Estuarine, Coastal and Shelf Science xxx (2013) 1–9

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 xxx

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

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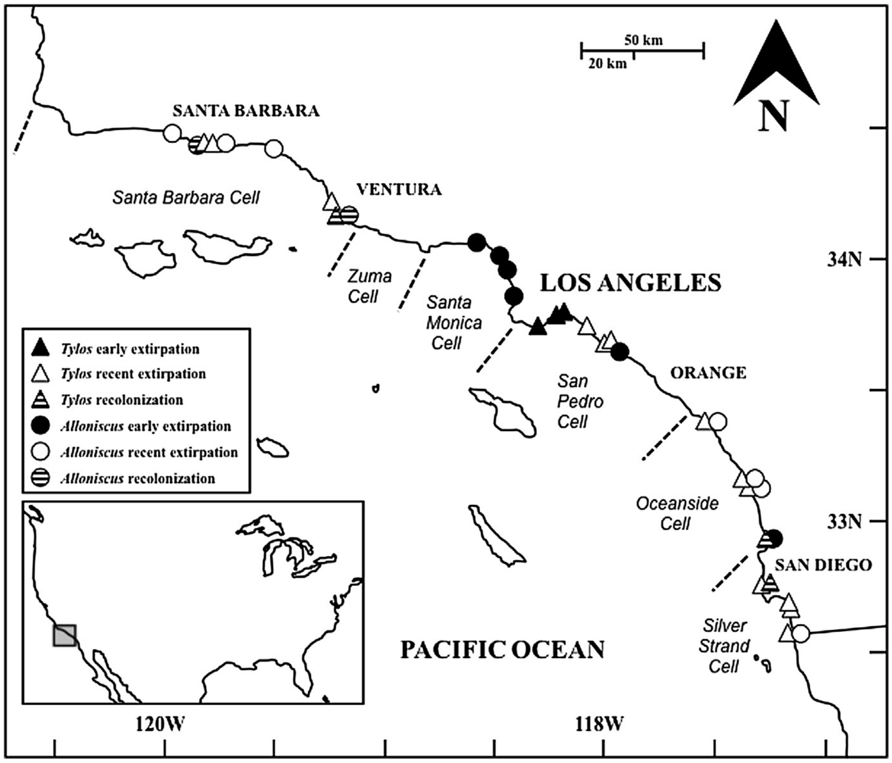

Fig. 1. Map of the southern California study area showing coastal counties and major littoral cells (separated by dotted lines, after Orme, 2011). Sites where changes in population status were found are indicated for *Tylos punctatus* (triangles) and *Alloniscus perconvexus* (circles) on the mainland coast. For both species, closed symbols indicate extirpations evident between early and middle period records and open symbols indicate those between the middle and recent records. Symbols with striped shading indicate colonization events (middle to late, or within the late period).

preferred food of *Tylos punctatus*. Burrowing behavior in intertidal oniscoidean isopods is sensitive to sediment texture and moisture levels (Holanov and Hendrickson, 1980; de Villiers and Brown, 2012; Viola et al., 2013). Seasonal patterns in surface activity have been reported for *T. punctatus*. Between March and November, this species actively foraged on the beach surface at night, while in the winter surface activity was reduced, with animals remaining buried in the sand or under wrack (Hamner et al., 1968, 1969). Maximum body lengths attained are 13 mm for *T. punctatus* (Hayes, 1969) and 16 mm for *Alloniscus perconvexus*. For *T. punctatus*, annual growth rate estimates ranged from 0.5 to 4 mm with a mean of 2 mm and males reached larger sizes than females (Hayes, 1969). These isopod species are relatively long-lived with late reproduction and low fecundity. For *T. punctatus*, Hamner et al. (1969) reported that few females reproduced before their third year producing one brood (mean of 13.6 young) per summer and most died soon after.

2.3. Data sources

We compiled historical and recent data on the distribution and abundance of *Tylos punctatus* and *Alloniscus perconvexus*, from museum records, published papers, theses, dissertations, books, technical reports and new field surveys. We obtained location information for a total of 118 beach sites, including sites where the two isopod species had been reported and sites where intertidal macroinvertebrate communities had been surveyed. Our data also included records from 37 additional sites on the California Channel Islands obtained from a variety of sources (Hewatt, 1946; US Bureau of Land Management, 1979; Straughan, 1982; Garthwaite et al., 1985; Dugan et al., 1995).

