Estuarine, Coastal and Shelf Science 150 (2014) 67–75

Contents lists available at SciVerse ScienceDirect

Estuarine, Coastal and Shelf Science

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

Local extirpations and regional declines of endemic upper beach invertebrates in southern California

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ARTICLE INFO

Article history:
Received 21 January 2013
Accepted 20 June 2013
Available online 28 June 2013

Keywords:
coastal armoring
erosion
beach management
indicator species
intertidal environment
range limit

ABSTRACT

Along the world's highly valued and populous coastlines, the upper intertidal zones of sandy beach ecosystems and the biodiversity that these zones support are increasingly threatened by impacts of human activities, coastal development, erosion, and climate change. The upper zones of beaches typically support invertebrates with restricted distributions and dispersal, making them particularly vulnerable to habitat loss and fragmentation. We hypothesized that disproportionate loss or degradation of these zones in the last century has resulted in declines of upper shore macroinvertebrates in southern California. We identified a suite of potentially vulnerable endemic upper beach invertebrates with direct development, low dispersal and late reproduction. Based on the availability of printed sources and museum specimens, we investigated historical changes in distribution and abundance of two intertidal isopod species (*Tylos punctatus*, *Alloniscus perconvexus*) in southern California. Populations of these isopods have been extirpated at numerous historically occupied sites: *T. punctatus* from 16 sites (57% decrease), and *A. perconvexus* from 14 sites (64% decrease). During the same period, we found evidence of only five colonization events. In addition, the northern range limit of the southern species, *T. punctatus*, moved south by 31 km (8% of range on California mainland) since 1971. Abundances of *T. punctatus* have declined on the mainland coast; only three recently sampled populations had abundances >7000 individuals m^{-1}. For *A. perconvexus* populations, abundances >100 individuals m^{-1} now appear to be limited to the northern part of the study area. Our results show that numerous local extirpations of isopod populations have resulted in regional declines and in greatly reduced population connectivity in several major littoral cells of southern California. Two of the six major littoral cells (Santa Barbara and Zuma) in the area currently support 74% of the remaining isopod populations. These isopods persist primarily on relatively remote, ungroomed, unarmored beaches with restricted vehicle access and minimal management activity. These predominantly narrow, bluff-backed beaches also support species-rich upper beach assemblages, suggesting these isopods can be useful indicators of biodiversity. The high extirpation rates of isopod populations on the southern California mainland over the last century provide a compelling example of the vulnerability of upper beach invertebrates to coastal urbanization. Climate change and sea level rise will exert further pressures on upper beach zones and biota in southern California and globally. In the absence of rapid implementation of effective conservation strategies, our results suggest many upper intertidal invertebrate species are at risk.

1. Introduction

Habitat loss, degradation and fragmentation are broadly recognized as major threats to biodiversity and to the survival of vulnerable species and populations (e.g. Wilcove et al., 1998; Fahrig, 2003; Henle et al., 2004; Ewers and Didham, 2006). Coastal development, human activities and management practices have been shown to significantly impact sandy beach habitats affecting ecosystem community structure and biodiversity. On urbanized coasts, beach ecosystems are challenged by a broad range of stressors including shoreline development, contaminants, human activities and management practices, such as grooming, nourishment and coastal armoring (Defeo et al., 2009). Placement of coastal armoring structures has been shown to reduce the overall width of beaches over large stretches of coastline (Orme et al., 2011). Shoreline retreat and erosion coupled with coastal armoring causes a disproportionate reduction of upper beach habitat relative to wet and saturated lower beach habitats which can eliminate wrack-associated and other macroinvertebrates (Dugan and Hubbard, 2006; Dugan et al., 2008; Jaramillo et al., 2012). Beach filling or nourishment projects can result in complete mortality of sandy intertidal biota (e.g. Peterson and Bishop, 2005; Schlacher et al., 2012). The widespread practice of beach

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http://dx.doi.org/10.1016/j.ecss.2013.06.017

grooming or raking also directly impacts wrack-associated and upper beach invertebrates (Llewellyn and Shackley, 1996; Dugan et al., 2003) as well as coastal strand and dune biota (Dugan and Hubbard, 2010).

As sea level rises, shoreline erosion accelerates, and human populations expand on coasts, the ecological consequences of all three of these intensifying pressures on beach ecosystems become increasingly apparent. The recognition of the impacts of these growing pressures and habitat losses on beach-dependent plants, and vertebrate species, including sea turtles, pinnipeds, birds, and fish, have generated special status designations and major conservation efforts (e.g. Oli et al., 2001; Donlan et al., 2003; Garcia et al., 2003; Maschinski and Wright, 2006). Less well recognized are the disappearances of once abundant intertidal invertebrate fauna from many beaches along urbanized coastlines (e.g. Nagano, 1980). These losses have the potential to alter the biodiversity and function of beach ecosystems on regional scales along developed coasts (Dugan et al., 2008; Defeo et al., 2009; Dugan and Hubbard, 2010).

For some coastal ecosystems, individual populations of organisms, even those in marginal and fragmented habitats (sinks), can persist through the influx of planktonic propagules and larvae produced by source populations. A subset of intertidal species may be more vulnerable to disturbances; these species include taxa that do not have planktonic larval stages and have low adult dispersal, (such as oniscoidean isopods, talitrid amphipods and flightless insects). On sandy beaches, a high proportion of intertidal invertebrate species can be direct developing taxa, lacking planktonic larval stages (e.g. >50% in California; Grantham et al., 2003). Brown (2000) recognized this issue and made a strong case for the vulnerability of these upper beach species, highlighting the African isopod, *Tylos granulatus*, as an example. A list of upper beach invertebrates that appear to exemplify these vulnerabilities in the southern California region appears in Table 1.

