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No lines in the sand: Impacts of intense mechanized maintenance regimes on sandy beach ecosystems span the intertidal zone on urban coasts

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ABSTRACT

As coastal population growth accelerates, intensive management practices increasingly alter urban shorelines, creating major conservation challenges. To evaluate key ecological impacts and identify indicators of coastal urbanization, we compared intertidal macroinvertebrate communities between urban beaches with intense maintenance regimes (sediment filling and grooming) and reference beaches lacking such maintenance in densely populated southern California. On urban beaches, intertidal communities were highly impacted with significantly reduced species richness, abundance, and biomass (effect sizes: 79%, 49%, 30%, respectively). Urban impacts affected macroinvertebrates across all intertidal zones, with greatest effects on upper intertidal wrack-associated taxa. On urban beaches altered intertidal communities were remarkably homogeneous across littoral cells in a biogeographically complex region. Functional diversity comparisons suggested degraded ecological functioning on urban beaches. No taxa flourished on urban beaches, but we identified several vulnerable indicator taxa. Our results suggest intense maintenance regimes on urban coasts are negatively impacting sandy beach ecosystems on a landscape scale. Beaches not subject to intense mechanized maintenance, can support high biodiversity, even near major urban centers.

1. Introduction

As human populations expand world-wide, a growing number of ecosystems are being profoundly altered by urbanization (McDonald et al., 2008; McKinney, 2002) including highly valued coastal ecosystems. Understanding the extent to which the structure and function of coastal ecosystems respond to impacts associated with urbanization is crucial to conserving these threatened ecosystems and the vital functions and services they provide. Bounded by land and sea, intertidal zones are recognized as some of the most vulnerable marine ecosystems to growing coastal urbanization (Halpern et al., 2007; Ruttenberg and Granek, 2011) as well as climate change (Harley et al., 2006). The identification of robust indicators of ecological condition will aid the management of vulnerable coastal ecosystems as urbanization expands. Sandy beaches make up a major component of many urban coasts and are highly valued as socioeconomic assets that support extensive recreation and tourism (Pendleton et al., 2001). Equally important but generally less valued are the unique biodiversity and irreplaceable ecosystem functions (e.g. nutrient cycling and wildlife support) of natural beach ecosystems (Dugan et al., 2010; Schlacher et al., 2008).

Beach ecosystems regularly experience a number of impacts associated with urbanization (e.g. artificial light, mechanized maintenance, pollution, recreation). We focus here on the major alteration of intertidal substrate associated with intense mechanized maintenance of sandy beaches that is often neglected in urban ecology. The widespread beach maintenance activities that we focus on here include the frequent raking and sifting of the intertidal and supralittoral zones – primarily the upper intertidal – using heavy equipment to remove wave-delivered macrophyte wrack, trash, and litter (grooming) and the addition of large quantities of non-native sand across all intertidal zones to create artificially wide beaches (sediment filling). Long stretches of the southern California coast are highly urbanized and nearly half of the beaches (> 160 km) are subject to some form of intense mechanized maintenance (Dugan et al., 2003; Patsch and Griggs, 2006). On urban beaches the scaling of these human impacts varies spatially from very local to landscape scales and temporally from weeks to decades (Defeo et al., 2009). At a local scale, mechanical maintenance results in the immediate direct and intense mortality of intertidal macroinvertebrates via grooming (e.g. Dugan et al., 2003; Llewellyn and Shackley, 1996; Zielinski et al., 2019) and beach filling episodes (e.g. Peterson et al., 2000, 2014; Speybroeck et al., 2006). The combination of frequent beach grooming and the retention of non-native coarse and poorly sorted sediment from past beach filling episodes (Leidersdorf et al., 1993) can alter habitat quality for intertidal macroinvertebrates (Dugan

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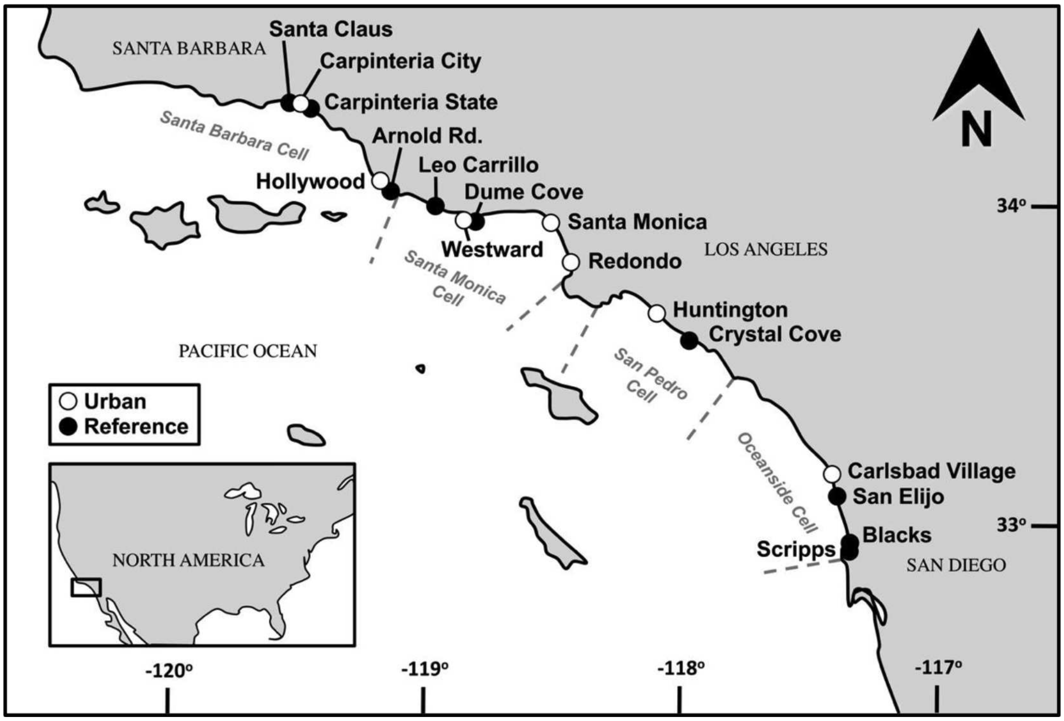

Fig. 1. Map of the study region with names and locations of the urban (white dot) and reference (black dot) sandy beach study sites surveyed and the littoral cell names and boundaries (dashed gray lines) on the coast of southern California, USA.

et al., 2000a, 2003; Manning et al., 2014; Viola et al., 2014) as well as the physical processes on beaches (Dugan and Hubbard, 2010; Komar, 1998; van der Wal, 1998).

The dramatic changes to the substrate of sandy beaches under urban management regimes can persist for decades on a variety of spatial scales (Peterson et al., 2014; Speybroeck et al., 2006). At a regional scale, littoral cells are important coastal landscape features that contain a complete sediment budget including sources (e.g. rivers, streams, bluffs), movement (e.g. onshore-offshore and longshore transport), and sinks (e.g. submarine canyons, coastal dunes) (Orme et al., 2011; Patsch and Griggs, 2006). These major features influence the quantity and quality of sandy beach habitat and can contribute to the biogeographic structure and biodiversity of intertidal macroinvertebrate communities (Claisse et al., 2018; Hubbard et al., 2014; Schooler 2018). In southern California, major beach filling episodes (totaling > 250 million cubic meters of sand) have considerably altered sediment dynamics in a number of the important littoral cells (Orme et al., 2011). The ecological effects of this landscape scale disruption of the natural sediment regime and associated environmental conditions of sandy beach ecosystems are not known.

The intertidal macroinvertebrate communities of sandy beaches are dominated by highly mobile burrowing taxa that constantly shift position to adjust to tides, waves, and changing beach conditions and rely on subsidies (e.g. wrack, phytoplankton) imported from adjacent ecosystems (Dugan et al., 2003; McLachlan and Brown, 2006). In temperate regions these endemic beach communities can be partitioned into two major groups based on functional traits and habitat requirements. Differences in traits associated with trophic guild, intertidal zonation, life history, and dispersal capability between these groups could influence their relative vulnerability and potential utility as indicators (Dugan et al., 2003; Schooler et al., 2017). Many biota of the wave-washed mid to lower intertidal zones of beaches are suspension or deposit feeders (hereon referred to as lower beach macroinvertebrates). Most of these lower beach taxa have dispersive planktonic larval stages that can facilitate recolonization following disturbance (Grantham et al., 2003; Jones et al., 2017; Schooler et al., 2017). Higher on the shore, biota inhabiting damp sand near the driftline rely on subsidies of macrophyte wrack for food and shelter (hereon referred to as wrack-associated macroinvertebrates). These taxa often have direct development and low dispersal abilities, traits that can make their populations more vulnerable to disturbance (Defeo et al., 2009; Hubbard et al., 2014; Schooler et al., 2017).

The effects of widespread urbanization on biodiversity, structure, and function of sandy beach ecosystems are beginning to be appreciated more broadly (e.g. Defeo et al., 2009). However, studies to date have largely focused on taxa or guilds with life history traits and ecological requirements that make them particularly vulnerable to disturbance (e.g. upper intertidal wrack-associated macroinvertebrates) (Bessa et al., 2014; Dugan et al., 2003; Hubbard et al., 2014; Schooler et al., 2017; Veloso et al., 2008). Although the potential impacts of widespread urban beach maintenance regimes on intertidal biodiversity of the entire sandy beach ecosystem are substantial, impacts to the diverse and abundant lower beach biota that represent key prey resources for fish and birds remain largely undescribed. To fill this critical gap, a quantitative analysis of the ecological impacts of intensive urban beach maintenance on macroinvertebrate biodiversity, community structure, and function across all intertidal zones of sandy beaches is needed.