The data we compiled were classified into three major time periods, early (1913–1955), middle (1969–1982) and recent (1996–2012). Most of the early records (1913–1955) of the distributions of *Tylos punctatus* and *Alloniscus perconvexus* provided only general location information, such as the name of the nearest city (Searle, 1905; Stafford, 1912, 1913; Thompson and Thompson, 1919; Johnson and Snook, 1927; Smithsonian National Museum of Natural History, 2012). The records from 1969 to 2012 generally provided more detailed location information including beach segment (although some of these have changed over time), and local landmarks. The records from this period often included density estimates. Published studies, reports, data archives and museum specimens associated with the majority of these later records came from: Hamner et al. (1969) three sites, Clark (1969) six sites, Hayes (1969, 1970; 1974; 1977) 26 sites, Craig (1973) three sites, Patterson (1974) nine sites, Parr et al., 1978 one site, Straughan (1982) 26 sites, and Dugan et al. (1995, 2000, 2003 and unpublished) 77 sites.

2.4. Field surveys

To investigate the distribution and persistence of the study species in the region, we re-surveyed 20 sites that had supported one or more of these upper beach isopod species in the past. Our surveys were conducted between 2010 and 2011 using a variety of sampling methods. For surveys focused solely on upper beach taxa, we sampled three shore normal transects at each site during daylight hours, taking thirty 10 cm cores to 20 cm depth, from the highest (seasonal maximum) wrack line to the lower (seaward) limit of the talitrid amphipod zone on each transect. Cores were sieved through 1.0–1.5 mm mesh bags to retain animals, placed in

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labeled plastic bags then frozen and sorted in the laboratory. For intertidal community biodiversity surveys, three shore normal transects were also sampled and core size and depth and sieve size were the same as described above. Community biodiversity survey methods are described in detail in Dugan et al. (2003) and Schooler et al., 2013. In all surveys, densities were expressed as number of individuals per meter of shoreline based on the intervals between cores. The lower limit for detecting populations of isopods with these methods and the zone widths encountered would be at a density of approximately 20 individuals m^{-1} of shoreline. At four of the 20 sites, we did not conduct quantitative surveys, but visually searched for surface burrows and excavated sand near and under wrack that was located at and above the high tide line.

3. Results

3.1. Early records

Our earliest records of these two endemic upper beach isopod species are more than 100 years old (e.g. *Alloniscus perconvexus* at Santa Barbara in 1876; Searle, 1905), however, we were not able to confirm how commonly these isopods were encountered on beaches in the study area prior to initial coastal urbanization in the 1920's and the intensive development in the 1950's following World War II. Since the first quantitative intertidal surveys of southern California beaches conducted in the 1970's, these isopods have been reported at only a small proportion (25%) of the beach sites surveyed. However, the earliest (40 years ago) of these quantitative surveys were conducted following the onset of major urban development and widespread beach grooming along the southern California coastline.

3.2. Extirpations

Our recent surveys indicated that populations of these isopod species are no longer present at the majority of the beaches they historically occupied along approximately 450 km of shoreline on the southern California mainland. Overall, our analysis found populations of upper beach isopods have been extirpated at nine of the 12 (75%) sites where they were reported in the early period (before 1955) (Fig. 1). These extirpations are clustered along the metropolitan Los Angeles coast. Populations of *Tylos punctatus* appear to have been eliminated from 16 of the 28 sites where they were reported in the early and middle periods for an estimated extirpation rate of 57% in less than 100 years (Fig. 1). The estimated extirpation rate for *Alloniscus perconvexus* in the study is comparable at 64%, based on the elimination of populations from 14 of 22 sites where they were reported in the early and middle periods (Fig. 1). *T. punctatus* abundance has declined dramatically in recent years at a site where it was first reported in 2002 (Broad Beach, Zuma littoral cell). South of the study area, there is little information on the distribution or densities of these species, but the extirpation of one documented population of *T. punctatus* at Hamner et al.'s (1968, 1969) study site, Estero Punta Banda, Baja California, Mexico, located 100 km south of the US/Mexico border was noted by Hayes and Hamner (pers. comm.).

