Estuarine, Coastal and Shelf Science 154 (2015) 184–193

Contents lists available at ScienceDirect

Estuarine, Coastal and Shelf Science

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

Large-scale dynamics of sandy beach ecosystems in transitional waters of the Southwestern Atlantic Ocean: Species turnover, stability and spatial synchrony

Diego Lercari [a, b, *], Omar Defeo [a, b]

[a] UNDECIMAR, Facultad de Ciencias, Iguá 4225, Montevideo, 11400, Uruguay
[b] GEPEIA, Centro Universitario de la Región Este, Ruta nacional N° 9 intersección con Ruta N° 15, Rocha, Uruguay

ARTICLE INFO

Article history:
Received 21 July 2014
Accepted 4 January 2015
Available online 10 January 2015

Keywords:
Uruguay
transitional waters
Río de la Plata
sandy beaches
morphodynamics
benthic macrofauna
species richness
seasonal dynamics

ABSTRACT

Transitional waters (TW) are interfaces between the terrestrial and freshwater environments and the sea. These ecotones are characterized by highly dynamic physico-chemical and hydro-morphologic conditions, resulting in a mosaic of habitats in which species are particularly well adapted to variability. However, sandy beach ecotones occurring along estuarine gradients are rarely addressed from the TW perspective. We conducted a 2-yr study to assess the seasonal dynamics of environmental and macrofaunal descriptors in 16 sandy beaches of the Uruguayan coast in TW defined by the widest estuary of the world (Rio de la Plata). A strong variability in environmental conditions was found at inner estuarine beaches, reflecting the seasonal dynamics of the estuarine discharge. The greatest abundance and species richness found in dissipative oceanic beaches were also characterized by their lowest temporal variability, indicating that macrofaunal communities were more stable towards oceanic conditions, where environmental variability was also lowest. Spatial synchrony was reflected in changes across seasons in the species richness in the TW system. A high turnover of species along spatio-temporal gradients occurring within the TW ecotone was observed. Mollusca and Polychaeta were absent in highly-variable estuarine beaches, irrespective of the morphodynamic state. A functional equivalence between species was found at the extremes of the salinity gradient. The environmental variables that best explained community patterns differed among seasons: in summer and autumn, salinity, wave period and beach width were the main explanatory factors, whereas temperature had a primary influence in winter and morphodynamic variables exerted a major influence in autumn. We highlight the need to consider concurrent variations in estuarine and morphodynamic variables when assessing the spatial distribution of macrofaunal species richness and abundance in sandy beaches occurring along TW.

1. Introduction

Populations of plants and animals gradually change along gradients of physical conditions, shaping distinct ecological communities within broadly defined ecosystems, such as forests, grasslands and estuaries (Ricklefs, 1990; Gaston, 2000). Every coastal habitat exists within a multi-dimensional mesh of environmental gradients, notably related to four main sources of variation: parameters that change across-shore (e.g. temperature, humidity), wave exposure, sand particle size and salinity (Raffaelli and Hawkins, 1996).

Transitional waters (TW) are 'bodies of surface water in the vicinity of river mouths which are partially saline in character as a result of their proximity to coastal waters but which are substantially influenced by freshwater flows' (Directive, 2000/60/EC). They comprise estuaries, deltas and coastal lagoons, defining ecosystems with unique functional and structural characteristics (Cognetti and Maltagliati, 2008; Basset et al., 2013). Indeed, TW are ecotones between land, sea and freshwater, characterized by highly dynamic physical, chemical and hydro-morphologic conditions, resulting in a mosaic of habitats in which species are particularly well adapted to variability (Elliott and Whitfield, 2011). Ecotone dimensions correspond to major discontinuity boundaries between different ecosystem types, shaping TW as multi-dimensional, hierarchically organised, ecotones. The hydrodynamic ecotone dimension (1st order) mainly reflects a spatial or temporal salinity gradient that

* Corresponding author. UNDECIMAR, Facultad de Ciencias, Iguá 4225, Montevideo, 11400, Uruguay.
E-mail address: lercari@fcien.edu.uy (D. Lercari).

http://dx.doi.org/10.1016/j.ecss.2015.01.011
0272-7714/

limits the local number of species (α diversity) for some groups by a filtering process from the regional species pool (Zobel, 1997; Mouillot et al., 2007). The spatio-temporal patchiness found in TW is likely to support high taxonomic turnover among locations (β diversity) and then a high regional γ diversity (Barbone and Basset, 2010). Additional ecotone dimensions occur at other TW interfaces, including the across-shore axis from the supralittoral to the sublittoral margins (Basset et al., 2013). The relative size (spatial dimension) and the temporal presence of these ecotones vary with locality and type of TW.

The dynamics of exposed sandy beach ecotones occurring along estuarine gradients has been rarely studied from the TW perspective. Exposed sandy beaches are relatively uncommon in TW such as estuaries, and large-scale macrofauna variations along estuarine gradients have been scarcely documented. Recent reviews in sandy beach ecology highlighted the need to consider a multiscale approach for ecosystem modelling, including the underlying processes and mechanisms (Defeo and McLachlan, 2005, 2011; Fujii, 2007; Schlacher et al., 2008). Alongshore patterns in a single beach affected by a salinity gradient showed an exponential decrease in species richness and abundance towards low salinities (Lercari et al., 2002; Lercari and Defeo, 2003). Temporal variations in freshwater discharges resulted in local short-term changes in community attributes (Defeo and Lercari, 2004). At the macroscale (hundreds of km), salinity range become an ecological master factor governing macrofaunal distribution patterns in sandy beaches located along an estuarine gradient (Lercari and Defeo, 2006). Tolerance to salinity changes varies among species according to the beach zone inhabited (intertidal species have lower tolerance than supralittoral ones) and development mode (species with planktonic larvae have lower tolerance than direct developers) (Barboza et al., 2012).