The combination of high natural biodiversity, strong biogeographic structure, and locally intense anthropogenic impacts on a densely populated urban coast (Claisse et al., 2018; Dugan et al., 2000a, 2003; Schooler et al., 2017) make sandy beaches of southern California an ideal ecosystem for assessing impacts associated with coastal urbanization. To investigate the responses of sandy beach ecosystems to widespread urban impacts, we compared the structure and function of intertidal macroinvertebrate communities of urban sandy beaches subject to intense mechanized maintenance regimes with those of reference beaches lacking mechanized maintenance. We evaluated the hypotheses that intense mechanized maintenance of sandy beaches associated with urbanization 1) degrades biodiversity, structure, and functioning of these ecosystems across all intertidal levels, 2) homogenizes community composition and assembly on a landscape scale that spans littoral cells, and 3) differentially impacts two key groups of

Table 1

The site names, coordinates, beach types, littoral cells, and dates surveyed for the 16 study beaches arranged by beach type then geographically from north to south. Subscript SP and/or MPA indicate that the study site is located in a California State Park (Santa Monica: Santa Monica State Beach, Carpinteria State: Carpinteria State Beach, Leo Carrillo: Leo Carrillo State Park, Dume Cove: Point Dume State Beach, Crystal Cove: Crystal Cove State Park, San Elijo: San Elijo State Beach) and/or Marine Protected Area (Westward and Dume Cove: Point Dume SMR, Crystal Cove: Crystal Cove SMCA, San Elijo: Swami's SMCA, Scripps: Matlahuayl SMR), respectively.

Site	Latitude	Longitude	Beach Type	Littoral Cell	Survey Date
Carpinteria City	34°23′38.9″N	119°31′33.6″W	Urban	Santa Barbara	October 6, 2014
Hollywood	34°10′13.1″N	119°13′59.7″W	Urban	Santa Barbara	September 1, 2015
Westward$_{\mathrm{MPA}}$	34°00′10.0″N	118°48′35.3″W	Urban	Santa Monica	September 21, 2009
Santa Monica$_{\mathrm{SP}}$	34°00′39.5″N	118°30′00.7″W	Urban	Santa Monica	October 22, 2014
Redondo	33°49′10.4″N	118°23′27.4″W	Urban	Santa Monica	August 31, 2015
Huntington	33°38′54.2″N	117°59′28.7″W	Urban	San Pedro	October 9, 2014
Carlsbad Village	33°09′29.5″N	117°21′13.9″W	Urban	Oceanside	October 8, 2014
Santa Claus	34°24′30.8″N	119°33′05.8″W	Reference	Santa Barbara	October 6, 2010
Carpinteria State$_{\mathrm{SP}}$	34°23′29.4″N	119°31′18.1″W	Reference	Santa Barbara	August 21, 2009
Arnold Rd.	34°07′11.9″N	119°09′36.1″W	Reference	Santa Barbara	October 21, 2010
Leo Carrillo$_{\mathrm{SP}}$	34°02′49.4″N	118°56′52.5″W	Reference	Santa Monica	September 30, 2011
Dume Cove$_{\mathrm{SP,\ MPA}}$	34°00′21.1″N	118°48′06.3″W	Reference	Santa Monica	October 12, 2011
Crystal Cove$_{\mathrm{SP,\ MPA}}$	33°34′40.2″N	117°50′51.5″W	Reference	San Pedro	September 29, 2011
San Elijo$_{\mathrm{SP,\ MPA}}$	33°01′29.6″N	117°17′11.9″W	Reference	Oceanside	October 29, 2011
Blacks	32°53′17.3″N	117°15′12.2″W	Reference	Oceanside	October 27, 2011
Scripps$_{\mathrm{MPA}}$	32°51′49.2″N	117°15′17.8″W	Reference	Oceanside	August 21, 2011

endemic intertidal taxa (wrack-associated and lower beach macroinvertebrates) that could serve as ecological indicators. We also explored the relative influence of selected environmental factors (e.g. sediment characteristics, macroalgal wrack, beach width) in the manifestation of urban impacts to intertidal and functional biodiversity and structure in sandy beach ecosystems.

2. Material and methods

2.1. Study area

Our study area spanned ~300 km of coastline in southern California from Carpinteria (34°24′30.8″N) to San Diego (32°51′49.2″N) (Fig. 1; Table 1). The 16 study beaches (seven urban and nine reference) were located in four major littoral cells (Santa Barbara, Santa Monica, San Pedro, and Oceanside; Patsch and Griggs, 2006; Fig. 1; Table 1). At least one urban and one reference study beach were located within each littoral cell. The study area spans a single biogeographic province, the Californian or California Transition Zone (Newman, 1979).

More than 160 km of the sandy shoreline in southern California are subject to some form of intense mechanized maintenance associated with urbanization (grooming, beach filling) (Dugan et al., 2003; Patsch and Griggs, 2006). For our comparisons, urban beaches (Fig. 2ab; Table 1) were defined as beaches that are subjected to a similar rate of locally intensive maintenance activities conducted using heavy equipment. These activities included decades of year-round frequent (at least weekly) mechanical grooming and past beach filling with imported sand resulting in artificially wide upper beach zones at our study sites (Orme et al., 2011, personal communication; Coastal Sediment Management Workgroup). These intensive maintenance activities strongly influence the morphology, physical characteristics, and profiles of urban beaches which are typically characterized by narrow, steep intertidal zones and wide, flattened upper beach zones devoid of wrack deposits and vegetation (Fig. 2ab; Dugan and Hubbard, 2010).

Anthropogenic influences, such as altered sediment budgets (Orme et al., 2011), that occur on regional and littoral cell scales can affect all beaches regardless of local management activities (Defeo et al., 2009). For this reason, we selected reference beaches that had never been subject to direct mechanized maintenance activities (grooming or beach filling) and exhibited the best attainable ecological condition for sandy beaches on an urban coast (*sensu* Stoddard et al., 2006) (Table 1). The morphology and profiles of these beaches were largely the result of natural coastal processes rather of than direct human interventions (Fig. 2cd).

2.2. Beach surveys

We sampled each of the study beaches once during daytime spring low tides in the late summer or fall (August to October), prior to strong late fall and winter storms that cause considerable beach erosion and a few months after the major spring recruitment pulses of many taxa. This is when intertidal diversity, abundance, and biomass are generally most stable for both beach types in the region (Dugan et al., 2003; Schooler et al., 2017) (Table 1). Our comparisons included beaches surveyed in different years as the variation in species richness, abundance, and biomass of macroinvertebrates among beaches in the study region tend to be much greater than observed interannual variation at individual beaches, particularly in the absence of major changes in disturbance regimes (Schooler et al., 2017). During the survey at each beach, all biotic and physical measurements were collected along three transects using the methods of Dugan et al. (2003), which we describe in more detail in the Supplementary material (Appendix S1).

To estimate biodiversity and community structure of intertidal macroinvertebrates, we collected a series of 150 core (diameter: 10 cm, depth: 20 cm) samples at uniform intervals along each of the three transects per site (total area sampled per site: 3.5 m^2), sieved the contents of 10 pooled cores (= one sample) through mesh bags (aperture: 1.5 mm), and preserved each sample in 10% buffered formalin. All macroinvertebrates retained in the samples were identified to the lowest taxonomic level possible, typically species, enumerated, and weighed to the nearest milligram blotted wet weight. Abundance and wet biomass values were expressed per meter wide strip of beach extending from the landward boundary to the low swash as recommended for the highly mobile fauna of this dynamic ecosystem (McLachlan and Brown, 2006).

We measured the cover and composition of drift macrophytes (kelp, algae, surfgrass) and other wrack using a line-intercept method on the same three transects sampled for macroinvertebrates. Measurements of wrack were grouped into two categories, macroalgal (brown, green, and red algae) and total (all macrophyte wrack and debris except tar and terrestrial vegetation) wrack. Mean (± SE) values for these groups were calculated for the three transects for each site and expressed as the area (m^2) of wrack per meter wide strip of beach (see above).

The following physical characteristics were averaged (± SE) across the three transects at each site: widths of total beach, upper beach, and active intertidal zones, slope at the water table outcrop (WTO), and mean grain sizes and sediment sorting at the WTO and high tide strandline (HTS). Dean's parameter (Ω), which is used to characterize

Fig. 2. Examples of urban and reference beach types. Photographs of examples of urban study beaches at a) Santa Monica and b) Huntington and of reference study beaches at c) Leo Carrillo and d) Crystal Cove. Aerial photographs are copyright © 2002–2015 Kenneth & Gabrielle Adelman, California Coastal Records Project, www.californiacoastline.org.

beaches by morphodynamic state, was calculated from breaker height divided by the breaker period and sand fall velocity (Short and Wright, 1983) for each site. In global scale comparisons, beaches with higher values of Dean's parameter have been associated with higher species richness and abundance (Barboza and Defeo, 2015; McLachlan, 1990).

2.3. Univariate analyses

To evaluate hypotheses concerning the response of diversity and key functional groups to urbanization on sandy beaches and potential utility as ecological indicators, we collated our data into three groups: the total intertidal macroinvertebrate community (hereon referred to as total community) and two major groups based on trophic guild, intertidal zonation, functional traits, and dispersal ability, the lower beach and wrack-associated macroinvertebrate groups. No taxa overlapped across the two major groups of macroinvertebrates, and all taxa (including predatory taxa) from the total intertidal community were assigned to one of these two groups.