3.3. Current distribution

We were able to currently document the presence of populations of one or both of these isopod species at only 29 sites in our southern California mainland study area (Fig. 2a, b). These records include only 12 of the 31 sites where populations of isopods had been reported in the early and middle periods (five not re-sampled). Twenty of the sites that now support at least one of these isopods were not surveyed before 1996. On the mainland we confirmed the presence of *Tylos punctatus* at 17 sites, and *Alloniscus perconvexus* at 25 sites, and both species occurred at 13 of these sites. These totals do not include five sites with older records of these species that we were not able to visit. Populations of one or both of these species are known to occur on a number of beaches on the California Channel Islands (Fig. 2a, b) but only three of these sites have been recently visited to confirm status of the populations. The majority of the remaining populations of these isopods (74%) are now concentrated in the two northern littoral cells (Santa Barbara and Zuma cells) in our study area. Several of the major littoral cells in the study area currently support only a few populations each (Santa Monica cell: one population of each species at a single site, San Pedro cell: four populations at two sites, Oceanside cell: five populations at three sites, Silver Strand cell: one population)(Fig. 2a, b). Of the 29 beach sites that currently support extant populations on the mainland, 16 are backed by coastal bluffs, seven are backed by vegetated coastal dunes, and six are backed by manmade structures (four by rock revetments).

3.4. Coastal impacts

Information on specific causes of extirpations of *Tylos punctatus* and *Alloniscus perconvexus* from individual beaches in southern California is limited, although both coastal erosion and management have strongly affected their upper beach habitat. There are some clear examples of large-scale beach habitat destruction, such as the development of the ports of Los Angeles (San Pedro) and Long Beach (Fig. 3), which eliminated beach habitat and at least two populations of *T. punctatus* (e.g. Johnson and Snook, 1927). Widespread mechanical beach grooming initiated in the 1960's, which severely alters upper beach habitat, coincides with a large gap in the modern distribution of *T. punctatus* and *A. perconvexus* along the urban Los Angeles coast in the central portion of our study area (Fig. 1). Most recently, a population of *T. punctatus* was present at an estimated abundance 713 m^{-1} of shoreline in a 2002 survey at Broad Beach near Malibu (Zuma littoral cell) but was not detected in quantitative sampling in 2010 (although we found one individual in wrack) after the installation of intertidal coastal armoring (rock and geotextile revetment) (Fig. 4).

3.5. Gaps in distributions

The maximum gaps between populations are currently much larger in size (>100 km) than the gaps between all reported localities for each of these species (about 30 km) in the study area (Figs. 1 and 2). Importantly, a gap of 107 km of coastline now separates the cluster of the remaining 12 northernmost mainland populations of *Tylos punctatus from* the southern populations (Fig. 2a). Similarly, a gap of 107 km is present between the 21 northern populations of *Alloniscus perconvexus* and the four remaining southern populations on the mainland (Fig. 2b). This major gap in distributions of both isopod species encompasses the entire Santa Monica littoral cell and all but the southern end of the San Pedro littoral cell.

Currently most of the isopod populations that are separated from other conspecific populations by 10 km or less are clustered in small stretches of the study coast. All eleven gaps of less than ten km for *Alloniscus perconvexus* populations occur across a 113 km stretch of coast in the Santa Barbara and Zuma littoral cells (25% of the study area), with ten of the gaps in a 51 km distance at the northern end (11%). For *Tylos punctatus*, six of the nine gaps less than ten km occur in the vicinity of its northern range limit at Rincon County Park, Santa Barbara littoral cell and along the Zuma littoral cell (69 km, 15% of the study area).

