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Biodiversity of coastal ecosystems: exploring spatial and temporal patterns in intertidal macroinvertebrate communities of sandy beaches

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Biodiversity of coastal ecosystems: exploring spatial and temporal patterns in intertidal macroinvertebrate communities of sandy beaches

A dissertation submitted in partial satisfaction of the
requirements for the degree Doctor of Philosophy
in Marine Science

by

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Nicholas Karraker Schooler

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2017 Schooler, N. K., Dugan, J. E., Hubbard, D. M., & Staughan, D. Local scale processes drive long-term changes in biodiversity of sandy beach ecosystems. Ecology and Evolution. 7:4822-4834. doi:10.1002/ece3.3064
2014 Schooler, N. K., Dugan, J. E., Hubbard, D. M. Detecting change in intertidal species richness on sandy beaches: calibrating across sampling designs. Estuarine, Coastal and Shelf Science. 150:58-66 doi: http://dx.doi.org/10.1016/j.ecss.2013.10.016

2014 Viola, S.M., Dugan, J. E., Hubbard, D. M., Schooler, N. K. Burrowing inhibition by fine textured beach fill: implications for recovery of beach ecosystems. Estuarine, Coastal and Shelf Science 150:142-148 doi: http://dx.doi.org/10.1016/j.ecss.2013.09.003

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2012 Schooler, N.K., Dugan, J. E., Page, H. M. First host record for the parasitoid rove beetle, *Aleochara sulcicollis* Mannerheim, 1843 (Coleptera: Staphylinidae) on the intertidal kelp fly *Fucellia ruftibia* Stein 1910 (Diptera: Anthomyiidae). The Coleopterists Bulletin 66(4):1-4. doi: http://dx.doi.org/10.1649/072.066.0404

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ABSTRACT

Biodiversity of coastal ecosystems: exploring spatial and temporal patterns in intertidal macroinvertebrate communities of sandy beaches

by

Nicholas Karraker Schooler

Biodiversity plays a vital role in the function, stability, and resilience of ecosystems. Concern about biodiversity loss and the alteration of ecological communities has driven major efforts to catalog and monitor species in ecosystems across the globe and to quantify relationships between biodiversity and ecosystem function. Evaluating responses of biodiversity and community structure to abiotic and biotic drivers, such as climate, disturbance, and species interactions requires comparisons across relevant spatial and temporal scales.

Located at the boundary between land and sea, coastal ecosystems and the biodiversity they support are subject to increasing threats from escalating anthropogenic and climatic impacts. Sandy beach ecosystems, which support unique macroinvertebrate communities and provide irreplaceable ecosystem functions (e.g. nutrient recycling and wildlife support), experience heavy human use and manipulations making them particularly vulnerable to urbanization and environmental change. For temperate sandy beaches the degree of vulnerability is expected to vary with major trophic guilds due to differences in functional,

trophic, and life history traits, with greater impacts expected for wrack-associated than lower beach species. To gain insights on mechanisms influencing ecological communities and functioning, I explored questions concerning responses of biodiversity, community structure, and composition of sandy beach ecosystems to environmental and anthropogenic factors operating over a range of temporal and spatial scales for my dissertation research. To evaluate these questions, we conducted 60 intertidal macroinvertebrate surveys at 41 study beaches spanning >1800 km of California coastline (~9 degrees of latitude) from 2009-2015. These were the first quantitative surveys ever conducted at many of these beaches.

In my first chapter, I addressed the important issue of comparing species richness across surveys conducted using different sampling methods by developing a calibration approach to adjust species richness for sampling effort. In my second chapter, I assessed the direction and magnitude of change in intertidal biodiversity over time by comparing values of species richness from surveys collected >30 years apart (1970s and 2009-11) using the calibration from my first chapter. In my third chapter, I evaluated ecological impacts of coastal urbanization by comparing intertidal macroinvertebrate communities between urban beaches with intense maintenance regimes and reference beaches lacking such maintenance. In my final chapter, I evaluated spatial patterns in biodiversity, structure, and composition and the role of environmental factors in structuring intertidal macroinvertebrate communities of sandy beaches at different spatial scales.

Overall, findings from my dissertation suggest sandy beaches are more diverse and biogeographically complex than generally acknowledged and that central and southern California beaches may represent a global biodiversity hotspot for intertidal macroinvertebrates. The peak in intertidal species richness of sandy beach

macroinvertebrates in temperate latitudes is not consistent with the well-known pattern of a negative trend in species richness with latitude reported for a wide range of ecosystems and taxa. My results highlight the importance of connectivity to donor ecosystems and the strong influence of subsidies on intertidal macroinvertebrate communities of sandy beaches, particularly that of drift macroalgae on wrack-associated species. The functional, trophic, and life history traits of wrack-associated macroinvertebrates, a major component of intertidal diversity (>40% of species), make this guild disproportionately vulnerable to human and climatic impacts compared with lower beach species. Human impacts associated with urbanization (e.g. mechanized grooming, sediment fills) strongly degraded intertidal macroinvertebrate biodiversity, structure, and function and appeared to influence sandy beach communities more at local than regional spatial scales. Though local scale processes masked the influence regional and global scale processes at most study beaches, we observed biodiversity declines consistent with habitat loss from sea-level rise.

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Chapter I. Detecting change in intertidal species richness on sandy beaches: calibrating across sampling designs

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Abstract

Detecting changes in the biodiversity of biotic communities is fundamental to evaluating ecological responses to anthropogenic and climatic drivers at multiple scales. Species richness, the simplest measure of biodiversity, can be strongly affected by sampling design, making comparisons among results of different studies challenging. We investigated the use of extrapolative species richness estimators to address these issues in comparing species richness results from two sampling designs that differed in area sampled for intertidal macroinvertebrates on exposed sandy beaches. The area sampled by the proportional area sampling design increased with beach width (0.4 m^2 to 3.0 m^2) across our sites. The area sampled by the fixed area sampling design (3.5 m^2) was independent of intertidal width. To obtain datasets for comparisons, we simultaneously used these sampling designs on nested intertidal grids at seven sandy beaches in central and southern California, USA. Observed species richness differed significantly ($p \leq 0.05$) between the two sampling designs and was consistently lower (3 to 10 species less) for the proportional area design compared to the

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fixed area design (8 to 35 vs. 12 to 38 species, respectively), except at the widest beach where sampling areas were most similar (3 m^2 vs. 3.5 m^2). All seven non-parametric species richness estimators provided higher estimates of richness for both designs (mean = 5.4 ± 3.8 species), but only four of the richness estimators reduced differences in richness obtained by the two designs to a non-significant level ($p \geq 0.05$) across the sites. The ratio of richness values (proportional area/fixed area) obtained by the two designs was strongly correlated with sampling area for observed richness and four of the seven estimators, suggesting these estimators did not uniformly correct for sampling area. When we used an extrapolation of sample-based rarefaction to adjust for sampling area, differences in species richness between sampling designs were reduced (mean difference = 0.9 ± 3.1 species) to within the 95% CI at every site and estimated species richness did not differ significantly among designs. Our results suggest that use of the extrapolative sample-based rarefaction approach could provide a means of calibrating species richness among sampling designs that differ in area sampled. This approach could allow more robust analyses and enable comparisons of species richness data collected across larger temporal and spatial scales. Such comparisons will provide needed opportunities to evaluate the responses of biodiversity to larger scale effects of human impacts and climate change in coastal ecosystems.

Keywords: Biodiversity; Ecosystems; Methodology; Macroinvertebrates; Extrapolation; Non-parametric estimators

Introduction

Biodiversity and its many components represent an underlying principle in many ecological models and conservation strategies (e.g. Gotelli and Colwell, 2001). Shifts in biodiversity may indicate climatic or anthropogenic environmental change or impacts on a variety of temporal and spatial scales (e.g. Vitousek, 1994; Pimm et al., 1995; Chapin III et al., 1997; Vitousek et al., 1997; Sagarin et al., 1999; Harley et al., 2006; Parmesan, 2006; Schlacher et al., 2008). Changes in biodiversity can affect ecosystem function (e.g. Chapin III et al., 2000; Hooper et al., 2005; Isbell et al., 2011), food web dynamics (e.g. Cardinale et al., 2000), and resilience to environmental change (e.g. Chapin III et al., 2000).

Evaluating the impacts of press drivers, such as climate change or anthropogenic disturbance, on the biodiversity of an ecosystem or community requires robust and accurate comparisons of data sets collected over time scales of appropriate length. One such press driver, climate change, has been studied less extensively in marine ecosystems (Hoegh-Guldberg and Bruno, 2010). Changes in temperature, UV exposure, sea-level, ocean circulation, and pH can influence biodiversity in marine ecosystems (Macpherson, 2002; Harley et al., 2006), but the paucity of data spanning sufficient time spans in marine ecosystems has made the identification of changes in marine biodiversity challenging (Richardson and Polocanska, 2008, Richardson et al., 2012). This data gap is particularly evident and critical for sandy beach ecosystems (Dugan et al., 2010; Richardson et al., 2012) which make up ~70% of the world's open-ocean coasts and have a high socioeconomic (e.g. Parsons and Powell, 2001; Klein et al., 2004) and ecological importance (e.g. Fairweather, 1990; Schlacher et al., 2007, Dugan et al., 2010).

The simplest and most commonly used way to describe biodiversity in terms of species is species richness, a measure of the total number of species observed in a given area or sample (Magurran, 1988). However, species richness can be strongly affected by sampling effort, area, and design, a major issue for estimating species richness in both marine and terrestrial ecosystems (Gotelli and Colwell, 2001; Colwell et al., 2012; Chase and Knight, 2013). These issues are particularly relevant for sandy beach ecosystems where biotic survey data are limited in many regions. To date, large scale evaluations of global patterns in intertidal biodiversity of beach ecosystems have usually relied on data from surveys that differ in sampling designs and effort, acknowledging that this could be a source of considerable uncertainty (Dexter, 1992; McLachlan and Dorvlo, 2005).

Comparisons of observed species richness or standardizations of observed species richness through the use of simple ratios of the number of species per unit area are unreliable and should never be used (Magurran and McGill, 2011). Instead, interpolative or extrapolative approaches to estimating species richness for the smallest or largest common sampling units (area), respectively, can be used to compare species richness on different spatial or temporal scales (Magurran and McGill, 2011).

Species-accumulation curves can be used to evaluate relationships between sampling effort and species richness, if applied properly (Chase and Knight, 2013). The appropriate level of sampling effort (area) needed to adequately determine species richness of intertidal infauna has been extensively considered for sandy beaches through the interpolation of rarefaction curves (Jaramillo et al., 1995; Brazeiro, 2001; Schoeman et al., 2003; Schlacher et al., 2008). The recommended sampling area for sandy beaches is ~4 m^2, which can be adjusted to scale with the diversity and width of a beach (Schlacher et al., 2008), was based on a balance between the accuracy, bias, and precision of an extrapolative approach to estimating true species richness through the use of non-parametric richness estimators (Schoeman et al., 2008). These extrapolative richness estimators provided more accurate estimates of species richness than observed values on sandy beaches (Foggo et al., 2003; Schoeman et al., 2003; Schoeman et al., 2008). Recent advances in estimates of richness allow the extrapolation of rarefaction (interpolation) curves to larger sampling effort with unconditional 95% confidence intervals (Colwell et al., 2012). This method yields species accumulation curves that are statistically very similar to interpolative results for a given dataset but has the advantage of allowing the use of all available data rather than a subset (Colwell et al., 2012). Importantly, species richness estimators and other extrapolative approaches to estimating richness could potentially be used to calibrate results between different sampling designs, including those that differ in sampling area (Basualdo, 2011).

Increased confidence in comparisons between samples taken with different methods decades apart could enable interesting and important inferences about change and stability in sandy beach and other coastal ecosystems. For example, in California, high-quality quantitative sampling of intertidal invertebrates on sandy beaches using a variety of sampling designs were initiated following the 1969 Santa Barbara oil spill continuing through the 1970s (Straughan, 1982). Decades later, intertidal surveys of California mainland beaches have primarily used a single sampling design (Dugan et al., 2003; Schooler et al., unpublished) that differs from those in earlier surveys.

Considering the number of different sampling designs used in intertidal surveys, the ability to calibrate results across designs is critical to identifying long-term and large-scale change in species richness for beaches and other ecosystems. In this study, we investigated the effect of sampling design on species richness by simultaneously employing two sampling designs over the same intertidal grid, effectively surveying an identical intertidal community at seven beaches. One design sampled an area that was proportional to intertidal width with randomly spaced sampling units (hereafter referred to as the proportional area sampling design). The second design sampled a fixed area of habitat that was independent of intertidal width using a consistent number of uniformly spaced sampling units (hereafter referred to as the fixed area sampling design). We compared observed species richness and evaluated the ability of several non-parametric species richness estimators to calibrate values of intertidal species richness across the two sampling designs. Lastly, we investigated the efficacy of estimating species richness using extrapolations of sample-based rarefaction curves to larger sampling areas as a calibration method.

Methods

Study sites

The central and southern California coast is characterized by microtidal modally intermediate beaches with mixed semidiurnal tides. In this study, the biodiversity of intertidal macrofauna was surveyed on seven sandy beaches ranging from Cayucos, California to San Diego, California (120°55’ W 35°25.986’N – 118°15’ W 32°51.832’N) (Fig. 1). Sites were chosen to represent a range of beach types that varied in richness, level of disturbance, and morphodynamic state across the geographic region and to include locations of intertidal surveys conducted several decades ago (Straughan, 1982).

Sampling design

We investigated the effect of sampling approach on values obtained for species richness of sandy beaches by comparing results of two stratified sampling designs, a proportional area sampling design and a fixed area sampling design, both previously used to survey intertidal macroinvertebrate biodiversity in California. At each site, we simultaneously employed the two designs (Straughan, 1982; Dugan et al., 2003) nested within the same intertidal grid, effectively sampling an identical intertidal community (Fig. 2). We conducted these surveys during spring low tides at seven beaches (Table 1) in daylight when invertebrate surface activity is minimal. All surveys were conducted in late summer and fall of 2009 when beaches are typically widest in the region except for the beach at Scripps (August 2011). Historic basepoints were identified for each site and a measuring tape was run from the base point to the low swash to act as a reference for the sampling grid. We used the same mesh size, core size, and core depth in all surveys.

The proportional area sampling design was adapted from methods used in sandy beach macrofaunal surveys in the 1970s by Patterson (1974) and Straughan (1982) in central and southern California. We used a stratified random quadrat sampling layout (Fig. 2) in which 3.0 m by 12.2 m (10 ft by 40 ft) strata were divided into four replicate contiguous 3.0 m by 3.0 m (10 ft by 10 ft) shore-parallel quadrats. These strata, extended from the 24-hour high tide line to the low swash level using the basepoint transect as a border for the survey grid. The number of strata (n = 0.03/m x intertidal width), and therefore the area sampled (range: 0.4 m^2 - 3.0 m^2), was dependent on intertidal width. In each quadrat, two cores with a diameter of 10 cm were taken to a depth of 20 cm at a random location and pooled to constitute one sample.

The fixed area sampling design was adapted from a uniform spacing sampling layout used in intertidal surveys conducted on the California coast by Dugan et al. (2003). Three shore-normal transects extended from the 24-hour high tide line to the low swash zone. Two of these transects were placed on the outer edges of the proportional area sampling design grid (including the basepoint transect) while the third was run at a random distance from the other two transects, nested within the proportional area sampling design survey grid. On each transect, 150 cores with a 10 cm diameter were taken to a depth of 20 cm at uniform intervals across the intertidal zone. The size of the interval between cores varied with intertidal width. Ten consecutive cores were taken and pooled at each 15 consecutive levels for a total of 15 samples per transect and 45 samples across the three replicate transects. The total sampling area was fixed at 3.5 m^2, independent of intertidal width. We determined *a priori* that the fixed area sampling design was the preferred method of sampling biodiversity based on the sampling design parameters recommended by Schlacher et al. (2008) as well as the total area sampled in each design.

For both sampling designs, each pooled core sample was placed in bags with 1.5 mm mesh apertures and sieved to remove sand and retain the macroinvertebrates, macroalgae, kelps, and other debris. Samples were placed in labeled plastic bags and returned to the laboratory where they were preserved in 10% buffered formalin. Macroinvertebrates in each sample were identified to the lowest taxonomic level possible and counted.

Analytical approach and data analysis

Observed species richness was calculated by totaling the number of unique macroinvertebrate taxa found in all transects for each sampling design at each site. We used a two-tailed paired t-test to determine if observed species richness differed significantly ($p \leq 0.05$) between the proportional area sampling design and fixed area sampling design across the study beaches.

To evaluate the ability of non-parametric extrapolative species richness estimators to adjust for the differences between these sampling designs, we calculated then compared estimates of true species richness from the observed richness for each sampling method and site. We used a species richness estimator program, EstimateS 9.0 (http://purl.oclc.org/estimates) to generate values for the seven non-parametric richness estimators commonly used in the literature: ACE, ICE, Chao 1, Chao 2, Jackknife 1, Jackknife 2, and Bootstrap (100 randomized iterations, Colwell, 2013) for our comparisons. For each species richness estimator we determined if values of estimated species richness yielded by the proportional area sampling design and fixed area sampling design differed significantly ($p \leq 0.05$) across the study beaches using two-tailed paired t-tests.

Finally, we evaluated a different type of extrapolative approach to estimating species richness for larger sample sizes, extrapolation of sample-based rarefaction curves (Colwell, 2013). Recent advances in extrapolation of sample-based rarefaction curves have improved this approach to estimating species richness for a given area relative to the interpolative approaches because it can utilize the entire suite of data collected while maintaining confidence in the estimate (Colwell et al., 2012). EstimateS 9.0 was used to compute the extrapolation of sample-based rarefaction curves with unconditional variance estimates (95% confidence intervals) for results from each of the samples collected using the proportional area sampling design at the seven beaches (Colwell et al., 2012; Colwell, 2013).

We compared the estimated richness of the extrapolated sample for the smallest area sampled (proportional area sampling design) to the observed richness of the sample for the largest area sampled (fixed area sampling design) for each beach. The resulting unconditional 95% confidence intervals (1.96 SE) for the proportional area sampling designs (Colwell et al., 2012; Colwell, 2013) were used to examine whether the estimated richness yielded by the two sampling designs differed significantly ($p \leq 0.05$) at individual beaches. Additionally, we tested whether the values of estimated species richness from this method differed significantly between the two sampling designs across the seven study beaches with a two-tailed paired t-test.

We investigated whether a sampling area-based calibration could improve comparisons of species richness among sampling designs by plotting the ratio of the richness from the proportional area sampling design to that of the fixed area sampling design (e.g. proportional/fixed richness, hereafter, richness ratio) as a function of area sampled for the observed and the estimated values of species richness for each of the seven sites. The goodness-of-fit of these relationships was analyzed using ordinary linear regression.

Results

Intertidal widths varied over six-fold among our sites, ranging from 21.3 m at Coal Oil Point to 143.4 m at Morro Bay (Table 1). For the proportional area sampling design, sampling area for individual beaches varied more than seven-fold as a function of intertidal width, ranging from 0.4 m^2 at the narrowest beach, Coal Oil Point, to 3.0 m^2 at the widest beach, Morro Bay. We consistently sampled greater surface areas using the fixed area sampling design compared to the proportional area sampling design (Table 1). At Morro Bay, the beach with the widest intertidal width, the area sampled using the proportional area sampling design was most similar to the area sampled in the fixed area sampling design (86%). At the narrowest beach Coal Oil Point the areas sampled by the two sampling designs were the least similar (11%) (Table 1).

Overall, we found a total of 72 sandy intertidal macroinvertebrate species (not including terrestrial incidentals) in a total combined sampling area of 34.7 m^2 for the seven beaches in our study. For the fixed area sampling design, a total of 67 species occurred in a total sampling area of 24.8 m^2, representing 93% of the combined pool of 72 species. Using the proportional area sampling design, a total of 58 species occurred in a sampling area of 9.9 m^2, representing 81% of the species pool. The minimum and maximum values of observed species richness across the seven sites were similar between the two sampling designs. Observed species richness for the seven sites ranged from 8 species at Point Dume to 35 species at Cayucos using the proportional area sampling design and 12 species at Point Dume to 38 species at Cayucos using the fixed area sampling design (Table 2).

The values of observed species richness differed significantly between the two sampling designs (Table 2). Values for observed species richness were greater for the fixed area sampling design than the proportional area sampling design (difference = 3–10 species) in all comparisons with one exception (Table 2, Fig. 3). At the widest beach, Morro Bay, 30 species were collected using the proportional area sampling design and 28 species were collected using the fixed area sampling design (Table 2).

When the seven non-parametric species richness estimators were applied to each sampling design across sites, they consistently produced higher values for species richness (mean = 5.4 ± 3.8 species, n = 14, range: 0.2–20.2 species) than observed richness. However, the mean difference in species richness between designs was slightly higher for the estimated richness than observed richness (Fig. 4). On average, the mean difference in observed richness between the two designs was 5.1 species (± 3.9 species, n = 7, range: -2–10 species), while the mean difference between the two designs for all estimators was 5.8

species (± 6.1 species, n = 49, range: -5.7–22.2 species). No single species richness estimator consistently reduced the difference in values of species richness between sampling designs across the seven sites (Table 2, Fig. 4). Their performance varied among the seven beaches, but at the beach with the largest difference in area sampled (3.1 m^2), Coal Oil Point, all estimators reduced the difference in richness between the sampling designs (8 to 4.0 species ± 1.1 species, n = 7, range: 0.9–7.8 species) (Fig. 4c). Five of the richness estimators also reduced the difference in values of species richness at three of the beaches, North Carpinteria (ACE and ICE), Point Dume (Chao 1 and Jackknife 2), and Scripps (ACE, Chao 1, and Chao 2) (Fig. 4d, f, and g). For four of the seven non-parametric richness estimators the values of estimated species richness for the two designs differ significantly (Table 2) suggesting that the richness estimators did not adjust for the differences in species richness between the two sampling designs.

The ratio of observed species richness (proportional area/fixed area) yielded by the two sampling designs yielded the highest correlation with area sampled across our seven study sites ($r^2 = 0.84$, $p<0.05$) (Fig. 5a). For four of the seven richness estimators (ACE, Chao 1, Jackknife 1, and Bootstrap), relationships between these ratios and area sampled were also significantly correlated ($p\leq0.05$), with the highest correlation for the ACE estimator ($r^2 = 0.82$) (Fig. 5b–h). The ratio of species richness (proportional area/fixed area) yielded by the extrapolation of the sample-based rarefaction curves was not significantly correlated (($r^2 = 0.04$, $p\geq0.05$) with area sampled.

Differences in richness between the two sampling designs were reduced (mean = 0.9 ± 3.1 species, n = 7, range: 3.6–4.2 species) at all but one of the beaches when adjusting for sampling area using the extrapolation of the sample-based rarefaction curve approach. At

Morro Bay, where sampling areas were most similar, the difference in estimated species richness was greater (1.3 species) than the difference in observed richness (Table 2). Overall, values of estimated species richness adjusted for sampling area by extrapolation did not differ significantly between the two sampling designs across our study beaches (Table 2).

By adjusting for sampling area, the estimate of species richness from the extrapolation of the sample-based rarefaction curve yielded a higher mean value of richness than the observed richness for the proportional area sampling design at all sites (mean = 4.3 ± 3.8 species , n = 7, range: 1.3–11.6 species) (Table 2). The observed species richness for the fixed area sampling design fell within the 95% confidence interval of the estimated richness from extrapolation of sample-based rarefaction curves for the proportional area sampling design at all sites (Fig. 6).

Discussion

We obtained very different results for species richness of intertidal invertebrates on open coast beaches using two sampling designs, despite the use of simultaneous sampling on the same nested intertidal grid. Sampling area differences between the two designs we used appear to represent the most important source of variation with regard to species richness values. Given the strength of species area relationships in most ecosystems, it is not surprising that our results indicated that the proportional area sampling design consistently undersampled the intertidal species pool as a result of the smaller sampling area on most of the beaches we surveyed. The more similar the sampling areas, the more similar species richness values would be expected to be for a given site and date. This idea is supported by our results from the widest beach, Morro Bay, where sampling area for the fixed area and proportional area designs were most similar and species richness values were comparable between the two designs.

Our results generally support the idea that an extrapolative approach to estimating species richness is a methodology that researchers may be able to use to standardize and compare this component of biodiversity across surveys and sampling designs. Observed richness is almost always an underestimate of true richness, an emphasis of Schoeman et al. (2008) and others. The use of extrapolative non-parametric species richness estimators for sandy beaches has provided more accurate estimates of true richness than observed values at both regional (Foggo et al., 2003) and survey levels (Schoeman et al., 2003; Schoeman et al., 2008). It has been suggested that non-parametric richness estimators could be used to compare estimates of species richness when sampling designs differ (Basualdo, 2011). However, these species richness estimators did not consistently or adequately account for differences in the richness of intertidal macroinvertebrates associated with sampling design in our comparisons. The inability of the species richness estimators to consistently yield comparable results for true richness among sampling designs in our analyses is likely related to the small proportion of the species pool sampled by both designs, resulting in large (20-40%) differences between values of observed species richness and the highest estimates of true species richness.

Non-parametric richness estimators conservatively predict the total richness of the species pool based on species-area relationships (Colwell, 2013). For this reason we expected the smallest difference between the observed and estimated richness to occur in surveys in which the highest proportion of beach was excavated. In agreement with our prediction, differences between values of observed and estimated species richness were lowest (7-16%) at the narrowest beach surveyed, Coal Oil Point, where approximately twice the intertidal width was excavated across all three transects for the fixed area sampling design.

The strong linear correlations for the ratios (proportional area/fixed area) of species richness for both observed and estimated richness values obtained by the two designs as a function of sampling area emphasized the influence of sampling area. The highest correlation we obtained was for the ratio of observed species richness as a function of sampling area. However, relationships between ratios of species richness and area sampled were significant for four of the seven richness estimators, including two that have been considered the most accurate estimators of true richness for sandy beaches, Chao 1 (Foggo et al. 2003) and Jackknife 1 (Schoeman et al., 2008). Those strong correlations for the four non-parametric richness estimators provide a potential means of calibrating between the sampling designs while maintaining more accurate estimates of true species richness.

Extrapolation using sample-based rarefaction curves provided the most effective approach to calibrating species richness values obtained by the two sampling designs we used on sandy beaches in our study. This approach, although not perfect, has been commonly used in the standardization of sampling effort in community biodiversity comparisons in other ecosystems (e.g. Gotelli and Colwell, 2001; Magurran and McGill, 2011; Colwell et al., 2012).

In our study, sampling area was the primary factor affecting differences in observed species richness between sampling designs. However, for those wishing to use the calibration approach described here to compare species richness results from different sampling designs, differences in other key sampling components, such as core depth and mesh size (see Schlacher et al 2008), if present, will also need to be explicitly considered.

Our results and those of others (Foggo et al., 2003; Schoeman et al., 2003; Schoeman et al., 2008) indicate that identifying changes in biodiversity on sandy beaches cannot be accomplished by simply comparing observed species richness, particularly when sampling designs differ. We were able to effectively calibrate differences in species richness between the two intertidal sampling designs used on sandy beaches by adjusting for area sampled with the extrapolation of sample-based rarefaction curves to a sampling area of 3.5 m^2. The approach we developed and tested to calibrate species richness estimates among different sampling designs could be used to allow more accurate comparisons of species richness across larger temporal and spatial scales. The evaluations made possible by this approach will provide needed opportunities to investigate responses of biodiversity of intertidal ecosystems to long term effects of human impacts and climate change.

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Figures

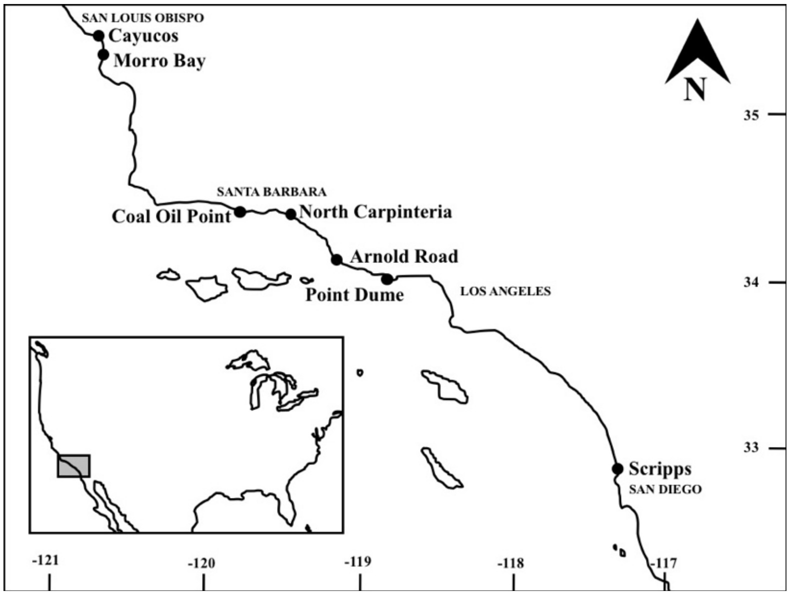

Figure 1. Map of the locations of sites sampled in this study on the southern and central California coast of the United States. Black dots indicate location of each site.

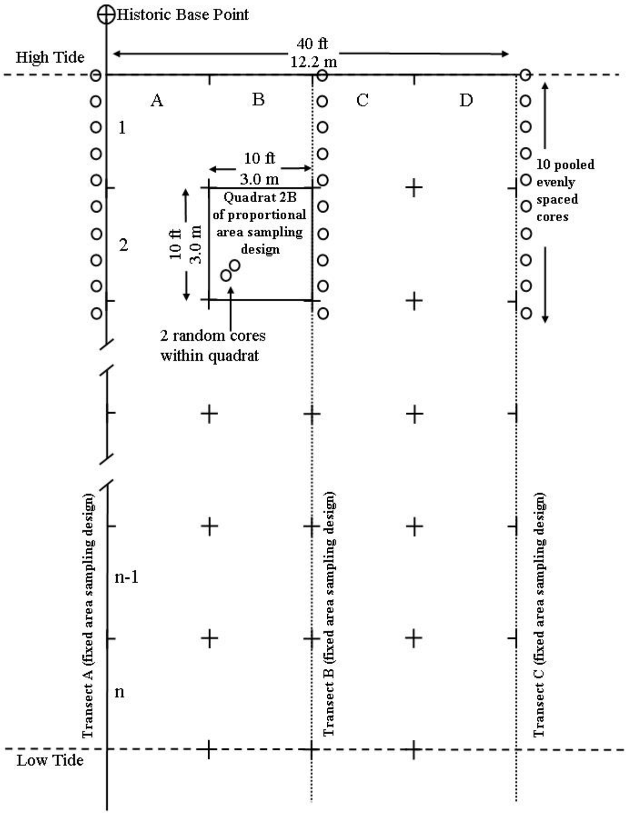

Figure 2. Diagram of the layout for the proportional area sampling design and the fixed area sampling design relative to the historic baseline transect, 24-hour high tide line, and low tide line. Figure is not drawn to scale.