For each of the three groups of intertidal macroinvertebrates, we calculated the mean values of abundance and biomass per meter (± SE) across the three transects for each study beach. Cumulative species richness was calculated and pooled across the three transects for each beach and group. An estimate of true species richness was generated for each site and group using EstimateS software (v.9.1; Colwell, 2013) from abundance data. For this analysis, we used the first order jackknife estimator (Jack1), which was determined to be the best estimator for use in beach ecosystems (Schoeman et al., 2008). Comparisons of biodiversity, community structure, and environmental characteristics between urban and reference beaches were evaluated using one-way ANOVA and estimates of effect size (η^2) were calculated using SPSS (v.17.0).

2.4. Functional traits and diversity

To evaluate whether functional diversity differed between urban and reference beaches, we compiled a species-by-traits matrix (Supplementary material; Table S1) that comprised 15 traits with 52 modalities (Supplementary material; Table S2). For our analyses of functional diversity, we calculated three multivariate indices, functional richness, functional evenness, and functional dispersion, to assess different components of functional diversity using the R Package *FD* (Laliberté et al., 2014). The R package *FD* uses a species-by-traits matrix to calculate the Gower dissimilarity for different functional traits. Axes from a principal coordinate analysis (PCoA) are then treated as new traits to compute functional diversity. PCoA axes corresponding to negative eigenvalues are imaginary and cannot be represented in Euclidean space, so we used a correction approach for the species-distance matrix (Lingoes, 1971). Functional evenness and dispersion can be weighted by using a species-abundance matrix and shifting the centroid closer to the more abundant species in multidimensional space, which we employed here because weighted values are considered good predictors of ecosystem functioning provided by animals (Gagic et al., 2015). These methods are described in more detail in the supplementary material (Appendix S1).

2.5. Multivariate analyses

We evaluated the null hypothesis that the macroinvertebrate

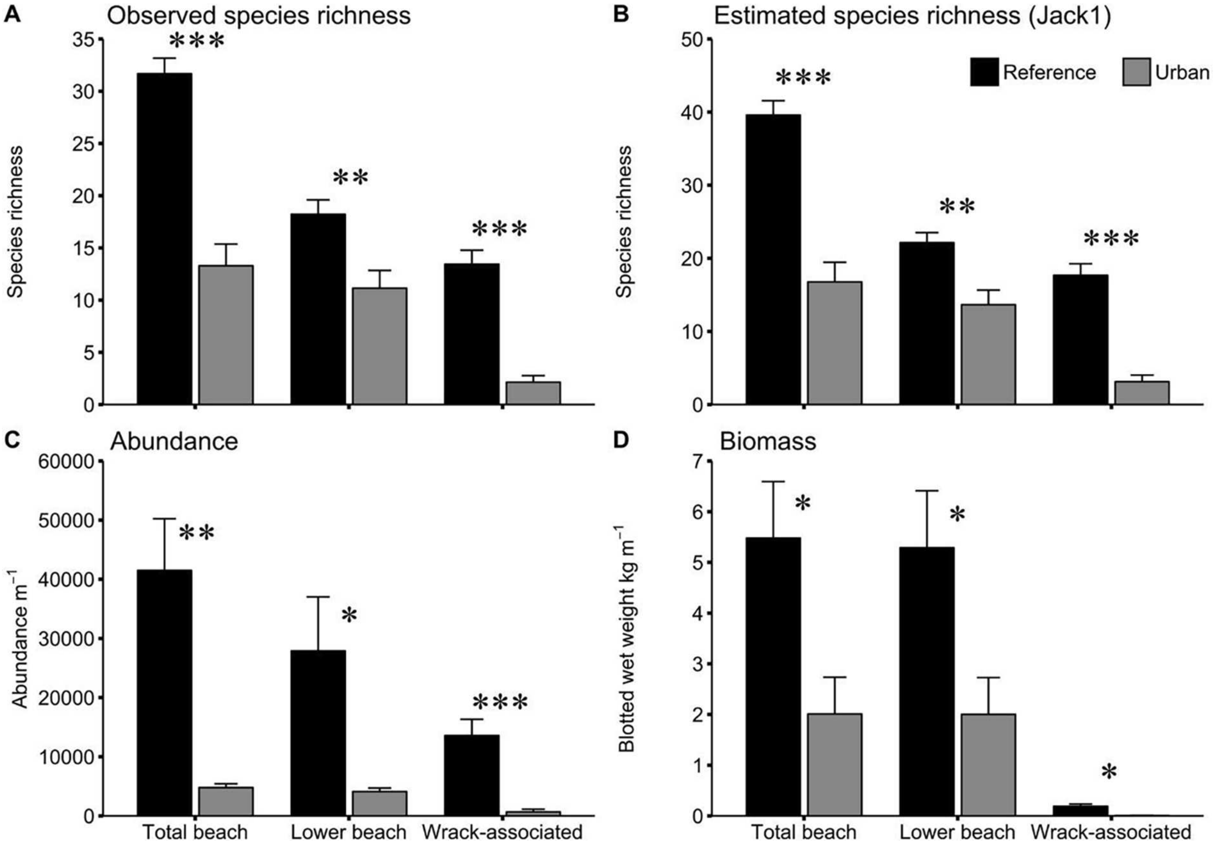

Fig. 3. Comparisons of the biodiversity and structure of the total beach, lower beach, and wrack-associated macroinvertebrates for reference (black, $N = 9$) and urban (grey, $N = 7$) study beaches. The bars represent the mean ± SE for A) observed species richness, B) estimated (Jackknife 1) species richness, C) abundance, and D) wet biomass ($* = P \leq 0.05$, $** = P \leq 0.01$, $*** = P \leq 0.001$). See Table 2 for effect sizes.

assemblage patterns (variance in the abundance-based or biomass-based data clouds) for the total intertidal community and the lower beach and wrack-associated macroinvertebrate groups did not differ between urban and reference beaches and across littoral cells using multivariate analyses. Abundance and wet biomass data were averaged across the three transects for each beach and grouped by beach type (urban or reference) and littoral cell (Santa Barbara, Santa Monica, San Pedro, or Oceanside) for these analyses. Macroinvertebrate assemblage patterns were analyzed using multivariate routines in the statistical software package PRIMER 6 (Clarke and Gorley, 2006) and PERMANOVA+ (Anderson et al., 2008) unless otherwise specified. Prior to analyses, abundance and biomass data were log (x + 1) transformed to minimize the influence of dominant taxa and used to compute Bray-Curtis dissimilarity matrices.

To examine macroinvertebrate assemblage patterns, we employed unconstrained non-metric multidimensional scaling ordination (nMDS). We tested for significant differences in macroinvertebrate assemblage patterns among the two beach types (urban and reference) using analysis of similarity (ANOSIM) (Clarke and Warwick, 1994). Using similarity of percentages (SIMPER) analysis, we identified the taxa contributing most to statistically significant differences among urban and reference beach macroinvertebrate assemblages. We used a one-factor permutational multivariate analysis of variance (PERMANOVA) to test for significant differences across littoral cells for each beach type (Anderson, 2001). Using a two-factor nested PERMANOVA with littoral cell as the fixed factor and beach type as the random factor nested within littoral cells, we tested for significant differences in the macroinvertebrate assemblage patterns between beach types nested within littoral cells.

To explore the influence of environmental factors (Supplementary material; Table S3) on macroinvertebrate assembly, we employed a nonparametric multivariate regression model (DistLM) using Bray-Curtis dissimilarity matrices derived from the transformed composition and abundance data. We used a *step-wise* selection procedure and *AIC* selection criterion (9999 permutations) to identify the environmental factors that significantly predicted variance in macroinvertebrate assembly for the total intertidal community and the lower beach and wrack-associated groups across all study beaches and among urban and reference beaches separately.

2.6. Indicator taxa

To identify taxa that could be used as indicators by showing an affinity for either urban beaches subject to intense mechanized maintenance or reference beaches without mechanized maintenance, we employed two analyses commonly used when comparing two habitat types, Indicator Species Analysis (ISA) and a multinomial species CLAssification Method (CLAM) (see Appendix S1 for more details). We compared these to the results from the SIMPER analysis (see previous section). Using multiple approaches to identifying indicator taxa can help account for any shortcomings of individual indicator analyses (Bicknell et al., 2014). We ran these analyses using abundance data for the lowest taxonomic level identified (typically species) and family because of the potential broader applicability for similar species belonging to the same family in other regions or ecosystems.