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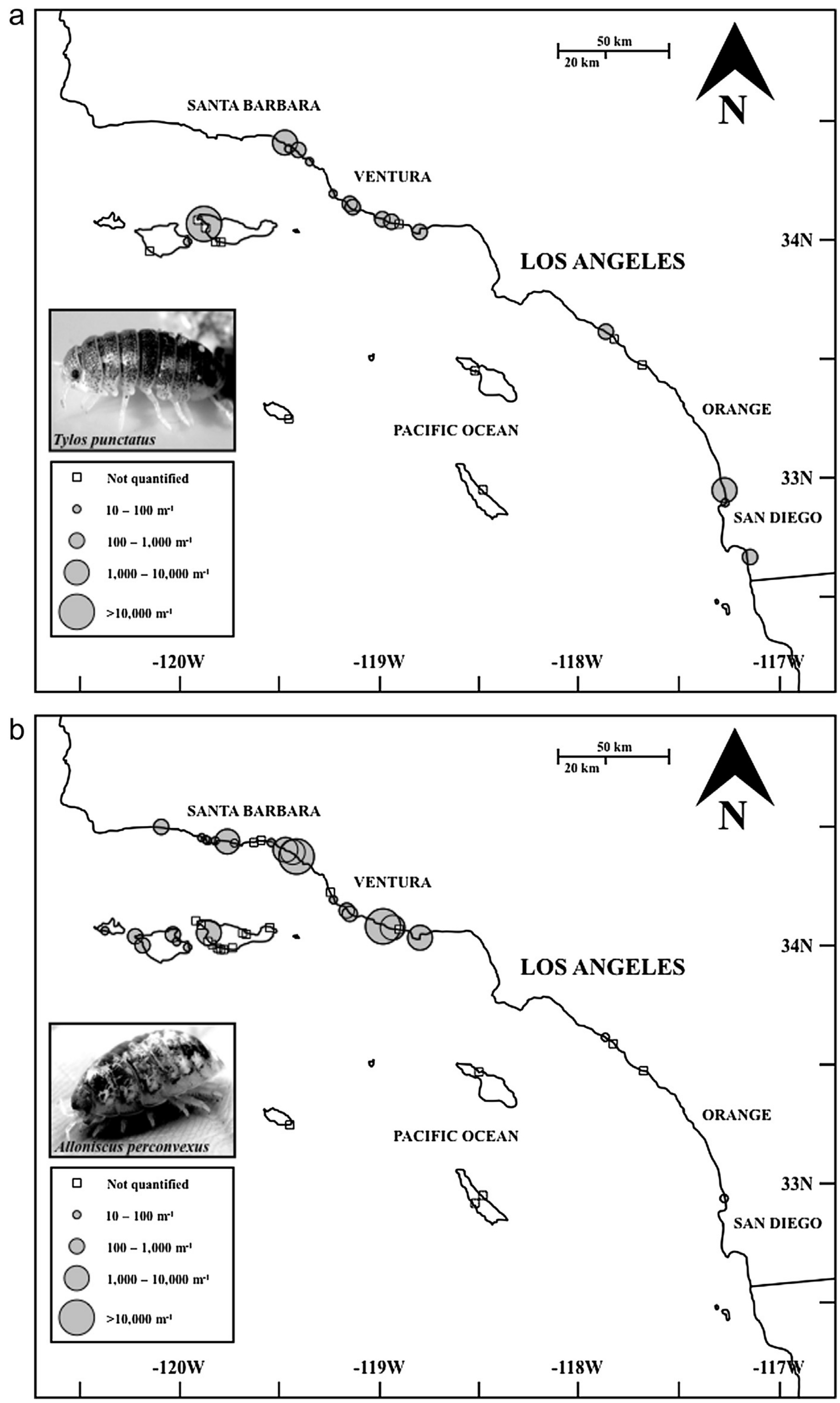

Fig. 2. Current confirmed distributions and abundance (where reported) of populations of (a) *Tylos punctatus*, and (b) *Alloniscus perconvexus* on the southern California mainland coast since 1996 and on the California Channel Islands (since 1977). The size of the gray circles indicates the relative abundance of populations at the sites. Small squares indicate the lack of information on abundance.

3.6. Population persistence

There are no data available to document year-to-year dynamics of populations of these isopod species over the decades at any site in California. However, museum specimens of *Tylos punctatus* collected at Torrey Pines in 1925, and observations from 1965 to 1966 (Hayes, 1969) combined with the current existence of a population appear to indicate 87 years of persistence at that site. Populations were also documented over a period of 89 years in Santa Barbara (1876, 1899 and 1965, Smithsonian National Museum of Natural History, 2012; Searle, 1905; Hamner et al., 1969). There may be one example of longer duration from Laguna based on a

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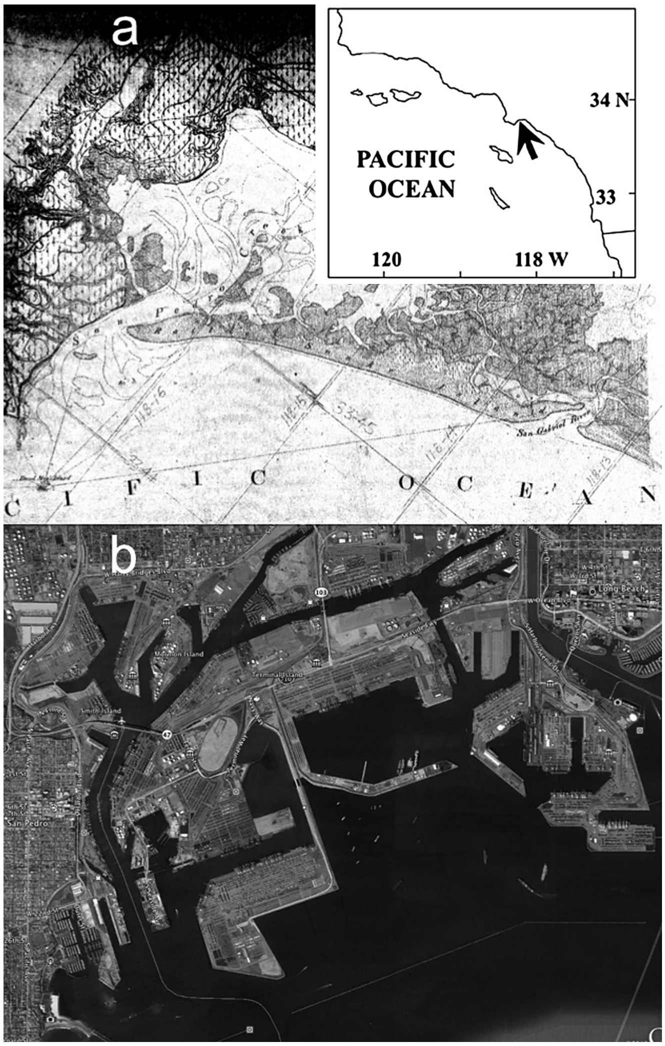