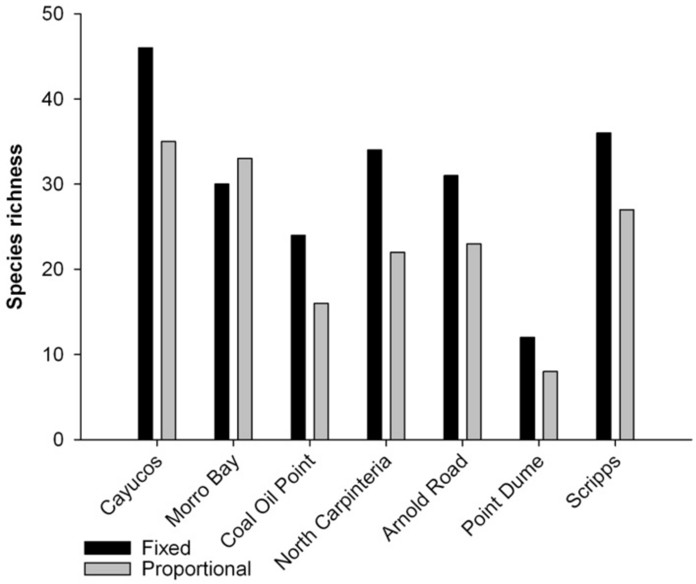

Figure 3. Observed species richness for the fixed area and proportional area sampling designs at all beaches.

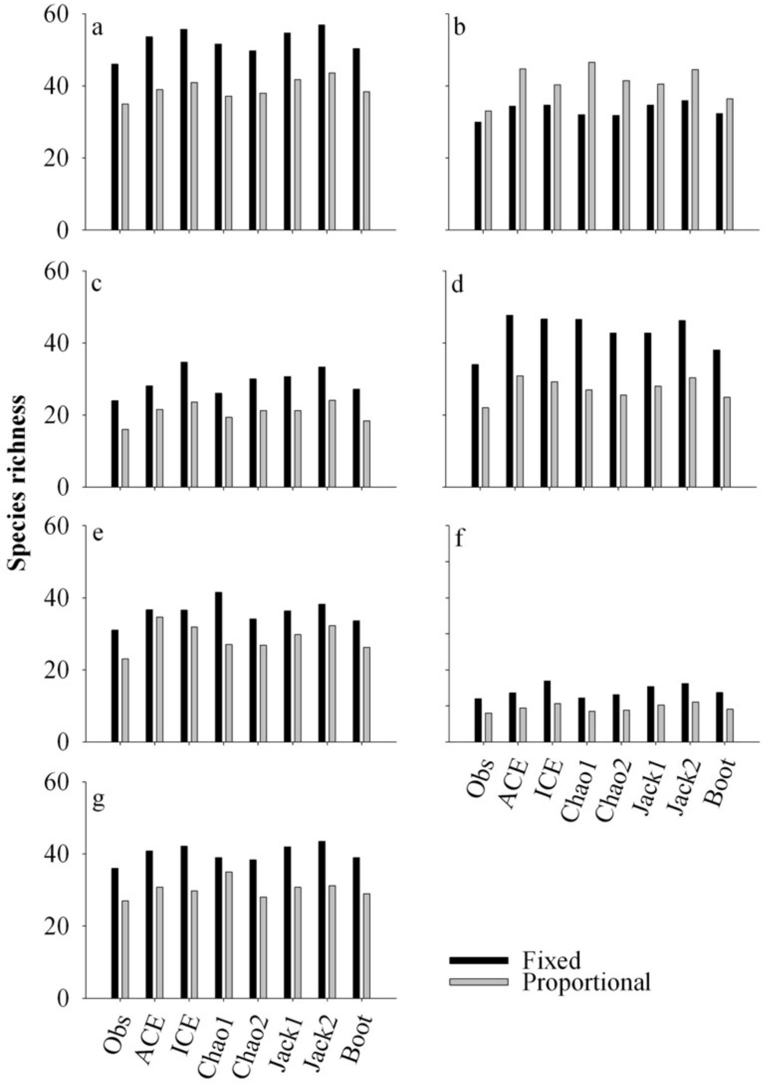

Figure 4. Differences in observed species richness (Obs) and species richness estimates (ACE, ICE, Chao1, Chao 2, Jackknife 1, Jackknife 2, and Bootstrap) between the fixed and proportional area sampling designs at a) Cayucos b) Morro Bay c) Coal Oil Point d) North Carpinteria e) Arnold Road f) Point Dume and g) Scripps.

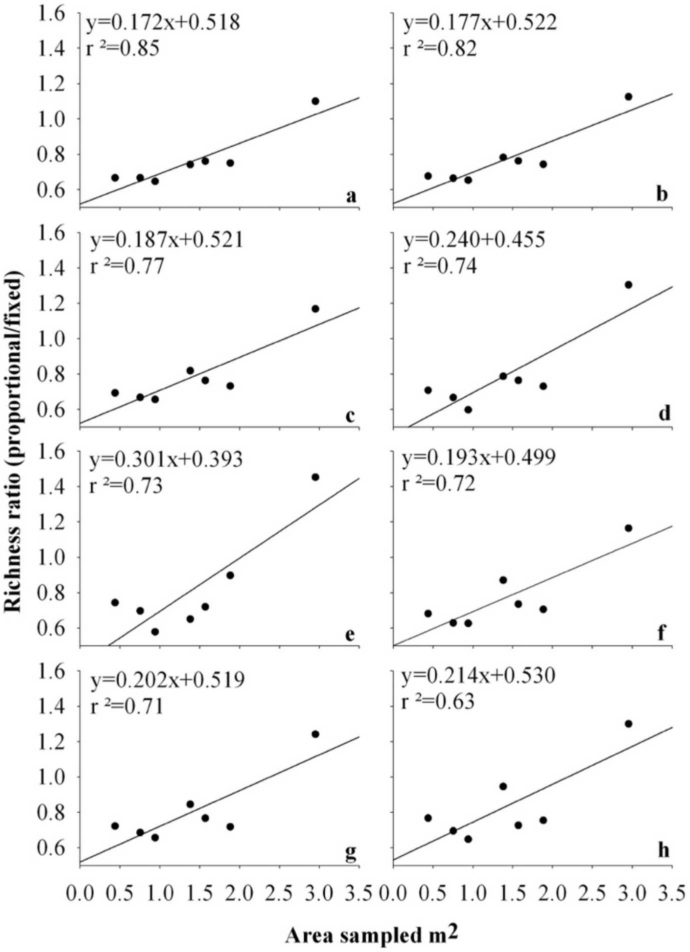

Figure 5. The relationship between the ratio of species richness from the proportional area sampling design to the species richness using the fixed area sampling design as a function of sampling area for a) observed species richness and for estimated species richness obtained from b) ACE c) Bootstrap 1 d) Jackknife 1 2 e) Chao 1 f) Chao 2 g) ICE and h) Jackknife 2 estimators for the seven study beaches. The regression equation and correlation coefficient are displayed on all graphs. Lines are shown for all significant regressions ($p<0.05$).

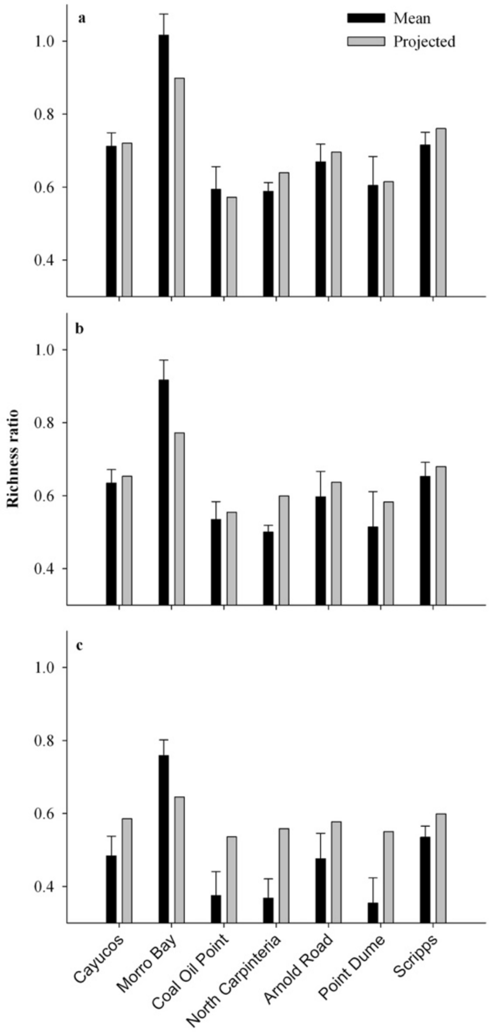

Figure 6. A comparison of the observed richness for the fixed area sampling design and the estimated mean richness for the proportional area design with 95% confidence intervals (1.96 SE). Estimates of richness are from the extrapolation of the sample-based rarefaction curve (ESBRC) of the proportional area design.

Tables

Table 1. Beach sites, sampling dates, intertidal widths, area sampled, and tide heights for the two sampling designs used in the study.

Site	Date	Total beach width m	Intertidal beach width m	Fixed sampling area m2	Proportional sampling area m2	Low ht m
Cayucos	October 3, 2009	128.0	76.2	3.53	1.57	0.15
Morro Bay	November 15, 2009	216.5	143.0	3.53	2.95	-0.21
Coal Oil Point	August 23, 2009	26.0	26.0	3.53	0.42	0.21
North Carpinteria	August 21, 2009	84.8	45.7	3.53	0.94	0.21
Arnold Road	August 22, 2009	118.6	67.1	3.53	1.38	0.21
Point Dume	September 21, 2009	89.5	36.6	3.53	0.75	0.06
Scripps	August 31, 2011	102.1	91.5	3.53	1.88	0.09

Table 2. Observed species richness, non-parametric richness estimates, and richness estimate using the extrapolation of the sample-based rarefaction curve approach (ESBRC) obtained for the two sampling designs at the study sites with the t-statistic and p-values from two-tailed paired t-tests comparing differences in species richness between the two sampling designs.

Site	Observed	ACE	ICE	Chao 1	Chao 2	Jack 1	Jack 2	Bootstrap	ESBRC
Fixed area sampling design									
Cayucos	38	47	46	45	44	48	50	43	38
Morro Bay	28	32	31	31	31	33	36	30	28
Coal Oil Point	25	29	29	27	27	30	29	28	25
North Carpinteria	32	41	42	46	52	43	50	37	32
Arnold Road	29	32	33	34	36	35	40	32	29
Point Dume	12	14	15	12	13	16	15	14	12
Scripps	33	35	37	35	37	40	43	36	33
Proportional area sampling design									
Cayucos	35	38	37	37	36	40	38	38	37
Morro Bay	30	36	36	37	35	37	41	33	31
Coal Oil Point	17	23	30	23	29	24	28	20	29
North Carpinteria	22	31	33	27	30	30	34	26	29
Arnold Road	23	25	26	24	25	28	29	26	26
Point Dume	8	9	11	9	9	11	12	9	10
Scripps	26	30	29	34	34	30	33	28	29
Two-tailed paired t-test									
t	3.46	3.04	2.18	1.90	1.81	3.18	2.39	3.47	0.75
p-value	0.01	0.02	0.07	0.11	0.12	0.02	0.05	0.01	0.48

Chapter II. Local scale processes drive long-term change in biodiversity of sandy beach ecosystems

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Abstract

Evaluating impacts to biodiversity requires ecologically informed comparisons over sufficient timespans. The vulnerability of coastal ecosystems to anthropogenic and climate change related impacts makes them potentially valuable indicators of biodiversity change. To evaluate multidecadal change in biodiversity, we compared results from intertidal surveys of 13 sandy beaches conducted in the 1970s and 2009-11 along 500 km of coast (California, USA). Using a novel extrapolation approach to adjust species richness for sampling effort allowed us to address data gaps and has promise for application to other data-limited biodiversity comparisons. Long-term changes in species richness varied in direction and magnitude among beaches and with human impacts but showed no regional patterns. Observed long-term changes in richness differed markedly among functional groups of intertidal invertebrates. At the majority (77%) of beaches, changes in richness were most evident for wrack-associated invertebrates suggesting they have disproportionate vulnerability to impacts. Reduced diversity of this group was consistent with long-term

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habitat loss from erosion and sea level rise at one beach. Wrack-associated species richness declined over time at impacted beaches (beach fill and grooming), despite observed increases in overall intertidal richness. In contrast richness of these taxa increased at more than half (53%) of the beaches including two beaches recovering from decades of off-road vehicle impacts. Over more than three decades, our results suggest that local scale processes exerted a stronger influence on intertidal biodiversity on beaches than regional processes and highlight the role of human impacts for local spatial scales. Our results illustrate how comparisons of overall biodiversity may mask ecologically important changes and stress the value of evaluating biodiversity change in the context of functional groups. The long-term loss of wrack-associated species, a key component of sandy beach ecosystems, documented here represents a significant threat to the biodiversity and function of coastal ecosystems.

Keywords: habitat loss, intertidal, macroinvertebrates, macrophyte wrack, marine, coastal, anthropogenic impacts, recovery, species richness, species-area curves

Introduction

On a global scale biodiversity is unequivocally considered to be declining due to species extinctions driven by climate change, development, and other human impacts (Pimm *et al.*, 1995; Sala *et al.*, 2000; Butchart *et al.*, 2010; Hoegh-Guldberg & Bruno, 2010; Gonzalez *et al.*, 2016). However, biodiversity declines have not been consistently observed at local and regional spatial scales (Sax & Gaines, 2003; Vellend *et al.*, 2013; Thomas, 2013; Dornelas *et al.*, 2014; Hautekèete *et al.*, 2015). As Earth's climate changes, determining whether and how biodiversity is decreasing and the processes responsible is the most pressing issue facing modern ecologists (Gonzalez *et al.*, 2016).

Shifts in geographic ranges of individual species in response to climate change have already been described extensively (e.g. Parmesan & Yohe, 2003; Burrows *et al.*, 2011; Chen *et al.*, 2011; Schoeman *et al.*, 2014). At the same time, human impacts can increase diversity at multiple scales through mechanisms including changing disturbance regimes (Devictor & Robert, 2009) and addition of exotic species (Bruno *et al.*, 2004). Despite a growing number of local scale long-term biodiversity studies (see Vellend *et al.*, 2013; Dornelas *et al.*, 2015), major gaps in the understanding of biodiversity change outside of developed nations and for underrepresented biomes seriously impede our ability to accurately quantify biodiversity change across the planet (Gonzalez *et al.*, 2016). For example, only a few studies have assessed long-term change in biodiversity for coastal ecosystems on a regional scale (e.g. Smith *et al.*, 2006; Zabin *et al.*, 2013; Elahi *et al.*, 2015; Novoa *et al.*, 2016) and none of these studies have addressed diversity change for sandy beach ecosystems, which dominate shorelines globally making up ~70% of open coasts (Schoeman *et al.*, 2014).

Understanding the responses of communities and ecosystems to climate forcing is critical for conservation (Harley *et al*., 2006; Gonzalez *et al*., 2016). Coastal ecosystems are expected to be particularly sensitive to sea level rise and warming as intertidal communities are exposed to extremes in abiotic conditions (Harley *et al*., 2006). Sandy beach ecosystems support diverse, endemic intertidal communities on a narrow strip of habitat between the land and sea (McLachlan *et al*., 1995; Dugan *et al*., 2010). Local scale anthropogenic drivers, including beach filling, grooming, armoring, off-road vehicle (ORV) use, fishing, and recreation, have been shown to impact beach ecosystems (Schlacher *et al*., 2007; Defeo *et al*., 2009), but data on scales sufficient to detect regional or global scale biodiversity change are lacking for these underrepresented biomes (Dugan *et al*., 2010; Schoeman *et al*., 2014, Gonzalez *et al*., 2016).

Ecosystems and species are not expected to be equally vulnerable to climate change and other stressors (Pacifici *et al*., 2015). Ecological theory and experiments have shown that declines in biodiversity could depress ecosystem stability and function and increase invasibility, which could lead to higher species richness (Cardinale *et al*., 2012; Tilman *et al*., 2014; Lefcheck *et al*., 2015; Gamfeldt *et al*., 2015). Analyses of overall biodiversity could mask important changes that may only be apparent in a subset of the community that shares specific ecological traits. Identifying the functional groups or taxa with traits that make them vulnerable to extinction could increase our ability to accurately detect meaningful change in community structure, identify the mechanisms responsible, and predict which aspects of biodiversity are most likely to be impacted by changes in specific environmental factors or processes (Elahi *et al*., 2015).

Sandy beaches are characterized by low *in situ* primary production and subsidies of marine macrophytes cast ashore as wrack provide food and shelter to an important component of the overall intertidal community, wrack-associated species (Fig. 1). The diverse invertebrates associated with wrack (Fig. 1) are highly sensitive to local impacts as well as climate change (Dugan *et al*., 2003, 2008, Hubbard *et al*., 2014). Climate change is likely to affect the availability of wrack through multiple processes: warming is expected to decrease productivity of kelps in upwelling areas (Schiel & Foster, 2015), while losses of beach habitat due to sea level rise and erosion will reduce retention of wrack on beaches (Revell *et al*., 2011, Vitousek *et al*., 2017). Wrack-associated invertebrates, moreover, are characterized by limited dispersal ability and direct development (Grantham *et al*., 2003) both of which likely reduce their resilience to disturbance (Dugan *et al*., 2003; Hubbard *et al*., 2014).

Here we evaluate the direction and magnitude of change in the biodiversity of sandy beach ecosystems in southern and central California, USA across more than three decades. We hypothesized that declines in overall species richness on beaches due to anthropogenic and climate change related impacts on habitat and food supply would be evident at both local and regional scales over this time span. We predicted that a vulnerable functional group, wrack-associated invertebrates, would exhibit greater declines in species richness and be most sensitive to local and regional stressors due to their low dispersal ability and life histories and their dependence on a variable cross-ecosystem subsidy.

Materials and Methods

Biodiversity surveys

Our 13 study beaches spanned ~500 km of coastline in California, USA, from Cayucos (35°26.058'N) to San Diego (32°44.523'N) (Fig. 2, Table 1). All beaches could be classified as intermediate morphodynamic type for both study periods. Extensive intertidal macroinvertebrate surveys were conducted in the 1970s by Patterson (1974) and Straughan (1982). We used data from a total of 214 surveys conducted at the 13 beaches from 1969 to 1980 (hereafter 1970s surveys) (Appendix S1). To address the lack of complete datasets on species abundance and biomass at all 13 sites, we relied on cumulative species lists (Table S1) and area sampled data compiled for each site for our comparisons between survey periods. We compiled cumulative lists of overall, wrack-associated, and low dispersal wrack-associated species for each site from Patterson (1974) and Straughan (1982). We calculated a cumulative sampling area for each study beach using the number of surveys conducted, active intertidal zone widths (distance from the 24 hour high tide line to the low swash limit), and sampling design for each survey based on Straughan (1982). We estimated the sampling area for wrack-associated invertebrates by calculating the area of the upper beach zone where wrack-associated species are found for each survey. This zone was smaller than the active intertidal zone and covered from the 24 h high tide line down to the lowest sample containing wrack-associated species (Dugan *et al*., 2013).

We resurveyed intertidal macroinvertebrate communities at the 13 study beaches from 2009 to 2011, conducting a total of 35 surveys, primarily in the late summer and fall (Table 1). Surveys were conducted during spring low tides in daylight when surface activity of invertebrates is minimal. We used sediment cores to collect samples, which were sieved through 1.5 mm mesh to retain macrofauna. Two different sampling designs were used, one similar to the sampling design in the 1970s survey period with a sample area that was proportional to and varied with active intertidal width and one with a fixed sampling area that was independent of active intertidal width (Table 1; Appendix S1; Fig. S1; Schooler *et al*., 2014). We chose to employ two survey methods in order to better calibrate for differences in sampling design and effort between survey periods (Schooler *et al*., 2014). The sampling design that was independent of active intertidal width and surveyed the most area is the preferred method by beach ecologists (Schlacher *et al*., 2008). Using this method to maximize sampling effort in the 2009-11 surveys, allowed a more robust evaluation of change in species richness between survey periods.

Beach characteristics

Physical attributes and macrophyte wrack are considered to be the key drivers of community structure on beaches, far more important than biological interactions (McLachlan *et al*., 1993; Dugan *et al*., 2003; Brown & McLachlan, 2010). For each survey, we measured active intertidal widths and collected sand samples for grain size analysis. Data on sand grain size and active intertidal beach width from fall surveys (August to November) for study beaches in the 1970s were extracted from Patterson, Straughan, and handwritten field and laboratory data sheets.

In the 1970s, sand samples were collected every 3.0 m along the basepoint transect spanning the width of the active intertidal. In 2009-11, sand samples were collected on each transect at the 24 h high tide line and water table outcrop, standard locations for calculating mean grain size (Brown & McLachlan, 2010). Sand was rinsed with fresh water, dried, and run through graded sieves in the laboratory. We calculated arithmetic mean grain size for each sand sample from the 2009-11 surveys using the R package ‘G2Sd’ (Gallon & Fournier, 2013). We measured the abundance of wrack as cover in the 2009-11 surveys using the methods of Dugan *et al*. (2003) which employs a line intercept method along each transect sampled for macroinvertebrates. A number of the physical characteristics recorded in the 1970s surveys were limited and often qualitative. Therefore it was not possible to make quantitative temporal comparisons of wrack cover and morphodynamic state across the survey periods.

Data analysis

Evaluating change in biodiversity

To estimate cumulative richness from the 2009-11 surveys we used rarefaction (when 1970s sample area < 2009-11) or extrapolation (1970s sample area > 2009-11) methods of Colwell *et al*. (2012) and Chao *et al*. (2014) to adjust observed species richness for differences in sampling areas among survey periods (hereafter adjusted species richness). Species-area curves with 95% confidence limits were generated for each site for the 2009-11 surveys using EstimateS software (version 9.0; Colwell, 2013), both for the overall intertidal community and wrack-associated macroinvertebrates. Where multiple sampling designs were employed in the recent surveys (nine beaches), we used data from the sampling design that yielded the greatest area sampled across the 2009-11 surveys to create species-area curves. Generally this was the fixed area design (eight of 13 beaches).

To compare adjusted species richness between sampling periods, we plotted the cumulative species number versus cumulative area sampled from the 1970s surveys on the species-area curves constructed from 2009-11 biodiversity data for each beach. The position of the value for the 1970s cumulative species richness and area with respect to the 95% confidence intervals of the species-area curves was used to assess the direction, magnitude, and significance of differences in species richness between time periods. We estimated the adjusted species richness from the 2009-11 surveys as the point on the species-area curve at the cumulative area sampled in the 1970s. The direction and magnitude of the difference in species richness between the survey periods was estimated by calculating the difference between the cumulative species richness from each 1970s survey and the estimated adjusted species richness from the 2009-11 surveys at the same beach for two categories of macroinvertebrates, overall and wrack-associated taxa.

We used these results to evaluate patterns in the direction and magnitude of change in species richness between survey periods. Change in richness was expressed as a percentage with positive and negative values representing increases and decreases in species richness over time, respectively.

Drivers of intertidal richness

Differences in active intertidal width and mean grain size between the 1970s and 2009-11 survey periods were evaluated with a one-way ANOVA (SPSS v.17.0) and also expressed as percentages. We used OLS regression to evaluate relationships among mean grain size, active intertidal width, and wrack cover (2009-11 only) with the overall and wrack-associated species richness adjusted for sampling area for our 2009-11 surveys (SPSS v.17.0). We inspected the residuals for these model regressions visually by using standard diagnostic plots to assess violations of model assumptions. Bearing in mind that sample sizes were small (n = 13), we found little evidence of heteroscedasticity, trends, or non-normality among residuals.

To evaluate impacts from climate change or other processes operating on regional spatial scales we looked for widespread declines in species richness across study beaches consistent with large-scale environmental drivers (e.g. sea level rise, sea surface temperature, wave height). To assess influence of local scale processes on species richness over time, we compiled information on disturbance activities (Table 1) and beach characteristics for each study beach. We evaluated responses of species richness to these potential regional and local drivers for three categories of macroinvertebrates: overall, wrack-associated, and low dispersal wrack-associated species.

Results

Biodiversity

A total of 109 species (89 total species in each survey period) of intertidal macroinvertebrates ($\overline{x}$ = 36.2 ± 5.0 SE species per site, *n* = 13, range = 11 – 64 species) were recorded in all beach surveys (249 surveys). No regional patterns in observed species richness were evident in either survey period (Fig. 3). Observed species richness varied > six-fold across the 13 study beaches but was similar in the two survey periods (1970s: 8 – 48 species per site, 2009-11: 8 – 55 species per site) (Fig. 3).

In both survey periods intertidal macroinvertebrate communities were dominated by Polychaeta (33%), Insecta (28%), and Crustacea (27%). Only one species, the sand crab *Emerita analoga*, was collected at every beach in both survey periods (Table S1). Other common taxa include the peracarid isopod, *Excirolana* sp., and the polychaetes, *Hemipodia* sp., *Nephtys californiensis*, and *Scolelepis bullibranchia*, which were collected at ≥ 11 of the 13 study beaches (Table S1). Two species, the talitrid amphipod, *Megalorchestia columbiana* and gastropod, *Callianax biplicata*, were collected at slightly less than half of the beaches in the 1970s and only one or two beaches in the 2009-11 surveys, the largest decline in occurrence we observed for species that were collected in both survey periods (Table S1).

Wrack-associated invertebrates made up greater than a third of the total observed macroinvertebrate species in each survey period (1970s: 34%, 2009-11: 39%) (Fig. 3). Species lacking planktonic larval stages and with limited dispersal abilities as adults made up more than a third of these wrack-associated taxa (1970s: 37% and 2009-11: 35%) and 12% of the total species (1970s: 13%; 2009-11: 14%). Eight wrack-associated species of peracarid Crustacea, all of which brood their young and have limited adult dispersal, were found including six species of talitrid amphipods (*Megalorchestia* spp.) and two oniscid isopods (*Alloniscus perconvexus* and *Tylos punctatus*) (Table 2; Table S1). At least one species of talitrid amphipod was collected at every beach with the exception of Westward (Table S1). Oniscid isopods were more restricted in distribution (nine beaches) (Table S1). Coleoptera were the most diverse order of wrack-associated macroinvertebrates with 24 species from six families observed across the survey periods at our study beaches (Table S1). Of these, four species are flightless with low dispersal ability (Table 2). Overall species richness of Coleoptera increased across the survey periods with five more species observed in 2009-2011 (Table S1).

Beach characteristics

No regional patterns of change in beach characteristics were evident across survey periods. Active intertidal width and mean sand grain size remained similar between survey periods at the majority of study beaches and significant differences in these parameters were limited to three beaches (Figs. 4, S2). Many beaches in the study region, including four of our study beaches, are subject to intense anthropogenic impacts, such as grooming and beach fills, as part of the local coastal management regime (Table 1).

Mean values of active intertidal width, which represents habitat area available for beach communities, varied at least five-fold among study beaches in both survey periods, with values ranging from 24 m to 183 m across sites during fall surveys (Fig. S2a). A significant difference in mean active intertidal width between survey periods was detected at only one site, Crystal Cove ($F = 14.52$, $P = 0.03$), which was wider (38%) in the 2009-11 surveys (Fig. 4a). The greatest loss of intertidal width between survey periods (24%) was observed at Coal Oil Point, but was not statistically significant (Fig. 4a).

Mean values of sand grain size varied more than three-fold among study beaches in both survey periods, ranging from 0.14 mm to 0.53 mm in fall surveys (Fig. S2b). Values for mean grain size were greater for the 2009-11 surveys than the 1970s surveys for the majority of beaches (10 beaches) and lower mean values were observed in the recent surveys at 25% of the beaches (three beaches) (Fig. 4b). Significant differences in values of mean sand grain size between survey periods were detected at only two sites, Coal Oil Point ($F = 6.27$, $P = 0.031$) and North Carpinteria ($F = 14.13$, $P = 0.033$), with greater values in recent surveys for both beaches (Fig. 4b).

The mean cover of macrophtye wrack varied more than sixty-fold ($\bar{x} = 1.8 \pm 0.5$ m^2 m^{-1}, range: 0.1 – 6.6 m^2 m^{-1}) among study beaches in the 2009-11 surveys (Fig. S3). Ungroomed beaches ($\bar{x} = 2.1$ m^2 m^{-1} $\pm$ 0.7 m^2 m^{-1}, $n = 9$, range = 0.2 – 6.6 m^2 m^{-1}) had four times the cover of wrack compared to urban beaches ($\bar{x} = 0.5$ m^2 m^{-1} $\pm$ 0.3 m^2 m^{-1}, $n = 3$, range = 0.1 – 1.1 m^2 m^{-1}) with the exception of Ocean Beach which had high cover of fresh wrack (3.6 m^2 m^{-1}) in the lower intertidal zone (Fig. S3; Table 1).

Drivers of intertidal richness

Local scale anthropogenic drivers

Although the multidecadal changes we detected in biodiversity varied in magnitude and direction among beaches, our analyses of values of adjusted species richness using species-area curves for overall and wrack-associated species revealed several trends across the survey periods (Figs. 5, 6; see Figures S4, S5 in Supporting Information for details) that were related to the history of human impacts (Table 1). A large component of the differences we detected in adjusted species richness across the survey periods was driven by wrack-associated species with ecologically important shifts in richness of this group evident for 77% (10) of the 13 beaches (Fig. 6). Differences detected in the richness of wrack-associated species exceeded those for overall adjusted species richness in magnitude at nine (69%) of the beaches and differed in direction at four (31%) of the beaches (Fig. 6). For beaches with no detectable anthropogenic impacts, overall and wrack-associated species richness increased significantly between the survey periods except for one beach where declines in species richness were consistent with habitat loss (Fig. 6b; white and black bars with asterisks). Where local scale anthropogenic drivers were identified on our study beaches, we observed ecologically important declines in the species richness of the wrack-associated and low dispersal wrack-associated groups (Fig. 6b; gray and gray hatched bars). For two beaches where ORV use was banned between survey periods, overall and wrack-associated species richness increased in a manner that was consistent with recovery from impacts (Fig. 6b; white hatched bars).

