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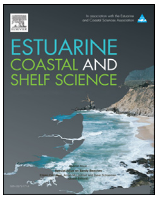

Small-scale spatial structuring of interstitial invertebrates on three embayed beaches, Sydney, Australia

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ABSTRACT

An understanding of ecological processes hinges upon an understanding of the spatial structuring of their key biotic components. Interstitial invertebrates are a ubiquitous and ecologically important component of sandy beach ecosystems. As many sandy beach taxa have limited dispersal, it may be expected that their populations exhibit a high degree of spatial structuring, yet the spatial scales across which they display baseline variability remain largely unknown. To assess (1) whether interstitial invertebrates display patchiness on embayed sandy beaches, (2) whether the size of patches they form is consistent across three geographically proximal beaches, (3) the key environmental correlates of this variation and (4) its taxonomic dependence, samples were collected at regular (0.5 m) intervals along 15 m long geomorphically similar stretches of three proximal intermediate beaches and analyses of spatial autocorrelation were conducted. On each of the three beaches, interstitial invertebrate communities formed patches of 2–4.5 m in diameter. Spatial structuring of invertebrate communities was driven by harpacticoid copepods and gastrotrichs, and corresponded to spatial structuring of sediments. Sediments, however, explained only 33% of spatial variation in faunal communities, indicating the importance of other abiotic and/or biotic factors. Our study highlights that even on seemingly homogeneous sandy beaches, faunal communities may display considerable small-scale spatial structuring. Examination of spatial structure may lead to a greater understanding of the ecological processes in this system.

1. Introduction

Sandy beaches comprise around 50–60% of Earth's coastline (Bird, 1996) and are of high ecological value (Defeo et al., 2009). Although often mis-labelled as biological deserts, they can support densities of interstitial invertebrates in excess of 10 million individuals per square metre of sediment surface (Kennedy and Jacoby, 1999). Meiofauna live in the interstitial environment between sand grains and are important in remineralising detritus, the dead organic matter which washes up on beaches (Coull, 1999). Larger macrobenthic invertebrates including crustaceans, molluscs and polychaete worms, actively burrow and ride the swash, feeding on phytoplankton, organic matter, or the interstitial biota (Defeo et al., 2009). Cumulatively, these invertebrates are an important prey resource for shorebirds and surf fishes (e.g. Coull, 1999; Peterson et al. 2006; Manning et al., 2013).

Sandy beaches are increasingly being modified by engineering aimed at protecting coastal infrastructure and public beach amenities from rising sea levels and beach erosion (Peterson and Bishop, 2005). So as to ascertain how engineering practices may be adapted to minimise ecological impacts to sandy beach ecosystems, assessments of impacts to interstitial invertebrates, a key component of the sandy beach ecosystem, are required. These typically involve the collection of replicate samples from control and impacted locations, where possible before and after the disturbance (Green, 1979). Such impact assessment requires detecting change on disturbed sandy beaches over and above background spatio-temporal variation. On exposed sandy beaches, however, few studies have examined the small scale patch formation and, hence, spatial variability of invertebrates (but see Gimenez and Yannicelli, 2000; Gingold et al., 2011). Further, there has been little consideration of how spatial patterns may depend on the taxonomic resolution of the study (Li et al., 1997). Lumping taxa together may mask small scale variation, which may be

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desirable if the goal is to assess impacts of large-scale disturbances, but undesirable if the disturbance is likely to act at small scale (Pik et al., 2002; Anderson et al., 2005).

Previous studies on sandy beach invertebrates have focused on how the dynamic physical environment, as defined by waves, currents and sediments, influences their abundance and diversity across scales of 100's of metres to kilometres (e.g. Nicholas and Hodda, 1999; Rodriguez et al., 2001, 2003; Lee and Riveros, 2012). These studies have found variation among sandy beach types and tidal elevations. It has been suggested that physical disturbance in energetic marine environments may homogenise and decrease heterogeneity within communities (Lambshead and Boucher, 2003; Gallucci and Netto, 2004). Sedimentological studies have found that foreshore areas of energetic sandy beaches contain sand which is well sorted and generally finer than adjacent inshore areas, suggesting that in the swash zone, processes of laminar swash and backwash might have a homogenising effect on the environment (Edwards, 2001). The assumption that physical disturbance prevents small-scale patchiness developing at the centimetre to metre scale of energetic sandy beaches has, however, rarely been tested.