Fig. 3. Example of historical loss of beach habitat. The coastline of San Pedro and Long Beach, California: (a) shortly after statehood in 1859, and (b) the same coastline decades after port development (2007). The area includes at least two sites, San Pedro and Long Beach and approximately 7 km of beach that formerly supported populations of *Tylos punctatus*. Photographs courtesy of Google Earth and http://www.caltsheets.org/

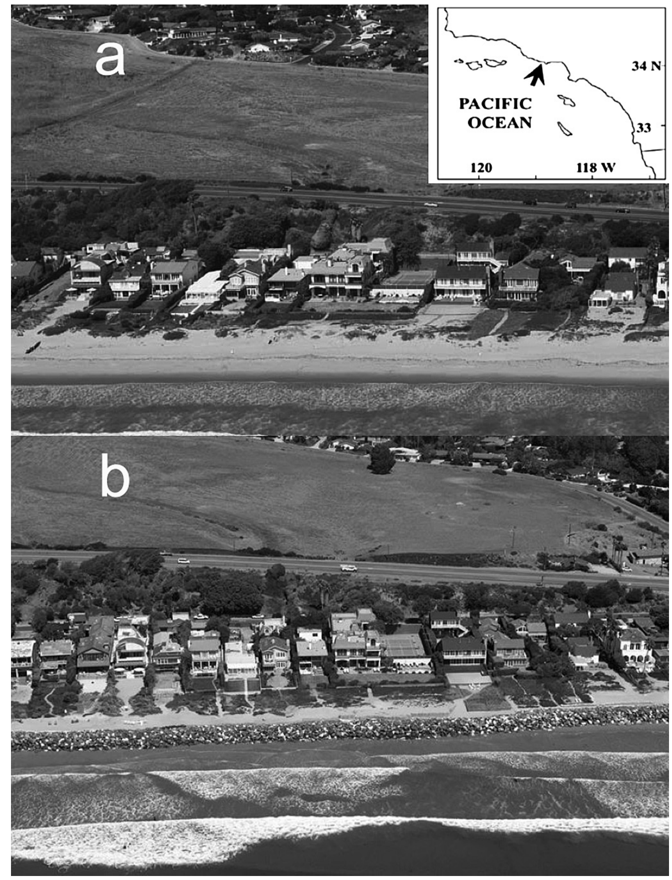

Fig. 4. Example of recent alteration of beach habitat. The coastline at Broad Beach, Los Angeles County in: (a) 2002 when *Tylos puntatus* abundance was estimated to be 714 m^{-1} of shoreline, and (b) 2010 when *Tylos puntatus* was not detected in quantitative sampling. The dry sand zone, coastal strand vegetation and connection between the dunes and the intertidal zone visible in the earlier photograph are not evident in 2010. Photographs courtesy of the California Coastal Records Project.

collection of *T. punctatus* made there in 1913, but we were not able to determine the exact location of the original collection. Populations of both species appear to have persisted continuously on the beaches of the California Channel Islands (Fig. 2) with intermittent reports of both species occurring at Christy Beach on Santa Cruz Island for over 73 years starting with a report by Hewatt (1946), observations by Straughan in the 1970's (Straughan, 1982), and our recent observations through 2012. However, overall our analysis found populations of at least one species of upper beach isopods remained at only two of the eleven (27%) of the sites identified on the mainland coast before 1950 (Torrey Pines and perhaps Laguna for which the early location was not specified).