For taxa to be identified as indicators of either heavily maintained urban beaches or reference beaches not subject to maintenance, we selected taxa that were consistently categorized as having an affinity for either urban or reference study beaches across both analyses (ISA and CLAM). We then evaluated these taxa against the results from the SIMPER analysis and only retained taxa that contributed most to statistically significant difference between urban and reference beach

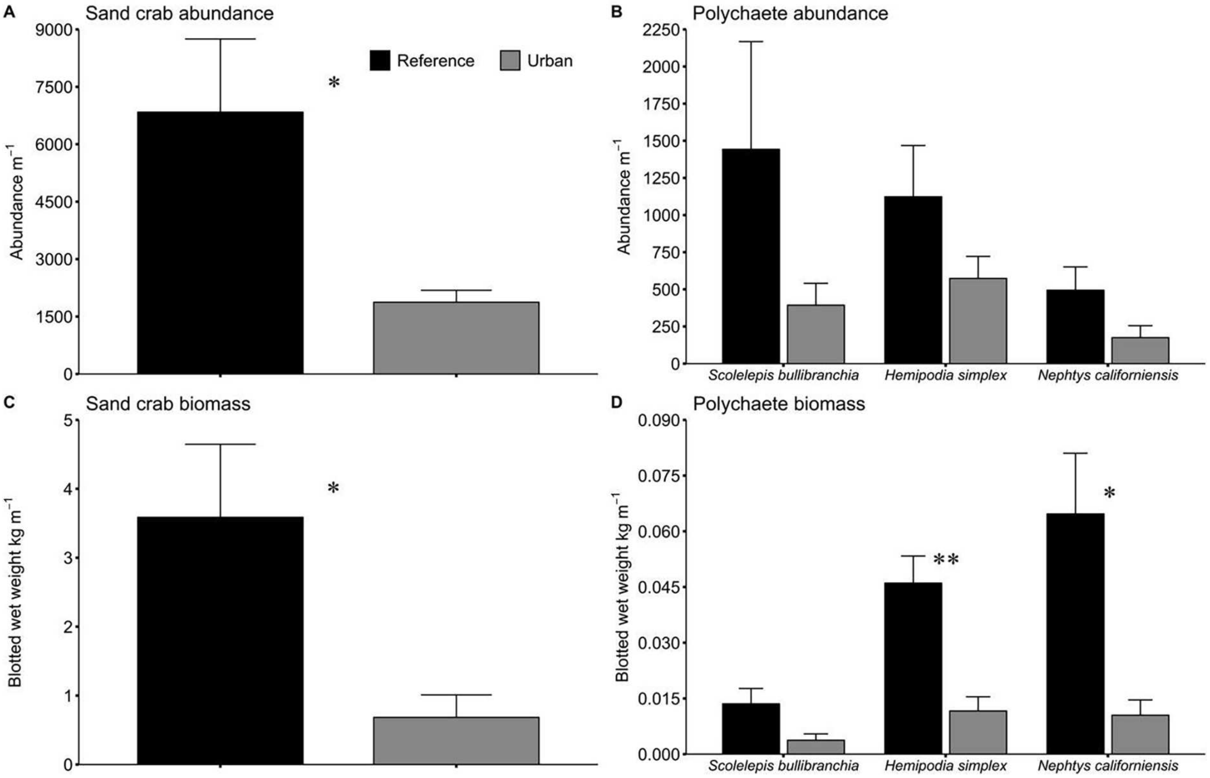

Fig. 4. Comparisons of the abundance and biomass of the four species of macroinvertebrates (all lower beach) that were present at every beach we sampled for reference (black, $N = 9$) and urban (grey, $N = 7$) study beaches. The bars represent the mean (± SE) abundance for A) sand crabs (*Emerita analoga*) and B) polychaetes and the wet biomass for C) sand crabs (*E. analoga*) and D) polychaetes ($* = P \leq 0.05$, $** = P \leq 0.01$).

assemblages (accounted for < 50 percent of the cumulative dissimilarity in the data cloud).

3. Results

3.1. Diversity, structure, and composition as ecological indicators

We recorded approximately half as many species of intertidal macroinvertebrates in our surveys on all urban (34 species) beaches compared with all reference (73 species) (Supplementary material; Table S4). Species richness varied more than fivefold (4–21 species) among urban beaches and almost twofold (25–40 species) among the reference beaches. Comparisons of mean values of observed and estimated richness indicated approximately half as many total intertidal species on urban compared with reference study beaches (Fig. 3). For all three groups of macroinvertebrates, total intertidal community, lower beach, and wrack-associated macroinvertebrates, mean values for observed and estimated species richness were significantly lower ($P \leq 0.01$) on urban compared with reference beaches (Fig. 3).

The relative species richness of the two major groups of intertidal macroinvertebrates also differed markedly across urban and reference beaches. Lower beach species were the dominant species group in terms of richness for urban and reference beaches but made up a higher percentage of the total intertidal species pool for urban (74%; 25 species) than reference (52%; 38 species) beaches. In contrast, wrack-associated species were a small component of the total intertidal species pool for urban (26%; 9 species) compared with reference (48%; 35 species) beaches. This difference in species richness between the major macroinvertebrate groups was reflected in intertidal community composition (Table S4). Community composition of urban beaches was dominated by crustaceans (38%) and polychaetes (32%) with a lower proportion of insects (18%) compared with reference beaches. In contrast, the composition of intertidal macroinvertebrate communities of reference beaches was dominated by insects (37%), crustaceans (30%), and polychaetes (23%).

Mean values of abundance of the total intertidal community and of the lower beach and wrack-associated macroinvertebrates differed significantly and were up to an order of magnitude lower on urban beaches compared with reference beaches (total community: $F = 13.4$, $P < 0.01$; lower beach: $F = 5.2$, $P = 0.04$; wrack-associated: $F = 16.6$, $P < 0.01$) (Fig. 3). Total intertidal abundance varied only a little over twofold among urban beaches (2,394–6,773 individuals m^{-1}) but over sevenfold among reference beaches (11,884 – 84,878 individuals m^{-1}). On urban beaches a lower beach species, *E. analoga*, (39%) dominated intertidal abundance. In contrast, on reference beaches, no single macroinvertebrate taxa dominated intertidal abundance and the most abundant taxa were wrack-associated talitrid amphipods, *Megalorchestia* spp. (23%).

Mean values of wet biomass of the total intertidal community and of the lower beach and wrack-associated macroinvertebrate groups were significantly lower on urban beaches than on reference beaches (total community: $F = 5.9$, $P = 0.04$; lower beach: $F = 5.2$, $P = 0.04$; wrack-associated: $F = 12.8$, $P < 0.01$) (Fig. 3). The mean wet biomass of the total intertidal community was dominated by lower beach macroinvertebrates on all beaches (urban: 97%, reference: > 99%). Sand crabs, *E. analoga*, made up the highest percentage of intertidal biomass on both urban (34%) and reference beaches (65%).

The average abundance and biomass of the majority (95%) of intertidal species were depressed on urban beaches compared with reference beaches. Those differences in abundance and biomass were significant ($P \leq 0.05$) for a subset of seven taxa that were found on a sufficient number of urban and reference beaches for comparisons (Table S4).

Four macroinvertebrates, all lower beach species, were present at every reference and urban beach we sampled (the sand crab, *Emerita analoga*, and three polychaetes, *Nephtys californiensis*, *Hemipodia*

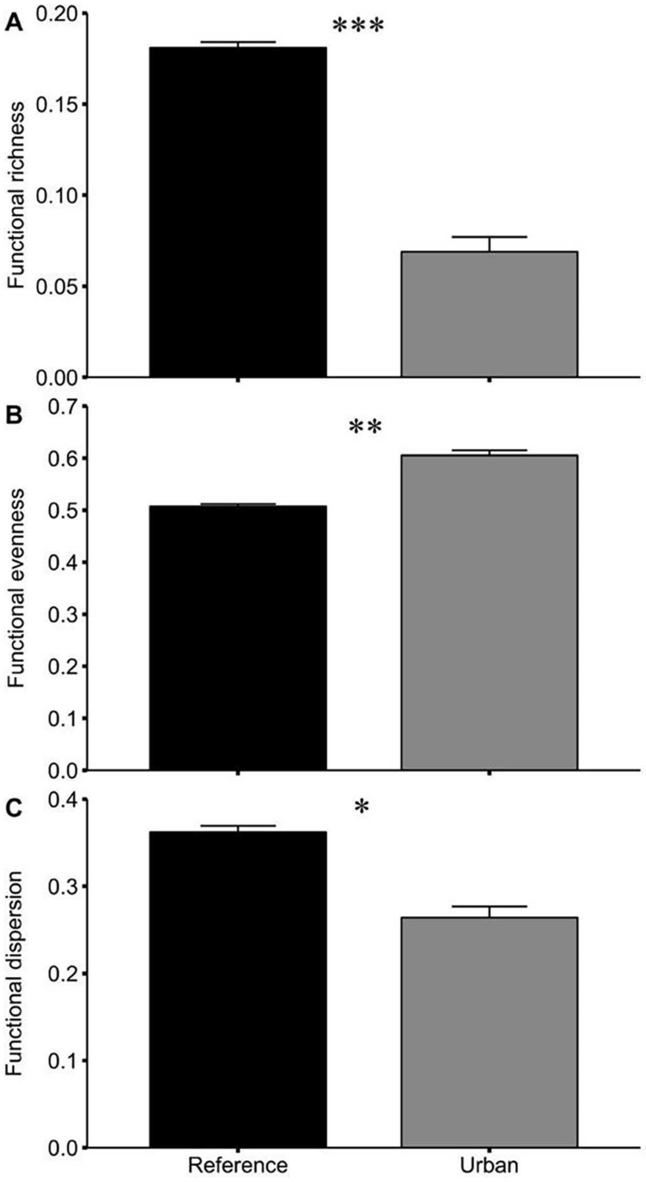

Fig. 5. Comparisons of the functional diversity of reference (black, $N = 9$) and urban (grey, $N = 7$) study beaches. The bars represent the mean ± SE for functional A) richness, B) evenness, and C) dispersion ($* = P \leq 0.05$, $** = P \leq 0.01$, $*** = P \leq 0.001$). See Table 2 for effect sizes.

simplex, and *Scolelepis bullibranchia*) (Table S4), albeit in depressed abundance and biomass on urban beaches (Fig. 4). In contrast, no species or taxa of upper beach macroinvertebrates occurred at every beach we sampled (Table S4).

Functional diversity indices of richness, evenness, and dispersion also differed significantly among urban and reference beaches (functional richness: $F = 26.8$, $P < 0.01$; evenness: $F = 12.1$, $P < 0.01$; dispersion: $F = 6.4$, $P = 0.02$), but the direction of those differences varied across the three indices. Similar to species richness (Fig. 3), mean values for functional richness and dispersion were 62% and 27% lower, respectively, on urban compared with reference beaches (Fig. 5). However, values for functional evenness were 19% higher on average for urban beaches (Fig. 5), which supported fewer specialized taxa that were also less abundant.