We also detected significant differences (Fig. 5ab) in overall and wrack-associated adjusted richness between survey periods at five of six beaches where no direct beach alterations were identified during or between survey periods (Table 1) (Fig. 6; white and black bars with asterisks). For these six beaches, cumulative overall and wrack-associated species richness in the 1970s varied ≥ three-fold among beaches (Fig. 3). Higher values for overall and wrack-associated adjusted richness were estimated in 2009-11 compared to 1970s surveys at four beaches (Figs. 5a, 6; white bars). Adjusted overall richness ranged from 17% (Dume Cove) to 84% higher (Crystal Cove) with a mean value of 48% higher species richness (Figs. 5a, 6a; white bars). In contrast, for one beach (Coal Oil Point), overall and wrack-associated adjusted richness was much lower (38% and 62%, respectively) in the 2009-11 surveys compared to the 1970s (Figs. 5b, 6; black bars), a result consistent with the observed loss of intertidal habitat estimated by intertidal width (Fig. 4). Notably, four species of talitrid amphipods with low dispersal abilities were reported at Coal Oil Point in the 1970s surveys compared to only one species in the 2009-11 surveys, a 75% decline in richness of this ecologically important genus (Table 2).

For degraded urban beaches that experienced continuous impacts from intensive grooming and major beach fills (Table 1) which commenced well before the 1970s surveys and continued throughout both survey periods, the adjusted richness of wrack-associated species declined despite increases in overall richness at three of four beaches (Fig. 6b; gray bars). Values of cumulative overall and wrack-associated species richness in the 1970s were low and varied three-fold and four-fold, respectively, among these beaches (Fig. 3). Overall adjusted richness at these four beaches was 45% higher on average in the 2009-11 surveys (Fig. 6a; gray bars). However at three of these beaches, the average value for adjusted richness of wrack-associated species was 41% lower in the 2009-11 surveys (Hollywood: 23%, Westward: 50%, and Torrance: 50%; Fig. 6b; gray bars). For wrack-associated species with low dispersal abilities, major differences in the number of species between survey periods were also evident at the fourth urban beach, Ocean Beach (Table 2). Two taxa, a talitrid amphipod and an oniscid isopod, recorded in the 1970s surveys were not detected at Ocean Beach in the 2009 or 2010 surveys, representing a loss of two genera, the greatest loss observed for any study beach despite gains in overall and wrack-associated adjusted richness (Table 2).

Beach fills conducted during and between the survey periods at one beach, Morro Bay, included large dredge pipes stretched across upper-beach habitat and our sampling area during the 2009 survey (Table 1). Despite these direct impacts, cumulative overall richness was high (34 species; Fig. 4) in the 1970s and little change (< 1%) in overall adjusted richness was estimated between the survey periods (Figs. 5c, 6a; gray hatched bars). In contrast, we observed declines (49%) for wrack-associated adjusted richness at this beach similar to that observed at two degraded urban beaches (50% at Westward and Torrance) (Fig. 6b; gray hatched bars). Moreover, a 60% decline in observed richness of wrack-associated species with low-dispersal ability was evident at this site (Table 2).

Our results on intertidal richness were consistent with recovery from intense ORV use at two beaches, Oceano Dunes and Arnold Road, where overall and wrack-associated adjusted richness were higher in the 2009-11 surveys (Figs. 5a, 6; white hatched bars). Both beaches were subject to intense ORV traffic during the 1970s (Table 1), but management changes prohibited ORVs about 15 years prior to our 2009-2011 surveys (1984 at Oceano Dunes and 1992 at Arnold Road). Overall adjusted richness was significantly higher in the 2009-11 surveys at both beaches but was only statistically significant for wrack-associated species at Oceano Dunes (Figs. 5a, 6; white hatched bars). Wrack-associated species with low dispersal not previously recorded in the 1970s surveys were detected in our 2009-11 surveys at both beaches, including talitrid amphipods at Oceano Dunes and oniscid isopods at

Arnold Road and Oceano Dunes (Table 2). At Oceano Dunes, three genera and five species of wrack-associated invertebrates not observed in the 1970s were found in our 2009-11 surveys (Table 2), the largest increase we observed in these taxa with low dispersal.

Environmental drivers

The responses of species richness to beach characteristics, including active intertidal width, sand grain size, and wrack abundance were not consistent across groups and survey periods. Overall adjusted species richness was negatively related to sand grain size in both survey periods (1970s: $r^2 = 0.38$, $P = 0.02$, $n = 13$; 2009-11: $r^2 = 0.47$, $P = 0.01$, $n = 13$), as was the adjusted richness of wrack-associated biota for the 2009-11 surveys ($r^2 = 0.30$, $P = 0.05$, $n = 13$) (Fig. S6). Relationships between mean active intertidal width and 1) overall species richness and 2) the richness of wrack-associated species were positive but not significant for both periods. Across the survey periods, we found no relationships between the observed change in overall or wrack-associated adjusted species richness and those in beach width or grain size for the 13 study beaches. For 2009-11 surveys the adjusted overall ($r^2 = 0.31$, $P = 0.05$, $n = 13$) and wrack-associated ($r^2 = 0.27$, $P = 0.07$, $n = 13$) species richness were positively related with the mean cover of wrack indicating the importance of this resource to biodiversity (Fig. S7).

Discussion

Wildlife populations that rely on sandy beaches as critical habitat, such as sea turtles and nesting plovers, are threatened worldwide, largely in response to human disturbance and habitat alteration (e.g. Schlacher *et al*., 2012). Our results documenting the loss of sandy beach invertebrate species that depend on macrophyte wrack, particularly those with limited dispersal, strongly echo trends observed for beach-dependent wildlife on urban coasts and highlight the importance on local scale processes. Disturbed beaches continued to lose species over more than three decades, while beaches recovering from impacts slowly gained species.

We observed an overall lack of regional declines in species richness and change in physical beach characteristics despite regional increases in sea surface temperature (SST), sea level rise, wave height, and storm frequency across the survey periods (Allan & Komar, 2006; Smith *et al.*, 2006; Ruggiero *et al.*, 2010; NOAA Tides & Currents, 2017). This suggests that processes operating at local scales are exerting a stronger influence on sandy beach biodiversity than regional or global scale drivers and highlight the importance of human impacts at local spatial scales. Our results are broadly consistent with studies across a range of ecosystems and communities showing that local and regional scale changes observed in biodiversity often do not clearly correspond with global biodiversity loss (Sax & Gaines, 2003; Vellend *et al.*, 2013; Thomas, 2013; Dornelas *et al.*, 2014; Elahi *et al.*, 2015; Hautekèete *et al.*, 2015). At a global scale, change in species number is the difference between the speciation and extinction rates, and increasing extinction rates have resulted in a net global loss of species over the last century (Sax & Gaines, 2003). At smaller spatial scales, immigration and emigration drive metacommunity dynamics that can obscure the signal of species extinctions at broader scales (Sax & Gaines, 2003; Gonzalez *et al.*, 2016). Our results demonstrate why a long-term and ecologically informed perspective is needed to reveal declines in biodiversity that may not be apparent in more broad-brush analyses (Gonzalez *et al.*, 2016).

The influence of local and regional processes on sandy beach biodiversity contrasts with results for rocky shores for the same eastern Pacific region over a similar time span (Smith *et al*., 2006). In rocky intertidal communities associated with mussels, fewer intertidal species of invertebrates were observed in 2002 compared to the 1960s and 1970s at sites across California (Smith *et al*., 2006). Based on these results Smith *et al*. (2006) concluded that the consistency of trends for observed species richness in intertidal mussel beds among sites suggested that large-scale processes impacted species richness over the past 30 years despite spatially varying intensities of human use and pollution across the study region. They attributed these changes to climate-change-driven warming and decreased phytoplankton productivity lowering food supply to mussel beds and decreasing pelagic larval survival. Although our study covered similar regions and time spans, we did not observe analogous local or regional declines in intertidal species richness for sandy beach communities. One potential factor in the disparate results for these two intertidal ecosystems is the relative importance of the wrack-associated fauna to intertidal biodiversity on beaches, compared to suspension-feeding animals that depend on phytoplankton. This diverse functional group lacks planktonic larval stages and largely depends on beached giant kelp (*Macrocystis pyrifera*) and other marine macrophytes from nearby kelp forests for food and shelter (Dugan *et al*., 2003; Lastra *et al*., 2008). Although giant kelp biomass has shown considerable local scale variability over the past three decades, no consistent regional patterns have emerged (Bell *et al*., 2015). Our results showing that change in wrack-associated species richness occurred over time, but the direction and magnitude of that change varied strongly among beaches are consistent with local scale resource availability and human impacts as drivers of diversity change rather than regional changes in productivity or pelagic larval survival as proposed for rocky shores.

Increases in species richness can be associated with higher connectivity caused by declines in regional barriers and the immigration or introduction of exotic species (Sax & Gaines, 2003). However, the higher richness of macroinvertebrate species we found in the 2009-11 surveys at approximately half of the study beaches was not due to the presence of exotic species. Although a small number of cryptogenic sandy beach macroinvertebrate species were found in our surveys (< 5% on average) during both survey periods, no known non-native intertidal species were observed. Globally, few exotic species of macroinvertebrates have been reported for sandy beach ecosystems (Defeo *et al*., 2009). This result contrasts with temperate regions and coastal ecosystems in general (Cohen & Carlton, 1998; Heard *et al*., 2012), which are often considered hotspots for biological invasions (Ruiz *et al*., 2011). Our finding of no exotic or invasive intertidal invertebrates at beaches representing a wide range in biodiversity and intensity of disturbance for a widespread coastal ecosystem suggests that the invasion potential may be smaller for beaches than other ecosystems.

Our results of significant increases in overall species richness over more than 30 years at four relatively unmanaged beaches as well as three impacted beaches were unexpected and indicates further study of these dynamic communities and the local drivers affecting biodiversity, including coastal management, is warranted. For two of the beaches the positive response in diversity was consistent with recovery from disturbance by ORV use. Similar increases in species richness found at the five other study beaches may have also responded to changes in coastal management across the survey periods, including the past establishment of marine reserves at Scripps and Crystal Cove. However, it is not possible to quantitatively evaluate these unexpected changes using our datasets and the limited information available on past coastal management activities. Monitoring of the biodiversity of sandy beach ecosystems that takes advantage of the recent establishment of a widespread (~1,350 km) network of marine protected areas overlapping the study region could provide an opportunity to gain insights into factors underlying the long-term changes in biodiversity we identified here.

Long-term changes we detected in richness differed substantially among functional groups of intertidal invertebrates. In particular, comparisons of overall species richness alone failed to capture the significant loss of a key functional group, the wrack-associated species, in sandy beach ecosystems across three decades. Wrack-associated taxa play a vital role in the breakdown and processing of macroalgal wrack and subsequent nutrient cycling on beaches (Lastra *et al*., 2008; Dugan *et al*., 2011) and are important prey for wildlife, particularly shorebirds including endangered species (Dugan *et al*., 2003). The lack of planktonic larval stages and the low dispersal abilities of some adult invertebrates (Table 2a) make wrack-associated species especially sensitive to anthropogenic impacts that directly affect their populations or the abundance of wrack subsidies that provide food and shelter (Hubbard *et al*., 2014). Removal or disturbance of wrack resources has been shown to strongly impact wrack-associated taxa and diversity (Llewellyn & Shackley, 1996; Dugan *et al*., 2003). The changes in richness of wrack-associated species we observed were consistent with the impacts of wrack removal and associated disturbance at four urban beaches subject to regular beach grooming (Hollywood, Westward, Torrance, and Ocean Beach) and one beach with heavy upper-beach habitat modification (beach fill and dredge pipes) during our surveys (Morro Bay). Despite a result of higher or no change in overall adjusted species richness values at these beaches, wrack-associated richness had declined by greater than

20% at all but one groomed beach in 2009-11 compared to the 1970s. Similarly, ORVs can severely impact wrack as well as dune vegetation and biota (Schlacher & Thompson, 2008; Davies *et al*., 2016). At two of our study beaches that were subject to intense ORV traffic during the 1970s, biodiversity increased across the survey periods likely in response to the elimination of ORV disturbance more than 15 years before our 2009-2011 surveys. In particular, richness of wrack-associated species, including five species with low dispersal never recorded in the 1970s, increased, indicating that recovery of these sensitive species may be possible given adequate time and sufficient local source populations.

Beach habitat loss associated with erosion and sea level rise is expected to result in declines in intertidal biodiversity where retreat of beaches is constrained by coastal bluffs or armoring (Dugan *et al*., 2008, 2013; Jaramillo *et al*., 2012; Schoeman *et al*., 2014). Our results were consistent with this prediction at only one site, Coal Oil Point, a narrow beach backed by a coastal bluff. There, both overall and wrack-associated species richness declined (38% and 62%, respectively) by 2009-11, concomitant with a 24% decrease in the active intertidal width, a 25% increase in mean sand grain size, and a 1.11 mm yr^{-1} increase in local monthly mean sea level (data from Santa Barbara Station 1973-2015; NOAA Tides & Currents, 2017). This loss and alteration of intertidal beach habitat likely resulted from a combination of sea level rise and climate forcing that increased wave height and storm frequency (Allan & Komar, 2006; Ruggiero *et al*., 2010), such as the Pacific Decadal Oscillation and El Niño-Southern Oscillation (Mantua *et al*., 1997; Revell *et al*., 2011; Barnard *et al*., 2012) and anthropogenic impacts to sediment supply (Revell & Griggs, 2006; Orme *et al*., 2011; Barnard *et al*., 2012). These factors, combined with the very limited scope for retreat due to the coastal bluff bounding this beach (Dugan *et al*., 2013), may explain why observed declines in species richness were so striking here compared to the other study beaches. Narrow beaches constrained by bluffs or armoring are common in central and southern California but are at risk of complete habitat loss from erosion and sea level rise (Vitousek *et al*., 2017). By 2100, 31% to 67% of all southern California beaches are projected to disappear due to erosion (Vitousek *et al*., 2017). These results illustrate regional (e.g. sea level rise and wave height) and local (e.g. sand starvation and armoring) processes that threaten biodiversity and ecosystem integrity of this widespread coastal ecosystem in the region and around the globe (Dugan *et al*., 2008, 2010, Schlacher *et al.* 2007, Schoeman *et al*., 2014).

The need for robust evaluations of shifts in biodiversity driven by climate and anthropogenic drivers at relevant temporal and spatial scales to inform conservation and management is growing (Magurran, 2010, Sternberg & Yakir, 2015). We were able to overcome differences in sampling effort and methodologies associated with comparisons of biodiversity across multi-decadal temporal scales by using an extrapolation approach (Colwell *et al*., 2012, Chao *et al*., 2014, Schooler *et al*., 2014). Using cumulative species richness values obtained from species lists to compare area-adjusted species richness across survey periods made it possible for us to identify and evaluate ecologically relevant differences in intertidal biodiversity over a multi-decadal time scale. Greater use of such methods could allow much needed temporal comparisons of biodiversity to be made in ecosystems with datasets that might otherwise be unsuitable for comparison, particularly underrepresented biomes and ecosystems outside of developed nations, to accurately quantify global biodiversity change (Gonzalez *et al*., 2016).

Our results highlight how the complexity of ecologically important change in biodiversity can be masked in comparisons of overall species richness (Elahi *et al.*, 2015). Identifying taxa and functional groups known to be vulnerable to specific impacts can be an important tool to inform *a priori* predictions of biodiversity change. Despite detecting declines in overall species richness at only one study beach, we found that ecologically important wrack-associated fauna vulnerable to disturbance, resource limitation, and habitat loss declined at numerous beaches, suggesting considerable alteration of the structure and function of a major coastal ecosystem has occurred in the region over three decades. We also found evidence that local impacts to this ecologically important component of intertidal biodiversity may be reversed with management changes that reduce disturbance of beaches and allow recovery of sensitive taxa. Shifts in species composition and loss or gain of key taxa, such as those we observed for wrack-associated species, can be as important as overall biodiversity change when the taxa are critical to ecosystem function (Hooper *et al.*, 2012; Orwin *et al.*, 2014; Lefcheck *et al.*, 2015). Our findings illustrate the value of using detailed long-term comparisons of community composition at local and regional scales in evaluating the status of biodiversity. These types of evaluations can inform policies intended to conserve and manage the endemic biodiversity of beaches and other vulnerable ecosystems.

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Biosketch: Nicholas Schooler, a PhD student at UC Santa Barbara, evaluates spatial and temporal patterns in coastal biodiversity under the supervision of Drs. Jenifer Dugan and Steven Gaines.

Author contributions: NKS, JED, and DMH designed the study. DS conducted 1970s surveys and provided data. NKS, JED, and DMH conducted 2009-11 surveys. NKS processed samples and analyzed data with JED. NKS, JED, and DMH wrote the manuscript.

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Figures

Figure 1. Macroalgal wrack, which is beach cast marine macrophytes, provides food and shelter for a large component of sandy beach macroinvertebrates. The large piles of wrack pictured here are composed primarily of giant kelp (*Macrocystis pyrifera*). The dense aggregation of burrows surrounding the wrack belong to low dispersal wrack-associated species, talitrid amphipods (*Megalorchestia* spp.), which are the primary consumers of wrack on sandy beaches.

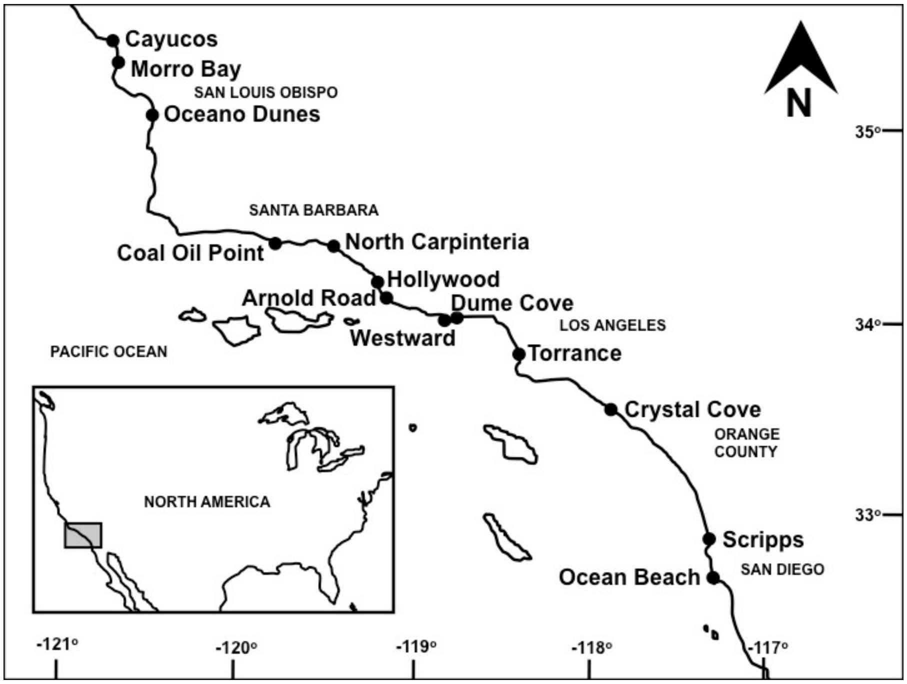

Figure 2. Map of the study region with names and locations of the sandy beach study sites (indicated by dots) surveyed on the coast of central and southern California, USA in the 1970s and in 2009-11 survey periods.

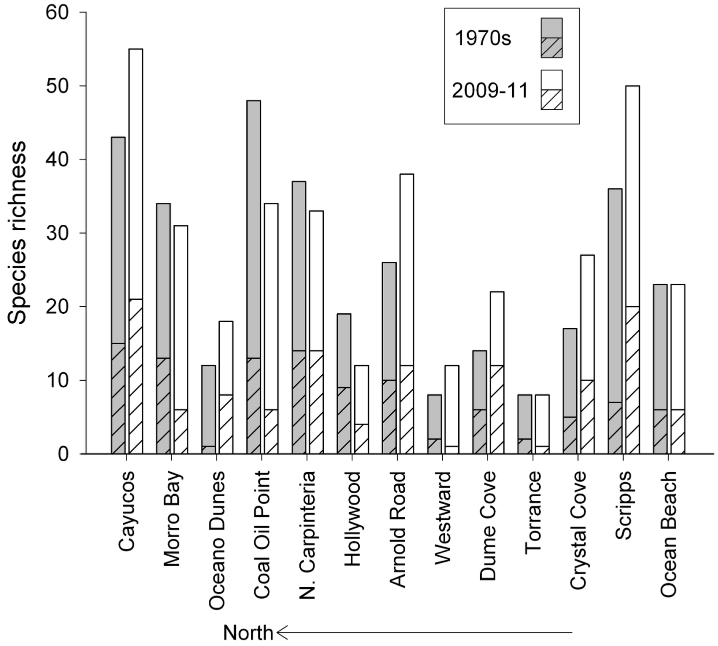

Figure 3. Values of cumulative observed species richness of macroinvertebrates at the study beaches for the 1970s and 2009-11 survey periods. The hatched bars indicate the values of observed richness for wrack-associated species for each survey period. Species richness values are not adjusted for sampling.

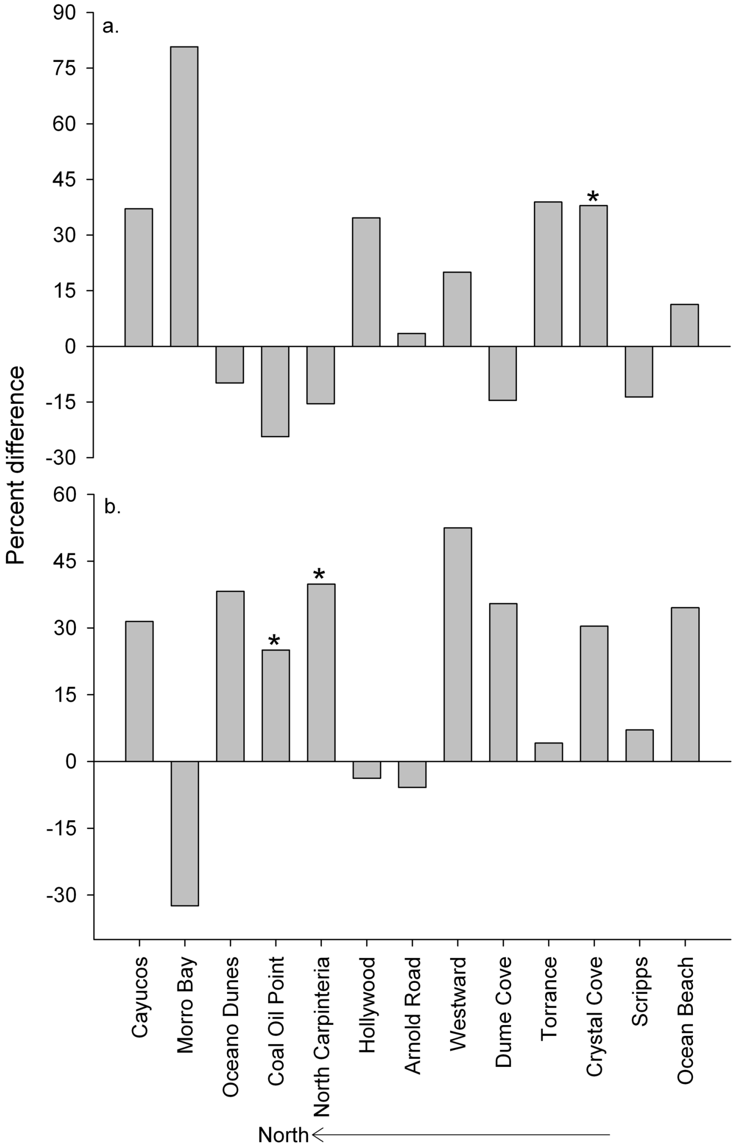

Figure 4. The direction of and percent difference observed in a) mean active intertidal width and b) mean grain size during fall (August-December) surveys for the study beaches between the 1970s and 2009-11 survey periods (* indicates sites where differences were significant at 0.05 level).

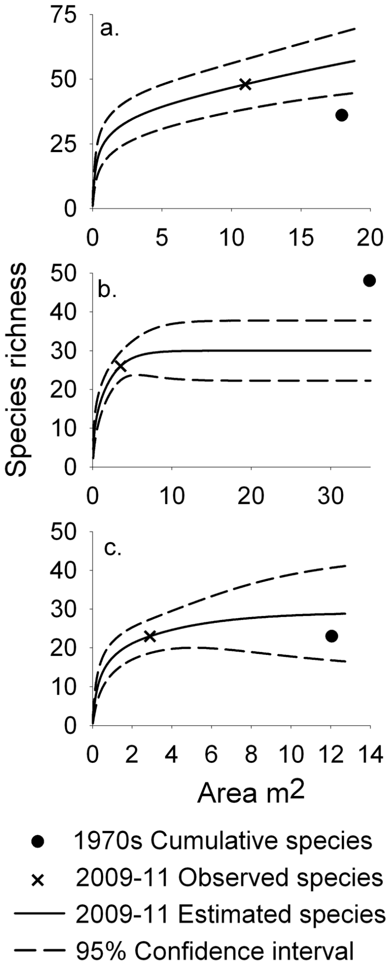

Figure 5. Example plots of species-area curves based on the 2009-11 surveys with unconditional 95% CI. The values of cumulative species number and sampling area in the 1970s surveys and the 95% CI of the 2009-2011 species area curves shown here were used to evaluate differences in species richness between survey periods. Adjusted species richness values were a) significantly higher (Scripps), b) significantly lower (Coal Oil Point), and c) did not differ significantly (Ocean Beach) in 2009-11 compared to 1970s surveys. See Figs. S4, S5 in Supplementary Information for species-area curves for all study beaches.

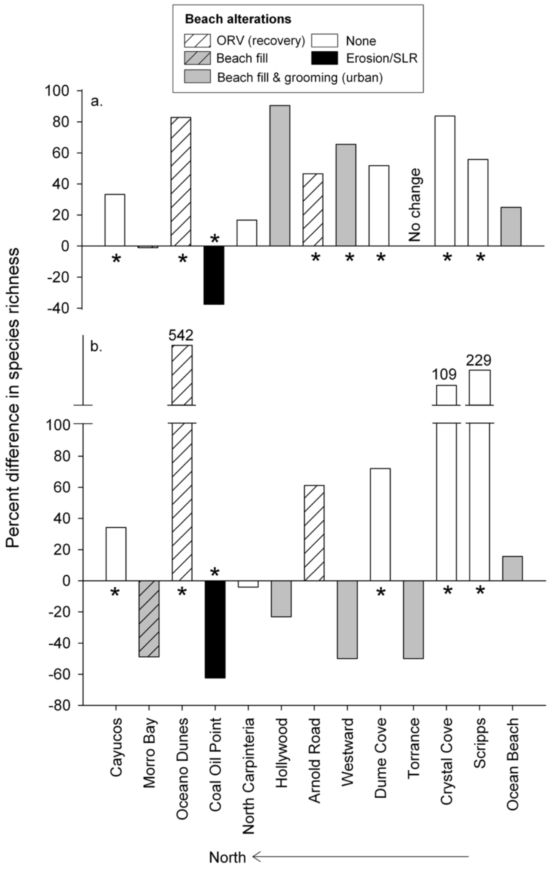

Figure 6. The direction of and percent difference reported in species richness between the 1970s and 2009-11 surveys for a) adjusted overall species richness and b) adjusted wrack-associated species richness. White bars = no direct beach alteration detected. White hatched bars = change consistent with recovery from off-road vehicle use. Gray bars = urban sites with continuous beach fills and grooming. Gray hatched bars = beach fill and upper beach habitat modification. Black bars = no direct beach alteration but overall and wrack-associated adjusted richness declines were consistent with habitat loss from erosion and sea level rise (SLR). Asterisk = sites with significant (95% CI) differences in adjusted richness. See also Figs. S4, S5 in Supporting Information.

Tables

Table 1. The names, coordinates of the basepoints (from Straughan 1982), years surveyed, cumulative active intertidal sampling area and number of surveys conducted for each survey period for the thirteen study beaches arranged from north to south. The numbers in parentheses represent the number of proportional area surveys. A total of 249 surveys were conducted in the 1970s (214 surveys) and 2009-11 (35 surveys). Collectively the repeated surveys from the 1970s sampled more than three times as much active intertidal area (226 m^2) as the 2009-11 surveys (71 m^2). Direct beach alteration activities (grooming, beach fill, and ORV use) are listed by study beach. The number of surveys using the proportional area design during the 2009-11 surveys appears in parentheses. Dredge pipes were stretched across the upper-beach habitat at one beach indicated by an asterisk in the Beach fill column.

