m apart, and its treatment determined previously by a random distribution. All patches were covered by a bird-net (1 cm mesh size) attached to the sand by aluminium pegs to prevent aeolian dispersion, and left in place for five days. This time gap was chosen because wrack in natural conditions loses exponentially most of the biomass in a few days, and most of the associated invertebrates are early colonizers (see Rodil et al., 2015b).

Specific information on the experimental UVR-treatments is available somewhere else (Rodil et al., 2015b). Briefly, four ambient solar radiation treatments were established by suspending cut-off filters immediately above the patches (10 cm), supported over 4-legged polyethylene squared structures (buried 5 cm into the sand) to modify the quality of the solar radiation: (a) The photosynthetically active radiation treatment (400–700 nm, Lee 226), which blocks radiation < 400 nm (i.e., UVA and UVB), but allows for full transmission of PAR (hereafter, P). (b) The PAR + UVA treatment (320–700 nm, Lee 130), which blocks UVB radiation (hereafter, PA). (c) The full sunlight treatment (PAR + UVA + UVB; 280–700 nm) using a commercial polyethylene film as a procedural control (hereafter, PAB), which allowed penetration of full spectrum light (>90% for PAR, UVA, and UVB). (d) The full sunlight with no filter as a control for filter artefacts (hereafter, C). Information on the solar radiation recorded through the filters is available somewhere else (Rodil et al., 2015b).