Using effect size as an index of relative sensitivity of ecological indicators to urban impacts revealed much greater impacts for species richness than for abundance or biomass for all three groups of intertidal macroinvertebrates (total intertidal community, lower beach, and wrack-associated macroinvertebrates) (Table 2). Furthermore, the effect sizes for species richness, abundance, and biomass of the two major macroinvertebrate groups was consistently greater for wrack-associated compared with lower beach macroinvertebrates (Table 2). The effect size for total species richness was also greater than for all three functional diversity indices (Table 2).

Table 2
Relative sensitivity, expressed as effect size (η^2), of ecological and environmental indicators of urban impacts detected for sandy beach ecosystems in this study. ($^{*}P \leq 0.05$, $^{**}P \leq 0.01$, $^{***}P \leq 0.001$).

Ecological indicators Biodiversity and structure	Effect size (η^2) Total	Lower beach	Wrack-associated
Observed species richness	79%***	44%**	78%***
Estimated species richness	78%***	48%**	80%***
Abundance	49%**	27%*	54%***
Biomass	30%*	27%*	48%*
Functional diversity indices			
Functional richness	65%***		
Functional evenness	31%**		
Functional dispersion	47%*		
Environmental indicators	**Effect size (η^2)**		
Mean grain size			
High tide strand (HTS)	52%**		
Water table outcrop (WTO)	54%**		
Beach width			
Upper beach	34%*		
Total beach wrack			
Macroalgal	28%*		
Total	35%*		

3.2. Macroinvertebrate assemblage patterns

Results of our multivariate analyses (abundance and biomass-based nMDS and one-way ANOSIM) indicated distinct clusters for urban and reference beaches that differed significantly ($P \leq 0.05$) for the total intertidal, lower beach, and wrack-associated macroinvertebrate groups (Fig. 6). Global R values indicated greater similarity in assemblage patterns between urban and reference beaches for the lower beach macroinvertebrates than for wrack-associated macroinvertebrates (Fig. 6). Results of our SIMPER analysis suggested several wrack-associated species *Megalorchestia benedicti*, *Megalorchestia corniculata*, *Fucellia rufitibia*, *Tylos punctatus*, *Megalorchestia californiana*, and the lower beach clam, *Donax gouldii* contributed most (cumulative percentage = 20%) to the statistically significant differences we found between intertidal communities on urban and reference beaches (Supplementary material; Table S5a).

Beach type (urban and reference) was an important factor in evaluating landscape scale differences in assemblage patterns (PERMANOVA) across littoral cells (Table 3). When beach type was excluded as a factor, there were no significant differences in the assembly of macroinvertebrates for both abundance and biomass-based analyses (PERMANOVA, $P > 0.05$) across littoral cells (Table 3a). However, when beach type was nested within littoral cell, the clusters differed significantly ($P \leq 0.05$) (Table 3a). Within beach types, assemblage patterns of intertidal macroinvertebrate groups generated by nMDS were significantly associated with littoral cells for the reference beaches (PERMANOVA, $P \leq 0.05$) but not for the urban beaches (PERMANOVA, $P > 0.05$) (Fig. 6, Table 3b).

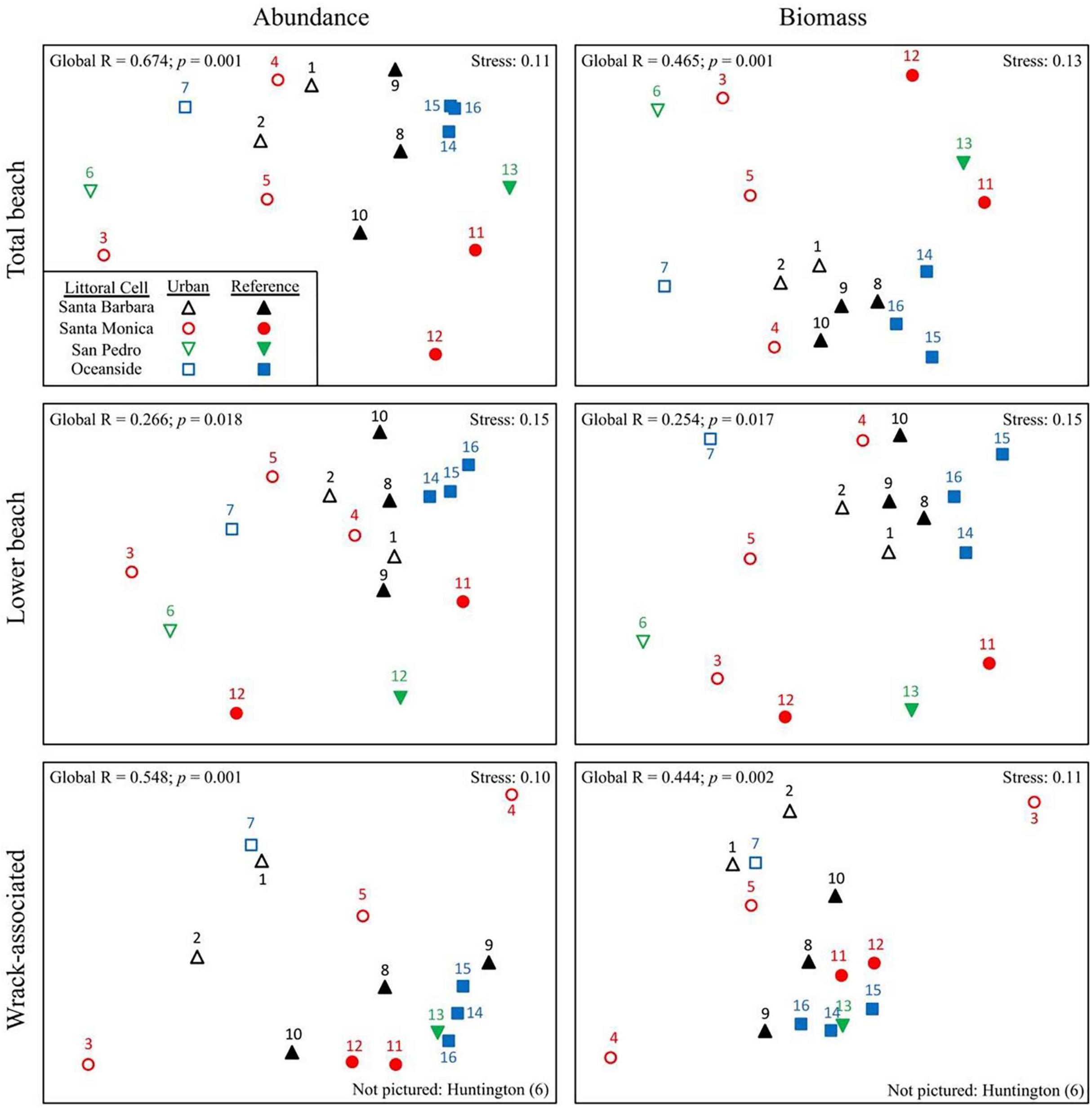

Fig. 6. Non-metric multidimensional scaling (nMDS) analysis comparing macroinvertebrate assemblages of urban and reference study beaches for the total beach, lower beach, and wrack-associated macroinvertebrates using log (x + 1) transformed abundance and wet biomass data. Global R and *P*-values displayed for each plot were computed using ANOSIM with beach type as the factor. Open symbols indicate urban study beaches and solid symbols indicate reference beaches. Symbol and color represent the littoral cell where study beaches are located (Santa Barbara = black triangle, Santa Monica = red circle, San Pedro = green inverted triangle, Oceanside = blue square). The numbers adjacent to symbols represent study beaches and are ordered by beach type then geographically from north to south (urban beaches: 1 = Carpinteria City, 2 = Hollywood, 3 = Westward, 4 = Santa Monica, 5 = Redondo, 6 = Huntington, 7 = Carlsbad Village; reference beaches: 8 = Santa Claus, 9 = Carpinteria State, 10 = Arnold Rd., 11 = Leo Carrillo, 12 = Dume Cove, 13 = Crystal Cove, 14 = San Elijo, 15 = Blacks, 16 = Scripps) as in Table 1. Huntington (urban) is not shown in the nMDS plot for wrack-associated macroinvertebrates because our samples contained no animals and so including this site would greatly distort the plot.

3.3. *Beach characteristics as environmental indicators*

Mean values of sediment grain size collected from the high tide strand line (HTS) and water table outcrop (WTO) levels (Table S3) differed significantly ($P \le 0.05$) among urban (0.22–0.51 mm) and reference beaches (0.20–0.34 mm). On average, grain sizes were greater (HTS = 43%, WTO = 27%) for the urban beaches (Fig. 7). Mean values of sediment sorting for the HTS and WTO were more similar across urban and reference beaches ranging from 1.27 to 1.53 and 1.27 to 1.51, respectively (Table S3). On average, sediment collected from the HTS and WTO was more poorly sorted (higher value) for the urban beaches than for reference beaches but those differences were not significant ($P > 0.05$) (Fig. 7).

Stranded marine macrophyte wrack on the study beaches was composed primarily of giant kelp, *Macrocystis pyrifera,* and surfgrass, *Phyllospadix torreyi*. Values of mean cover of macroalgal and total wrack were significantly lower on urban beaches compared with reference beaches ($P \le 0.05$, Fig. 7; Table S3). The mean cover of total wrack varied by more than two orders of magnitude across urban study beaches (range: 0.007–0.9 $m^2\,m^{-1}$) and over an order of magnitude among the reference study beaches (range: 0.3–4.9 $m^2\,m^{-1}$) (Table S3).