Beach name	**Coordinates**	**Years surveyed**	**1970s**		**2009-11**		**Large-scale beach alteration**		
			Area m^2	**Surveys**	**Area m^2**	**Surveys**	**Grooming**	**Beach fill**	**ORV use**
Cayucos	35°26'06.2"N, 120°53'18.7"W	1973-74; 2009-10	10.1	7	8.6	3 (2)	No	No	No
Morro Bay	35°22'33.8"N, 120°51'50.8"W	1973-74; 2009	12.5	8	6.5	2 (1)	No	Both*	No
Oceano Dunes	35°02'14.6"N, 120°37'58.5"W	1974; 2010	4.2	3	2	1 (1)	No	No	1970s
Coal Oil Point	34°24'33.2"N, 119°52'09.9"W	1969-78; 2009-11	34.9	52	7	6 (5)	No	No	No
North Carpinteria	34°23'29.4"N, 119°31'18.1"W	1970-71, 73-75, 78; 2009	36.6	35	4.5	2 (1)	No	No	No
Hollywood	34°10'13.1"N, 119°13'59.7"W	1971-74, 78; 2009	34.7	28	1.3	1 (1)	Both	Both	No
Arnold Road	34°07'17.5"N, 119°09'37.6"W	1971-74, 78; 2009-11	38.6	24	12.5	6 (4)	No	No	1970s
Westward	34°00'10.9"N, 118°48'34.4"W	1975-78; 2009-10	5.8	8	5	3 (2)	Both	Both	No
Dume Cove	34°00'21.8"N, 118°48'06.5"W	1971; 2011	2	6	2.1	1 (0)	No	No	No
Torrance	33°49'09.8"N, 118°23'25.1"W	1974-80; 2009	11.7	16	0.9	1 (1)	Both	Both	No
Crystal Cove	33°34'41.2"N, 117°50'52.3"W	1970-71; 2011	5.1	7	3.1	1 (0)	No	No	No
Scripps	32°51'49.2"N, 117°15'16.7"W	1975-78; 2009-11	17.9	10	14.5	6 (5)	No	No	No
Ocean Beach	32°44'52.3"N, 117°15'10.3"W	1975-78; 2009-10	12.1	10	2.9	2 (2)	Both	Both	No

Table 2. a) Wrack-associated species with low dispersal known from the study region and b) the cumulative number of species and genera collected at each study beach in each survey period. NC = not collected in this study. Differences of >1 species or genus across study periods are indicated in bold.

a. Low dispersal wrack-associated species

- Crustacea:
  - Talitridae:
    - *Megalorchestia benedicti*
    - *Megalorchestia californiana*
    - *Megalorchestia columbiana*
    - *Megalorchestia corniculata*
    - *Megalorchestia minor*
    - *Megalorchestia pugettensis*
  - Alloniscidae:
    - *Alloniscus perconvexus*
  - Tylidae:
    - *Tylos punctatus*
- Arachnida:
  - Bdellidae:
    - *Neomolgus littoralis*
- Insecta:
  - Carabidae:
    - *Akephorus marinus*
  - Curculionidae:
    - *Emphyastes fucicola*
  - Melyridae:
    - *Endeodes* sp. (NC)
  - Staphylinidae:
    - *Thinopinus pictus*
    - *Hadrotes crassus* (NC)
  - Tenibrionidae:
    - *Coelus ciliatus*
    - *Coelus globosus* (NC)

b. Number of low dispersal wrack-associated species and genera collected

LOCATION	GENERA		SPECIES	
	1970s	2009-11	1970s	2009-11
Cayucos	3	4	6	7
Morro Bay	2	1	**5**	**2**
Oceano Dunes	**0**	**3**	**0**	**5**
Coal Oil Point	2	1	**5**	**1**
North Carpinteria	3	2	**5**	**3**
Hollywood	2	2	4	3
Arnold Road	3	4	6	6
Westward	0	0	0	0
Dume Cove	**2**	**5**	**4**	**8**

Supplementary material

Appendix S1. Detailed methods for the 1970s and 2009-11 biodiversity surveys.
1970s biodiversity surveys:

Basepoints described by Straughan (1982) for each site were used to locate the start of a transect line that was laid out from the basepoint to the water's edge (low swash) at low tide (Fig. S1). Surveys were conducted during spring low tides year round. Study beaches were only selected if they were surveyed during the late summer or fall. Samples were collected using cores or quadrats along this transect spanning the active intertidal zone (24 h high tide line to the low swash) employing a variety of sampling designs (Straughan, 1982). Samples were sieved through 1.5 mm mesh to retain macroinvertebrates for counting and identification.

2009-11 biodiversity surveys:

At each site, we stretched a transect tape from the same basepoint used by Straughan (1982) (Table 1) in the 1970s to the low swash (Fig. S1). The proportional area surveys consisted of a contiguous grid of 3.0 x 3.0 m quadrats in four shore-normal columns and y along-shore rows (y = active intertidal width/3.0 m) that spanned the active intertidal. Within each quadrat, two sediment cores (10 cm diameter, 20 cm depth) were randomly collected and pooled as a sample. The fixed area (3.5 m^2) survey design was similar to that used in intertidal surveys conducted by Dugan *et al*. (2003). We collected 150 cores at uniform intervals along each of three shore-normal transects randomly spaced along-shore (450 cores per site) from the 24 h high tide line to the low swash. Cores were pooled in contiguous groups of 10 to make 15 total samples per transect. Slightly less area was sampled at Dume Cove and Crystal Cove (Table 1) using the fixed area survey design because samples collected landward of the 24 h high tide line were excluded. Each pooled core sample was sieved through 1.5 mm mesh to remove sand and retain macrofauna, placed in labeled plastic bags, and returned to the laboratory where they were preserved in 10% buffered formalin. Macroinvertebrates were counted and identified to the lowest taxonomic level possible, typically species. Inconsistencies in taxonomic identification and nomenclature between study periods were addressed by consulting the literature and taxonomic specialists. Species that do not normally inhabit beaches or are considered parasitic were excluded from our analyses.

References:

Dugan, J. E., Hubbard, D. M., McCrary, M. D. & Pierson, M. O. (2003) The response of macrofauna communities and shorebirds to macrophyte wrack subsidies on exposed sandy beaches of southern California. *Estuarine, Coastal and Shelf Science*, 58, 25–40.

Straughan, D. (1982) *Inventory of the natural resources of sandy beaches in Southern California*. Report, Allan Hancock Foundation and Institute for Marine and Coastal Studies, University of Southern California, Los Angeles.

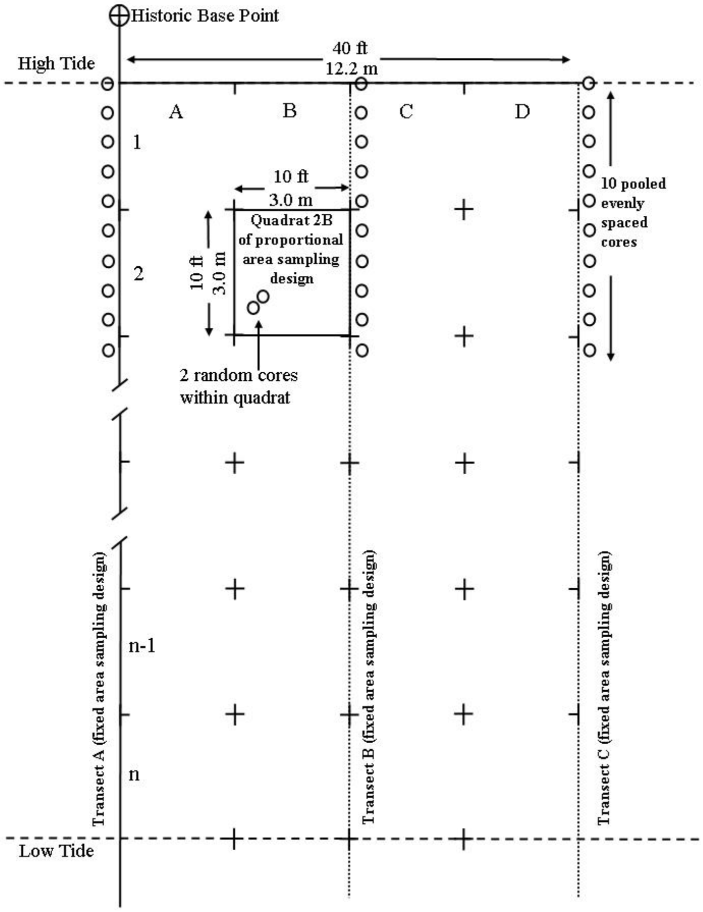

Figure S1. Diagram of the layout for the proportional area sampling design and the fixed area sampling design relative to the historic baseline transect, 24 h high tide line (high tide), and low swash (low tide). Figure is not drawn to scale. The diagram was first published by Schooler *et al.* (2014) and permission for reuse was given by Elsevier.

References:

Schooler, N. K., Dugan, J. E. & Hubbard, D. M. (2014) Detecting change in intertidal species richness on sandy beaches: calibrating across sampling designs. *Estuarine, Coastal and Shelf Science*, 150, 58–66.

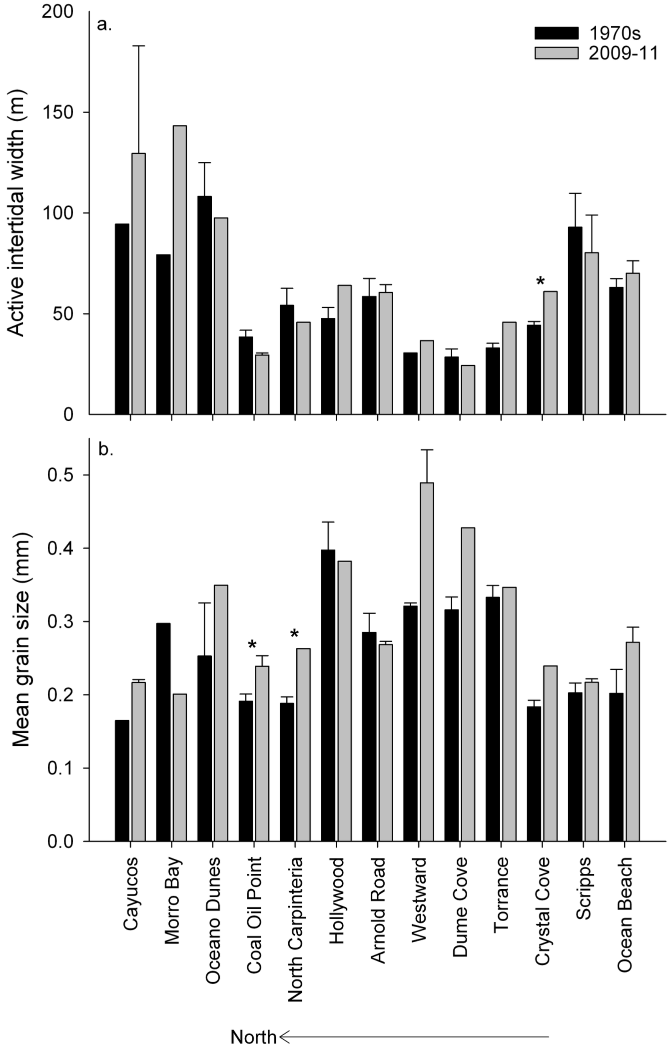

Figure S2. Mean values (± 1 SE) for a) active intertidal width and b) mean grain size during fall (August-December) surveys for beaches in the 1970s and 2009-11 (* indicates significant differences ($P \leq 0.05$)). SEs are not reported for sites where only one survey was conducted in 2009-11 except for Westward where active intertidal width was the same in both the 2009 and 2010 surveys.

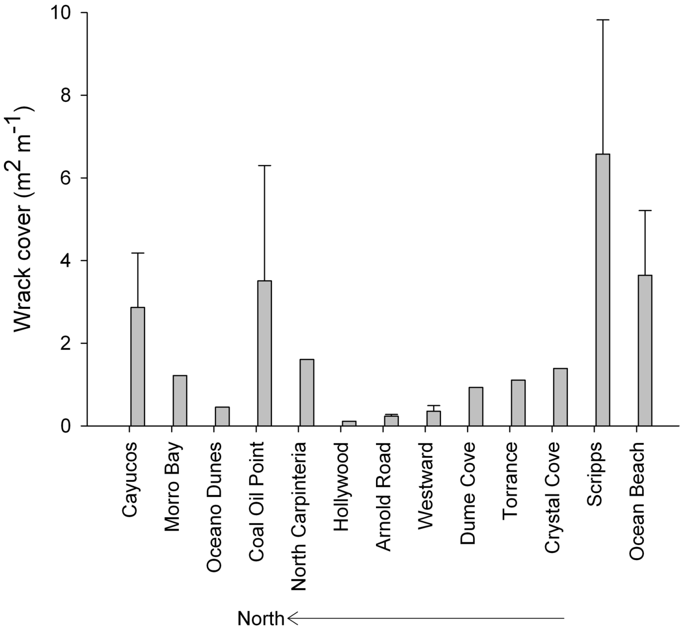

Figure S3. Mean values (± 1 SE) for wrack cover for beaches in the 2009-11 surveys. SEs are not reported for sites where only one survey was conducted in 2009-11.

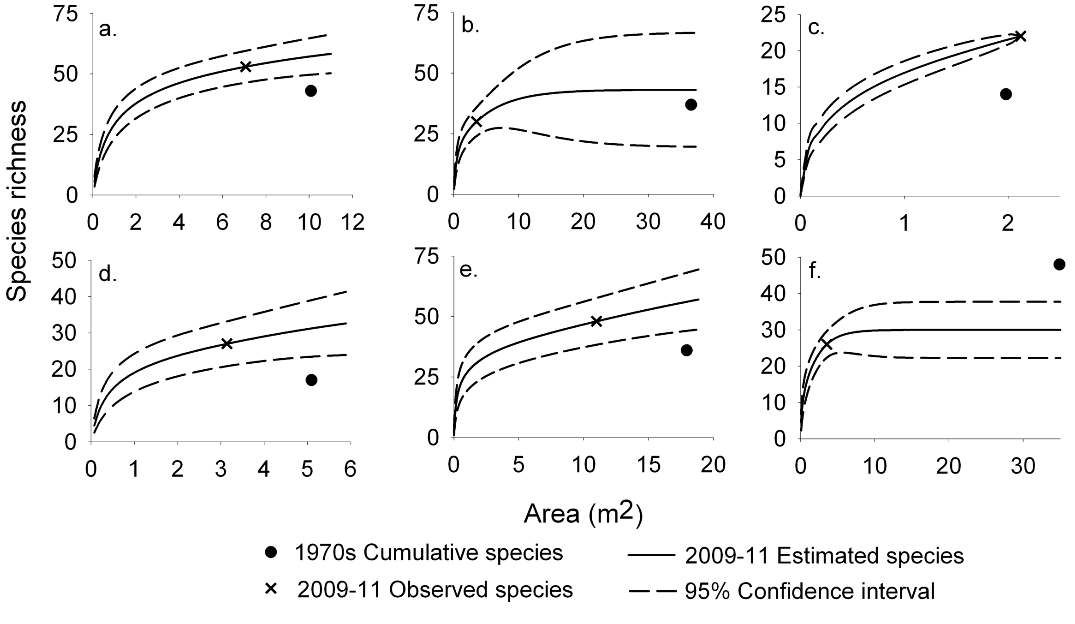

Figure S4. Plots of species-area curves based on the 2009-2011 surveys with unconditional 95% CI for six beaches where no direct beach alteration during or between survey periods were detected. The values of cumulative species number and sampling area in the 1970s surveys and the 95% CI of the 2009-2011 species area curves shown here were used to evaluate differences in species richness between survey periods. The plots are organized by increases or decreases in richness between periods and geography. Species richness values were higher in the 2009-11 surveys at a) Cayucos, b) North Carpinteria, c) Dume Cove, d) Crystal Cove, and e) Scripps and lower in the 2009-11 surveys at f) Coal Oil Point.

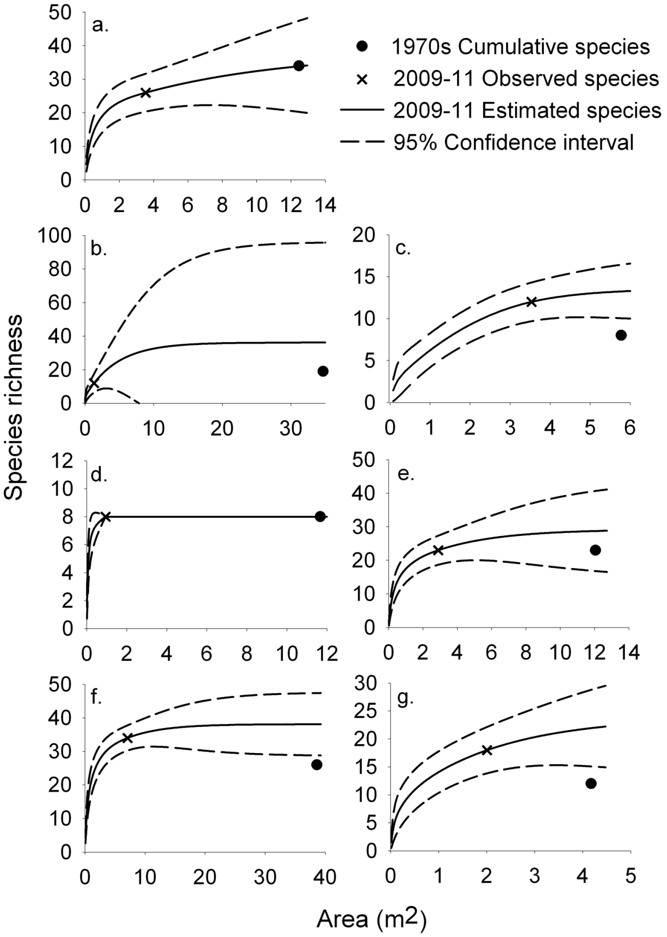

Figure S5. Plots of species-area curves based on the 2009-2011 surveys with unconditional 95% CI for seven beaches where direct beach alteration during or between survey periods were detected. The cumulative species number and sampling area in the 1970s surveys and the 95% CI of the 2009-2011 species area curves shown here were used to evaluate differences in species richness between the survey periods. The plots are organized by direct alteration type. Beach fill and upper beach alteration occurred at a) Morro Bay. Beach fills and grooming occurred at b) Hollywood, c) Westward, d) Torrance, and e) Ocean Beach. Off-road vehicle use occurred during the 1970s surveys at f) Arnold Rd and g) Oceano Dunes.

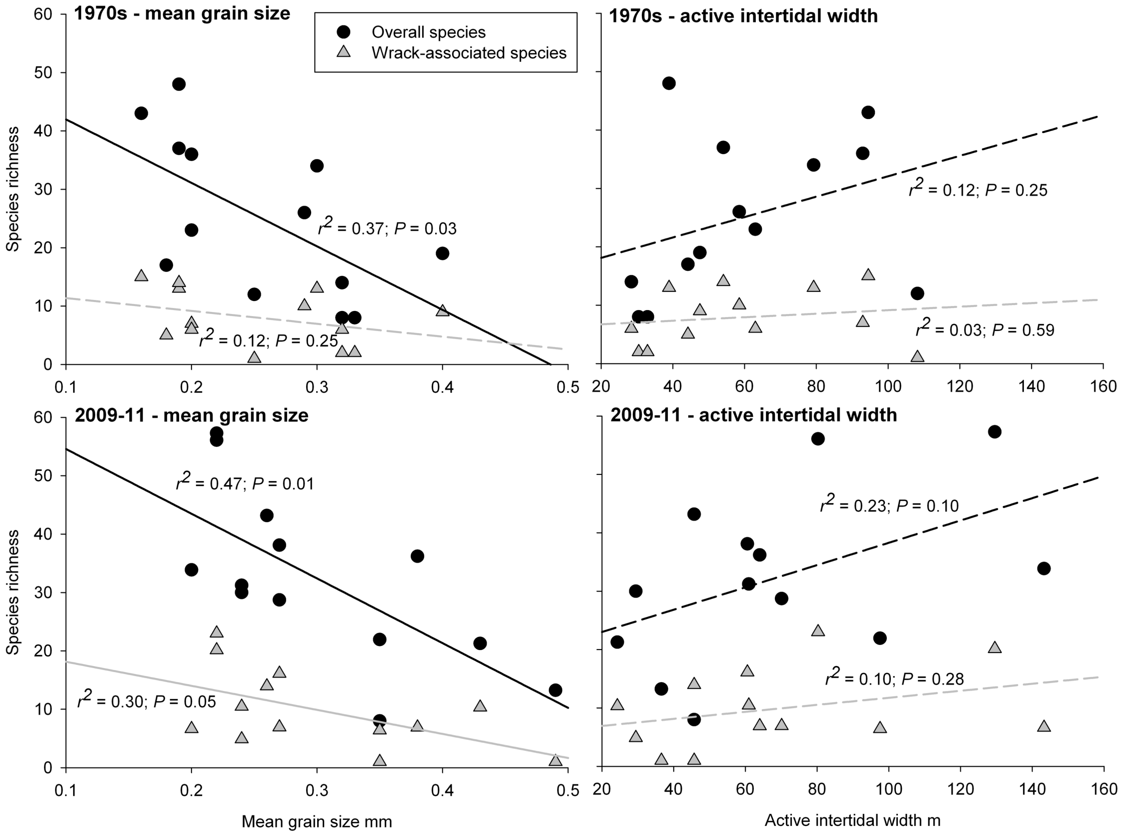

Figure S6. The relationships between overall (black) and wrack-associated (gray) species richness as a function of mean grain size (left) and active intertidal width (right) for the 1970s (top) and 2009-11 (bottom) surveys. The regression correlation coefficients and *P*-values are displayed on the graphs adjacent to the lines with which they correspond. Relationships that are significant ($P \leq 0.05$) are indicated by a solid line.

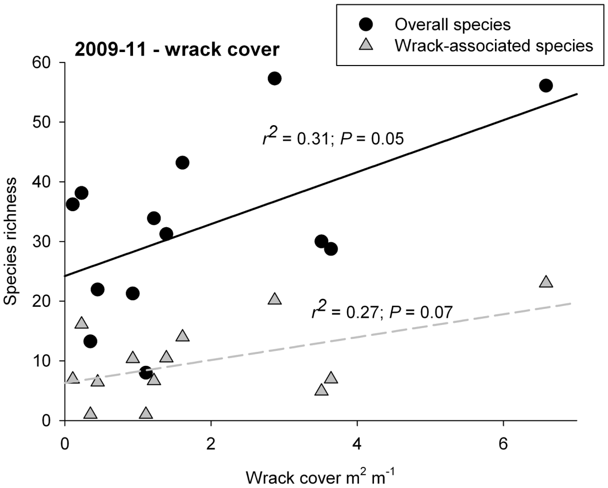

Figure S7. The relationships between overall (black) and wrack-associated (gray) species richness as a function of wrack cover. The regression correlation coefficients and *P*-values are displayed on the graphs adjacent to the lines with which they correspond. Relationships that are significant ($P \leq 0.05$) are indicated by a solid line.

Table S1. Cumulative macroinvertebrate species list for the 1970s (red) and 2009-11 (black) surveys. Study beaches listed left to right are arranged geographically from north to south, respectively. An "X" indicates that the species was present in at least one survey and was included in species richness counts. A "0" indicates that the species was present in at least one survey but was not included in species richness counts. Species names preceded by an asterisk were not included in total species counts. Wrack associated species are indicated by a "†" and low dispersal wrack-associated species are indicated by a "§".

Taxa	Cayucos		Morro Bay		Oceano Dunes		Coal Oil Point		North Carpinteria		Hollywood		Arnold Rd.		Westward		Dume Cove		Torrance		Crystal Cove		Scripps		Ocean Beach	
	1970s	09-11	1970s	09-11	1970s	09-11	1970s	09-11	1970s	09-11	1970s	09-11	1970s	09-11	1970s	09-11	1970s	09-11	1970s	09-11	1970s	09-11	1970s	09-11	1970s	09-11
ARTHROPODA - 61 spp																										
CRUSTACEA - 29 spp																										
MYSIDACEA - 4 spp																										
Acanthomysis californica		X																								
Archaeomysis grebnitzkii	X	X	X	X	X	X					X	X	X	X		X								X		
Archaeomysis maculata										X			X	X		X		X						X		
Metamysidopsis elongata									X																	
AMPHIPODA - 15 spp																										
Megalorchestia benedicti §	X	X	X	X			X		X	X		X	X	X			X	X			X	X		X		
Megalorchestia californiana §	X	X	X	X		X	X				X		X				X	X			X	X				
Megalorchestia columbiana §	X	X	X				X				X		X				X	X								
Megalorchestia corniculata §	X						X	X	X	X				X							X	X	X	X	X	
Megalorchestia minor §	X		X			X			X		X	X	X	X				X		X						
Megalorchestia pugettensis §						X																				
Americhelidium sp.	X		X	X	X	X	X	X	X	X	X	X	X	X		X						X				
Eohaustorius sawyeri	X	X		X	X		X	X	X	X				X												
Eohaustorius washingtonianus	X	X	X	X	X	X	X	X	X					X			X				X	X	X	X	X	X
Gibberosus devaneyi																							X	X		
Gibberosus myersi														X												
Harpiniopsis spp.											X		X													
Heterophoxus spp.							X																			
Mandibulophoxus gilesi		X									X			X		X						X				
Paraphoxus sp.	X	X					X	X						X								X	X	X	X	X
ISOPODA - 5 spp																										
Alloniscus perconvexus §		X				X			X			X		X				X				X				
Tylos punctatus §											X			X			X	X			X	X	X	X	X	
Ancinus granulatus							X																			
Excirolana sp.	X	X	X	X		X	X	X	X	X		X	X	X	X		X		X	X	X		X	X		
Gnorimosphaeroma noblei		X						X										X				X			X	X
DECAPODA - 5 spp																										
Blepharipoda occidentalis	X	X									X		X	X		X	X		X				X	X		
Lissocrangon stylirostris	X																									
Emerita analoga	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X
Isocheles pilosus		X																								
Lepidopa californica		X		X			X	X	X	X				X	X								X	X	X	X
ARACHNIDA - 1 spp																										
Neomolgus littoralis §																		X								
INSECTA - 31 spp																										
COLEOPTERA - 25 spp																										
Aleochara arenaria †									X																	
Aleochara sulciollis †	X	X							X	X														X		
Bledius fenyesi †								X	X	X				X								X		X		
Bledius montratus †	X	X	X	X																						
Bledius ornatus †							X																			
Cafius canescens †	X	X	X				X		X	X	X			X					X					X		
Cafius lithocharinus †							X				X													X	X	
Cafius luteipennis †									X															X		
Cafius seminitens †		X								X																
**Cafius* spp. larvae/eggs †	0							X										X								
Pontamalota opaca †														X				X								
Pontomalota californica †	X	X				X																				
Tarphiota fucicola †		X								X														X		
Tarphiota geniculata †		X												X										X		
Thinopinus pictus §	X	X	X				X		X	X																
*Staphylinidae larva/pupa †	0		0				0						X										X		0	
Akephorus marinus §		X				X							X	X												
Cercyon sp. †		X		X			X	X	X	X	X		X									X	X	X		X
Euspilotus scissus †		X				X																				
Hypocaccus gaudens †	X	X	X																			X	X	X		
Neopachylopus aeneipunctatus †																								X		
Neopachylopus sulcifrons †										X																
**Neopachylopus* sp. †			X				X											X								
Coelus ciliatus §													X													
Epantius obscurus †																								X		
Phalaria rotunda †		X								X	X		X	X				X				X		X		
Emphyastes fucicola §		X																X					X	X	X	X
*Unknown beetle larva †														0			X								0	
*Unidentified Coleoptera †															X		X				X					
DIPTERA - 7 spp																										
Coelopa vanduzeei †		X	X	X			X	X	X	X														X	X	X
Dolichipodidae †	X						X																			
Empididae †										X				X										X		X
Fucellia sp. †	X	X	X			X	X	X	X	X	X	X							X			X		X	X	X
Hydrophorus spp. †	X		X																							
Thoracochaeta johnsoni †		X	X	X					X							X								X		X
Sphaeroceridae †	X																									
*Unidentified Cyclorrhapha †	0		0		X		0		0		0		X						0				X		0	
*Unknown diptera †							0								X											
MOLLUSCA - 4 spp																										
Callianax biplicata	X	X	X				X		X														X		X	
Donax gouldii									X	X	X		X	X						X			X	X	X	X
Siliqua spp.	X	X	X		X																					
Tivela stultorum	X	X	X	X					X	X			X	X									X	X		
NEMERTEA - 5 spp																										
Amphiporus sp.							X																X			
Cerebratulus californiensis	X	X	X																				X		X	
Paranemertes californica	X	X	X	X			X	X	X	X			X	X							X	X	X	X		X
Paranemertes peregrina							X																			
Zygeupolia rubens	X						X		X				X										X		X	
*Unidentified nemertea		X	X	X				X		X		X		X							X			X		X
ANNELIDA - 36 spp																										
POLYCHAETE - 36 spp																										
Arabella iricolor complex							X	X										X				X				
Arenicola brasiliensis								X																		X
Paraonella platybranchia		X		X		X			X					X							X	X		X		X
Amastigos acutus								X	X	X																
Decamastus sp.																								X		
Heteromastus sp.		X						X																		
Notomastus sp.							X	X																X		
Notomastus sp. D																						X				
*Unidentified Capitellidae							0																X	0		
Maldanidae																							X			
Cirriformia sp.							X	X														X				
Timarete luxuriosa							X																			
Typosyllis sp.								X																		
Eteone dilatae	X	X	X	X		X	X	X	X																	
Eteone pacifica							X																			
Thoracophelia dillonensis	X	X	X	X			X	X	X	X								X					X	X	X	
Thoracophelia mucronata	X	X	X	X		X	X	X	X								X				X		X	X	X	X
Glycera macrobranchia	X	X		X																						
Hemipodia sp.	X		X	X	X		X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X
Hesionella mccullochae							X																			
Magelona pitelkai	X	X		X			X																X	X		
Nephtys caecoides		X		X																				X		
Nephtys californiensis	X	X	X	X	X	X	X	X	X	X	X		X	X	X	X	X	X	X	X	X	X	X	X	X	X
Mooreonuphis stigmatis																							X			
Onuphis sp. E														X									X	X		
Orbinia johnsoni	X	X					X																	X		
Leitoscoloplos pugettensis	X	X	X	X																						
Scoloplos armiger complex					X		X	X	X	X												X	X	X		
Scoloplos acmeceps					X		X																X			
*Orbiniidae	0				0		0					X											0		X	X
Pisione sp.														X												
Dispio uncinata	X	X	X	X			X	X						X						X			X	X	X	X
Pygospio californica	X	X	X	X		X	X	X	X	X														X		
Scolelepis bullibranchia	X	X	X	X			X	X	X	X	X	X	X	X	X	X		X	X	X	X	X	X	X	X	X
Scolelepis squamata complex							X	X						X				X			X	X	X	X		X
Scolelepis sp. B							X																			
Scoletoma sp.	X	X	X	X	X		X	X	X	X				X			X	X			X	X	X	X	X	
Saccocirrus sp.																X										
OTHER - 2 spp																										
Unknown Oligochaeta		X		X						X			X	X		X										
Unknown Nematoda													X													

Chapter III. No lines in the sand: impacts of coastal urbanization on sandy beach ecosystems span the intertidal zone

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Abstract

As coastal population growth accelerates, infrastructure development, and intensive management practices increasingly alter shorelines, creating major conservation challenges. To evaluate ecological impacts of coastal urbanization, we compared intertidal macroinvertebrate communities between urban beaches with intense maintenance regimes and reference beaches lacking such maintenance in densely populated southern California. Intertidal macroinvertebrate communities were highly impacted on urban beaches with significantly reduced species richness (-58%), abundance (-88%), and biomass (-63%). These impacts affected all macroinvertebrate guilds on urban beaches, but effects were greatest for upper intertidal wrack-associated taxa. The altered intertidal communities of urban beaches were remarkably homogeneous compared with reference beaches across the biogeographically complex study region. Functional diversity comparisons suggested degraded ecological functioning on urban beaches. No taxa flourished on urban beaches, but we identified several vulnerable taxa. Our results indicate intense maintenance regimes on urban coasts strongly degraded biodiversity and functioning of sandy beach ecosystems across all intertidal zones.