In other sedimentary environments, such as mudflats, sediment-dwelling invertebrates form patches of centimetres to metres (e.g. Findlay, 1981; Blanchard, 1990). The limited dispersal of many interstitial invertebrates (Remane, 1952; Bell and Sherman, 1980), inter-organism and animal–microhabitat interactions drive this small-scale spatial structuring (Findlay, 1981). The assumption that sandy beach fauna are homogeneous in abundance and diversity across small scales of centimetres to metres neglects to consider that physical processes may, in some instances, lead to small scale variation in sediment properties, such as grain size and skewness (Sun et al., 1993; Woodroffe, 2003), which in turn may influence interstitial invertebrates via effects on porosity, permeability, oxygen supply (Giere, 2009 p. 260), stability (i.e. settling velocity), the amount of interstitial space (McLachlan, 1978) and/or food availability (Fisher and Sheaves, 2003). Further, the assumption of homogeneity across small scales is based on the premise that biological interactions on sandy beaches are weak. There is evidence that predation and prey selectivity may influence distribution (Moens et al., 2000) and sediment structure may influence predation efficiency (Gallucci et al., 2005).

Here we use spatial autocorrelation (Cliff and Ord, 1969) to test the null hypothesis that interstitial invertebrates of exposed sandy beaches exhibit no spatial structuring at the scale of centimetres to metres. We test this hypothesis in the highly dynamic environment of the swash zone of three south-east Australian beaches which are classified as intermediate morphodynamic types (Wright and Short, 1984). We expect that contrary to the null hypothesis, on each of the three beaches we will find clear patterns of spatial structuring that in many instances reflect patterns of small-scale spatial variation in sediment grain size. We expect that scales of patchiness will vary among taxa, according to differences in their juvenile and adult dispersal capability, and differences in key functional traits, such as feeding mode and body size, that influence inter-organism and animal–microhabitat interactions. We also predict that on sandy beaches, as in other marine environments (Blanchard, 1990; Gallucci et al., 2009), spatial patterning will be sensitive to taxonomic resolution which tends to lump taxa across multiple functional groups.

2. Materials and methods

2.1. Study site and sampling methods

Our study considered small scale variation in interstitial invertebrates on three embayed intermediate beaches (*sensu* Short, 2007) along the northern coastline of Sydney, Australia: Collaroy-Narrabeen Beach, Newport Beach and Palm Beach (Fig. 1). Embayed, intermediate-type beaches dominate south eastern Australia, and are typically separated by rocky reefs that extend a few hundred metres offshore, compartmentalising the sand resources and sedimentary processes of each. All three beaches were of easterly orientation with an increasing wave energy gradient from south to north. The southern third of each beach was protected by prominent headlands and attached reefs from high energy waves that are typically of a south-south-east direction. The dominant form of each beach was transverse bar and rip, grading to rhythmic bar and beach (Short, 2007). Each beach was comprised mainly of 'marine' derived medium size quartz grains with shell fragments (Short and Wright, 1981) and experienced a spring tidal range averaging 1.6 m. Study sites were subject to regular cleaning (grooming) during the spring-summer period, but were outside of areas of beach nourishment.

On each beach, we assessed the spatial scales of alongshore variation in invertebrate abundances within a single tidal elevation stratum, the upper swash zone. We focused our sampling within a single elevational stratum because faunal communities differ among elevations (McLachlan, 1980). On each beach we identified a section of shoreline with similar wave obliquity, shore slope and distance from the southerly headland to the other beaches (see Table 1 for a full summary of the environmental characteristics of each). Within each stretch, we established a 15 m long transect that followed the upper swash zone, within the zone of saturation, above the low tide swash

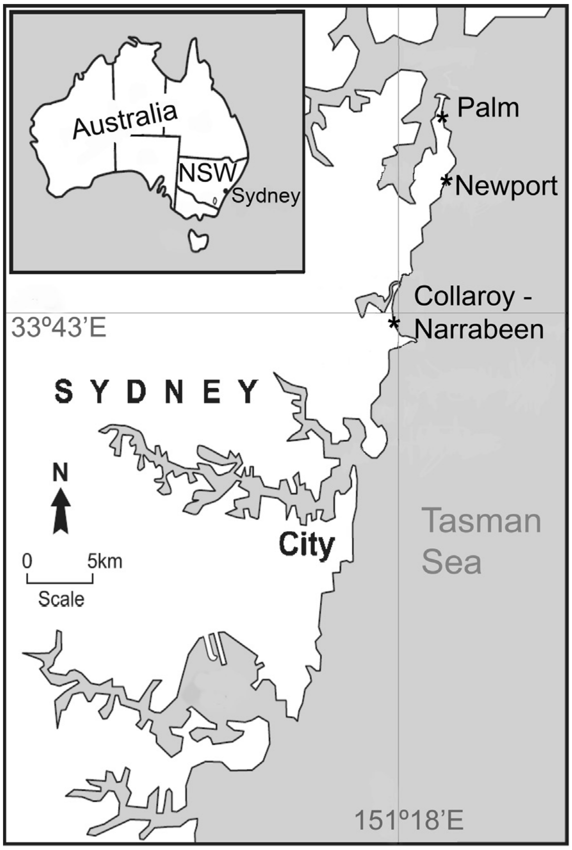

Fig. 1. The location of the three embayed beaches sampled along the northern coastline of Sydney, New South Wales (NSW), Australia. Stars indicate the location of the 15 m transect on each beach.