Observed mean values of total beach widths (landward boundary to

Table 3

Results from PERMANOVA (999 permutations) testing for significant differences in total community and lower beach and wrack-associated macroinvertebrate species assemblages using transformed abundance and biomass data among urban and reference beach types with A) littoral cells as a fixed factor and beach type as the random factor nested within littoral cell and B) littoral cell as a single factor. Asterisks specifies significant differences.

A.	Littoral cell		Littoral cell (beach type)	
	pseudo-*F*	*p*-value	pseudo-*F*	*p*-value
Total abundance	0.64	0.80	2.61	* < 0.01
Lower beach abundance	1.11	0.42	1.73	*0.03
Wrack-associated abundance	0.57	0.89	2.38	* < 0.01
Total biomass	0.91	0.55	2.43	* < 0.01
Lower beach biomass	1.38	0.28	1.64	* < 0.01
Wrack-associated biomass	0.71	0.73	2.04	* < 0.01

B.	Littoral cell – urban		Littoral cell – reference	
	pseudo-*F*	*p*-value	pseudo-*F*	*p*-value
Total abundance	0.86	0.70	2.14	* < 0.01
Lower beach abundance	0.87	0.61	2.55	* < 0.01
Wrack-associated abundance	1.22	0.28	1.08	0.42
Total biomass	0.94	0.61	2.80	* < 0.01
Lower beach biomass	0.96	0.55	2.59	*0.01
Wrack-associated biomass	1.06	0.31	1.49	0.11

low swash) varied over threefold across the urban (range: 75–297 m) and reference (range: 47–162 m) study beaches (Table S3). The mean values of total beach width were consistently greater on urban beaches than on reference beaches in our surveys, but those differences were not significant ($P > 0.05$) (Fig. 7). However, the mean widths of upper beach zones (dry sand landward of HTS) varied more than fourfold for urban beaches and contributed greatly to the wider average total beach width observed for those beaches (Table S3). Mean values of width of the upper beach zone differed significantly ($P \le 0.05$) between urban (range: 27–240 m) and reference (range: 5–40 m) beaches (Fig. 7). Much of the upper beach habitat present on urban beaches was highly disturbed above the active intertidal zone and devoid of wrack, vegetation, and animals. The mean values of the width of the active intertidal zone varied over fourfold among reference beaches (range: 29–130 m) but were less variable among urban study beaches, ranging from 42 to 62 m (Table S3). Mean values of width of active intertidal zones were less on average for urban compared with reference beaches, but those differences were not significant ($P > 0.05$) (Fig. 7).

Overall, beach profiles seaward of the high tide line of the urban and reference study beaches were relatively similar with intermediate intertidal slopes and comparable wave regimes. This was supported by the results for morphodynamic state estimated by Dean's parameter (Ω) measured during our surveys which indicated that all study beaches were intermediate type ($1 < \Omega < 6$) (Short and Wright, 1983) (Table S3). Values of Dean's parameter did not differ significantly ($P > 0.05$) among urban ($\bar{x} = 2.9 \pm 0.3$; $n = 7$; range: 1.7–3.8) and reference ($\bar{x} = 2.3 \pm 0.3$; $n = 9$; range: 1.3–4.2) beaches (Fig. 7). Likewise, beach slopes at the WTO did not differ significantly among urban ($\bar{x} = 3.9 \pm 0.6$; $n = 7$; range: 1.5–6.0) and reference ($\bar{x} = 2.9 \pm 0.6$; $n = 9$; range: 1.1–7.2) beaches (Fig. 7).

As an index of relative sensitivity of environmental indicators, effect size of urban impacts was greater for mean grain size than beach width or macrophyte wrack cover (Table 2). For macrophyte wrack subsidies, the effect size was slightly greater for total macrophyte wrack compared with macroalgal wrack (Table 2).

3.4. Environmental drivers

Environmental drivers that affect habitat quality and food availability on beaches – sediment characteristics (measured as HTS and WTO mean grain size and sorting) and wrack abundance (measured as total and macroalgal wrack cover) – explained a significant ($P \le 0.05$) amount of the variance in total intertidal, lower beach, or wrack-associated community assemblage patterns for the 16 study beaches in our models using DistLM. None of the other environmental characteristics reported to influence intertidal assemblage patterns on sandy beaches elsewhere (Dean's parameter, beach slope at the WTO, total beach width, and width of the active intertidal zone) explained additional variance in total intertidal, lower beach, or wrack-associated community assembly of our 16 study beaches spanning ∼300 km of coastline. When we compared all beaches (urban and reference – 16 beaches), mean grain size at the HTS and total wrack cover explained a significant percentage of variance (35%) for the total intertidal community ($P \le 0.05$) (Table 4). For the two macroinvertebrate groups, significant percentages of the variability in the lower beach and wrack-associated macroinvertebrates were explained by three sediment characteristic parameters (HTS grain size and sorting, WTO sorting = 46%) and by total wrack cover (18%), respectively ($P \le 0.05$) (Table 4).

When we compared reference beaches alone, these same two factors (sediment characteristics and wrack abundance) also explained a significant amount of the variance in intertidal community assembly across all intertidal levels (total community = 50%, lower beach = 35%, wrack-associated = 49%) ($P \le 0.05$) (Table 4). However, across urban beaches alone, sediment sorting was the only environmental variable that explained a significant proportion of the variability ($P \le 0.05$), but this was only for the total intertidal community (30%) and the lower beach macroinvertebrates (34%) (Table 4).

3.5. Indicator taxa identification

Overall, six species and four families were consistently identified as indicator taxa across the two analyses (ISA, CLAM) and contributed considerably (< 50% cumulative contribution) to dissimilarity in macroinvertebrate assemblages (SIMPER) across urban and reference beaches (Table 5). All of these taxa had an affinity for the reference beaches not subject to maintenance (Table 5). Except for the lower beach amphipod family Haustoriidae, all the indicator species and families identified across the three analyses were wrack-associated macroinvertebrates including the talitrid amphipod species *M. benedicti*, *M. californiana*, and *M. corniculata*, the peracarid isopod species and families *Alloniscus perconvexus* (Alloniscidae) and *Tylos punctatus* (Tylidae), and the kelp fly species and family *Fucellia rufitibia* (Anthomyiidae) (Table 5). Talitridae, which includes species of the genus *Megalorchestia* (*Megalorchestia minor* was the only congener not identified as an indicator species), was not identified across the three analyses as an indicator family. The families Alloniscidae and Tylidae were only represented by a single species in our surveys (*A. perconvexus* and *T. punctatus*, respectively) (Table S4). There were several notable differences between the two indicator analyses (ISA and CLAM). For ISA, we identified four more species and eight more families of indicator taxa than the CLAM analysis. However, the only indicators of urban beaches (species: *Hemipodia simplex* and *M. minor*; family: Glyceridae and Spionidae) were identified by the CLAM analysis (Supplementary material; Table S5).

4. Discussion

Our findings indicate that the significant declines reported in biodiversity and structure of marine and coastal ecosystems in response to urbanization and anthropogenic pressures that affect ecosystem function (Lotze et al., 2006; Palumbi et al., 2009; Worm et al., 2006) should be extended to include sandy beach ecosystems. Our results illustrate how the biodiversity, composition, and structure of the entire intertidal macroinvertebrate community of sandy beach ecosystems are potentially valuable as indicators of the impacts from widespread