Keywords: Beaches; Disturbance; Urbanization; Biodiversity; Functional Diversity; Biotic homogenization; Intertidal zone; Invertebrates; Macrophyte Wrack; Indicator Species

Highlights

- Evaluated macroinvertebrate community responses to urban impacts for sandy beaches
- Strong negative responses (>50%) of biodiversity and community structure to urban impacts
- Urban impacts spanned intertidal zone and were stronger for wrack-associated taxa
- Functional diversity useful in assessing urban impacts to beaches (-62% FRic)
- Intertidal communities of urban beaches homogeneous compared to reference beaches

Introduction

As human populations expand world-wide, a growing number of ecosystems are being profoundly altered by urbanization (McDonald *et al.* 2008, McKinney 2002). Defined as growth in the size and the number of people inhabiting cities, urbanization is accompanied by the intensive alteration of natural landscapes for human use (Grimm *et al.* 2008). Along the coasts where 41% of the world's people already live and population growth is accelerating (Martínez *et al.* 2007, Nordstrom 2000, de Sherbinin *et al.* 2012), the alteration of coastal ecosystems from a natural to an urban state is widespread on land and increasing rapidly (Baird 2009, Rakodi & Treloar 1997, Seto *et al.* 2011). Although intense habitat alteration in the ocean is limited (Ruttenberg & Granek 2011) and the ecological consequences are not well studied (Halpern *et al.* 2008), urbanization can indirectly degrade adjacent marine ecosystems (Halpern *et al.* 2007, 2008, Lotze *et al.* 2006, Martínez *et al.* 2007, Worm *et al.* 2006).

Understanding the extent to which the structure and function of coastal ecosystems at the marine-land interface 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 & Granek 2011) and climate change (Harley *et al.* 2006). 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). Characterized by low *in situ* primary production, sandy beach food webs rely on subsidies, such as wrack (wave-delivered macrophytes and other debris), carrion, and phytoplankton, from adjacent ecosystems (McLachlan & Brown 2006). Two major trophic guilds of endemic intertidal macroinvertebrates inhabit beaches in temperate regions (Dugan *et al.* 2003, Schooler *et al.* 2017). In the mid to lower intertidal zones many biota are suspension or deposit feeders (hereon referred to as lower beach macroinvertebrates). Many of these taxa have dispersive planktonic larval stages that can facilitate recolonization following disturbance (Grantham *et al.* 2003, Schooler *et al.* 2017). Higher on the shore, biota inhabiting damp sand near the driftline rely on macrophyte wrack for food and shelter (hereon referred to as wrack-associated macroinvertebrates). These taxa often have direct development and low dispersal, making populations particularly vulnerable to disturbance (Hubbard *et al.* 2014, Schooler *et al.* 2017).

Along urbanized coasts, management regimes of sandy beaches vary from intensive to minimal or no maintenance (McLachlan *et al.* 2013). This provides an opportunity to evaluate the influence of the impacts of differing management regimes on beach ecosystems. Many urban beaches regularly experience intense disturbance from mechanized maintenance that result in mortality or exclusion of species and the loss of ecological function (Defeo *et al.* 2009, Schlacher *et al.* 2007). Like most temperate coastal regions, 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 & Griggs 2006). Beach maintenance activities include cleaning and sifting of the intertidal and supralittoral zones using heavy equipment to remove trash, litter, and wrack (grooming), adding large quantities of non-native sand to create artificially wide beaches (beach filling), and seasonal building and flattening of large winter berms (3-4 m high) using intertidal sand moved by bulldozers.

The scaling of impacts to urban beaches varies from very local to landscape spatial scales while temporal impacts can range from weeks to decades (Defeo *et al.* 2009). For example, littoral cells are important coastal landscape scale features that contain a complete sediment budget including sources (e.g. rivers, streams, bluffs), transport paths (e.g. onshore-offshore and alongshore), and sinks (e.g. submarine canyons, coastal dunes) (Orme *et al.* 2011, Patsch & Griggs 2006). These major features contribute to the biogeographic complexity of sandy beach macroinvertebrate communities along the California coast (Claisse *et al*. 2018, Schooler *et al. in prep*). In southern California, major beach filling episodes (totaling > 250 million cubic meters of sand) have considerably altered sediment dynamics on large spatial and temporal scales in a number of the important regional littoral cells (Orme *et al.* 2011). At the local scale, sediment fills strongly degrade beach ecosystems (Manning *et al.* 2014, Peterson *et al.* 2000, 2014, Speybroeck *et al.* 2006). However, the effects of disruption of the natural sediment budget and associated environmental conditions of littoral cells linked to urbanization are not well documented and potentially may represent important landscape scale drivers of the biodiversity and structure of sandy beach ecosystems.

The effects of widespread urbanization on biodiversity, structure, and function of sandy beach ecosystems are just beginning to be appreciated more broadly (e.g. Defeo *et al.* 2009). Although ecological impacts to beaches and dunes associated with urbanization appear to be extensive and persistent in many parts of the world, studies to date have largely focused on taxa or guilds with life history traits and ecological requirements that make them vulnerable to disturbance (e.g. wrack-associated macroinvertebrates) (Dugan *et al.* 2003, Hubbard *et al.* 2014, Schooler *et al.* 2017, Veloso *et al.* 2008). However, the potential for broader impacts of urbanization on the biodiversity of the entire sandy beach ecosystem is substantial. Despite this, ecological impacts of widespread urban beach maintenance regimes on 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, biogeographic complexity, and locally intense anthropogenic impacts on a densely populated urban coast (Claisse *et al.* 2018, Dugan *et al.* 2000, 2003, Schooler *et al.* 2017) make sandy beaches of southern California an ideal ecosystem for assessing impacts associated with coastal urbanization on biodiversity and ecosystem function. To investigate the responses of sandy beach ecosystems to these 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 explored the role of selected environmental factors in observed variation in intertidal and functional biodiversity and structure in these ecosystems. 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 including across biogeographically distinct littoral cells, and 3) differentially impacts key trophic guilds of endemic intertidal taxa.

Material and Methods

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). More than 160 km of the sandy shoreline in southern California has been subject to some form of intense mechanized maintenance (grooming, beach filling, berm building) (Dugan et al 2003, Patsch & Griggs 2006). The 16 study beaches (seven urban and nine reference) were located in a single biogeographic province, the Californian or California Transition Zone (Briggs 1974, Newman 1979, Valentine 1966) but in four littoral cells (Santa Barbara, Santa Monica, San Pedro, and Oceanside; Patsch & Griggs 2006; Fig. 1; Table 1). At least one urban and one reference study beach were located within each littoral cell.

For our comparisons, urban beaches (Fig. 2ab; Table 1) were defined as beaches that are subjected to locally intensive maintenance activities that are conducted using heavy equipment. For our study, these activities included regular mechanical grooming and beach filling with imported sand on all beaches, as well as winter berm building on a subset of the beaches. The morphology, physical characteristics, and profiles of urban beaches are strongly influenced by these maintenance activities. The profiles of urban beaches are characterized by narrow, steep intertidal zones and wide, flat upper beach zones devoid of wrack deposits and vegetation (Fig. 2ab; Dugan & Hubbard 2010).

Anthropogenic influences that occur on regional and littoral cell scales, such as altered sediment budgets (Orme *et al.* 2011), can affect all beaches regardless of local management activities and impacts (Defeo *et al.* 2009). For this reason, we selected reference beaches that lacked mechanized maintenance activities and exhibited the best attainable ecological condition for sandy beaches on an urban coast (*sensu* Stoddard *et al.* 2006). These reference beaches (Fig. 2cd, Table 1) were not subject to the intensive maintenance activities of beach filling, berm building, or grooming. The morphology and profiles of these beaches are largely the result of natural coastal processes rather of than direct human interventions (Fig. 2cd).

Beach surveys

We sampled each of the study beaches once during daytime spring low tides in the late summer or fall (August to October) between 2009 and 2015 (Table 1). At each beach, we established three shore-normal transects that extended from the landward boundary of the beach (sea bluff, dune toe, or manmade infrastructure) to the low swash zone at the time of low tide. At three of the urban beaches with artificially wide upper beach zones that exceeded 100 m (Hollywood, Santa Monica, and Huntington), we estimated the landward boundary for the three transects based on high water mark remnants and stranded marine debris from spring high tides and measured the remaining distance (used for total and upper beach zone widths) between the tops of the transects and the bounding manmade infrastructure using a distance measuring wheel. The distances between transects were randomly selected and, to minimize any disturbance of the mobile fauna in adjacent transects prior to sampling, a 10 m buffer zone was added between transects. During the survey at each beach, all biotic and physical measurements were collected along these three transects using the methods of Dugan *et al*. (2003).

To estimate biodiversity and community structure of intertidal macroinvertebrates, we collected a series of 150 core samples at uniform intervals (0.2 m to 1.2 m – depending on the width of the beach) along each transect totaling 450 cores per site. The top core collected on each transect corresponded to the landward boundary (or estimated landward boundary for three artificially wide beaches described above) of the beach and the lowest core corresponded to the low swash level at the time of low tide. Each of the cylindrical cores (0.0078 m^2, 10 cm diameter) was taken to a depth of 20 cm. To facilitate handling, each set of ten successive cores was pooled in a mesh bag with an aperture of 1.5 mm then sieved in the swash zone to remove sand and retain macroinvertebrates. After sieving macroinvertebrates, each set of ten cores were placed in a labeled plastic bag. In the laboratory, samples were preserved in 10% buffered formalin. This sampling design yielded a total sampling area of 3.5 m^2 at each beach.

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 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 & 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. The width of all macrophyte wrack, debris, wood, trash, and tar that intersected the transect line was measured, categorized, and recorded. Cover of wrack was totaled for each transect and expressed as the area (m^2) of wrack per meter wide strip of beach (see above). 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 wrack cover were calculated for the three transects for each site.

On each transect we measured total beach width from the landward boundary to low swash level and identified and measured the widths of two intertidal zones, the upper beach zone width (landward boundary to 24 h high tide strandline (HTS)), and active intertidal zone width (HTS to low swash level). We also measured a number of other environmental factors that have been shown to influence macroinvertebrate community structure (McLachlan *et al.* 1993, 1996) including sand grain size, wave height, wave period, and beach slope at the water table outcrop (WTO) for each transect. We collected sand samples for grain size analysis at the HTS and the WTO on each transect. Sand samples were rinsed with fresh water, dried, and measured using graded sieves in the laboratory. We calculated the geometric mean (mean grain size) and sediment sorting (standard deviation) of grain size distribution using the geometric method of moments for each sand sample using the R package *G2Sd* (Gallon & Fournier, 2013).

The following physical characteristics were averaged (± SE) across the three transects at each site: total beach, upper beach, and active intertidal widths, WTO slope, and mean grain sizes and sediment sorting at the WTO and HTS. Dean's parameter (Ω), which is used to characterize beaches by morphodynamic state, was calculated from breaker height divided by the breaker period and sand fall velocity (Short & Wright 1983). Beaches can be categorized into three types based on morphodynamic state: reflective ($\Omega < 1$), intermediate ($1 < \Omega < 6$), and dissipative ($\Omega > 6$) (Short & Wright 1983). In global scale comparisons, beaches with higher values of Dean's parameter (more dissipative) have been associated with higher species richness and abundance (Barboza & Defeo 2015, McLachlan 1990).

Univariate analyses

To evaluate hypotheses concerning the response of diversity and key functional groups to urbanization on sandy beaches, we collated our data into three groups: the total intertidal macroinvertebrate community (hereon referred to as total community) and two trophic guilds, the lower beach and wrack-associated macroinvertebrate groups we described in the introduction. No taxa overlapped across the two trophic guilds of macroinvertebrates, and all taxa (including predatory taxa) from the total intertidal community were assigned to one of these two guilds.

For each of the three groups of intertidal macroinvertebrates, we calculated the mean values of Simpson's diversity index (1/D), Shannon index ($e^{H'}$), and abundance and biomass per meter ± standard error (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).

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 (Table 2). We selected traits that related directly to vulnerability and important ecological functions (nutrient cycling and wildlife support) of beach ecosystems and cannot be summarized using one functional trait. Due to the lack of existing databases with trait information for sandy beach macroinvertebrates, we compiled information regarding the traits of each species to build a species-by-traits matrix from the literature, personal observations, and several online databases (Table 2). When information regarding traits was not available at the species level, the trait of the next highest taxonomic level was used or the trait was left blank.

For our analyses of functional diversity, we calculated three multivariate indices, functional richness (FRic), functional evenness (FEve), and functional dispersion (FDis), to assess different components of functional diversity using the R Package *FD* (Laliberté *et al.* 2014). FRic represents the amount of functional space occupied and is computed by calculating the minimum convex hull space occupied by the given species assemblage relative to the total species assemblage (Villéger *et al.* 2008). A higher value indicates that more niche space is occupied (Mason *et al.* 2005). FEve describes the evenness of abundance distributed in functional trait space and is independent of other diversity indices (Villéger *et al.* 2008). It is calculated by summing the branch lengths of the minimum spanning tree that is required to connect all species in an assemblage weighted by abundance (Villéger *et al.* 2008). High values can indicate that all occupied niche space is utilized equally (Mason *et al.* 2005). FDis is the spread of species in multidimensional trait space and is computed by calculating the mean distance of individual species to the abundance weighted centroid of all species in the community (Laliberté & Legendre 2010). High values can indicate high niche differentiation and thus low resource competition (Mason *et al.* 2005).

The R package *FD* (Laliberté *et al.* 2014) 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). FEve and FDis 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).

Multivariate analyses

We evaluated the null hypothesis that the macroinvertebrate 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 guilds 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, and Oceanside) for these analyses. Macroinvertebrate assemblage patterns were analyzed using multivariate routines in the statistical software package PRIMER 6 (Clark & 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 & 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 S2) 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 (9,999 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 guilds across all study beaches and among urban and reference beaches separately.

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). 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.

The ISA uses a species-abundance matrix to compute an indicator value (IV), which is the degree to which a particular species exhibits specificity (uniqueness to a particular beach type) and fidelity (frequency of occurrence in a particular beach type) for two beach types, urban and reference (Dufrêne & Legendre 1997). The statistical significance of this value is calculated using a Monte Carlo randomization procedure (PC-ORD v.7).

In contrast, CLAM uses pooled abundance data from two groups to classify taxa into four categories instead of just the two for ISA. In addition to group A (urban) and group B (reference) specialists, CLAM categorizes taxa as generalists and too rare to classify (Chazdon *et al.* 2011). We pooled abundance data for urban and reference beaches and set a conservative super-majority threshold (K = 0.667, p = 0.001) to classify indicator taxa into the above categories using CLAM (Chao & Lin 2011), an iterative program that implements the classification procedures above.

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

Results

Diversity, structure, and composition

We recorded more than twice as many species of intertidal macroinvertebrates in our surveys on all reference (73 species) compared with all urban (34 species) beaches (Supplementary material; Table S3). Species richness varied almost twofold (25 – 40 species) among the reference beaches and value of species richness were quite similar for the reference beaches across all littoral cells. For the urban beaches, species richness varied more than fivefold (4 – 21 species) among beaches. On urban beaches, more species were collected on average from the two beaches in the Santa Barbara littoral cell (19.5 ± 1.5 species, range = 18 – 21) than the five beaches (10.8 ± 1.9 species, range = 4 – 15) across the other three littoral cells.

Four macroinvertebrates, all lower beach species, were present at every beach we sampled – the sand crab, *Emerita analoga,* and three polychaetes, *Nephtys californiensis*, *Hemipodia simplex*, and *Scolelepis bullibranchia.* Wrack-associated talitrid amphipods, *Megalorchestia* spp., were collected at every beach except for three of the urban beaches, Westward, Santa Monica, and Huntington. The smallest of the five talitrid species, *Megalorchestia benedicti,* was recorded at all reference beaches and only one urban beach, Redondo. A different species, *Megalorchestia minor* was the most common talitrid collected at urban beaches (57% of urban beaches).

Comparisons of mean values of observed and estimated richness also indicated more than twice as many total intertidal species on reference compared with urban study beaches (Fig. 3). The size of this effect in species richness was greater for observed and estimated values (effect size, η^2 = 79% and 78%, respectively) than for abundance or biomass (Fig. 3). For total intertidal community, lower beach, and wrack-associated macroinvertebrates, the mean values for observed and estimated species richness were significantly lower ($P \leq 0.05$) on urban than on reference beaches (Fig. 3). However, the relative differences in mean values of observed and estimated species richness among reference and urban beaches varied between guilds and effect sizes were much greater for wrack-associated (η^2 = 78% and 80%, respectively) than for lower beach macroinvertebrates (η^2 = 44% and 48%, respectively) (Fig. 3).

The relative species richness of the two guilds of intertidal macroinvertebrates differed markedly across urban and reference beaches. Lower beach species were the dominant species guild in terms of richness for urban and reference beaches and made up a higher percentage of 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 guild richness was reflected in intertidal community composition (Table S3). Overall composition of the intertidal macroinvertebrate communities of reference beaches was dominated by insects (37%), crustaceans (30%), and polychaetes (23%). In contrast, community composition of urban beaches was dominated by crustaceans (38%) and polychaetes (32%) with the proportion of insects (18%) reduced by half.

Similar to results above for species richness, Simpson's diversity and Shannon indices indicated lower diversity of macroinvertebrates across all intertidal levels on urban compared with reference beaches (Fig. 3). The values of these indices differed significantly ($P \leq 0.05$) for the total community (Shannon: $F = 4.6$, $P = 0.05$) and the wrack-associated macroinvertebrates (Simpson's: $F = 10.8$, $P < 0.01$; and Shannon: $F = 14.9$, $P < 0.01$) but not for the lower beach macroinvertebrates (Simpson's: $F = 0.03$, $P = 0.87$; and Shannon: $F = 0.3$, $P = 0.62$) (Fig. 3).

Mean values of abundance of the total intertidal community and the lower beach and wrack-associated macroinvertebrates were up to an order of magnitude greater and differed significantly on reference beaches compared with urban beaches (total community: $F = 13.4$, $P < 0.01$; lower beach: $F = 5.2$, $P = 0.04$; wrack-associated: $F = 16.6$, $P < 0.01$). Effect sizes were greater for the wrack-associated than the lower beach macroinvertebrates (total community: 49%; lower beach: 27%; wrack-associated: 54%) (Fig. 3). Total intertidal abundance varied over sevenfold among the reference beaches (11,884 – 84,878 individuals m^{-1}) but only a little over twofold among the urban beaches (2,394 – 6,773 individuals m^{-1}).

The mean biomass of the total intertidal community was dominated by lower beach macroinvertebrates on all beaches (urban: 97%, reference: > 99%). Values for biomass of the total intertidal community and the lower beach and wrack-associated macroinvertebrates were also significantly greater on reference beaches than on urban 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). As we found for abundance, effect sizes for mean biomass among reference and urban beaches were greater for the wrack-associated than for lower beach macroinvertebrates or total community (total community: 30%; lower beach: 27%; wrack-associated: 48%) (Fig. 3).

On reference beaches, no single macroinvertebrate taxa truly dominated intertidal abundance and the most abundant taxa were the wrack-associated talitrid amphipods *Megalorchestia* spp. (23%), followed by lower beach bean clams *Donax gouldii* (17%), hippid crabs *E. analoga* (16%), and polychaetes *Thoracophelia mucronata* (15%). In contrast, on urban beaches the lower beach species *E. analoga* (39%) dominated intertidal abundance. For the five species of talitrid amphipods, the most abundant on reference beaches was *Megalorchestia corniculata* and the most abundant on urban beaches was *Megalorchestia minor*. The latter species was present in very low numbers on urban beaches relative to reference beaches (more than half as abundant).

Intertidal biomass was dominated by the lower beach hippid crab, *E. analoga* on both reference beaches (65%) and urban beaches (34%). One large lower beach crab species, *B. occidentalis* was also an important component of the intertidal biomass on reference and urban beaches (10% and 40%, respectively).

The average abundance and biomass of the majority (95%) of intertidal species were higher on reference than on urban beaches. Those differences were significant ($P \leq 0.05$) for a subset of taxa, including three wrack-associated (*Megalorchestia* spp., a flightless curculionid beetle *Emphyastes fucicola*, and a staphylinid beetle *Bledius fenyesi*) and four lower beach macroinvertebrates (*E. analoga,* an amphipod *Paraphoxus* sp., a nemertean *Paranemertes californica*, and a polychaete *Nephtys californiensis* (biomass only)).

Functional diversity indices of richness, evenness, and dispersion also differed significantly among urban and reference beaches (FRic: $F = 26.8$, $P < 0.01$; FEve: $F = 12.1$, $P < 0.01$; FDis: $F = 6.4$, $P = 0.02$), but the direction of those differences varied across the three indices. Similar to species richness (Fig. 3), mean values for functional richness (FRic) and dispersion (FDis) were 62% and 27% lower, respectively, on urban compared with reference beaches (Fig. 4). However, values for functional evenness (FEve) were 19% higher on average for urban beaches (Fig. 4), which supported fewer specialized taxa that are less abundant.

Macroinvertebrate assemblage patterns

Results of our multivariate analyses (nMDS and one-way ANOSIM) using beach type (urban and reference) indicated distinct clusters that differed significantly ($P \leq 0.05$) for the total intertidal community and for the lower beach and wrack-associated macroinvertebrate guilds (Fig. 5). Global R values indicated greater similarity in assemblage patterns between reference and urban beaches for the lower beach macroinvertebrates than for wrack-associated macroinvertebrates (Fig. 5). Results of our SIMPER analysis suggested the wrack-associated species *M. benedicti, M. corniculata, Fucellia rufitibia*, *Tylos punctatus*, *M. californiana*, and the lower beach clam*, D. gouldii* contributed most (cumulative percentage = 20%) to the statistically significant differences between intertidal communities on reference and urban beaches (Supplementary material; Table S4a).

Beach type (urban and reference) was an important factor in evaluating landscape scale differences in assemblage patterns (PERMANOVA) across littoral cells. When beach type was excluded as a factor, there were no significant differences in the assembly of macroinvertebrates (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). Littoral cells were significantly associated (PERMANOVA, $P \leq 0.05$) with the assemblage patterns of intertidal macroinvertebrate groups generated by nMDS for the reference beaches but not for the urban beaches (PERMANOVA, $P > 0.05$) (Fig. 5, Table 3b).

Beach characteristics

Mean values of sediment grain size collected from the high tide strand line (HTS) and water table outcrop (WTO) levels ranged from 0.22 to 0.51 mm and 0.20 to 0.34 mm, respectively (Table S2) and differed significantly ($P \leq 0.05$) among urban and reference beaches. On average, grain sizes were greater (HTS = 43%, WTO = 27%) for the urban beaches (Fig. 6). Mean values of sediment sorting for the HTS and WTO, ranged from 1.27 to 1.53 and 1.27 to 1.51, respectively (Table S2). On average, sediment collected from the HTS and WTO was better sorted (lower value) for the reference beaches than for urban beaches but those differences were not significant ($P > 0.05$) (Fig. 6).

The overall intertidal profiles of the study beaches were relatively similar with intermediate intertidal slopes and comparable wave regimes. This was supported by the values for morphodynamic type estimated by Dean's parameter (Ω) measured during our surveys which indicated that all study beaches were intermediate in morphodynamic type ($1 < \Omega < 6$) (Short & Wright 1983) (Table S2). Values of Dean's parameter did not differ significantly ($P > 0.05$) among urban ($\overline{x} = 2.9 \pm 0.3$; $n = 7$; range: 1.7–3.8) and reference ($\overline{x} = 2.3 \pm 0.3$; $n = 9$; range: 1.3–4.2) beaches (Fig. 6). Likewise, beach slopes at the WTO also did not differ significantly among urban ($\overline{x} = 3.9 \pm 0.6$; $n = 7$; range: 1.5–6.0) and reference ($\overline{x} = 2.9 \pm 0.6$; $n = 9$; range: 1.1–7.2) beaches (Fig. 6).

Observed mean values of total beach widths (landward boundary to low swash) varied over threefold across the urban (range: 75 – 297 m) and reference (range: 47 – 162 m) study beaches (Table S2). The mean values of total beach width of urban beaches were consistently greater than on reference beaches in our surveys, but those differences were not significant ($P > 0.05$) (Fig. 6). 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 S2). Mean values of width of the upper beach zone differed significantly ($P \leq 0.05$) between urban (range: 27 – 240 m) and reference (range: 5 – 40 m) beaches (Fig. 6). Much of the upper beach habitat zone present on urban beaches was highly disturbed above the intertidal range and devoid of wrack, vegetation, and animals. The mean values of active intertidal zone width 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 S2). Mean values of active intertidal zone widths were greater on average for reference compared with urban beaches, but those differences were not significant ($P > 0.05$) (Fig. 6).

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 higher on reference beaches compared with urban beaches ($P \leq 0.05$, Fig. 6; Table S2). The mean cover of total wrack varied by more than an order of magnitude among the reference study beaches (range: 0.3 – 4.9 m^2m^{-1}) and over two orders of magnitude across urban study beaches (range: 0.007 – 0.9 m^2m^{-1}) (Table S2).

Environmental drivers

Two types of environmental drivers that affect the 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 ($P \leq 0.05$) amount of the variance in intertidal community and trophic guild 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 intertidal community or trophic guild assembly of our 16 study beaches. When we compared all beaches (reference and urban – 16 beaches), mean grain size at the HTS and total wrack cover explained a significant percentage of variance (35%) for the total intertidal community ($P \leq 0.05$) (Table 4). For the two trophic guilds, significant percentages of the variability in the lower beach and wrack-associated macroinvertebrates were explained by three sediment characteristics (HTS grain size and sorting, WTO sorting = 46%) and total wrack cover (18%), respectively ($P \leq 0.05$) (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%) ($P \leq 0.05$) (Table 4). However, across urban beaches alone, sediment sorting was the only environmental variable that explained a significant proportion of the variability ($P \leq 0.05$), but this was only for the total intertidal community (30%) and the lower beach macroinvertebrate guild (34%) (Table 4).

Indicator taxa

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). All the indicator species identified across the three analyses were wrack-associated species including the talitrid amphipods *M. benedicti*, *M. californiana*, and *M. corniculata*, the peracarid isopods *Alloniscus perconvexus* and *Tylos punctatus*, and the kelp fly *Fucellia rufitibia*. The indicator families included three wrack-associated macroinvertebrate families (Alloniscidae, Tylidae, and Anthomyiidae) and one lower beach macroinvertebrate family (Haustoriidae) (Table 5). 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: *H. simplex* and *M. minor*; family: Glyceridae and Spionidae) were identified by the CLAM analysis (Supplementary material; Table S4).

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 have been strongly altered by the widespread maintenance regimes (grooming, sediment fills, and berm building) prevalent on urban beaches. Urban beaches, which make up a large proportion of the southern California sandy shoreline (Dugan *et al*. 2003, Patsch & 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 effects on biodiversity (species richness). In contrast, the reference beaches we studied appeared to be representative of the high biodiversity in the region (Claisse *et al.* 2018) with values of species richness, abundance, and biomass that are considered globally high for open coast sandy beaches (McLachlan *et al.* 1996).

In comparison to our results, observed ecological responses to urbanization in the terrestrial biome have been more variable (decrease, increase, or no change), however declines in the number of species were observed in the majority of terrestrial studies, particularly for invertebrates (McKinney 2008). Substantial declines in observed local scale biodiversity and structure in response to heavy manipulation of landscapes (>90% habitat loss) (Ewers & Didham 2006) are expected to have severe consequences by inhibiting important ecological functions (Hooper *et al.* 2012, Spaak *et al.* 2017). For sandy beaches, this suggests that the magnitude of loss that we observed in intertidal biodiversity and structure in response to intensive management regimes is weakening important ecological resources and functions, such as the supply and processing of organic matter (e.g. macroalgal wrack) that are important for nutrient cycling (e.g. Dugan *et al.* 2011, Lastra *et al.* 2008, 2018) and food web support of higher trophic levels (e.g. fish, birds, mammals) (e.g. Hubbard & Dugan 2003, Huijbers *et al*. 2013, Polis & Hurd 1996, Vargas-Fonseca *et al.* 2016).

Functional diversity can predict ecosystem function and vulnerability more reliably than species diversity (Gagic *et al.* 2015). The alteration of landscapes for human use associated with urbanization can selectively filter out specialist species with more restricted habitat and resource requirements causing functional diversity to decline more than species richness (Croci *et al.* 2008, Mouillot *et al.* 2013).

Functional diversity measures provided useful and unique insights on the impacts of urbanization on ecosystem function on sandy beaches. In our study, functional richness (-62%) declined more than the species richness (-58%). Two of the three functional diversity indices tested declined in response to urbanization, but evenness did not decline. Inverse responses of functional richness and functional evenness to urbanization such as we found are not common and has been attributed to declines in specialist species (Filippi-Codaccioni *et al.* 2009), such as the specialized wrack-associated guild on sandy beaches. However, the implications of these results for ecosystem function have not been explored. 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 less niche space was occupied. If niche space relating to important ecological functions is unoccupied or underutilized, ecosystem function could be weakened or degraded (Mason *et al.* 2005). In our study, 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 study beaches. Furthermore, the lower functional dispersion we observed for urban beaches suggests a low degree of niche differentiation and weakened ecosystem functioning on beaches with intensive management regimes. Our results suggest functional diversity measures could provide a valuable tool in elucidating biodiversity-ecosystem function relationships for sandy beach ecosystems.