Another source of variability in sandy beach ecotones is defined by their morphodynamic characteristics. Beach morphodynamics play a key role in determining the structure of sandy beach communities, with species richness increasing from reflective (steep slope, coarse grains) to dissipative (gentle slopes, fine grains) beaches (reviewed in Defeo and McLachlan, 2013). In this context, sandy beaches occurring in TW are affected by the highly dynamic hydro-morphologic conditions that characterize these systems, resulting in weaker wave action and a decrease in wave period and swash width at inner estuarine conditions (Lercari and Defeo, 2006). However, the dynamics of these intertidal ecotones in TW has yet to be resolved. This uncertainty arises partly from two main issues: firstly, the traditional comparison of only one pair of sites in sandy beach studies (e.g. high and low salinities, one dissipative vs. one reflective beach) cannot distinguish between linear and nonlinear changes in increasing severity of the gradients. Secondly, although salinity is a major explanatory driver of diversity patterns, little is known about how temporal variations in complex TW systems affect structural and functional changes in sandy beach communities occurring inside TW.

This paper describes a 2-yr study to assess the spatial and temporal dynamics of the environment and the macrobenthic community on sandy beach ecotones occurring along the Rio de la Plata, the widest estuary of the world that defines a TW system in the Southwestern Atlantic Ocean. According to the theoretical frameworks developed for estuaries (Attrill, 2002; Basset et al., 2013) and sandy beaches (Defeo and McLachlan, 2005), we predict: 1) a lower number of species and abundance in sandy beaches affected by high salinity variability, and in those with reflective characteristics; 2) a higher community stability in less variable environments (both in terms of salinity and beach morphodynamics); 3) a replacement (turnover) of species along the TW gradient maintaining functional redundancy, and 4) changes in community structure across seasons occurring synchronically (spatial synchrony) among beaches.

2. Materials and methods

The Rio de la Plata estuary, located at 35°S on the Atlantic coast of South America, constitutes a major TW system with unique characteristics. It drains the second largest basin of the continent with an average freshwater flow of 22,000 $m^3\ s^{-1}$ (Simionato et al., 2001). This large and microtidal estuary covers more than 400 km from the head to the mouth (200 km wide) with a broad permanent connection to the sea. The estuary is characterized by seasonal variations in river inputs, being highly sensitive to the atmospheric forcing, especially to wind-induced turbulence. The strong seasonal variability is controlled by the balance between onshore and offshore winds, the river discharge, the tides and the Coriolis force (Simionato et al., 2001).

The study covered 400 km in the TW of the Uruguayan coast, where we selected eight beaches along 150 km of the Río de la Plata estuary (inner beaches) and eight beaches along 250 km of oceanic shores (outer beaches) outside the mouth of the estuary. Sampling sites were selected considering, whenever possible, close pairs of beaches with the same salinity range but markedly different morphodynamic features. Biological samples on each beach were taken every 2 months from July 1999 to May 2001, along three transects perpendicular to the shoreline, spaced 8 m apart, from the base of the dunes to the lower limit of the swash zone. Sampling units (SUs) on each transect were done every 4 m with a sheet metal cylinder, 27 cm in diameter and 40 cm deep, and the material was sieved through a 0.5 mm mesh. In order to cover the entire beach habitat, the number of samples taken on each beach and sampling event varied according to the beach width, which was measured as the distance between the base of the dunes and the lower limit of the swash zone, where water moves over the beach face after a broken wave collapses on the sand (Lercari and Defeo, 2006). The organisms retained were fixed in 5% formalin, counted and identified to the species level (whenever possible). Sampling on each beach was made at the same time of the day in order to minimize daily effects associated with sampling conditions. Following Defeo (1996), macrofaunal abundance was expressed as individuals per strip transect (ind m^{-1}). The total number of species recorded on each beach was considered as a measure of α diversity (Barboza et al., 2012).

At each beach, salinity and water temperature were measured at the surf zone with an YSI 33 thermosalinometer, wave height was visually estimated and wave period was determined with a stopwatch. At each SU, we measured temperature at the surface and 15 cm depth, sand compaction (kg cm^{-2}), and beach slope (Emery, 1961). Sediment samples were also collected at each SU to estimate granulometric variables (Folk, 1974), sediment moisture and organic matter content (weight differences between wet, dry and incinerated samples, respectively). The amount of wrack or carcasses deposited on all the beaches can be considered negligible. Swash width was measured as the distance between upper and lower swash limits at sampling time. Mean estimates for each beach and sampling date were obtained by averaging individual SU estimates.

Alongshore patterns in salinity were modelled by season, and the best model was selected according to the coefficient of determination (r^2) and statistical significance. Beach morphodynamics were assessed by Dean's parameter Ω (Short, 1996):

$$\Omega = \frac{Hb \cdot 100}{Ws \cdot T}$$

where Hb is breaker height (m), Ws is sand fall velocity (cm s^{-1}) and T is wave period (sec). Annual mean values of Ω were employed to classify beaches according to their morphodynamic features.