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Ghost crab populations respond to changing morphodynamic and habitat properties on sandy beaches

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ABSTRACT

The morphodynamic state and habitat properties of microtidal sandy beaches largely account for variations in macrofauna structure. In ecological theory, the habitat harshness hypothesis and the habitat safety hypothesis explain variations in macrofauna populations of the intertidal and supratidal zones of sandy beaches. The former hypothesis states that intertidal macrofauna should increase from reflective to dissipative beaches. The latter hypothesis supports the idea that supratidal species are more successful on reflective beaches, given their relative independence from the swash. However, trends in abundance of supratidal species, particularly crustaceans, have been unclear and further investigation is therefore needed. This study tested the two hypotheses on the largest invertebrate intertidal-to-supratidal crustacean on sandy beaches, namely the ghost crab (genus *Ocypode*). Variations in ghost crab burrow density, abundance, size and across-shore distribution were measured on four warm-temperate microtidal sandy beaches in KwaZulu-Natal, South Africa. Burrow numbers increased with beach morphodynamic state, while average burrow size decreased. The steepest, narrowest and most inundation-prone beach represented the least hospitable environment for the ghost crabs. The results that are reported here tend to support the habitat harshness hypothesis. However, the relevance of i) individual physical variables, ii) tidal action, and iii) the ecology of various species, in shaping ghost crab population dynamics, is also discussed. The results contribute to the knowledge regarding population dynamics of intertidal and supratidal crustaceans across beach types.

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1. Introduction

Sandy beaches are unique ecotones, as they represent the most prominent partitioning environment between the continents and the ocean, constituting 70% of the world's coastlines (Bascom, 1980; Schlacher and Thompson, 2013b). They offer essential extractive and non-extractive ecosystem services (e.g. food, habitat, water storage, nutrient cycling, coastal protection, recreation), aside from having intrinsic values (Defeo et al., 2009; Everard et al., 2010; Schlacher et al., 2014).

Sandy beaches are unstable and mobile environments; the habitat is the result of a combination of abiotic factors, from climate to sea conditions and tides. The morphology and dynamics of sandy beaches are ultimately determined by sediment particle size, wave height and period, and topography (Short and Wright, 1983; Short, 1996). The result of the interplay of these features is a range of beach morphodynamic types, from reflective to dissipative.

Reflective beaches are narrow and steep with coarse sand, and have a dynamic and turbulent swash with short wave periods. Dissipative beaches are wider, flatter, have finer sand particles and gentle swashes, with waves of longer period that dissipate in the surf zone. Between these extremes sit a range of intermediate beach types (Defeo and Gómez, 2005; Defeo and McLachlan, 2005).

Beach morphodynamic types are defined by a compound index of beach state, namely the dimensionless fall velocity or Dean's parameter Ω (Short, 1996). Dean's parameter Ω, which is essentially a measure of the ability of the predominant wave energy to erode sand (Defeo and McLachlan, 2005), is calculated as $|Hb \div (Ws \cdot T)|$, where Hb = wave breaker height (m), Ws = sediment fall velocity (m s^{-1}) and T = wave period (s). On microtidal beaches (tide range <2 m), a value of $\Omega = 1$ typically marks the threshold from the reflective to the intermediate state, while a value of $\Omega = 6$ marks the transition from the intermediate to the dissipative state (Wright and Short, 1984); in a study by Harris et al. (2011a) on microtidal beaches in South Africa, reflective beaches were classified as <27.49 m wide, reflective-intermediate beaches between 27.49 m

and 47.03 m wide, intermediate-dissipative beaches between 47.04 m and 64.10 m wide, and dissipative beaches >64.10 m wide.

When classifying all open coast beach systems (e.g. macrotidal, embayed), Short (1996) determined that values of $\Omega < 2$ denote a reflective beach; $2 < \Omega < 5$ denotes a beach of intermediate state, and $\Omega > 5$ indicates a dissipative beach. Wright and Short (1984, 1996) established that while beaches can be categorized into reflective, intermediate, and dissipative morphodynamic states, considerable variability still occurs within each category. For example, despite the small range of Ω values, beaches of the intermediate group exhibit the greatest variation; also, dissipative beaches are largely dynamic spatially and temporally, with Ω values going up to 30 (Wright and Short, 1984).

The diversity of beach types, characterized by the interaction of tides, waves and sand, can account for and explain variations in macrofauna structure on sandy beaches, including species richness, abundance, and morphological and life history traits. Therefore, understanding the spatial variation of sandy beach macrofauna, from the micro-scale to the macro-scale, has always been a pivotal theme in sandy beach and coastal ecology (Defeo and McLachlan, 2005; McLachlan and Dorvlo, 2007a; Schlacher et al., 2008; Defeo and McLachlan, 2013; Dugan et al., 2013; Schlacher and Thompson, 2013a; Veas et al., 2014). The large interest in determining the structure of macrofauna species on sandy beaches and its relation to external drivers has been increasing over the recent years, due to i) the overall importance of sandy beach macrofauna in ecosystem food webs and in the equilibrium of sandy beach ecosystems; and ii) the importance of many key species as 'signals' of natural and anthropogenic ecosystem changes (Scapini and Morgan, 2002; McLachlan and Brown, 2006; Harris et al., 2011b; Gonçalves et al., 2013).