As local scale losses of intertidal species accumulate on urban coasts, the resulting regional scale declines and fragmentation of remaining populations of these species need to be documented and recognized along with the implications for reduced biodiversity and ecosystem integrity and function. In this study we identified a suite of species that may be particularly vulnerable to the disproportionate loss and degradation of upper beach habitats in the last century in southern California (Table 1). Using published literature, unpublished dissertations, theses and reports, museum records and field surveys, we investigated changes in the distribution and abundance of selected upper beach invertebrate species over time.

2. Methods

2.1. Study area

Our study area spanned the southern California mainland coast between Point Conception and the Mexican border (approximately 450 km). The area contains six major littoral cells (Orme et al., 2011, Fig. 1) and spans five coastal counties. The study area is highly populated and includes the major population centers of the metropolitan Los Angeles area (18.1 million people) and the greater San Diego area (>3 million people). Development of the coast, including expansion of harbors, contributed several hundred million cubic meters of sediment (ranging in size from fines to cobbles) to the coast between 1920 and 1950. Individual projects, such as improvements at San Diego harbor between 1936 and 1946 placed as much as 30.6 million m^3 of sediment on the shoreline. As the surplus of sediments added to the coast from big projects faded in recent decades, the severe reduction of natural sand supply has become apparent as beaches have narrowed, coastal erosion accelerated (Griggs et al., 2005) and textural changes have become apparent (Kuhn and Shepard, 1984). The annual sediment deficit in southern California due to dams trapping sand in reservoirs has been estimated to be 1.02 million $m^3\ y^{-1}$ for more than 50 years (Griggs et al., 2005). For almost a century, responses to sand-starved beaches and coastal erosion in southern California have included extensive coastal armoring and beach nourishment projects (Orme et al., 2011). More than 120 km (27%) of the wave exposed southern California mainland coast is armored (Griggs et al., 2005). Management of southern California beaches includes other elements such as beach raking or grooming, berm building, driving and dredge disposal (Defeo et al., 2009). Mechanical beach grooming is particularly widespread affecting approximately 161 km (45%) of the beaches on the southern California mainland (Dugan et al., 2003).

Table 1
Upper intertidal and coastal strand invertebrate species that appear to be vulnerable to declines in abundance or reduced distributions on southern California beaches. #adults capable of flight, *Coastal strand zone.

Species	Taxon	Common name (family)
Tylos punctatus	Isopoda	Isopod (Tylidae)
Alloniscus perconvexus	Isopoda	Isopod (Alloniscidae)
Megalorchestia spp.	Amphipoda	Beachhoppers (Talitridae)
Dychirius marinus	Coleoptera	Beetle (Carabidae)
Cincindela spp.#	Coleoptera	Tiger beetle (Cincindelidae)
Thinopinus pictus	Coleoptera	Pictured rove beetle (Staphylindae)
Hadrotes crassus	Coleoptera	Rove beetle (Staphylindae)
*Coelus globosus**	Coleoptera	Globose dune beetle (Tenebrionidae)
Endeodes spp.	Coleoptera	Soft-winged flower beetle (Melyridae)

2.2. Study organisms

After evaluating the availability of information on distributions of potentially vulnerable species (Table 1) over time in the study area, we focused on two species of intertidal oniscoidean isopods inhabiting the upper zones of beaches on the Pacific coast of North America. The tylid isopod *Tylos punctatus* (Oniscoidea, Tylidae) is a beach endemic species that was described in 1909 based on a specimen collected in San Diego, California, USA. The distribution of *T. punctatus* extends from its current northern range limit in the study area near Carpinteria, California, USA to central Baja California, Mexico. *T. puncatus* is also reported to occur on the shores of the Sea of Cortez, Gulf of California, Mexico. However, both Lee (2013) and Hamner et al. (1969) have suggested that Pacific coast populations are deeply divergent or a separate species from the lineage found in the Gulf of California. The distribution of the alloniscid isopod, *Alloniscus perconvexus*, (Oniscoidea, Alloniscidae) another beach endemic species extends along the coast both north and south of the study area from British Columbia, Canada to Baja California, Mexico. *Alloniscus perconvexus* was described by Dana in 1854 based on a specimen collected in California.

These two beach isopod species are typical peracarid crustaceans with low fecundity that brood their young and have low dispersal rates. They apparently have very similar ecological niches, playing a significant role in kelp wrack consumption and processing (Hayes, 1969). However, no studies have made direct comparisons of their distribution, behavior or feeding in field settings. These isopods are prey for shorebirds and fish. Although tolerant of immersion in salt water, these species of oniscoidean isopods have no planktonic or swimming life stages (Brusca, 1966). Inhabiting upper intertidal and supralittoral zones of open coast sandy beaches, these and other sandy beach oniscoidean isopod species burrow in the sand near the high tide line during the day emerging at night to feed on wave cast macroalgal wrack and carrion (Ricketts et al., 1992; Brown and Odendaal, 1994; Carlton, 2007). Hayes (1969) reported that giant kelp, *Macrocystis pyrifera*, was the