From the middle period to the present, there are six other sites with records of populations of these isopods spanning at least four decades: Silver Strand State Beach (San Diego County) first surveyed by Clark (1969), Horse Pastures [now called Crystal Cove State Park, Orange County], Little Dume [actually Big Dume Cove, Los Angeles County], Hope Ranch (Santa Barbara County) starting with surveys by Patterson (1974), Arco [now called Haskell's, Santa Barbara County] and Isla Vista (Santa Barbara County) first surveyed by Craig (1973). The estimated persistence of populations first identified by surveys between 1969 and 1971 was six out of 18 (33%). For populations at sites first surveyed between 1996 and 1999, 10 out of 11 populations (91%) were detected in 2010 and 2011. The exception to this was the dramatic decline of *Tylos punctatus* populations at Broad Beach (Zuma littoral cell)(see above).

3.7. Range limits

The reported northern range limits for the southern isopod species, *Tylos punctatus*, all fell within the Santa Barbara littoral cell. Hamner (1969) reported the northern range limit of *T. punctatus* on beaches near the Santa Barbara wharf, which have been groomed regularly since that report. In 1971, *T. punctatus* was collected eight km further west at Hope Ranch by Patterson (1974), a record verified by specimens archived at the Santa Barbara Museum of Natural History. We re-surveyed the Hope Ranch site and ten other sites with suitable upper beach habitat within 25 km (five east and five west) between 1996 and 2010 without detecting *T. punctatus*. It should be noted that *Alloniscus perconvexus* was present at a subset of those sites, including Hope Ranch. The northernmost mainland population of *T. punctatus* found in our current surveys was at Rincon County Park in the Santa Barbara littoral cell. This result indicates that the northern range limit of *T. punctatus* shifted southward by 31 km between 1971 and 1996 (a shift equivalent to 8% of the California mainland range).

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3.8. Colonizations

Colonization or recovery events appear to be very limited for these species in the study area (Fig. 1). We found only five instances that were consistent with colonization of formerly unpopulated sites (but which might have been associated with populations below the detection limits of earlier surveys) in the records for these isopods. There are only three sites where populations are known to have colonized and persisted; all of which are located within a few kilometers of sites that have apparently supported persistent populations. In the San Diego area, Hayes (1969) found neither isopod species in his surveys at Scripps Beach or Ocean Beach. Hayes (1969) transplanted more than 1000 *Tylos punctatus* to Scripps Beach in 1967. Straughan (1982) reported *T. punctatus* at both Scripps Beach and Ocean Beach a few years later. We subsequently collected a few *T. punctatus* at the Scripps Beach site in 2011 but not in 2009 or 2010. Grooming resumed at that site in 2012, despite its status as a marine reserve. Populations of both isopod species have been documented for decades at Black's Beach located approximately one km to the north of Scripps Beach. At Ocean Beach, however, neither isopod was detected in our surveys in 2009 or 2010. At the south end of the Santa Barbara littoral cell, during years of heavy off-road vehicle use at Ormond Beach, Straughan (1982) found no upper beach isopods present in multiple surveys (1971–1978). In 1996, more than a decade after vehicles were excluded from that site, we surveyed her site once and found *T. punctatus*. In 2009–2011, both species of isopod were present in our surveys. Again, nearby populations of both species were present on beaches at Mugu Naval Air Station located immediately to the south. Lastly, on a beach on the University of California main campus in Santa Barbara, *Alloniscus perconvexus* was not detected in our quantitative surveys between 1996 and 2001. Our 2011 survey and subsequent observations indicate it recolonized this beach, which is located ~3 km downcoast from a population of these isopods at Isla Vista. This recovery may be associated with sand dynamics that resulted in widening of these bluff-backed beaches in recent years (Barnard et al., 2012).

3.9. Population abundance

Estimated abundances of endemic upper beach isopods surveyed in southern California reported in this and previous studies ranged over three orders of magnitude from 21 to 31,000 individuals m^{-1} of shoreline. Population abundance information is not available for the early periods and the earliest abundance estimates we could find were made in 1967 (San Diego).

For *Tylos punctatus* the highest abundance estimate ever reported was 31,000 individuals m^{-1} of shoreline at Carlsbad Beach in the Oceanside littoral cell in the late 1960s (Hayes, 1969). However, *T. punctatus* was not detected in our surveys at that location in 2010, 2011 or 2012 after sandy upper beach habitat had been converted to cobble by erosion. The highest abundance of *T. punctatus* recorded in recent years was observed on Santa Cruz Island (>20,000 individuals m^{-1} in 2011) (Fig. 2a). For the mainland coast, the highest values of abundance of *T. punctatus* recorded in recent years were <10,000 individuals m^{-1} (Fig. 2a). Peak abundance estimates ranging from 7000 to 9000 m^{-1} were found at three sites between 1996 and 2010, which were located in three different littoral cells (Santa Barbara, Zuma and Oceanside) (Fig. 2a).