In urban areas, another outcome of the modification of the physical environment intended to fit the narrow needs of humans is often biological homogenization (McKinney 2006). This 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 beach management regimes. These intense maintenance activities appear to have the potential to homogenize intertidal and functional diversity, which could degrade ecosystem function and increase vulnerability to environmental change on regional (Olden *et al*. 2004) and global scales (Groffman *et al.* 2014).

Major groupings of organisms, particularly taxonomic groups or feeding guilds, are often reported to respond differently to disturbance associated with urbanization (Barrett & Guyer 2008, McKinney 2002). For sandy beaches, both of the major guilds of 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 guilds. Overall, intensive maintenance activities on urban beaches affected the wrack-associated macroinvertebrates disproportionately and far more strongly (> 80% declines; η^2: > 48%) than the lower beach macroinvertebrates (> 39% declines; η^2: > 27%). Several factors relating to life history, resource dependence, and intertidal zonation likely contributed to the different responses of the guilds we observed to impacts from urban beach maintenance regimes. Groups of 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). 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 due to their dependence on a particular resource (e.g. macrophyte wrack) that is present but actively removed by maintenance activities (Dugan *et al.* 2003). Furthermore, these taxa inhabit upper intertidal zones located near the driftline where the frequency and intensity of disturbance by maintenance activities on urban beaches is generally greater, thus directly altering their habitat (e.g. Dugan *et al.* 2003, González *et al.* 2014, Hubbard *et al.* 2014, Schooler *et al.* 2017, Veloso *et al.* 2006, 2008, Weslawski *et al.* 2000ab). 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 far more vulnerable to urban beach management regimes than the macroinvertebrates of the lower intertidal zones.

Due to their sensitivity to disturbance, these wrack-associated macroinvertebrates may be useful as indicators of the ecological condition of sandy beaches on urban coasts in California and elsewhere. We identified several species (three talitrid amphipods, two peracarid isopods, and a kelp fly) and families (two peracarid isopods, a kelp fly, and lower beach amphipod) that are particularly vulnerable to urban impacts. Upper beach fauna have previously been identified as useful indicator taxa for monitoring sandy beach ecological condition because of their vulnerability to anthropogenic disturbance (trampling, off-road vehicles, grooming, and beach fills) and habitat loss (sea-level-rise and coastal squeeze) (Gonçalves *et al.* 2013, Gonçalves & Marques 2017, 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 these indicator taxa could be used to monitor declines in ecological condition across the intertidal zone in response to urbanization as well as potential recovery from impacts unrelated to urbanization (e.g. oil spills) for sandy beaches.

Unlike findings for other ecosystems where species 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 for more than 90% of the intertidal species were lower on urban than reference beaches, 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

& 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 traits that are characteristic of early successional species typically found in managed urban habitats (McKinney 2002). These traits include: high abundance on beaches not subject to maintenance (reference beaches), long-distance larval dispersal capability, capable of settling in large numbers, and extensive geographic distributions. This set of traits could be used to identify the types of species that may be able to tolerate coastal urbanization at some level. Of note, these taxa were not restricted to a single feeding guild and included filter feeders, predators, and deposit feeders.

Our study results and those of others (Dugan *et al.* 2003, Dugan & Hubbard 2010, Hubbard *et al.* 2014, Manning *et al.* 2014, Peterson *et al.* 2000, 2014, Schooler *et al.* 2017, Wooldridge *et al.* 2016) suggest that changes in habitat quality and resource availability that persist over sufficient time scales can inhibit the settlement and recovery of sandy beach biota and result in profound lasting impacts to macroinvertebrate communities across the entire intertidal. Our findings showed that variability in environmental characteristics associated with food availability and habitat quality – wrack abundance and sediment characteristics (size and sorting) – influenced differences we observed in intertidal community assembly between urban and reference beaches. In addition to the immediate direct and intense mortality of intertidal macroinvertebrates from grooming (e.g. Llewellyn & Shackley 1996) and beach filling episodes (e.g. Peterson *et al.* 2000), the combination of frequent beach grooming with heavy equipment and the retention of non-native coarse and poorly sorted sediment from past beach filling episodes (Leidersdorf *et al.* 1993) can alter and homogenize habitat quality for intertidal macroinvertebrates (Dugan *et al.* 2000, 2003, Viola *et al.* 2014) as well as the physical processes on beaches (Dugan & Hubbard 2010, Komar 1998, van der Wal 1998). Enhancing levels of biodiversity and function of urban beach ecosystems over the long term could be possible under revised management regimes that limit the spatial scale and frequency of different maintenance activities (beach grooming and filling) and seek to better match natural conditions (grain size and sorting, and wrack availability) (Peterson *et al.* 2014, Speybroeck *et al.* 2006, Weslawski *et al.* 2000b).

Conclusion

In conclusion, our comparisons showed a very strong response of sandy beach ecosystems to intense mechanized maintenance associated with coastal urbanization. Our results highlight the significant influence and regional scale of anthropogenic impacts associated with urbanization on the biodiversity, structure, and community composition of the entire community of intertidal macroinvertebrates and suggest these impacts 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 and could contribute to regional losses of coastal biodiversity. With global estimates that 24% of beaches are currently eroding (Luijendijk *et al.* 2018) and a projected loss of up to 67% of beaches in California by 2100 (Vitousek *et al.* 2017), conservation of the unique biodiversity and function of the remaining beach ecosystems in the face of expanding human populations along the coasts will be urgently needed. At present, sandy beaches are primarily managed for human use and recreation in many regions (McLachlan *et al*. 2013). Our results could be used to inform the development of more ecologically sensitive management approaches that achieve a greater balance between the vital socioeconomic and irreplaceable ecological functions of these threatened iconic coastal ecosystems.

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Figures

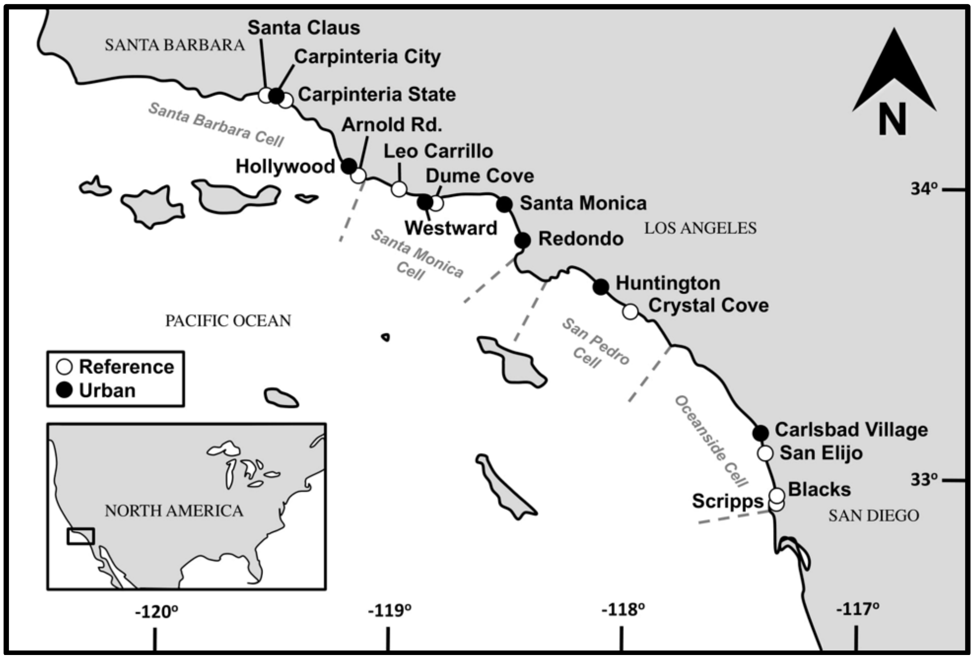

Figure 1. Map of the study region with names and locations of the reference (white dot) and urban (black dot) sandy beach study sites surveyed and the littoral cell names and boundaries (dashed gray lines) on the coast of southern California, USA.

Figure 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

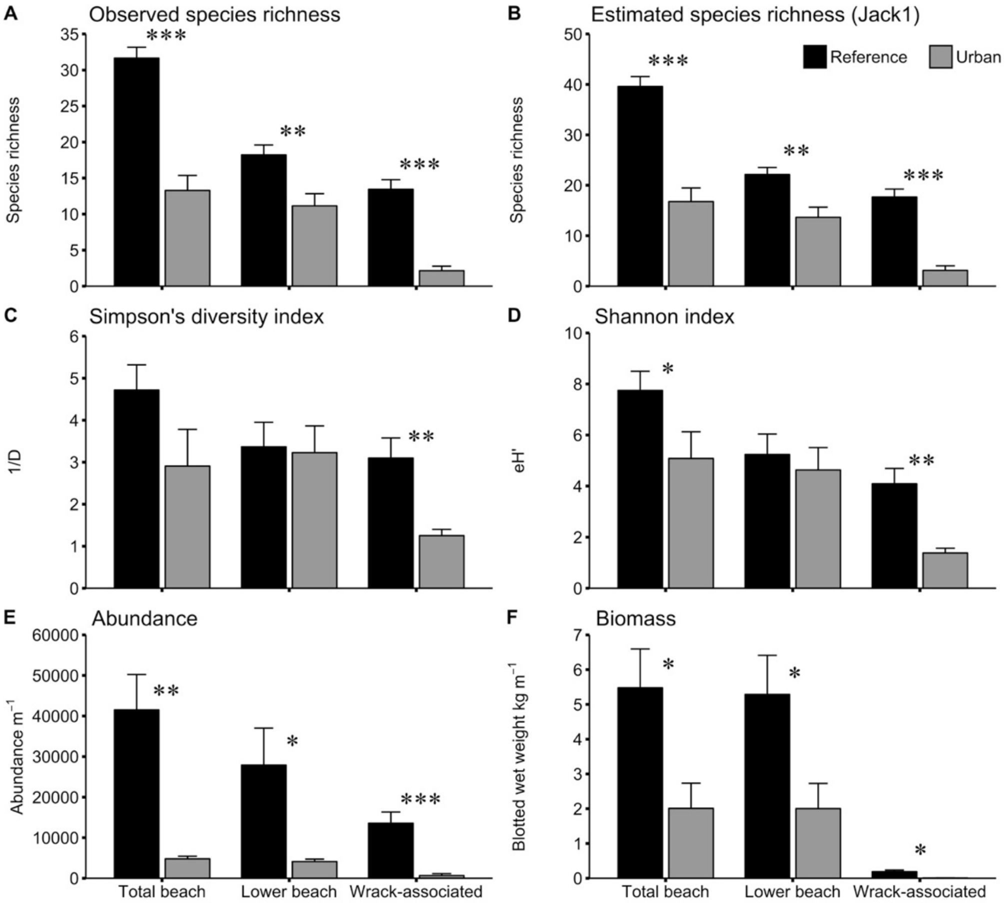

Figure 3. Comparisons of the biodiversity and structure of the total beach, lower beach, and wrack-associated macroinvertebrates for reference (black, $N = 9$) and urban (grey, $N = 7$) study beaches. The bars represent the mean ± SE for A) observed species richness, B) estimated (Jackknife 1) species richness, C) Simpson's diversity index, D) Shannon index, E) abundance, and F) biomass ($* = P \leq 0.05$, $** = P \leq 0.01$, $*** = P \leq 0.001$).

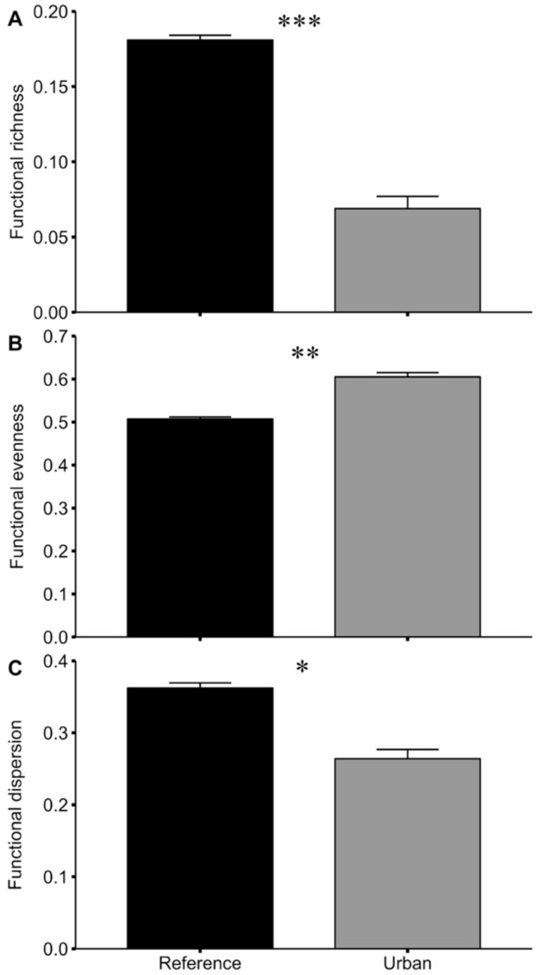

Figure 4. Comparisons of the functional diversity of reference (black, $N = 9$) and urban (grey, $N = 7$) study beaches. The bars represent the mean ± SE for functional A) richness (FRic), B) evenness (FEve), and C) dispersion (FDis) (* = $P \leq 0.05$, ** = $P \leq 0.01$, *** = $P \leq 0.001$).

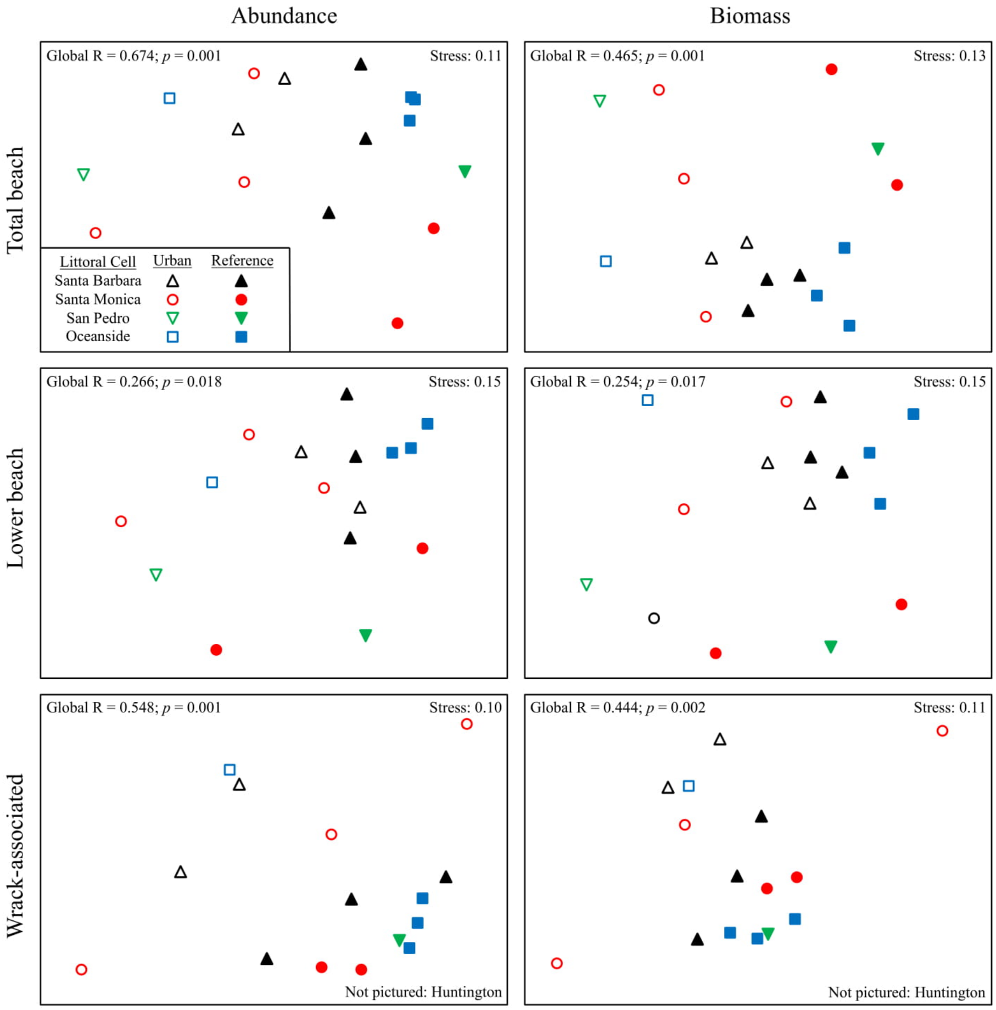

Figure 5. Non-metric multidimensional scaling (nMDS) analysis comparing macroinvertebrate assemblages of urban and reference study beaches for the total beach, lower beach, and wrack-associated macroinvertebrates using log (x+1) transformed abundance and biomass data. Global R and *p*-values displayed 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). 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.

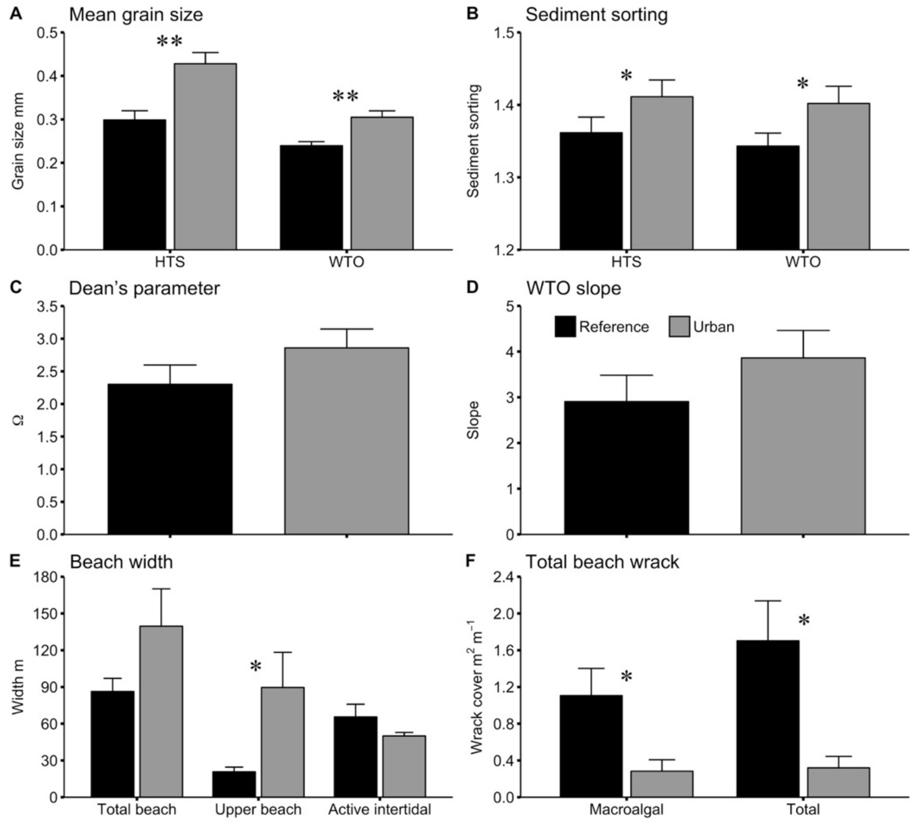

Figure 6. Comparisons of beach characteristics for reference (black, *N* = 9) and urban (grey, *N* = 7) study beaches. The bars represent the mean ± SE for A) mean grain size at the high tide strandline (HTS) and water table outcrop (WTO), B) sediment sorting at the HTS and WTO, C) Dean's parameter, D) WTO slope, E) total beach, upper beach, and active intertidal zone widths, and F) macroalgal and total wrack cover for the total beach (* = $P \leq 0.05$, ** = $P \leq 0.01$).

Tables

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.

Site	Latitude	Longitude	Beach Type	Littoral Cell	Survey Date
Santa Claus	34°24'30.8"N	119°33'05.8"W	Reference	Santa Barbara	October 6, 2010
Carpinteria State	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	34°02'49.4"N	118°56'52.5"W	Reference	Santa Monica	September 30, 2011
Dume Cove	34°00'21.1"N	118°48'06.3"W	Reference	Santa Monica	October 12, 2011
Crystal Cove	33°34'40.2"N	117°50'51.5"W	Reference	San Pedro	September 29, 2011
San Elijo	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	32°51'49.2"N	117°15'17.8"W	Reference	Oceanside	August 21, 2011
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	34°00'10.0"N	118°48'35.3"W	Urban	Santa Monica	September 21, 2009
Santa Monica	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

Table 2. Biological traits, modalities, and descriptions for the sandy beach macroinvertebrate community. Compiled from the literature, personal observations, and several online databases including Oregon Estuarine Invertebrates Database (scholarsbank.uoregon.edu/xmlui/handle/1794/11968), WoRMS (www.marinespecies.org), SCAMIT (scamit.org), Polytraits (polytraits.lifewatchgreece.eu), and SeaLifeBase (www.sealifebase.org).

Trait	**Modality**	**Description**
Size	Extra small	< 0.0002 g
	Small	0.0002 - 0.01 g
	Medium	0.01 - 0.03 g
	Medium-large	0.03 - 0.08 g
	Large	0.08 - 0.5 g
	Extra large	> 0.5 g
Beach zone	Upper	Dry upper beach sand that is not inundated with water at high tide
	Wrack	Primarily exposed high intertidal where wrack is deposited
	Middle	Equally exposed and submerged mid intertidal
	Lower	Primarily submerged lower intertidal
Primary food source	Terrestrial plants	Live terrestrial plants such as coastal strand plants
	Wrack	Marine macrophytes (kelp, algae, surf grass)
	Detritus	Organic matter that is interstitial, suspended, on the surface
	Plankton	Suspended phytoplankton and zooplankton
	Invertebrates	Live or dead invertebrates
Feeding guild	Grazer	Feeds on wrack or terrestrial plants
	Deposit	Collects food interstitially or from substrate surfaces
	Suspension	Collects suspended food
	Omnivore	Feeds on plants, wrack, and animals
	Scavenger	Primarily consumes dead animals
	Predator	Primarily kills prey
Terrestrial plants	1	Feeds on terrestrial plants
	0	Does not feed on terrestrial plants
Wrack	1	Feeds on wrack
	0	Does not feed on wrack
Detritus	1	Feeds on detritus
	0	Does not feed on detritus
Plankton	1	Feeds on plankton
	0	Does not feed on plankton
Invertebrates	1	Feeds on invertebrates
	0	Does not feed on invertebrates
Carrion	1	Feeds on carrion
	0	Does not feed on carrion
Dependence on wrack	1	Depends of wrack for shelter
	0	Does not depend on wrack for shelter
Respiratory mode	Air	Oxygen intake from air
	Water	Oxygen intake from water
	Both	Oxygen intake from air and water
Adult motility	Low - Marine	Infaunal burrowers - Polychaetes
	High - Marine	Epibenthic swimmers - Crustaceans and some Polychaetes
	Low - Terrestrial	Incapable of flight - Crustaceans, some Coleopterans
	High - Terrestrial	Capable of flight - Dipterans, most Coleopterans
Larval motility	Brooded	Eggs remain with and/or are cared for by adult (low dispersal)
	Eggs	Eggs not cared for by adult (low dispersal)
	Short planktonic	Larval planktonic stage < 10 days (moderate dispersal)
	Long planktonic	Larval planktonic stage > 10 days (high dispersal)
Biogeographic range	Local	Range restricted to 1-100 km of the NE Pacific
	Regional	Range restricted to 100-500 km of the NE Pacific
	NE Pacific	Range restricted to 500-10,000 km of the NE Pacific
	E Pacific	Range restricted to the eastern Pacific
	Pacific	Range restricted to Pacific
	Cosmopolitan	Range not restricted to Pacific

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

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 reference and urban 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	117.27	4.91	0.25	< 0.01
		Total wrack cover*	116.85	2.12	0.10	0.02
	Lower beach	HTS sediment sorting	112.07	5.33	0.28	< 0.01
		HTS mean grain size	111.65	2.13	0.10	0.02
		WTO sediment sorting	111.31	1.89	0.08	0.04
	Wrack-associated	Total wrack cover*	129.2	2.99	0.18	< 0.01
Reference beaches	Total	HTS mean grain size	63.58	3.24	0.32	< 0.01
		Total wrack cover*	62.91	2.07	0.18	0.03
	Lower beach	WTO mean grain size	62.46	3.73	0.35	< 0.01
	Wrack-associated	HTS mean grain size	65.93	2.9	0.29	0.03
		Macroalgal wrack cover*	64.86	2.44	0.20	0.04
Urban beaches	Total	HTS sediment sorting	50.81	2.11	0.30	0.03
	Lower beach	HTS sediment sorting	48.84	2.55	0.34	0.02
	Wrack-associated	None	-	-	-	-

Table 5. Results from ISA, CLAM, and SIMPER analyses for A) species and B) families showing ISA classification (reference or urban beaches) type, indicator value (IV), p-value; CLAM classification (reference, urban, 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. See supplementary material Table S4 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

Supplementary Material

Table S1. Species by site matrix from all species from the literature, personal observations, and several online databases including Oregon Estuarine Invertebrates Database (scholarsbank.uoregon.edu/xmlui/handle/1794/11968), WoRMS (www.marinespecies.org), SCAMIT (scamit.org), Polytraits (polytraits.lifewatchgreece.eu), and SeaLifeBase (www.sealifebase.org). NA specifies where data was unavailable, so it was left blank for the analyses.