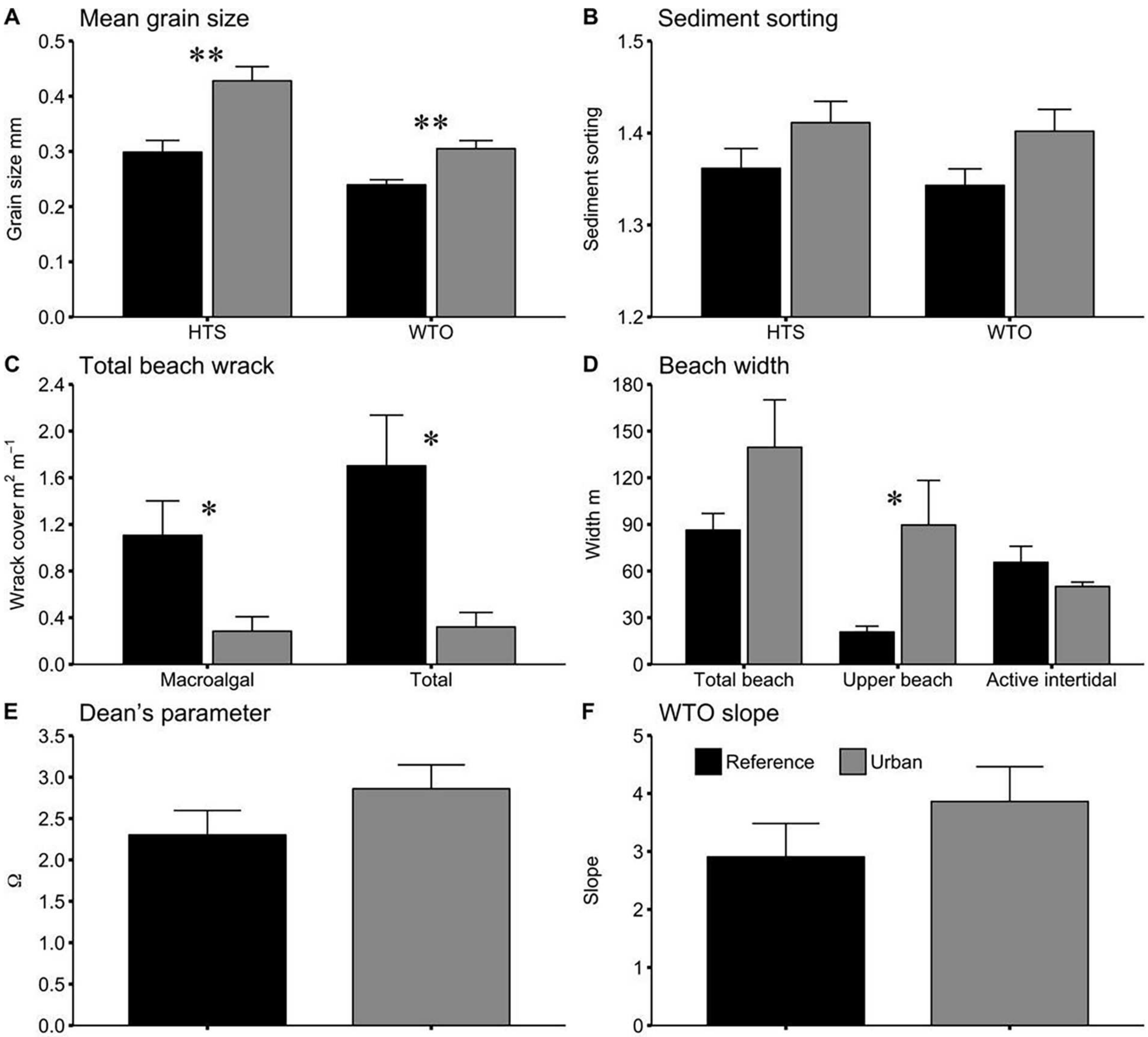

Fig. 7. Comparisons of beach characteristics for reference (black, $N = 9$) and urban (grey, $N = 7$) study beaches. The bars represent the mean ± SE for A) mean grain size at the high tide strandline (HTS) and water table outcrop (WTO), B) sediment sorting at the HTS and WTO, C) macroalgal and total wrack cover for the total beach, D) total beach, upper beach, and active intertidal zone widths, E) Dean's parameter, and F) WTO slope ($* = P \leq 0.05$, $** = P \leq 0.01$). See Table 2 for effect sizes.

Table 4
DistLM results showing significant environmental drivers of sandy beach macroinvertebrate assembly patterns, *AIC*, pseudo-*F*, variance, and *P*-values for the total community and lower beach and wrack-associated macroinvertebrates for all study beaches combined and urban and reference study beaches alone. Asterisk specifies log transformed data.

Beach type	Community	Environmental driver	*AIC*	pseudo-*F*	Variance	*P*-value
All beaches	Total	HTS mean grain size	117.3	4.9	0.25	< 0.01
		Total wrack cover*	116.9	2.1	0.10	0.02
	Lower beach	HTS sediment sorting	112.1	5.3	0.28	< 0.01
		HTS mean grain size	111.7	2.1	0.10	0.02
		WTO sediment sorting	111.3	1.9	0.08	0.04
	Wrack-associated	Total wrack cover*	129.2	3.0	0.18	< 0.01
Urban beaches	Total	HTS sediment sorting	50.8	2.1	0.30	0.03
	Lower beach	HTS sediment sorting	48.8	2.6	0.34	0.02
	Wrack-associated	None	–	–	–	–
Reference beaches	Total	HTS mean grain size	63.6	3.2	0.32	< 0.01
		Total wrack cover*	62.9	2.1	0.18	0.03
	Lower beach	WTO mean grain size	62.5	3.7	0.35	< 0.01
	Wrack-associated	HTS mean grain size	65.9	2.9	0.29	0.03
		Macroalgal wrack cover*	64.9	2.4	0.20	0.04

Table 5

Results from ISA, CLAM, and SIMPER analyses for A) species and B) families showing ISA classification (urban or reference beaches) type, indicator value (IV), *p*-value; CLAM classification (urban, reference, generalist, or too rare to classify) type; SIMPER percent contribution to dissimilarity (Contrib.%), and SIMPER cumulative percentage contribution to dissimilarity (Cum.%). Asterisk indicates lower beach macroinvertebrate families. Taxa included here were identified across all analytical techniques (ISA: p-value < 0.01, CLAM: Urban or Reference, SIMPER: Cum.% < 50) as indicator taxa. Note that the families Alloniscidae and Tylidae are only represented by a single species (also identified as indicators) in our analysis. See Supplementary material Table S5 for a complete list of all species and families.

A.	Indicator Species Analysis			CLAM	SIMPER	
Species	Classification	IV	*p*-value	Classification	Contrib.%	Cum.%
Fucellia rufitibia	Reference	73.3	0.01	Reference	3.15	< 50
Megalorchestia benedicti	Reference	91.8	< 0.01	Reference	4.44	< 50
Megalorchestia californiana	Reference	55.6	0.03	Reference	2.99	< 50
Megalorchestia corniculata	Reference	55.4	0.05	Reference	3.33	< 50
Alloniscus perconvexus	Reference	55.6	0.03	Reference	2.43	< 50
Tylos punctatus	Reference	66.7	0.01	Reference	3.08	< 50

B.	Indicator Species Analysis			CLAM	SIMPER	
Family	Classification	IV	*p*-value	Classification	Contrib.%	Cum.%
Haustoriidae*	Reference	69.7	0.02	Reference	4.06	< 50
Anthomyiidae	Reference	73.4	0.01	Reference	4.45	< 50
Alloniscidae	Reference	55.6	0.03	Reference	3.48	< 50
Tylidae	Reference	66.7	0.01	Reference	4.35	< 50

maintenance regimes (grooming and sediment filling) prevalent on urban beaches. Urban beaches, which make up a large proportion of the southern California shoreline (Dugan et al., 2003; Patsch and Griggs, 2006) supported significantly reduced intertidal species richness (−58%), abundance (−88%), and biomass (−63%) compared with reference beaches in the same region with the strongest effect size on species richness ($\eta^2 = 79\%$). This result suggests that species richness is a highly sensitive indicator of urban impacts on sandy beach ecosystems. In contrast, the reference beaches we studied that were not subject to intense maintenance regimes appeared to be representative of the high marine biodiversity in the region (Claisse et al., 2018; Schooler et al., 2017) with values of species richness, abundance, and biomass that are considered globally high for open coast sandy beaches (see McLachlan et al., 1996), despite being located on a densely populated urban coast with high human use.

Substantial declines in local scale biodiversity and structure in response to heavy manipulation of landscapes (> 90% habitat loss) (Ewers and Didham, 2006) are expected to cause severe ecosystem consequences by inhibiting important ecological functions (Hooper et al., 2012; Spaak et al., 2017). For sandy beaches, the magnitude of local and landscape scale losses in intertidal biodiversity and structure we observed in response to intensive management regimes is weakening important ecological resources and functions. These include the availability and processing of key subsidies of imported organic matter (e.g. macroalgal wrack) that enhances nutrient cycling (e.g. Dugan et al., 2011; Lastra et al., 2008, 2018; Lowman et al., 2019), growth of sand trapping vegetation (Dugan and Hubbard, 2010), and intertidal secondary production leading to food web support of higher trophic levels (e.g. fish, birds, mammals) (e.g. Hubbard and Dugan, 2003; Huijbers et al., 2013; Vargas-Fonseca et al., 2016).

Functional diversity can predict ecosystem function and vulnerability more reliably than species diversity (Gagic et al., 2015). Of the three functional diversity indices used in this study to evaluate the effects of urban impacts on the ecological function of sandy beach ecosystems, the effect size of urban impacts was strongest for functional richness ($\eta^2 = 65\%$). In our study, both functional and species richness were significantly lower (> 55% declines) on urban beaches and effect size of both were higher ($\eta^2 > 65\%$) than other diversity measures (e.g. functional dispersion). This result suggests species and functional richness may be the most sensitive indicators of urban impacts on the biodiversity and functioning of sandy beach ecosystems.

The use of multiple functional diversity measures provided unique new insights on the impacts of urban management regimes to ecosystem function of sandy beaches and their potential utility as ecological indicators. Two of the three functional diversity indices we tested were lower in response to mechanized beach maintenance, but the third, functional evenness, was higher. Inverse responses of functional richness and functional evenness to urbanization are not common and have been attributed to declines in specialist species (Filippi-Codaccioni et al., 2009). This is consistent with the declines we observed in the specialized wrack-associated species on urbanized sandy beaches. However, implications of our results on functional diversity for ecosystem functioning warrant further investigation. Although abundance was more evenly distributed across occupied niche space (higher functional evenness) on urban study beaches, the lower functional richness value we found could indicate that less niche space was occupied on these impacted beaches. If niche space relating to important ecological functions is unoccupied or underutilized, ecosystem function could be weakened or degraded (Mason et al., 2005). The disproportionate impacts to wrack-associated macroinvertebrates we observed suggests that niche space that facilitates nutrient cycling (macroalgal processing by intertidal consumers), was either unoccupied or underutilized on urban beaches. Furthermore, the lower functional dispersion we observed for urban beaches indicates a low degree of niche differentiation and weakened ecosystem functioning (Mason et al., 2005). Our results suggest functional diversity measures could provide valuable insights on biodiversity-ecosystem function relationships for sandy beaches and other impacted ecosystems.

Biological homogenization is another common outcome of the intense modification of the physical environment in urban areas (McKinney, 2006). This impact has consequences for biodiversity and ecosystem function on ecological and evolutionary scales (Clavel et al., 2011; Olden et al., 2004). Our finding that intertidal macroinvertebrate assemblages of urban beaches did not differ significantly across the major coastal landscape features of littoral cells while those of reference beaches did is suggestive of biological homogenization associated with urban management regimes on beaches. These intense maintenance regimes appear to have the potential to homogenize biological and functional diversity, which could not only degrade ecosystem function but also increase vulnerability to environmental change on regional (Olden et al., 2004) and global scales (Groffman et al., 2014).