Recent peak estimates for population abundance of *Alloniscus perconvexus* were higher than those obtained for *Tylos punctatus* on the mainland coast, reaching maximum values of 20,920 individuals m^{-1} at Oil Piers and 11,075 individuals m^{-1} at Deer Creek, both in the Santa Barbara littoral cell in 2010 (Fig. 2b). Importantly, in the four major southern littoral cells, population abundance of *A. perconvexus* did not exceed 100 individuals m^{-1} at any site (Fig. 2b). All of the populations with abundances >100 individuals m^{-1} of this species were found at sites in the two northern littoral cells (Santa Barbara and Zuma) (Fig. 2b).

Where these two isopod species co-occurred in earlier and our surveys, an inverse relationship in abundance was apparent (Fig. 5). Differences in the mean abundance between the two species increased significantly as the mean abundance of *Tylos punctatus* increased. This relationship was significant for all surveys conducted between 1969 and 2011 ($r = 0.870$, $n = 19$, $p < 0.001$), and also for the surveys conducted between 1996 and 2011 ($r = 0.773$, $n = 18$, $p < 0.001$). Although this result is consistent with competition between the two species, we could not adequately evaluate potential mechanisms underlying this pattern due to a lack of supporting experimental or observational data and the fragmentation and restricted distribution of populations of both species in the region.

4. Discussion

The high extirpation rates of populations of upper beach isopods on the mainland coast of southern California over the last century found by our analyses provide a compelling example of the vulnerability of upper beach biota to habitat loss and alteration associated with coastal development and beach management practices. Our study also identified major gaps in distributions and declines in abundance of two invertebrate species endemic to the upper intertidal zones of sandy beaches. Our results for two species of beach isopods on the southern California mainland strongly support Brown's (2000) predictions concerning the vulnerability of populations of upper beach invertebrates, particularly those with low dispersal abilities and low reproductive rates. They also support our hypothesis that a disproportionate loss and alteration of upper intertidal zones of beaches in the study area due to development, armoring, grooming and other factors has been associated with declines in the diversity and distribution of upper intertidal macroinvertebrates.

Endemic upper beach isopods may be sensitive indicators of beach ecosystem conditions because of their life history attributes, limited dispersal and habitat requirements (Brown, 2000). The extensive loss of populations of both isopod species across the southern California mainland coast is probably associated with widespread anthropogenic stressors detailed in the study area description, many of which disproportionately affect upper intertidal habitats. For example, the majority of the 161 km of groomed beaches are located in the Santa Monica and San Pedro littoral cells where a major gap in isopod distributions now exists, despite the

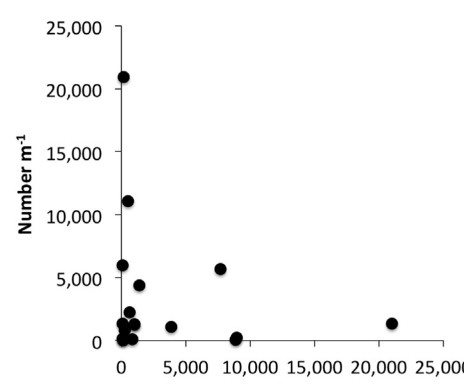

Fig. 5. Abundance of *Tylos punctatus* (*x*-axis) and *Alloniscus perconvexus* (*y*-axis) at 18 sites where they co-occurred in samples between 1996 and 2011.

relatively wide sandy beaches (Orme et al., 2011). Although early records are limited for southern California, we consider it likely that populations of other species of invertebrates of the upper intertidal beach with narrow habitat preferences and/or low dispersal abilities (Table 1) have suffered comparable declines and fragmentation of their distributions (e.g. Nagano, 1980 for tiger beetles).

Most of the currently known populations of these isopods occur on unarmored beaches that lack routine beach grooming and have limited vehicle access and minimal management manipulations associated with recreation. These include areas requiring more effort (hikes, stairs) for visitors or vehicles to access, a military base, and California State Parks with high levels of resource protection. The isolated but relatively undisturbed and lightly visited beaches of the California Channel Islands appear to support persistent populations of both species (Garthwaite et al., 1985) attesting to the ability of small populations of these species to remain viable. On the mainland coast, many of the remaining populations of isopods occur on narrow bluff-backed pocket beaches that retain sufficient sand volumes and suitable upper beach habitat. These narrow beaches also support species-rich assemblages of upper beach invertebrates, suggesting these isopods may be useful as indicators of biodiversity. Populations of isopods are also present on some beaches backed by artificial rock revetments that are presently above the reach of regular tidal influence.

