Estuarine, Coastal and Shelf Science 150 (2014) 102–110

Contents lists available at SciVerse ScienceDirect

Estuarine, Coastal and Shelf Science

journal homepage: www.elsevier.com/locate/ecss

Geographic variation in sandy beach macrofauna community and functional traits

I.F. Rodil [a,c,*], T.J. Compton [b], M. Lastra [a]

[a] Departamento de Ecología y Biología Animal, Universidad de Vigo, Campus As Lagoas-Marcosende, 36310 Vigo, Spain
[b] Department of Marine Ecology, NIOZ Royal Netherlands Institute for Sea Research, PO Box 59, 1790 AB Den Burg, Texel, The Netherlands
[c] National Institute of Water and Atmospheric Research (NIWA), P.O. Box 11-115, Hillcrest, 3216 Hamilton, New Zealand

ARTICLE INFO

Article history:
Received 30 November 2012
Accepted 21 June 2013
Available online 1 July 2013

Keywords:
boosted regression trees
exposed sandy beaches
feeding guilds
functional traits
geographic variation
taxonomic groups
Spain

ABSTRACT

Sandy beaches are a common ocean-dominated ecosystem along the north coast of Spain. We conducted field surveys at 39 beaches distributed between 1° and 9°W, ca. 2000 km along this geographic region to document broad patterns of macrobenthic communities, and to describe their association with variables characterising both the beach environment and the characteristics of the adjacent ocean waters. Macrofaunal functional traits are considered to be an informative measure that can be useful for many ecosystem-level questions, as they are based on what organisms do (i.e., their ecological function) rather than on their identification alone. Boosted regression-trees analysis showed that the occurrence of the main taxonomic groups and feeding guilds were differentially associated with the prevailing beach features along this coastline. The occurrence (presence/absence) of molluscs was best explained by the concentration of chlorophyll-*a* and wave exposure whereas those of crustaceans and polychaetes were best explained by an ensemble of variables including beach slope, sea surface temperature and grain size. A comparison of the feeding guilds demonstrated that the occurrence of suspension feeders was best explained by chlorophyll-*a* and wave exposure, whereas the occurrence of deposit feeders was best explained by beach slope, sea surface temperature and chlorophyll-*a*. The occurrence of predators and scavengers was best explained by sea surface temperature and beach slope. Based on the patterns presented here, we confirm that the upwelling events that occur regularly on this coastline are a structuring agent for beach communities. Future work needs to examine the role of the oceanographic conditions of the region for they might represent the driving forces behind large-scale shifts in macrofauna communities.

1. Introduction

Several levels of taxonomic complexity can be examined when considering marine macrobenthic diversity (Gray, 1997). Species-specific traits within a community are considered an informative measure that can be very useful for many ecosystem-level questions and comparisons across regions and along environmental gradients (e.g., Padilla and Allen, 2000; Petchey and Gaston, 2006). Functional traits describe organisms that share a similar physiological or ecological role, e.g., deposit feeders, bioturbators, predators (Bonsdorff and Pearson, 1999). Over large scales, patterns of functional traits have been suggested to vary, following environmental gradients (Broitman et al., 2001). However, few studies have examined how these traits change with respect to the environmental conditions over large scales (Bustamante et al., 1995; Broitman et al., 2001; Barboza et al., 2012).

Exposed sandy beaches are harsh environments strongly stressed by physical variables where macrofauna distribution has been typically related to beach morphodynamic factors, such as slope and sediment characteristics (Defeo and McLachlan, 2005). Consequently, few studies have dealt with the importance of biological interactions as a factor controlling the structure of benthic communities (Dugan et al., 2004), and characteristics such as food availability and primary productivity have been largely ignored (Cisneros et al., 2011; Rodil et al., 2012). Furthermore, beaches are marine ecosystems with very low *in situ* primary production (McLachlan and Brown, 2006). In these systems, allochthonous inputs, like surf phytoplankton, stranded macrophytes and carrion represent the major food sources for the macrofaunal beach

* Corresponding author. Present address: CIIMAR, Interdisciplinary Centre of Marine and Environmental Research, University of Porto, Rua dos Bragas 289, 4050-123 Porto, Portugal.
E-mail address: ibantxorodil@gmail.com (I.F. Rodil).

0272-7714/$ – see front matter © 2013 Elsevier Ltd. All rights reserved.
http://dx.doi.org/10.1016/j.ecss.2013.06.019

community (Colombini and Chelazzi, 2003; Dugan et al., 2003). Macrobenthic species are integral to the cycling of nutrients on beaches and their return to the coastal waters, and are also a fundamental food source to higher trophic levels (e.g., Peterson et al., 2006; McLachlan and Brown, 2006). The availability of allochthonous inputs in beach systems can have cascading effects with consequences for the distribution and abundance of macrofauna (e.g., Dugan et al., 2003; Lastra et al., 2008) and the composition of feeding guilds. For example, beaches with large wrack inputs are often dominated by scavengers and predators (Inglis, 1989; Dugan et al., 2003). On the other hand, beaches with low wave exposure are often associated with high sediment organic content and dominated by deposit feeders (Rodil et al., 2007; Bergamino et al., 2011). Furthermore, suspension feeders can be very abundant in situations where high phytoplankton supply and good feeding conditions in the beach swash occur (McLachlan and Brown, 2006).