Taxa	Size	Beach_zone	Primary_food_source	Feeding_guild	Terrestrial_plants	Wrack	Detritus	Plankton	Invertebrates	Carrion	Dependence_on_wrack	Respiratory_mode	Adult_motility	Larval_motility	Biogeographic_range
Scoletoma_zonata	Large	Lower	Detritus	Deposit	0	0	1	0	0	0	0	Water	Low_marine	Brooded	Cosmopolitan
Arabella_iricolor	Large	Lower	Detritus	Omnivore	0	0	1	0	1	0	0	Water	Low_marine	Brooded	Cosmopolitan
Hemipodia_simplex	Medium_large	Lower	Invertebrates	Predator	0	0	0	0	1	0	0	Water	Low_marine	Long_planktonic	Cosmopolitan
Nephtys_caecoides	Medium	Lower	Invertebrates	Predator	0	0	0	0	1	0	0	Water	High_marine	Long_planktonic	NE_pacific
Nephtys_californiensis	Large	Lower	Invertebrates	Predator	0	0	0	0	1	0	0	Water	High_marine	Long_planktonic	Pacific
Paraonella_platybranchia	Small	Lower	Detritus	Deposit	0	0	1	0	1	0	0	Water	Low_marine	NA	Pacific
Dispio_sp	Medium	Lower	Detritus	Deposit	0	0	1	0	0	0	0	Water	Low_marine	Short_planktonic	Regional
Pygospio_californica	Extra_small	Lower	Detritus	Omnivore	0	0	1	0	1	0	0	Water	Low_marine	Short_planktonic	Pacific
Scolelepis_bullibranchia	Medium	Middle	Detritus	Deposit	0	0	1	0	0	0	0	Water	Low_marine	Brooded	Regional
Scolelepis_squamata	Medium	Middle	Detritus	Deposit	0	0	1	0	0	0	0	Water	Low_marine	Short_planktonic	Cosmopolitan
Cirriformia_sp	Medium_large	Lower	Invertebrates	Predator	0	0	0	0	1	0	0	Water	Low_marine	Long_planktonic	Pacific
Amastigos_acutus	Small	Lower	Detritus	Deposit	0	0	1	0	0	0	0	Water	Low_marine	NA	NE_pacific
Capitellidae	Medium_large	Lower	Detritus	Deposit	0	0	1	0	0	0	0	Water	Low_marine	Brooded	NA
Notomastus_D	Medium	Lower	Detritus	Deposit	0	0	1	0	0	0	0	Water	Low_marine	Long_planktonic	NE_pacific
Thoracophelia_dillonensis	Small	Middle	Detritus	Deposit	0	0	1	0	0	0	0	Water	Low_marine	Long_planktonic	NE_pacific
Thoracophelia_mucronata	Small	Middle	Detritus	Deposit	0	0	1	0	0	0	0	Water	Low_marine	Long_planktonic	NE_pacific
Orbinia_johnsoni	Medium	Lower	Detritus	Deposit	0	0	1	1	0	0	0	Water	Low_marine	Eggs	Cosmopolitan
Scoloplos_armiger	Medium	Lower	Detritus	Deposit	0	0	1	1	0	0	0	Water	Low_marine	Eggs	Cosmopolitan
Saccocirrus_sp	Extra_small	Lower	Detritus	Deposit	0	0	1	0	0	0	0	Water	Low_marine	Long_planktonic	NE_pacific
Eohaustorius_sawyeri	Small	Lower	Detritus	Deposit	0	0	1	0	0	0	0	Water	Low_marine	Brooded	NE_pacific
Eohaustorius_washingtonianus	Small	Lower	Detritus	Deposit	0	0	1	0	0	0	0	Water	Low_marine	Brooded	NE_pacific
Parallorchestes_sp	Small	Lower	Wrack	Grazer	0	1	1	0	0	0	0	Water	Low_marine	Brooded	NE_pacific
Gibberosus_devaneyi	Small	Lower	Detritus	Suspension	0	0	1	1	0	0	0	Water	Low_marine	Brooded	Local
Gibberosus_myersi	Small	Lower	Detritus	Suspension	0	0	0	1	0	0	0	Water	Low_marine	Brooded	Cosmopolitan
Americhelidium_sp	Small	Lower	Detritus	Deposit	0	0	1	0	0	0	0	Water	Low_marine	Brooded	NE_pacific
Paraphoxus_sp	Small	Lower	Detritus	Suspension	0	0	1	0	1	0	0	Water	Low_marine	Brooded	NE_pacific
Mandibulophoxus_gilesi	Small	Lower	Detritus	Suspension	0	0	1	0	1	0	0	Water	Low_marine	Brooded	NE_pacific
Lepidopa_californica	Extra_large	Lower	Invertebrates	Scavenger	0	0	0	0	1	1	0	Water	High_marine	Long_planktonic	NE_pacific
Blepharipoda_occidentalis	Extra_large	Lower	Invertebrates	Scavenger	0	0	0	0	1	1	0	Water	High_marine	Long_planktonic	NE_pacific
Emerita_analoga	Extra_large	Lower	Plankton	Suspension	0	0	0	1	0	0	0	Water	High_marine	Long_planktonic	E_pacific
Excirolana_chiltoni	Small	Middle	Invertebrates	Scavenger	0	0	0	0	1	1	0	Water	High_marine	Brooded	NE_pacific
Excirolana_linguifrons	Small	Middle	Invertebrates	Scavenger	0	0	0	0	1	1	0	Water	High_marine	Brooded	NE_pacific
Archaeomysis_grebnitzkii	Small	Lower	Plankton	Suspension	0	0	1	1	1	0	0	Water	High_marine	Brooded	Cosmopolitan
Archaeomysis_maculata	Small	Lower	Plankton	Suspension	0	0	1	1	1	0	0	Water	High_marine	Brooded	NE_pacific
Donax_gouldii	Large	Lower	Plankton	Suspension	0	0	1	1	0	0	0	Water	Low_marine	Long_planktonic	NE_pacific
Tivela_stultorum	Extra_large	Lower	Plankton	Suspension	0	0	1	1	0	0	0	Water	Low_marine	Short_planktonic	NE_pacific
Callianax_biplicata	Extra_large	Lower	Invertebrates	Predator	0	0	0	0	1	1	0	Water	High_marine	Eggs	NE_pacific
Paranemertes_californica	Medium	Lower	Invertebrates	Predator	0	0	0	0	1	0	0	Water	Low_marine	Long_planktonic	NE_pacific
Nemertean_A	Medium	Lower	Invertebrates	Predator	0	0	0	0	1	0	0	Water	Low_marine	Eggs	NA
Nemertean_B	Medium_large	Lower	Invertebrates	Predator	0	0	0	0	1	0	0	Water	Low_marine	Eggs	NA
Neomolgus_littoralis	Extra_small	Wrack	Invertebrates	Predator	0	0	0	0	1	0	1	Air	Low_terrestrial	Eggs	Cosmopolitan
Akephorus_marinus	Small	Wrack	Invertebrates	Predator	0	0	0	0	1	0	1	Air	Low_terrestrial	Eggs	NE_pacific
Emphyastes_fucicola	Medium	Wrack	Wrack	Grazer	0	1	0	0	0	0	1	Air	Low_terrestrial	Eggs	NE_pacific
Euspilotus_scissus	Small	Wrack	Invertebrates	Scavenger	0	0	0	0	1	1	1	Air	High_terrestrial	Eggs	NE_pacific
Hypocaccus_gaudens	Small	Wrack	Invertebrates	Scavenger	0	0	0	0	1	1	1	Air	High_terrestrial	Eggs	NE_pacific
Neopachylopus_aeneipunctatus	Medium	Wrack	Invertebrates	Scavenger	0	0	0	0	1	1	1	Air	High_terrestrial	Eggs	NE_pacific
Neopachylopus_sulcifrons	Medium_large	Wrack	Invertebrates	Scavenger	0	0	0	0	1	1	1	Air	High_terrestrial	Eggs	NE_pacific
Cercyon_fimbriatus	Small	Wrack	Invertebrates	Omnivore	0	1	0	0	1	0	1	Air	High_terrestrial	Eggs	NE_pacific
Oedemeridae	Small	Upper	NA	NA	NA	NA	NA	NA	NA	NA	1	Air	NA	Eggs	NA
Aleochara_sulciollis	Small	Wrack	Invertebrates	Predator	0	0	0	0	1	1	1	Air	High_terrestrial	Eggs	Pacific
Bledius_fenyesi	Small	Wrack	Wrack	Ominvore	0	1	0	0	1	1	1	Air	High_terrestrial	Eggs	NE_pacific
Cafius_canescens	Medium	Wrack	Invertebrates	Predator	0	0	0	0	1	1	1	Air	High_terrestrial	Eggs	NE_pacific
Cafius_luteipennis	Medium	Wrack	Invertebrates	Predator	0	0	0	0	1	1	1	Air	High_terrestrial	Eggs	NE_pacific
Cafius_seminitens	Medium	Wrack	Invertebrates	Predator	0	0	0	0	1	1	1	Air	High_terrestrial	Eggs	NE_pacific
Cafius_sulcicollis	Medium	Wrack	Invertebrates	Predator	0	0	0	0	1	1	1	Air	High_terrestrial	Eggs	Regional
Pontomalota_opaca	Small	Wrack	Invertebrates	Predator	0	0	0	0	1	1	1	Air	High_terrestrial	Eggs	NE_pacific
Tarphiota_geniculata	Extra_small	Wrack	Invertebrates	Predator	0	0	0	0	1	1	1	Air	High_terrestrial	Eggs	NE_pacific
Thinopinus_pictus	Large	Wrack	Invertebrates	Predator	0	0	0	0	1	1	1	Air	Low_terrestrial	Eggs	NE_pacific
Coelus_ciliatus	Medium_large	Upper	Plants	Grazer	1	0	0	0	0	0	1	Air	Low_terrestrial	Eggs	NE_pacific
Coelus_globosus	Medium_large	Upper	Plants	Grazer	1	0	0	0	0	0	1	Air	Low_terrestrial	Eggs	NE_pacific
Epantius_obscurus	Small	Upper	Wrack	Grazer	0	1	0	0	0	0	1	Air	High_terrestrial	Eggs	NE_pacific
Phaleria_rotundata	Medium	Upper	Wrack	Grazer	0	1	0	0	0	0	1	Air	High_terrestrial	Eggs	NE_pacific
Fucellia_costalis	Medium	Wrack	Wrack	Grazer	0	1	0	0	0	0	1	Air	High_terrestrial	Eggs	NE_pacific
Fucellia_rufitibia	Small	Wrack	Wrack	Grazer	0	1	0	0	0	0	1	Air	High_terrestrial	Eggs	NE_pacific
Coelopa_vanduzeei	Small	Wrack	Wrack	Grazer	0	1	0	0	0	0	1	Air	High_terrestrial	Eggs	NE_pacific
Empididae	Extra_small	Wrack	Wrack	Grazer	0	1	0	0	0	0	1	Air	High_terrestrial	Eggs	NA
Thoracochaeta_johnsoni	Extra_small	Wrack	Wrack	Grazer	0	1	0	0	0	0	1	Air	High_terrestrial	Eggs	NE_pacific
Formicidae	Small	Upper	Invertebrates	Predator	0	0	0	0	1	0	1	Air	Low_terrestrial	Eggs	NA
Megalorchestia_benedicti	Medium	Wrack	Wrack	Grazer	0	1	0	0	1	1	1	Both	Low_terrestrial	Brooded	NE_pacific
Megalorchestia_californiana	Medium_large	Wrack	Wrack	Grazer	0	1	0	0	1	1	1	Both	Low_terrestrial	Brooded	NE_pacific
Megalorchestia_columbiana	Medium	Wrack	Wrack	Grazer	0	1	0	0	1	1	1	Both	Low_terrestrial	Brooded	NE_pacific
Megalorchestia_corniculata	Medium_large	Wrack	Wrack	Grazer	0	1	0	0	1	1	1	Both	Low_terrestrial	Brooded	NE_pacific
Megalorchestia_minor	Medium	Wrack	Wrack	Grazer	0	1	0	0	1	1	1	Both	Low_terrestrial	Brooded	NE_pacific
Alloniscus_perconvexus	Medium_large	Upper	Wrack	Grazer	0	1	0	0	1	0	1	Air	Low_terrestrial	Brooded	NE_pacific
Tylos_punctatus	Medium_large	Upper	Wrack	Grazer	0	1	0	0	1	0	1	Air	Low_terrestrial	Brooded	NE_pacific

Table S2. Beach characteristics for each site and beach type (mean and SE) arranged by beach type then geographically from north to south. Upper beach macroalgal, upper beach total wrack cover, and percent cover were not used in DistLM analysis.

			Mean grain size (mm)		Sorting		Beach width (m)			Cover (m^2 m^{-1})				Percent cover			
Site	Dean's parameter	WTO slope	HTS	WTO	HTS	WTO	Total	Upper	Active intertidal	Total macroalgae	Upper beach macroalgae	Total wrack	Upper beach wrack	Total macroalgae	Upper beach macroalgae	Total wrack	Upper beach wrack
Reference Mean	**2.30**	**2.91**	**0.30**	**0.24**	**1.36**	**1.34**	**86.3**	**20.7**	**65.5**	**1.11**	**0.67**	**1.70**	**1.14**	**1.32**	**6.35**	**2.14**	**9.47**
Reference SE	**0.29**	**0.58**	**0.02**	**0.01**	**0.02**	**0.02**	**10.7**	**3.8**	**10.4**	**0.30**	**0.31**	**0.43**	**0.43**	**0.38**	**3.12**	**0.57**	**3.90**
Santa Claus	4.22	2.53	0.30	0.23	1.34	1.27	58.7	21.5	37.1	0.777	0.023	0.787	0.030	1.324	0.108	1.341	0.139
Carpinteria State	1.25	2.83	0.28	0.25	1.31	1.29	84.2	30.7	53.5	1.537	0.650	1.653	0.697	1.825	2.115	1.964	2.267
Arnold Rd.	2.50	2.53	0.32	0.22	1.34	1.34	77.5	39.9	37.6	0.143	0.063	0.320	0.173	0.185	0.159	0.413	0.435
Leo Carrillo	2.56	3.10	0.34	0.27	1.42	1.43	78.3	12.7	65.7	3.100	2.923	4.927	4.340	3.957	23.079	6.289	34.263
Dume Cove	1.66	7.17	0.44	0.28	1.48	1.39	47.3	18.1	29.3	0.097	0.087	1.390	1.333	0.204	0.480	2.937	7.380
Crystal Cove	2.40	3.00	0.30	0.25	1.40	1.40	80.5	4.7	75.8	1.280	1.020	1.413	1.067	1.590	21.549	1.756	22.535
San Elijo	1.37	2.33	0.22	0.21	1.32	1.34	93.0	10.5	82.5	1.113	0.800	1.563	1.207	1.197	7.619	1.681	11.492
Blacks	2.50	1.10	0.26	0.22	1.36	1.34	162.0	32.0	130.0	0.960	0.327	1.273	0.620	0.593	1.020	0.786	1.935
Scripps	2.26	1.57	0.23	0.20	1.27	1.30	95.0	16.6	78.4	0.947	0.163	1.993	0.790	0.996	0.986	2.098	4.769
Urban Mean	**2.86**	**3.86**	**0.43**	**0.30**	**1.41**	**1.40**	**139.6**	**89.6**	**50.0**	**0.28**	**0.08**	**0.32**	**0.10**	**0.32**	**0.28**	**0.36**	**0.32**
Urban SE	**0.29**	**0.60**	**0.03**	**0.01**	**0.02**	**0.02**	**30.5**	**28.7**	**2.9**	**0.12**	**0.06**	**0.12**	**0.07**	**0.14**	**0.24**	**0.14**	**0.26**
Carpinteria City	2.21	4.03	0.32	0.22	1.37	1.38	75.0	33.4	41.6	0.160	0.013	0.180	0.013	0.213	0.040	0.240	0.040
Hollywood	3.54	1.50	0.37	0.32	1.35	1.40	175.5	126.0	49.5	0.010	0.010	0.077	0.077	0.006	0.008	0.044	0.061
Westward	3.26	5.60	0.51	0.32	1.43	1.34	95.0	52.9	42.1	0.480	0.040	0.490	0.050	0.505	0.076	0.516	0.095
Santa Monica	1.68	4.10	0.44	0.34	1.37	1.47	297.0	239.7	57.3	0.007	0.003	0.007	0.003	0.002	0.001	0.002	0.001
Redondo	3.76	3.27	0.44	0.33	1.42	1.35	91.3	44.6	46.7	0.867	0.047	0.917	0.057	0.949	0.105	1.004	0.127
Huntington	3.12	2.57	0.42	0.29	1.53	1.36	166.0	103.8	62.2	0.010	0.010	0.077	0.033	0.006	0.010	0.046	0.032
Carlsbad Village	2.45	5.97	0.50	0.32	1.41	1.51	77.3	26.6	50.7	0.453	0.453	0.493	0.493	0.586	1.704	0.638	1.855

Table S3. Macroinvertebrate species list for reference and urban study beaches. Study beaches listed left to right are arranged first by beach type then geographically from north to south. An "X" indicates that the species was present. Taxa identified to lowest taxonomic level with genus and species in italics. Lowest taxonomic level names preceded by an asterisk were included in site species counts but not total species counts. Total community and lower beach and wrack associated macroinvertebrate species counts tallied at the bottom of the table.

						Reference (N = 9)									**Urban (N = 7)**						
Trophic guild	**Phylum**	**Class**	**Order**	**Family**	**Lowest taxonomic level**	**Santa Claus**	**Carpinteria State**	**Arnold Rd.**	**Leo Carrillo**	**Dume Cove**	**Crystal Cove**	**San Elijo**	**Blacks**	**Scripps**	**Carpinteria City**	**Hollywood**	**Westward**	**Santa Monica**	**Redondo**	**Huntington**	**Carlsbad Village**
Lower beach	Annelida	Polychaeta	Eunicida	Lumbrineridae	*Scoletoma zonata*	X	X		X	X	X	X	X	X	X			X			
Lower beach	Annelida	Polychaeta	Eunicida	Oenonidae	*Arabella iricolor*				X	X	X										
Lower beach	Annelida	Polychaeta	Phyllodocida	Glyceridae	*Hemipodia simplex*	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X
Lower beach	Annelida	Polychaeta	Phyllodocida	Nephtyidae	*Nephtys caecoides*							X		X				X			
Lower beach	Annelida	Polychaeta	Phyllodocida	Nephtyidae	*Nephtys californiensis*	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X
Lower beach	Annelida	Polychaeta	Scolecida	Paraonidae	*Paraonella platybranchia*			X	X		X				X	X					
Lower beach	Annelida	Polychaeta	Spionida	Spionidae	*Dispio* sp.	X		X	X			X	X	X		X		X	X		
Lower beach	Annelida	Polychaeta	Spionida	Spionidae	*Pygospio californica*		X								X						
Lower beach	Annelida	Polychaeta	Spionida	Spionidae	*Scolelepis bullibranchia*	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X
Lower beach	Annelida	Polychaeta	Spionida	Spionidae	*Scolelepis squamata*			X		X	X	X									
Lower beach	Annelida	Polychaeta	Terebellida	Cirratulidae	*Cirriformia* sp.						X										
Lower beach	Annelida	Polychaeta		Capitellidae	*Amastagos acutus*		X								X						
Lower beach	Annelida	Polychaeta		Capitellidae	*Capitellidae								X								X
Lower beach	Annelida	Polychaeta		Capitellidae	*Notomastus* sp. D						X										
Lower beach	Annelida	Polychaeta		Opheliidae	*Thoracophelia dillonensis*		X			X			X	X							
Lower beach	Annelida	Polychaeta		Opheliidae	*Thoracophelia mucronata*				X				X	X							
Lower beach	Annelida	Polychaeta		Orbiniidae	*Orbinia johnsoni*									X							
Lower beach	Annelida	Polychaeta		Orbiniidae	*Scoloplos armiger*	X	X		X		X	X	X	X	X			X			
Lower beach	Annelida	Polychaeta		Saccocirridae	*Saccocirrus* sp.												X				
Lower beach	Arthropoda	Malacostraca	Amphipoda	Haustoriidae	*Eohaustorius sawyeri*	X	X	X	X						X						
Lower beach	Arthropoda	Malacostraca	Amphipoda	Haustoriidae	*Eohaustorius washingtonianus*			X			X	X	X	X		X					X
Lower beach	Arthropoda	Malacostraca	Amphipoda	Hyalidae	*Parallorchestes* sp.						X										
Lower beach	Arthropoda	Malacostraca	Amphipoda	Megaluropidae	*Gibberosus devaneyi*								X	X							
Lower beach	Arthropoda	Malacostraca	Amphipoda	Megaluropidae	*Gibberosus myersi*	X		X				X	X								
Lower beach	Arthropoda	Malacostraca	Amphipoda	Oedicerotidae	*Americhelidium* sp.		X	X			X	X	X			X	X		X		
Lower beach	Arthropoda	Malacostraca	Amphipoda	Phoxocephalidae	*Paraphoxus* sp.						X	X	X	X							
Lower beach	Arthropoda	Malacostraca	Amphipoda	Phoxocephalidae	*Mandibulophoxus gilesi*			X			X					X	X				
Lower beach	Arthropoda	Malacostraca	Decapoda	Albuneidae	*Lepidopa californica*	X	X	X	X			X	X	X	X	X		X	X		X
Lower beach	Arthropoda	Malacostraca	Decapoda	Blepharipodidae	*Blepharipoda occidentalis*	X			X			X		X	X	X	X		X		
Lower beach	Arthropoda	Malacostraca	Decapoda	Hippidae	*Emerita analoga*	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X
Lower beach	Arthropoda	Malacostraca	Isopoda	Cirolanidae	*Excirolana chiltoni*	X	X	X				X	X	X	X				X		
Lower beach	Arthropoda	Malacostraca	Isopoda	Cirolanidae	*Excirolana linguifrons*			X	X												
Lower beach	Arthropoda	Malacostraca	Mysida	Mysidacea	*Archaeomysis grebnitzkii*			X					X		X		X				
Lower beach	Arthropoda	Malacostraca	Mysida	Mysidacea	*Archaeomysis maculata*	X	X	X		X			X				X				
Lower beach	Mollusca	Bivalvia	Veneroida	Donacidae	*Donax gouldii*	X	X	X				X	X	X	X	X		X	X		X
Lower beach	Mollusca	Bivalvia	Veneroida	Veneridae	*Tivela stultorum*	X	X	X					X	X	X	X		X			
Lower beach	Mollusca	Gastropoda	Neogastropoda	Olivellidae	*Callianax biplicata*				X			X	X								
Lower beach	Nemertea	Enopla	Monostilifera	Emplectonematidae	*Paranemertes californica*	X	X	X	X		X	X	X	X	X	X					
Lower beach	Nemertea				Unknown Nemertea sp. 1	X			X			X	X	X	X	X		X			X
Lower beach	Nemertea				Unknown Nemertea sp. 2		X		X												
Wrack-associated	Arthropoda	Arachnida	Trombidiformes	Bdellidae	*Neomolgus littoralis*					X											
Wrack-associated	Arthropoda	Insecta	Coleoptera	Carabidae	*Akephorus marinus*			X													
Wrack-associated	Arthropoda	Insecta	Coleoptera	Curculionidae	*Emphyastes fucicola*	X			X	X	X	X	X	X							
Wrack-associated	Arthropoda	Insecta	Coleoptera	Histeridae	*Euspilotus scissus*	X															
Wrack-associated	Arthropoda	Insecta	Coleoptera	Histeridae	*Hypocaccus gaudens*						X			X							
Wrack-associated	Arthropoda	Insecta	Coleoptera	Histeridae	*Neopachylopus aeneipunctatus*	X			X	X				X							
Wrack-associated	Arthropoda	Insecta	Coleoptera	Histeridae	*Neopachylopus sulcifrons*	X	X		X			X									
Wrack-associated	Arthropoda	Insecta	Coleoptera	Hydrophilidae	*Cercyon fimbriatus*	X	X		X		X	X	X	X					X		
Wrack-associated	Arthropoda	Insecta	Coleoptera	Oedemeridae	Oedemeridae			X													
Wrack-associated	Arthropoda	Insecta	Coleoptera	Staphylinidae	*Aleochara sulciollis*		X				X	X	X								
Wrack-associated	Arthropoda	Insecta	Coleoptera	Staphylinidae	*Bledius fenyesi*	X	X		X		X	X		X							
Wrack-associated	Arthropoda	Insecta	Coleoptera	Staphylinidae	*Cafius canescens*		X		X	X				X							
Wrack-associated	Arthropoda	Insecta	Coleoptera	Staphylinidae	*Cafius luteipennis*				X												
Wrack-associated	Arthropoda	Insecta	Coleoptera	Staphylinidae	*Cafius seminitens*		X		X										X		
Wrack-associated	Arthropoda	Insecta	Coleoptera	Staphylinidae	*Cafius sulcicollis*				X												
Wrack-associated	Arthropoda	Insecta	Coleoptera	Staphylinidae	*Pontomalota opaca*				X	X											
Wrack-associated	Arthropoda	Insecta	Coleoptera	Staphylinidae	*Tarphiota geniculata*			X	X	X		X									
Wrack-associated	Arthropoda	Insecta	Coleoptera	Staphylinidae	*Thinopinus pictus*		X		X				X								
Wrack-associated	Arthropoda	Insecta	Coleoptera	Tenebrionidae	*Coelus ciliatus*				X	X		X			X						
Wrack-associated	Arthropoda	Insecta	Coleoptera	Tenebrionidae	*Coelus globosus*					X											
Wrack-associated	Arthropoda	Insecta	Coleoptera	Tenebrionidae	*Epantius obscurus*							X									
Wrack-associated	Arthropoda	Insecta	Coleoptera	Tenebrionidae	*Phaleria rotundata*			X		X	X	X	X	X							
Wrack-associated	Arthropoda	Insecta	Diptera	Anthomyiidae	*Fucellia costalis*				X		X			X							
Wrack-associated	Arthropoda	Insecta	Diptera	Anthomyiidae	*Fucellia rufitibia*	X	X		X	X	X	X	X	X				X	X		
Wrack-associated	Arthropoda	Insecta	Diptera	Coelopidae	*Coelopa vanduzeei*				X							X					
Wrack-associated	Arthropoda	Insecta	Diptera	Empididae	Empididae		X					X	X	X							
Wrack-associated	Arthropoda	Insecta	Diptera	Sphaeroceridae	*Thoracochaeta johnsoni*	X								X		X	X				
Wrack-associated	Arthropoda	Insecta	Hymenoptera	Formicidae	Formicidae				X												
Wrack-associated	Arthropoda	Malacostraca	Amphipoda	Talitridae	*Megalorchestia benedicti*	X	X	X	X	X	X	X	X	X					X		
Wrack-associated	Arthropoda	Malacostraca	Amphipoda	Talitridae	*Megalorchestia californiana*	X			X	X	X	X									
Wrack-associated	Arthropoda	Malacostraca	Amphipoda	Talitridae	*Megalorchestia columbiana*					X											
Wrack-associated	Arthropoda	Malacostraca	Amphipoda	Talitridae	*Megalorchestia corniculata*	X	X				X	X	X	X	X						X
Wrack-associated	Arthropoda	Malacostraca	Amphipoda	Talitridae	*Megalorchestia minor*	X		X	X	X					X	X			X		X
Wrack-associated	Arthropoda	Malacostraca	Isopoda	Alloniscidae	*Alloniscus perconvexus*	X		X	X	X	X										
Wrack-associated	Arthropoda	Malacostraca	Isopoda	Tylidae	*Tylos punctatus*			X	X	X	X		X	X							
					Total intertidal species richness	30	29	28	40	25	30	34	34	35	21	18	11	13	15	4	11
					Lower beach species richness	17	18	20	18	9	17	20	24	21	18	15	10	12	10	4	9
					Wrack-associated species richness	13	11	8	22	16	13	14	10	14	3	3	1	1	5	0	2

Table S4. Results from ISA, CLAM, and SIMPER analyses for A) species and B) families showing ISA classification (reference or urban beaches) type, indicator value (IV), p-value; CLAM classification (reference, urban, generalist, or too rare to classify) type; SIMPER percent contribution to dissimilarity (Contrib.%), and SIMPER cumulative percentage contribution to dissimilarity (Cum.%). Bold text specifies taxa identified across all analytical techniques (ISA: p-value < 0.01, CLAM: Urban or Reference, SIMPER: Cum.% < 50) as indicator taxa, which are included in Table 5 of the manuscript.

A.		Indicator Species Analysis			CLAM	SIMPER	
Trophic assemblage	Species	Classification	IV	*p*-value	Classification	Contrib.%	Cum.%
Lower beach	*Scoletoma zonata*	Reference	70.2	0.01	Generalist	2.5	<50
Lower beach	*Arabella iricolor*	Reference	33.3	0.21	Too rare	0.82	>50
Lower beach	*Hemipodia simplex*	Reference	52	0.29	Urban	0.73	>50
Lower beach	*Nephtys caecoides*	Reference	13.3	0.85	Too rare	0.84	>50
Lower beach	*Nephtys californiensis*	Reference	55.5	0.12	Generalist	1.24	>50
Lower beach	*Paraonella platybranchia*	Reference	20.5	0.63	Too rare	1.35	>50
Lower beach	*Dispio* sp.	Reference	42	0.39	Generalist	2	>50
Lower beach	*Pygospio californica*	Urban	8.3	0.74	Too rare	0.46	>50
Lower beach	*Scolelepis bullibranchia*	Reference	54.5	0.29	Generalist	1.44	>50
Lower beach	*Scolelepis squamata*	Reference	44.4	0.09	Too rare	1.42	>50
Lower beach	*Cirriformia* sp.	Reference	11.1	1.00	Too rare	0.3	>50
Lower beach	*Amastagos acutus*	Urban	7.9	1.00	Too rare	0.78	>50
Lower beach	*Notomastus* sp. D	Reference	11.1	1.00	Too rare	0.4	>50
Lower beach	*Thoracophelia dillonensis*	Reference	44.4	0.09	Too rare	1.52	>50
Lower beach	*Thoracophelia mucronata*	Reference	33.3	0.21	Reference	1.49	>50
Lower beach	*Orbinia johnsoni*	Reference	11.1	1.00	Too rare	0.39	>50
Lower beach	*Scoloplos armiger*	Reference	57.6	0.09	Generalist	2.71	<50
Lower beach	*Saccocirrus* sp.	Urban	14.3	0.44	Too rare	0.46	>50
Lower beach	*Eohaustorius sawyeri*	Reference	35.9	0.19	Generalist	1.78	>50
Lower beach	*Eohaustorius washingtonianus*	Reference	43.9	0.14	Reference	2.11	<50
Lower beach	*Parallorchestes* sp.	Reference	11.1	1.00	Too rare	0.25	>50
Lower beach	*Gibberosus devaneyi*	Reference	22.2	0.47	Too rare	0.49	>50
Lower beach	*Gibberosus myersi*	Reference	44.4	0.09	Too rare	1.23	>50
Lower beach	*Americhelidium* sp.	Reference	33.1	0.46	Too rare	1.31	>50
Lower beach	*Paraphoxus* sp.	Reference	44.4	0.09	Too rare	1.49	>50
Lower beach	*Mandibulophoxus gilesi*	Urban	15	0.93	Generalist	1.21	>50
Lower beach	*Lepidopa californica*	Reference	43.8	0.61	Generalist	1.82	>50
Lower beach	*Blepharipoda occidentalis*	Urban	31.1	0.75	Generalist	1.48	>50
Lower beach	*Emerita analoga*	Reference	53.3	0.01	Generalist	0.84	>50
Lower beach	*Excirolana chiltoni*	Reference	48.5	0.18	Generalist	2.21	<50
Lower beach	*Excirolana linguifrons*	Reference	22.2	0.48	Too rare	0.6	>50
Lower beach	*Archaeomysis grebnitzkii*	Urban	13.2	1.00	Generalist	1.28	>50
Lower beach	*Archaeomysis maculata*	Reference	48.3	0.05	Too rare	1.53	>50
Lower beach	*Donax gouldii*	Reference	39.1	0.71	Generalist	3.02	<50
Lower beach	*Tivela stultorum*	Reference	35.9	0.35	Generalist	2.16	<50
Lower beach	*Callianax biplicata*	Reference	33.3	0.22	Too rare	1.04	>50
Lower beach	*Paranemertes californica*	Reference	71	0.01	Generalist	2.73	<50
Lower beach	Nemertean A	Reference	31.4	0.72	Generalist	1.92	>50
Lower beach	Pink nemertean	Reference	22.2	0.47	Too rare	0.75	>50
Wrack-associated	*Neomolgus littoralis*	Reference	11.1	1.00	Too rare	0.26	>50
Wrack-associated	*Akephorus marinus*	Reference	11.1	1.00	Too rare	0.28	>50
Wrack-associated	*Emphyastes fucicola*	Reference	77.8	<0.01	Too rare	2.32	<50
Wrack-associated	*Euspilotus scissus*	Reference	11.1	1.00	Too rare	0.27	>50
Wrack-associated	*Hypocaccus gaudens*	Reference	22.2	0.47	Too rare	0.62	>50
Wrack-associated	*Neopachylopus aeneipunctatus*	Reference	44.4	0.09	Too rare	1.1	>50
Wrack-associated	*Neopachylopus sulcifrons*	Reference	44.4	0.09	Too rare	1.25	>50
Wrack-associated	*Cercyon fimbriatus*	Reference	68.8	0.01	Too rare	2.08	<50
Wrack-associated	*Oedemeridae*	Reference	11.1	1.00	Too rare	0.28	>50
Wrack-associated	*Aleochara sulciollis*	Reference	44.4	0.09	Too rare	1.23	>50
Wrack-associated	*Bledius fenyesi*	Reference	66.7	0.01	Too rare	2.34	<50
Wrack-associated	*Cafius canescens*	Reference	44.4	0.09	Too rare	1.22	>50
Wrack-associated	*Cafius luteipennis*	Reference	11.1	1.00	Too rare	0.2	>50
Wrack-associated	*Cafius seminitens*	Reference	12.9	1.00	Too rare	0.73	>50
Wrack-associated	*Cafius sulcicollis*	Reference	11.1	1.00	Too rare	0.2	>50
Wrack-associated	*Pontomalota opaca*	Reference	22.2	0.47	Too rare	0.47	>50
Wrack-associated	*Tarphiota geniculata*	Reference	44.4	0.09	Too rare	0.98	>50
Wrack-associated	*Thinopinus pictus*	Reference	33.3	0.21	Too rare	0.84	>50
Wrack-associated	*Coelus ciliatus*	Reference	22.6	0.50	Too rare	1.1	>50
Wrack-associated	*Coelus globosus*	Reference	11.1	1.00	Too rare	0.49	>50
Wrack-associated	*Epantius obscurus*	Reference	11.1	1.00	Too rare	0.24	>50
Wrack-associated	*Phaleria rotundata*	Reference	66.7	0.01	Too rare	2.28	<50
Wrack-associated	*Fucellia costalis*	Reference	33.3	0.21	Too rare	0.95	>50
Wrack-associated	***Fucellia rufitibia***	**Reference**	**73.3**	**0.01**	**Reference**	**3.15**	**<50**
Wrack-associated	*Coelopa vanduzeei*	Reference	6.3	1.00	Too rare	0.69	>50
Wrack-associated	*Empididae*	Reference	44.4	0.09	Too rare	1.12	>50
Wrack-associated	*Thoracochaeta johnsoni*	Urban	14.5	0.94	Too rare	0.99	>50
Wrack-associated	Formicidae	Reference	11.1	1.00	Too rare	0.2	>50
Wrack-associated	***Megalorchestia benedicti***	**Reference**	**91.8**	**<0.01**	**Reference**	**4.44**	**<50**
Wrack-associated	***Megalorchestia californiana***	**Reference**	**55.6**	**0.03**	**Reference**	**2.99**	**<50**
Wrack-associated	*Megalorchestia columbiana*	Reference	11.1	1.00	Too rare	0.48	>50
Wrack-associated	***Megalorchestia corniculata***	**Reference**	**55.4**	**0.05**	**Reference**	**3.33**	**<50**
Wrack-associated	*Megalorchestia minor*	Urban	28.6	0.92	Urban	2.72	<50
Wrack-associated	***Alloniscus perconvexus***	**Reference**	**55.6**	**0.03**	**Reference**	**2.43**	**<50**
Wrack-associated	***Tylos punctatus***	**Reference**	**66.7**	**0.01**	**Reference**	**3.08**	**<50**