Major assemblages of organisms, particularly taxonomic groups or feeding guilds, are often reported to respond differently to disturbance associated with urbanization (Barrett and Guyer, 2008; McKinney, 2002). For sandy beaches, both of the major groups of intertidal macroinvertebrates responded significantly to intensive mechanized maintenance regimes associated with urbanization. Biodiversity and structure of both wrack-associated and lower beach macroinvertebrates were reduced on urban beaches, with strongest effects on species richness for both of the major macroinvertebrate groups. Overall, the wrack-associated macroinvertebrates were affected disproportionately and far more strongly ($>$ 80% declines; η^2: $>$ 48%) than the lower beach macroinvertebrates ($>$ 39% declines; η^2: $>$ 27%) by intensive maintenance regimes on urban beaches. Factors related to life history, resource dependence, habitat requirements, and intertidal zonation likely contributed to the different observed responses of the two major groups to urban impacts. Taxa limited by dispersal, such as wrack-associated macroinvertebrates, which depend primarily on the reproduction of resident populations, are expected to exhibit higher spatial variation in community structure than species with long-distance larval dispersal (Grantham et al., 2003; Rodil et al., 2018; Soininen et al., 2007). As a result, populations of these taxa may be less resilient to impacts from disturbance associated with urbanization. The strength of the response and the severity of the impacts for these taxa is also related to their dependence on a particular resource (e.g. macrophyte wrack) that is removed frequently by maintenance activities (Dugan et al., 2003). Furthermore, these taxa inhabit upper intertidal zones located near the driftline where the sand is more frequently and intensely disturbed by maintenance activities on urban beaches (e.g. Dugan et al., 2003; Dugan and Hubbard, 2010; González et al., 2014; Hubbard et al., 2014; Schooler et al., 2017; Veloso et al., 2006, 2008; Weslawski et al., 2000a,b). Overall, for the majority of wrack-associated macroinvertebrates, their low dispersal potential, reliance on macrophyte wrack for food and shelter, and use of the more frequently and intensely disturbed upper intertidal zones as habitat appear to make them more vulnerable to urban beach management regimes than the macroinvertebrates of the lower intertidal zones.

Due to their sensitivity to disturbance, wrack-associated macroinvertebrates may be especially useful as indicators of the ecological condition across the intertidal of sandy beaches on urban coasts in California and elsewhere. We identified several wrack-associated species (three talitrid amphipods, two peracarid isopods, and a kelp fly) and families (peracarid isopods and kelp flies) that are particularly vulnerable to urban impacts. However, inconsistencies among the taxa identified at the species and family levels suggest caution is warranted when considering the broad utility of indicators at higher taxonomic levels (e.g. family) in assessing impacts. For example, we identified three out of the four species of talitrid amphipods as being vulnerable to urban impacts, but our analysis did not identify the family (Talitridae) of these species as an indicator. This result suggests that a functional approach to ecological indicators may have broader applicability than higher taxonomic levels.

For sandy beach ecosystems, upper beach and wrack-associated fauna have previously been identified as useful indicator taxa for monitoring ecological condition around the world because of their vulnerability to anthropogenic disturbance (trampling, off-road vehicles, grooming, and beach filling) and habitat loss (sea-level-rise and coastal squeeze) (e.g. Cardoso et al., 2016; Gonçalves et al., 2013; Gonçalves and Marques, 2017; González et al., 2014; Hubbard et al., 2014; Schlacher et al., 2014, 2016; Schooler et al., 2017; Veloso et al., 2008). We suggest that the presence/absence and relative abundance and biomass of indicator taxa belonging to these vulnerable functional groups could be used to monitor declines in ecological condition across the intertidal zone in response to urbanization as well as potential recovery from impacts both related and unrelated to urbanization (e.g. oil spills) for sandy beaches.

Unlike findings for other ecosystems where species (e.g. birds) adapted to or exploited urbanization (Blair, 1996; Kark et al., 2007), no intertidal macroinvertebrate taxa consistently flourished on urban compared with reference beaches. Values of mean abundance and biomass were lower on urban than reference beaches for more than 90% of the intertidal species, and no taxa were consistently identified as indicators of urban beaches. Changes in biotic interactions (e.g. strong competitive abilities, predator release, and exploitation of abundant resources) that permit certain species to thrive in an intensely disturbed urban setting (Marzluff, 2001), are generally considered to be less important in structuring sandy beach macroinvertebrate communities than physical processes (McLachlan et al., 1993; McLachlan and Brown, 2006). Intense anthropogenic disturbance combined with a limited role of competitive interactions appear to make it less likely for such adapters and exploiters to flourish in the frequently disturbed intertidal zones of urban sandy beaches.

While no taxa flourished on urban beaches, the four lower beach taxa found consistently on urban beaches, albeit in depressed abundance and biomass (*E. analoga*, *H. simplex*, *S. bullibranchia*, and *N. californiensis*), share some life history traits that are characteristic of early successional species typically found in managed urban habitats (McKinney, 2002). These traits relate to the recruitment and recolonization of disturbed habitat and include high abundance on beaches not subject to maintenance impacts (reference beaches), long-distance larval dispersal capability, capable of settling in large numbers, and extensive geographic distributions. This set of life history traits could be used to identify species whose populations may be able to persist at some level with coastal urbanization. However, the need for specific environmental characteristics, such as sediment selectivity (e.g. substrate generalist species vs substrate sensitive/specialist species) may limit recolonization of intensely maintained urban beaches by these intertidal taxa (Alexander et al., 1993). The coarser sediment we observed on urban beaches may favor taxa that are considered more effective burrowers (Che and Dorgan, 2010) or substrate generalist taxa that can burrow in a wide range of sediment grain sizes (Dugan et al., 2000b; McLachlan et al., 1995; Van Tomme et al., 2013; Viola et al., 2014). Further investigation into sediment requirements, particularly for coarse grain sediment, is needed to identify the relative vulnerability or tolerance of species to the intense alteration of substrate on urban beaches.

Our results and those of others suggest that the combination of widespread distribution and sensitivity to human impacts of two groups, lower beach hippid crabs (Burnett, 1971; Powell et al., 2002; Siegel and Wenner, 1984; Wenner, 1988) and wrack-associated talitrid amphipods (Bessa et al., 2014, 2017; Dugan et al., 2003; Fanini et al., 2009; Gonçalves et al., 2013; Hubbard et al., 2014; Scapini et al., 2015, 2019), make them excellent candidates as indicator taxa for use in monitoring the ecological condition of sandy beaches across the intertidal zone. In our study region, the absence and/or significant reductions in abundance and biomass of these two potential indicator taxa from upper and lower beach zones on urban beaches is comparable to results of Cardoso et al. (2016) for beaches in Brazil. The similarity of findings from geographically distinct regions highlight the potential broad utility of these intertidal taxa as ecological indicators of impacts to open coast sandy beaches.

Our study results and those of others (Dugan et al., 2003; Dugan and Hubbard, 2010; Fanini et al., 2009; Hubbard et al., 2014; Manning et al., 2014; Peterson et al., 2000, 2014; Schooler et al., 2017; Wooldridge et al., 2016) indicate that anthropogenic changes in habitat quality and resource availability that persist over sufficient time scales can inhibit the recovery of intertidal biota and result in profound lasting impacts to macroinvertebrate communities across the entire intertidal zone of sandy beaches. We show that variability in two environmental characteristics associated with food availability and habitat quality – wrack abundance and sediment characteristics (size and sorting) – that are directly altered by beach management regimes, strongly influence intertidal community assembly. Strongest effect sizes (η^2: $>$ 50%) across beach types were for substrate (mean grain size), which was much coarser on urban beaches in our study. This finding suggests that revising beach management regimes to limit the spatial scale and frequency of different intense maintenance activities (beach grooming and filling) and to better match natural conditions (grain size and sorting, and wrack availability) (Peterson et al., 2014; Speybroeck et al., 2006; Weslawski et al., 2000b; Zielinski et al., 2019) could be used to achieve higher levels of biodiversity and function of urban beach ecosystems.

5. Conclusion

In conclusion, our comparisons highlight the significant and regional scale of anthropogenic impacts associated with urbanization (grooming and sediment filling) on the biodiversity, structure, and community composition of the entire community of intertidal macroinvertebrates of sandy beach ecosystems in an urbanized region. Our results suggest these strong impacts could contribute to regional losses of biodiversity and degrade the ecological stability, resilience, and function of these widespread coastal ecosystems. The presence, even in relatively high abundance or biomass, of a few macroinvertebrate species on an urban beach does not equate to an ecologically functional or healthy beach. Our results strongly suggest that a number of macroinvertebrate taxa that share common functional traits are extremely vulnerable to urbanization making them highly sensitive indicators of urban impacts. The overall diversity, structure, and composition of macroinvertebrates across the entire intertidal could also be informative indicators of urban impacts on beaches, while use of functional diversity indices can provide additional value to evaluations of impacts. At present, sandy beaches are primarily managed for human use and recreation in many regions (McLachlan et al., 2013). In the face of expanding human populations along the coasts and global estimates that 24% of beaches are currently eroding (Luijendijk et al., 2018) with a projected loss of up to 67% of beaches in California by 2100 (Vitousek et al., 2017), coastal monitoring and management goals urgently need to include enhancement and conservation of the unique biodiversity and function of remaining beach ecosystems. Our results for urban beaches can inform the development of ecologically sensitive management approaches that achieve a greater balance between the vital socioeconomic and the irreplaceable ecological functions of these threatened coastal ecosystems.

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Appendix A. Supplementary data

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