Over the last 25 years, a number of ecological theories regarding macrofauna structure on sandy beaches have been proposed. The autecological hypothesis was applied to sandy beaches by McLachlan (1990), asserting that the structure of macrofauna communities on sandy beaches is determined by independent responses of each species to physical drivers in the environment. McLachlan (1990) also proposed the swash control hypothesis, asserting that the distribution of sandy beach macrofauna along a morphodynamic gradient is limited by the swash climate. McArdle and McLachlan (1991, 1992) and McLachlan et al. (1993) refined this hypothesis into the swash exclusion hypothesis (reviewed by Defeo and McLachlan, 2005), pertinent to intertidal communities (e.g. Defeo et al., 2001). The claim of this hypothesis is that species richness, abundance and biomass increase from reflective to dissipative beaches; the harshness of the swash climate (predominantly characterized by an increase in the frequency of swashes crossing the effluent line, the line separating saturated and unsaturated sands) on reflective beaches precludes the establishment of species in the intertidal zone. McLachlan et al. (1995) added that at the extreme reflective beach state, supratidal species would be the only ones capable of surviving the harsh conditions of the habitat.

Brazeiro (2001) criticized the exclusive role that the swash exclusion hypothesis gives to the hydrodynamic aspect of the beach environment, emphasizing the importance of other factors, including sediment texture, the availability of organic matter, and erosion-accretion dynamics. Acknowledging the interspecific variability of ecological and life history traits that characterizes sandy beach macrofauna, Brazeiro (2001) introduced a hypothesis of multicausal environmental severity, accounting for the possibility of different factors affecting species differently.

Shifting focus from the community to the population level of species in the swash zone and landward of this zone, the habitat harshness hypothesis (Defeo et al., 2003; Defeo and Martínez, 2003) affirms that not only species richness, but also characteristics of populations, from abundance to reproductive rates, improve along a continuum from reflective to dissipative beaches. The harsh conditions of reflective beaches force organisms to spend more energy on maintenance, thus limiting energy expenditure on reproduction, resulting in greater mortalities in the population. After testing the habitat harshness hypothesis, a number of studies concluded that beach morphodynamic state alone is an insufficient predictor of species abundances; this conclusion was based on results being either unclear or opposite to what was originally predicted, particularly on abundances of supratidal species (Defeo et al., 1997; Giménez and Yannicelli, 1997; Defeo et al., 2003; Defeo and Martínez, 2003; Defeo and Gómez, 2005; McLachlan and Dorvlo, 2005; Caetano et al., 2006; Gómez and Defeo, 2012; Barboza et al., 2013).

In order to explain the newly observed patterns concerning supratidal species on sandy beaches, Defeo and Gómez (2005) introduced the habitat safety hypothesis, which takes into account swash climate, sediment effects and life history traits of species. According to this hypothesis, supratidal species exhibit greater fitness indicators on reflective beaches, as opposed to intertidal species. This is the result of the relative independence of supratidal species from the swash and independent active movement of these species across the shore. Furthermore, the hypothesis claims that, thanks to their steep slope and relatively inundation-free backshores, reflective beaches provide a safer habitat (Short, 1996) to supratidal forms than dissipative beaches. Supratidal crustaceans in particular have been found to be most abundant on reflective beaches, also thanks to good burrowing abilities and to the tough exoskeleton, providing protection against abrasion from coarse sediment (Defeo and McLachlan, 2011); additional advantage has been attributed to scavenger and predator crustaceans living on the supratidal zone of sandy beaches of all morphodynamic states (Defeo and McLachlan, 2005, 2011).

Notwithstanding the large amount of data that have been produced to test hypotheses concerning the structure of macrofauna communities and populations on sandy beaches in response to beach morphodynamics and other habitat properties, further work is still required on supratidal species (Defeo and Gómez, 2005). Understanding the population dynamics of these species is particularly sought after, as values denoting fitness (e.g. abundance) are customarily used as a tool to evaluate the health of the ecosystem and assess the impact of human-driven changes to the ecosystem.

From tropical to temperate regions around the world, the ghost crab of the genera *Ocypode* and *Hoplocypode* is the largest invertebrate predator of exposed sandy beaches (Sakai and Türkay, 2013; Lucrezi and Schlacher, 2014). Being adapted to semi-terrestrial habitats, this burrower can cover the entire extent of the beach-face, from the swash to the dunes and beyond, also occupying a key locus at the land—sea interface, both as predator and prey (Lucrezi and Schlacher, 2014). Ghost crabs respond clearly to a variety of human stressors on sandy beaches, from recreation (e.g. trampling and four-wheel driving; Lucrezi et al., 2009; Schlacher and Lucrezi, 2010) to engineering interventions (armoring and nourishment; Lucrezi et al., 2009; Schlacher et al., 2012), urbanization (Noriega et al., 2012), pollution (Schlacher et al., 2011) and human-induced climatic changes, such as increasing storm intensity (Hobbs et al., 2008; Lucrezi et al., 2010).

Despite the wide use of population dynamics and the structure of ghost crab species to measure the effect of human impact on sandy beaches, research exploring the variation in ghost crab populations across beaches with different morphodynamic states