Due to the strong influence of sediment transport and dynamics associated with littoral cells (e.g. Griggs et al., 2005), we expect connectivity will be much greater among populations of upper beach biota within littoral cells than across littoral cells. The 100 km gaps now present in the ranges of the two isopods (Fig. 1) on densely populated urban coast in the vicinity of metropolitan Los Angeles (Santa Monica and San Pedro littoral cells) suggest that distributions of these animals are now severely fragmented. The largest gaps between all documented historic populations were roughly 30 km on the mainland coast for both species. The historic gaps were likely smaller than 30 km if undocumented populations were present in the study area. The large gaps and small number of adjacent population pairs has resulted in reduced potential for connectivity between the northern and southern populations remaining in our study area and within the Santa Monica and San Pedro littoral cells. Beaches with high potential for connectivity or colonization from known populations (e.g. within 10 km) are now mostly limited to the Santa Barbara and Zuma littoral cells. However, the low number of colonization and re-colonization events we were able to document in our dataset does not augur well for natural recovery of isopods on mainland beaches, particularly in the four southern littoral cells.

Habitat fragmentation and connectivity of populations of these and other upper beach species will be further affected by sea-level rise associated with climate change. As sea level rises, the narrow bluff-backed beaches where most of these populations persist in the study area will have little potential for retreat. Only a small fraction (<10%) of the 450 km of southern California coast will have the potential to provide suitable upper beach habitat under a scenario of 140 cm of sea-level rise by 2100 (Revell et al., 2011; NOAA, 2012). Most of the potential for shoreline retreat and restoration in the region under this scenario appears to be in the eastern Santa Barbara littoral cell, where as much as 12 km of relatively undeveloped shoreline might be able to accommodate retreat geomorphically if the economic and political elements of conservation planning are achieved. Successful conservation strategies for coastal endemic species such as these isopods and those in Table 1 will likely require assisted migration, transplantation of species and associated communities to new sites, and restoration of degraded areas capable of accommodating sea-level rise.

Urbanized coastal southern California has been recognized as a hotspot of endangerment and extinction for terrestrial flora and fauna (e.g. Dobson et al., 1997). Biota of the upper beach and coastal strand zones of this region appear to fit this pattern. Based on our results, we suggest that populations of two beach endemic isopods, *Tylos punctatus* and *Alloniscus perconvexus,* are now fragmented and declining across much of their historically occupied southern California range. Our estimates for the extirpation rates of these isopods seem to be lower in the most recent period than in earlier decades. However, there are far fewer extant populations and two recent examples, including the armoring of one site (2006) and the resumption of grooming at a designated marine reserve (2012), suggest that the current coastal management framework is not sufficient to protect the remaining populations of these isopods. Given the prospects for continued population losses posed by human activities, coastal erosion, sea-level rise and climate change, these two beach isopods could be considered imperiled species on the southern California coastline.

Acknowledgments

We are very grateful to M. Clark, R. Garthwaite, W. Hamner, W. Hayes, F.G. Hochberg, D. Pryor, D. Straughan, and S. Taiti for generously sharing their records, expertise and long-term perspectives on the study animals and area. We would also like to thank L. Hurtado, R. Wetzer, and J. Wright for their expert assistance. We gratefully acknowledge our crew of student field and laboratory assistants for their willing and cheerful help with field surveys and sample processing. We thank California State Parks for permission to conduct field surveys at numerous state beaches in the study area. We also thank the University of California Natural Reserve System for providing research access to the Scripps Coastal Reserve, Santa Cruz Island Natural Reserve and Coal Oil Point Natural Reserve for field surveys. This research was supported by funding from the California Sea Grant Program (Project R/ENV 210, including a Sea Grant Traineeship to N. Schooler and Project R/MPA-24 through the California Ocean Protection Council), the UCSB Coastal Fund, and the Santa Barbara Coastal Long Term Ecological Research project (National Science Foundation award no. OCE-0620276).

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Please cite this article in press as: Hubbard, D.M., et al., Local extirpations and regional declines of endemic upper beach invertebrates in southern California, Estuarine, Coastal and Shelf Science (2013), http://dx.doi.org/10.1016/j.ecss.2013.06.017