Exposed beaches are among the most common coastal ecosystems along the northern Spanish shoreline. This large geographic extent across a relatively constant latitude provides an ideal system to examine the roles of nutrition and physical environmental descriptors in shaping the composition of taxonomic groups and feeding guilds. Specifically, one of the main oceanographic features of this coast is a seasonal upwelling event involving a characteristic offshore equatorward-flowing current that promotes the uplifting of deep, cold and nutrient-rich ocean waters to the surface (Figueiras et al., 2002). This process fertilizes coastal waters and enhances phytoplankton growth, and thus sustains one of the largest and most diverse marine ecosystems in the world (Figueiras et al., 2002; Bode et al., 2006; Lastra et al., 2006). Several studies have demonstrated that large-scale oceanographic processes, acting over 100s of kms, can influence the local dynamics of marine communities (e.g., Bustamante et al., 1995; Broitman et al., 2001; Cardoso and Defeo, 2003; Contreras and Jaramillo, 2003; Blanchette et al., 2009). These studies have led to the hypothesis that differences in nutrients and/or chlorophyll concentrations, driven by the upwelling of cooler, nutrient-rich waters can influence the local dynamics of intertidal assemblages (Bustamante et al., 1995; Broitman et al., 2001). For example, along the north coast of Spain, beach-specific species follow a longitudinal gradient that is associated with increasing primary productivity from east to west, in accordance with the source of upwelling (Lastra et al., 2006; Rodil et al., 2012).

In this contribution, we examined the role of a number of abiotic factors in describing the geographic variation of representative macrobenthic assemblages across 39 beaches along the north coast of Spain. Our main aims were to identify the principle descriptors of geographic patterns of community structure, to determine which functional trait provides the best correlations with environmental data, and how such relationships are influenced by introducing surrogates of food supply (chlorophyll-*a* and sea surface temperature) into the models. We used boosted regression-tree analysis (BRTs) to examine these patterns as this approach can automatically model complex functions and the interactions between variables (De'ath, 2007; Elith et al., 2008). We hypothesize that the geographic variability of the community assemblages, in terms of taxonomic groups and feeding guilds, will be driven by the longitudinal gradient related to the specific oceanographic conditions from this region. Due to the clear associations between allochthonous inputs and feeding guilds, we expect that the local dynamics of the macrofauna community assemblages in relation to patterns of functional trait abundances will be influenced not only by the prevailing environmental conditions, but also by the food supply processes modulated through a large geographic extent.

2. Methods

2.1. Location and sampling procedure

Thirty-nine exposed beaches were sampled from 1995 to 1999 along the north coast of Spain (Fig. 1) (data compiled from Rodil and Lastra, 2004; Lastra et al., 2006; Rodil et al., unpublished) during spring tides between September and October to reduce seasonal variability in the biological and environmental predictors (Jaramillo et al., 2001). This coastline is characterised by mesotidal beaches with a wide range of morphodynamic characteristics across more than 2000 km of coastline from 42° 07′ N, 1° 46′ W to 43° 22′ N, 8° 49′ W (Fig. 1). At each beach, one sediment core was collected at each of 10 equally spaced levels from above the drift line to the swash zone (0.05 m^2, 15 cm deep) along 3 randomly chosen transects ($n = 30$) during low tide (see Lastra et al., 2006). Samples were sieved (1 mm mesh) and the macrofauna were sorted from the sediments, identified and counted in the laboratory. Samples for the determination of the granulometric and morphodynamic characteristics were collected in triplicate at the same sites.

Eight environmental variables were measured across all beaches. Beach slope was determined by Emery's profiling technique (Emery, 1961). Mean grain size (MGS) was calculated by means of a Coulter LS 200 laser diffraction particle size analyser (μm). Shear strength (SS) explored the sediment compacting force using a Pilcon shear vane tester (kilopascals). Relative tide range (RTR) indicated the importance of tides versus waves in controlling morphodynamics (RTR = TR/H_b, where TR is spring tide range and H_b is breaker height, both in m). The 20-point rating system (McLachlan, 1980) was used to estimate the wave exposure (exposure rating system: ER). Dean's index (Ω) was used to characterize the beach morphodynamic type ($\Omega = (H_b/W_s)^*$ Tb, where H_b is breaker height (m), W_s is sand fall velocity (m s^{-1}) and Tb is wave period (s)). Thus, $\Omega < 2$ characterise reflective, $\Omega > 5$ dissipative and $2 < \Omega < 5$ intermediate beaches (McLachlan and Brown, 2006).

Maximum sea surface temperature (SST, °C) and maximum chlorophyll-*a* concentrations (chl*a*, mg m^{-3}) along the coast of Spain were obtained from Bio-Oracle (http://www.oracle.ugent.be/) (see Tyberghein et al., 2012). Specifically, these values were obtained by averaging temperature and chlorophyll-*a* estimates from monthly climatologies (http://oceancolor.gsfc.nasa.gov/) across the period from 2002 to 2009. These estimates provide proxies of seasonality and temporal variation in food and nutrient supply (e.g., Lastra et al., 2006; Rodil et al., 2012; Tyberghein et al., 2012). We used the standardised data (according to zero mean and unit variance) available at the Bio-Oracle website in order to minimise variation between the extreme values.

2.2. Macrobenthic community and functional traits

To quantify compositional patterns of beach macrofaunal assemblages across this coastline, we examined macroinvertebrate occurrences (presence/absence) pooled into taxonomic groups and functional traits based on feeding guilds (Supplementary Table S1), (McLachlan and Brown, 2006). Macrobenthos is well represented on beaches, including crustaceans, polychaetes, and molluscs as the most common taxonomic groups (Table S1) that can be used as a first overview of the beach macrofauna distribution. The feeding guilds of species were defined as the feeding mode that they practice the majority of the time: suspension feeders; deposit feeders; scavengers and predators (Table S1).