B.		Indicator Species Analysis			CLAM	SIMPER	
Trophic assemblage	Family	Classification	IV	*p*-value	Classification	Contrib.%	Cum.%
Lower beach	Lumbrineridae	Reference	70.2	0.02	Generalist	3.51	<50
Lower beach	Oenonidae	Reference	33.3	0.21	Too rare	1.18	>50
Lower beach	Glyceridae	Reference	52	0.30	Urban	1.04	>50
Lower beach	Nephtyidae	Reference	55.5	0.12	Generalist	1.77	>50
Lower beach	Paraonidae	Reference	20.5	0.64	Too rare	1.89	>50
Lower beach	Spionidae	Reference	56.1	0.09	Urban	2.03	>50
Lower beach	Cirratulidae	Reference	11.1	1.00	Too rare	0.41	>50
Lower beach	Capitellidae	Reference	19.5	0.68	Generalist	1.95	>50
Lower beach	Opheliidae	Reference	55.6	0.03	Reference	3.11	>50
Lower beach	Orbiniidae	Reference	57.9	0.08	Generalist	3.85	<50
Lower beach	Saccocirridae	Urban	14.3	0.43	Too rare	0.65	>50
Lower beach	**Haustoriidae**	**Reference**	**69.7**	**0.02**	**Reference**	**4.06**	**<50**
Lower beach	Hyalidae	Reference	11.1	1.00	Too rare	0.34	>50
Lower beach	Megaluropidae	Reference	55.6	0.03	Too rare	2.08	>50
Lower beach	Oedicerotidae	Reference	33.1	0.45	Too rare	1.82	>50
Lower beach	Phoxocephalidae	Reference	40	0.13	Generalist	2.69	>50
Lower beach	Albuneidae	Reference	43.8	0.61	Generalist	2.54	>50
Lower beach	Blepharipodidae	Urban	31.1	0.76	Generalist	2.08	>50
Lower beach	Hippidae	Reference	53.3	0.01	Generalist	1.19	>50
Lower beach	Cirolanidae	Reference	58.1	0.08	Generalist	3.23	>50
Lower beach	Mysidacea	Reference	37.9	0.28	Generalist	2.46	>50
Lower beach	Donacidae	Reference	39.1	0.71	Generalist	4.22	<50
Lower beach	Veneridae	Reference	35.9	0.36	Generalist	2.98	>50
Lower beach	Olivellidae	Reference	33.3	0.21	Too rare	1.51	>50
Lower beach	Emplectonematidae	Reference	71	0.01	Generalist	3.8	<50
Lower beach	Nemertea	Reference	40.7	0.45	Generalist	2.88	>50
Wrack-associated	Bdellidae	Reference	11.1	1.00	Too rare	0.39	>50
Wrack-associated	Carabidae	Reference	11.1	1.00	Too rare	0.38	>50
Wrack-associated	Curculionidae	Reference	77.8	0.00	Too rare	3.3	>50
Wrack-associated	Histeridae	Reference	77.8	0.01	Too rare	3.3	<50
Wrack-associated	Hydrophilidae	Reference	68.8	0.02	Too rare	2.91	>50
Wrack-associated	Oedemeridae	Reference	11.1	1.00	Too rare	0.38	>50
Wrack-associated	Staphylinidae	Reference	90.5	<0.01	Generalist	4.49	<50
Wrack-associated	Tenebrionidae	Reference	67	0.02	Generalist	3.57	<50
Wrack-associated	**Anthomyiidae**	**Reference**	**73.4**	**0.01**	**Reference**	**4.45**	**<50**
Wrack-associated	Coelopidae	Reference	6.3	1.00	Too rare	1	>50
Wrack-associated	Empididae	Reference	44.4	0.09	Too rare	1.53	>50
Wrack-associated	Sphaeroceridae	Urban	14.5	0.93	Too rare	1.37	>50
Wrack-associated	Formicidae	Reference	11.1	1.00	Too rare	0.31	>50
Wrack-associated	Talitridae	Reference	71.5	<0.01	Generalist	5.51	<50
Wrack-associated	**Alloniscidae**	**Reference**	**55.6**	**0.03**	**Unmanaged**	**3.48**	**<50**
Wrack-associated	**Tylidae**	**Reference**	**66.7**	**0.01**	**Unmanaged**	**4.35**	**<50**

Chapter IV. Biogeographic patterns and drivers of intertidal macroinvertebrate communities of sandy beaches on the northeastern Pacific coast

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Abstract

Biogeographic patterns are often used as a foundation for spatially explicit conservation strategies across diverse ecosystems. We evaluated the congruence of existing biogeographic patterns for a threatened coastal ecosystem by investigating spatial patterns in biodiversity, structure, and composition, as well as the role of environmental factors in organizing intertidal macroinvertebrates of sandy beach ecosystems (35 beaches) spanning the coast of California, USA. The high biodiversity we found suggests that sandy beaches of central and southern California may represent a global biodiversity hotspot for intertidal macroinvertebrates. Our results showed strong patterns in the biodiversity, structure, and composition of intertidal macroinvertebrates across >1800 km of temperate zone shoreline (~9º latitude) in California. Although species richness declined with latitude across the study region, when we incorporated data on species richness from a wider latitudinal extent (>40º latitude including tropics) of northeastern Pacific beaches in our comparisons, peak species

richness occurred in the temperate zone of southern California. Our results for intertidal fauna of northeast Pacific beaches were not consistent with the well-known pattern of a negative trend in species richness with latitude reported for a wide range of ecosystems and taxa. However, our results are consistent with latitudinal patterns for a major subsidy source to beaches – marine macroalgae. The assembly of intertidal macroinvertebrate communities of sandy beaches and of the two major trophic guilds, lower beach and wrack-associated species, were generally congruent with existing biogeographic units for marine coastal ecosystems across a range of spatial scales (e.g. provinces, ecoregions, bioregions, littoral cells) in most comparisons. Sea surface temperature, a strong predictor of marine biogeographic structure across a wide range of taxa and ecosystems, explained the highest percentage of the variance (>20%) in the assembly of intertidal macroinvertebrates of beaches, including both trophic guilds. The distinctive functional, trophic, and life history traits characteristic of intertidal trophic guilds on sandy beaches may underlie the observed differences in biogeographic patterns and structure compared with other marine coastal communities and ecosystems. Our results for sandy beach ecosystems revealed the importance of connectivity to donor ecosystems and the strong influence of trophic subsidies, particularly drift macroalgae for wrack-associated species, in biodiversity and structure of recipient communities, a topic rarely considered in biogeographic analyses. These results highlight the need to investigate a wide range of ecosystems, taxa, and processes at sufficient spatial scales in order to assess the efficacy of using biogeographic information for conservation and management purposes.

Introduction

Quantitative predictions of the responses of ecological communities to changes in the environment at different spatial scales (Pielou 1979, Attwood et al 1997) are needed to inform conservation and management strategies. Biogeographic information and patterns such as the distribution of biodiversity have served as a key foundation for conservation efforts in terrestrial and aquatic ecosystems (Lourie & Vincent 2004, Whittaker et al 2005, Noss et al 2012). The hundreds of distinct biogeographic units (realms, provinces, regions) identified to date using a broad array of information (e.g. species distributions, geomorphological features, temperature) from a range of terrestrial (Olson et al 2001), freshwater (Abell et al 2008), and coastal marine (Spalding et al 2007) ecosystems underpin much of our current understanding of ecological responses to environmental changes as well as current conservation approaches. Identifying relevant biogeographic patterns at the spatial scales necessary for conservation requires detailed information that is difficult and labor intensive to obtain. This often limits the scope and utility of available biogeographic information for developing comprehensive strategies for the conservation and management of diverse ecosystems. As a consequence, the application of existing biogeographic data to conservation may lead to inaccurate representation of patterns and inadequate protection of the many ecosystems for which such information is limited or lacking (Whittaker et al 2005, Riddle et al 2011, Hortal et al 2015).

Situated at the edge of land and sea, marine intertidal ecosystems are threatened by climatic and human impacts (Harley et al 2006). Using biogeographic patterns to inform the conservation of these vulnerable ecosystems requires understanding how these patterns vary across the entire range of intertidal ecosystems, including rocky and soft sediment shores.

Evaluating the efficacy of broadly applying existing biogeographic information across taxa and ecosystems helps to identify areas where refinement is needed and conservation efforts may be underperforming (Costello et al 2017).

In general, existing biogeographic patterns for many marine ecosystems appear to be relatively consistent across taxa and ecosystems and can be generally predicted by a few oceanographic variables such as sea surface temperature (SST) (Spalding et al 2007, Belanger et al 2012). However, differences in the range of functional, trophic, and life history traits present among communities may strongly affect those basic patterns (e.g. Claudet et al 2010, Williams et al 2010, Violle et al 2014). Biogeographic patterns for widespread but understudied intertidal ecosystems may not fit into existing schema, especially for sandy beaches that support a suite of endemic taxa with particular functional and life history attributes (McLachlan & Brown 2006). For example, the classical pattern of a negative association between richness and latitude has been shown to apply across a wide range of ecosystems and taxa (Willig et al 2003). However, global analyses have generated contrasting results about latitudinal gradients in species richness for sandy beach ecosystems (Dexter 1992, Defeo & McLachlan 2013).

Unlike rocky and muddy shores, sandy beaches are characterized by low *in situ* primary production and food webs supported by imported organic matter (McLachlan & Brown 2006). In temperate latitudes, intertidal macroinvertebrate communities of beaches are made up of two actively mobile trophic guilds, lower beach and wrack-associated species, that depend on subsidies from adjacent marine ecosystems, including phytoplankton and drift macroalgae (wrack) (Dugan et al 2003, Liebowitz et al 2016, Morgan et al 2018). Biodiversity decreases with latitude and peaks in the tropics for the majority of marine and terrestrial taxa (Gaston 2000, Willig et al 2003). However, one of the major sources of trophic subsidies to sandy beaches, marine benthic macroalgae, exhibit peaks in biodiversity and biomass in temperate latitudes (Kerswell 2006). For temperate northeastern Pacific sandy beaches, up to 40% of intertidal macroinvertebrate species are strongly associated with drift macroalgae (Dugan et al 2003, Schooler et al 2017). The strong influence of macroalgal subsidies on intertidal structure and composition of these wrack-associated macroinvertebrates and the wildlife they support (e.g. shorebirds) has been demonstrated in a number of studies of beaches (Dugan et al 2003, Hubbard & Dugan 2003, Ince et al 2007, Schooler et al 2017). For these reasons, we hypothesized that macroalgal subsidies strongly influence biogeographic patterns in sandy beach communities.

Importantly, a relatively high proportion of the endemic macroinvertebrate species of sandy beaches are direct developing taxa with limited scope for long-distance dispersal compared to other marine ecosystems where the dispersal of young can be enormous compared to terrestrial ecosystems (Grantham et al 2003, Kinlan & Gaines 2003). These biota (e.g. peracarid crustaceans, insects) lack planktonic larval stages and depend largely on the reproduction of local resident populations. This suite of life history traits, particularly for the wrack-associated species, make them especially vulnerable to habitat loss, degradation, and alteration and in need of additional conservation efforts (Dugan et al 2003, Defeo et al 2009, Hubbard et al 2014, Schooler et al 2017). We suggest that the suite of life history traits of these specialized intertidal biota could potentially lead to greater isolation among populations resulting in higher spatial variability in the assembly of macroinvertebrate communities on sandy beaches than found in other coastal marine ecosystems. Evaluating the distributions of these types of taxa could also provide needed information on the role of dispersal in shaping biogeographic patterns.

Examining general ecological theories, patterns, and paradigms across a wide range of biota and ecosystems can provide new insights on their overall applicability. The unique nature of sandy beaches and their endemic intertidal fauna make this an ideal ecosystem for investigating the relevance of existing ecological principles (Schlacher et al 2015). The importance of material connectivity to donor ecosystems, such as kelp forests and seagrass beds, for sandy beaches (Dugan et al 2003, Liebowitz et al 2016), adds an important additional level of complexity that is rarely addressed in biogeographic analyses or conservation approaches.

To describe overall biodiversity patterns and evaluate the relevance of biogeographic patterns and environmental drivers for intertidal macroinvertebrate communities of open coast sandy beaches, we surveyed 35 beaches spanning the coast of California, USA. Our surveys provided the first quality baseline biogeographic scale data on sandy beaches for the northeastern Pacific region and represents the first large-scale study of the intertidal community ecology of sandy beach ecosystems of the entire California coast spanning >1800 km and nine degrees of latitude. We used a range of spatial scales (e.g. local, landscape, regional) to assess how our results for sandy beaches compared to existing coastal biogeographic, latitudinal, and landscape patterns for the region and the world. We examined predictions that variability in the biogeographic structure and composition 1) among coastal marine ecosystems and 2) between trophic guilds (lower beach and wrack-associated) of sandy beach ecosystems could arise from differences in functional, trophic, and life history traits of the biota and the relative influence of ocean and land-based environmental factors. We specifically evaluated the hypothesis that subsidies from donor ecosystems, particularly the supply of drift macroalgae, could strongly influence biogeographic patterns in macroinvertebrates of sandy beaches in the northeastern Pacific.

Methods

Study area

The >1800 km of open coast shoreline we studied is dominated by sandy beach habitat (sandy beach: 45.8%, rocky intertidal: 33.4%, California MLPA Initiative, 2009). We quantitatively surveyed intertidal biota of 35 open coast sandy beaches extending from 41°58’20” N, 124°12’20” W (Clifford Kamph Memorial Park) to 32°51’49 N, 117°15’16” W (Scripps Institution of Oceanography) over a six-year period from 2009 to 2015 (Fig. 1, Table 1). For the majority (68%) of the study beaches, these were the first quantitative full community macroinvertebrate surveys ever conducted. Our intertidal surveys were part of a major baseline monitoring program for a statewide network of Marine Protected Areas (MPAs – https://www.wildlife.ca.gov/conservation/marine/mpas/network). Fifteen of our study beaches are located within an MPA (Table 1). All study beaches are > 1 km in length, largely influenced by natural coastal processes, and not subject to locally intensive anthropogenic activities (e.g. sediment fills, grooming, armoring, recreational off-road vehicle use). All beaches were surveyed at least once during the study. For the subset of beaches surveyed multiple times during the study period, we selected the survey with the same sampling method and effort as other beaches (3.5 m^2) and highest species richness for use in our analyses.

The 35 study beach locations span two major marine biogeographic provinces, three ecoregions, four biogeographic regions (hereafter bioregions), and 25 littoral cells. The two biogeographic provinces, the Cold Temperate Northeast Pacific (NEP) or Oregonian province (18 beaches) and the Warm Temperate NEP or Californian province (17 beaches), are divided by biological and physical characteristics at Point Conception (Valentine 1966, Briggs 1974, Spalding et al 2007) (Fig. 1, Table 1). Nested within the two major marine biogeographic provinces are three marine ecoregions (Spalding et al 2007) and four marine bioregions (Hall 1960, 1964, Valentine 1966, Blanchette et al 2008). Within the Cold Temperate NEP province, our study beaches are distributed across two ecoregions divided at Cape Mendocino (Fig. 1, Table 1). These include six beaches in the Oregon, Washington, & Vancouver Coast and Shelf (hereafter OR, WA, & Vancouver) ecoregion and 12 beaches in the Northern California ecoregion (Fig. 1, Table 1). The two bioregions in the Cold Temperate NEP, Mendocinian (14 beaches) and Montereyan (4 beaches), are divided at Monterey Bay (Fig. 1, Table 1). For the Warm Temperate NEP province our study beaches are distributed in one ecoregion (Southern California Bight: 17 beaches) and two bioregions (Southern Californian: 11 beaches and Ensenadian: 6 beaches divided at Santa Monica Bay) (Fig. 1, Table 1). The California coast can also be divided into 25 distinct self-contained compartments called littoral cells that consist of a series of sediment sources, longshore transport, and sinks (Habel & Armstrong 1978, Patsch & Griggs 2006). We surveyed beaches in 13 of the 25 major littoral cells in California: nine beaches in the Santa Barbara cell, five beaches in the Oceanside cell, one beach in the Laguna cell, and two beaches in each of the remaining ten littoral cells (Fig. 1, Table 1).

Beach surveys

We surveyed the study beaches during daytime spring low tides once in the summer or fall (July to November). We measured abundance and diversity of macroinvertebrates, standing stock and composition of wrack, and the physical characteristics of each beach using the methods employed by Dugan et al (2003) and Schooler et al (*Chapter III*). At each beach, we established three shore-normal transects that extended from the landward boundary of the beach to the low swash zone at the time of low tide. The distances between these transects were randomly selected, but we allowed at least a 10 m buffer between transects to minimize any disturbance of the lower beach mobile fauna in adjacent transects.

To estimate intertidal macroinvertebrate biodiversity and community structure, we collected 150 evenly spaced cores (10 cm diameter and to a depth of 20 cm) per transect and sieved the contents through mesh bags with 1.5 mm aperture. This yielded a total sampling area of 3.5 m^2 per study site. The samples from each transect were pooled and 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 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 & Brown 2006).

We measured the cover and composition of wrack using a line-intercept method on the same three transects sampled for macroinvertebrates. The width of all macrophyte wrack (kelp, algae, surfgrass), debris, wood, trash, and tar that intersected the transect line was measured, categorized, recorded, and expressed as m^2 of wrack per meter of beach.

We measured intertidal zone widths from the landward boundary to low swash for each transect. We also measured a number of other environmental factors that have been shown to influence macroinvertebrate community structure (McLachlan et al 1993, 1996) including sand grain size, wave height, wave period, and beach slope at the water table outcrop

(WTO) for each transect. We collected sand samples for grain size analysis at the 24 h high tide strandline (HTS) and the WTO on each transect. Sand samples were rinsed with fresh water, dried, and measured using graded sieves in the laboratory. We calculated the geometric method of moments mean (mean grain size) and standard deviation (sediment sorting) of the distribution of sediment for each sand sample using the R package *G2Sd* (Gallon & Fournier, 2013).

We compiled additional data on five environmental variables for each study beach. We measured beach length as the sandy shoreline distance between two boundaries (e.g. headland, estuary, or river) and beach orientation as compass degrees of the shore-normal line (0°/360° = North) in Google Earth. We extracted remotely sensed oceanographic data on SST, chlorophyll concentration, and salinity averaged monthly from 2000 to 2014 for each study beach. Annual SST, chlorophyll concentration, and salinity at a 0.08° resolution were accessed from Bio-ORACLE v2 (http://bio-oracle.org/) (Assis et al 2017) and extracted using the R packages *raster* and *rgdal*.

Data analyses

To evaluate hypotheses concerning the response of diversity and key functional groups and the relative importance of different environmental factors in structuring community assemblages on sandy beaches, we divided our data into three groups: the total intertidal macroinvertebrate community (hereon referred to as total community) and two trophic guilds. The two trophic guilds, the lower beach and wrack-associated macroinvertebrate groups described in Schooler et al (*Chapter III*), differ in functional, trophic, and life history traits as well as intertidal location. All taxa (including predatory taxa) from the total intertidal community were assigned to one of these two guilds. Species that do not normally inhabit beaches or are considered parasitic were excluded from our analyses. For each group of intertidal macroinvertebrates, we calculated the mean values of abundance and biomass per meter ± standard error (SE) across the three transects for each study beach. Cumulative species richness was calculated and pooled across the three transects for each beach and trophic guild.

In addition to wrack type (e.g. *Macrocystis*, *Phyllospadix*, wood), measurements of wrack were grouped into two larger categories – macroalgal (kelp and algae) and total (all macrophyte wrack and debris except tar and terrestrial vegetation) wrack. Macroalgal wrack is an important food source for upper intertidal wrack-associated macroinvertebrates and provides shelter. Total wrack includes additional types of wrack that provide shelter but are not consumed by macroinvertebrates of sandy beaches (e.g. wood). Values for mean (± SE) cover of wrack were calculated for the three transects for each site. The following physical characteristics were averaged (± SE) across the three transects at each site: total beach width, WTO slope, and mean grain sizes and sediment sorting at the WTO and HTS. Dean's parameter (Ω), which is used to characterize beaches by morphodynamic state, was calculated from breaker height divided by the breaker period and sand fall velocity (Short & Wright 1983). Beaches can be categorized into three types based on this morphodynamic state parameter: reflective ($\Omega < 1$), intermediate ($1 < \Omega < 6$), and dissipative ($\Omega > 6$) (Short & Wright 1983). In global scale comparisons, beaches with higher values of Dean's parameter (more dissipative) have been associated with higher species richness and abundance (McLachlan 1990, Barboza & Defeo 2015).

We explored latitudinal gradients in biotic (community richness, abundance, and biomass) and abiotic (environmental factors) factors using non-parametric Spearman's rank correlation (ρ). The high density of study beaches in the Santa Barbara littoral cell (change in longitude >> change in latitude; see Fig. 1) precluded the use of OLS linear regression by violating key assumptions (e.g. normality).

We used multivariate analyses to evaluate the null hypothesis that the total community and the lower beach and wrack-associated macroinvertebrate assemblages did not differ across biogeographic units (provinces, ecoregions, bioregions) or littoral cells. Abundance and wet biomass data were averaged across the three transects for each beach and grouped by biogeographic unit and littoral cell for these analyses. Macroinvertebrate community assemblage patterns were analyzed using multivariate routines in the statistical software package PRIMER 6 (Clark & 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. Transformed data were then used to compute Bray-Curtis similarity matrices. All environmental factors except for SST were log (x+1) transformed to reduce skewness.

To examine assemblage patterns and how they may relate to previously described biogeographic units and littoral cells, we employed unconstrained non-metric multidimensional scaling ordination (nMDS). We used a one-factor permutational multivariate analysis of variance (PERMANOVA) to test for significant differences across provinces, ecoregions, bioregions, and littoral cells (Anderson 2001). We made direct pairwise comparisons between provinces, ecoregions, and bioregions by testing for significant differences in community assemblages using analysis of similarity (ANOSIM) (Clarke & Warwick 1994).

To compare beta diversity as turnover (the rate of change in community assembly along a gradient of distance alongshore) between lower beach and wrack-associated assemblages, we constructed distance-decay of similarity plots (as in Nekola & White 1999) by plotting the alongshore distance and log transformed similarity for every pairwise comparison of study beaches ($n = 595$). Similarity in community assembly was computed using Bray-Curtis similarity matrices derived from the transformed composition and abundance data. We fitted a line to each plot using OSL regression and compared the slopes for the lower beach and wrack-associated assemblages using *ANCOVA* in R. For comparisons between groups of taxa, a steeper slope is indicative of higher biogeographic structuring (Soininen et al 2007).

To explore the influence of the fourteen environmental factors (Table S1) on intertidal community assembly, we employed a nonparametric multivariate regression model (DistLM) using Bray-Curtis similarity matrices derived from the transformed composition and abundance or biomass data. We used a *step-wise* selection procedure and *AIC* selection criterion (9,999 permutations) to identify the environmental factors that significantly predicted variance in the data clouds for the total community and the lower beach and wrack-associated macroinvertebrates across all study beaches.

To better evaluate the pure contribution of the environmental factors independent of spatial patterns, we used a method of variance partitioning. This method controls for inflated type I errors in assessing the environmental components under spatial autocorrelations by computing the adjusted R^2 values for each partition (Borcard et al 1992). Each environmental factor can be broken down into the following four non-overlapping partitions: the pure environmental variable independent of spatial structure ([*env*]), the environmental influence that cannot be uncoupled from the spatial component ([*env+space*]), the pure spatial component that is independent of the environment ([*space*]), and the residuals that are unexplained by space or the environment ([*residual*]) (Borcard et al 1992). Variance partitioning is generally based on partial redundancy analysis (RDA), so to make variance partitioning analogous to the distance-based models we built using DistLM, we based the partitioning on distance-based redundancy analysis (dbRDA) instead of RDA. To do this, we retransformed a Bray Curtis distance matrix (derived from the transformed composition and abundance or biomass data) into a rectangular object by performing a principal coordinates analysis (PCoA) using the R package *ade4* (Dray & Dufour 2007) then extracted the retransformed distance matrix. To calculate the adjusted R^2 values for each partition of each environmental variable, we used the function *varpart* in the R package *vegan* (Oksanen et al 2007) using the retransformed compositional data, transformed environmental data, and spatial data (site coordinates). To test the significance of the influence of the independent partitions on community assembly, we used the function *anova* in R.

Results

Biodiversity and structure

A total of 130 macroinvertebrate taxa ($\overline{x}$ = 27.3 ± 1.6 SE species per site; *n* = 35) were recorded in our quantitative beach surveys (Table S2). For the total macroinvertebrate community, species richness was dominated by insects (35%), crustaceans (27%), and polychaetes (26%) with mollusks, nemerteans, and arachnids making up the remaining 12% of the taxa (Table S2). The sand crab, *Emerita analoga*, and at least one of the six species of talitrid amphipods, *Megalorchestia* spp. ($\overline{x}$ = 2.4 ± 0.2 SE species per site; range = 1 – 4 species), were recorded at every study beach (Table S2).

Clear spatial patterns in intertidal macroinvertebrate species richness, abundance, and biomass were detected across >1800 km of coastland and ~9° of latitude. The total number of species decreased significantly with latitude ($\rho = -0.46$, $P = 0.006$, $n = 35$) (Fig. 2). Total species richness ranged more than fourfold across the study region from 11 to 49 species (Fig. 3, Table S3), the latter being the most macroinvertebrate species ever recorded for a single open coast sandy beach survey (Defeo & McLachlan 2013, Harris et al 2014, Barboza & Defeo 2015, Schooler et al 2017, *Chapter III*). The majority (51%) of species observed in our surveys were only recorded from study beaches north (36 species) or study beaches south (30 species) of Point Conception. The two major groups, lower beach ($\overline{x} = 16.5 \pm 0.9$ SE species per site; $n = 35$; range = 4 – 26 species) and wrack-associated ($\overline{x} = 10.8 \pm 1.0$ SE species per site; $n = 35$; range = 2 – 26 species) species, represented 55% (72 species) and 45% (58 species) of the total species, respectively (Table S2). Species richness for the lower beach ($\rho = -0.27$, $P = 0.11$, $n = 35$) and wrack-associated ($\rho = -0.38$, $P = 0.02$, $n = 35$) assemblages were negatively correlated with latitude, but the correlation was only significant for wrack-associated species (Fig. 2).

Large-scale latitudinal patterns in intertidal abundance of macroinvertebrates were evident only for the wrack-associated assemblage, which varied over two orders of magnitude ($\overline{x} = 13{,}636 \pm 3{,}768$ SE individuals m^{-1}; $n = 35$; range = 274 – 103,090 individuals m^{-1}) and declined significantly with latitude ($\rho = -0.55$, $P = 0.001$, $n = 35$) (Fig. 2). Abundance of the total community ($\overline{x} = 61{,}776 \pm 11{,}664$ SE individuals m^{-1}; $n = 35$; range = 2,408 – 320,915 individuals m^{-1}) and lower beach macroinvertebrates ($\overline{x} = 48{,}140 \pm 9{,}993$ SE individuals m^{-1}; $n = 35$; range = 365 – 280,048 individuals m^{-1}) also varied more than two orders of magnitude across the study coast but did not exhibit significant trends with latitude (Table S3; Fig. 4).

Lower beach and wrack-associated macroinvertebrates represented 78% and 22% of the total community abundance, respectively, and the abundance of wrack-associated macroinvertebrates exceeded that of lower beach macroinvertebrates for eight (23%) of the study beaches (Table S3; Fig. 4). The most abundant taxa belonging to each of the two trophic guilds were the sand crab, *E. analoga* (lower beach: 35%, total: 27%), and talitrid amphipods, *Megalorchestia* spp. (wrack-associated: 79%, total: 18%) (Fig. S1).

Strong latitudinal patterns were also evident in intertidal biomass. Biomass increased significantly with latitude for the total community ($\rho = 0.37$, $P = 0.03$, $n = 35$) and the lower beach assemblage ($\rho = 0.38$, $P = 0.03$, $n = 35$). Total biomass varied more than two orders of magnitude across the study region from 0.3 kg m^{-1} to 82.9 kg m^{-1} ($\bar{x} = 10.9 \pm 2.9$ SE kg m^{-1}; $n = 35$) (Table S3; Fig. 4). The lower beach sand crab, *E. analoga*, was the major component of sandy beach biomass, representing >75% of total community (77%) and lower beach macroinvertebrate (78%) biomass (Fig. S1). Biomass of the wrack-associated assemblage, which represented only 2% of the total intertidal biomass, decreased significantly with latitude ($\rho = -0.48$, $P = 0.004$, $n = 35$) and also varied over two orders of magnitude across the study area ($\bar{x} = 0.2 \pm 0.1$ SE kg m^{-1}; $n = 35$; range = 0.006 – 1.7 kg m^{-1}) (Table S3; Figs. 2 & 4).

Multivariate analyses of community composition and structure

Patterns in community similarity across the study region and within biogeographic units (province, ecoregion, and bioregion) and littoral cells generated by non-metric multidimensional scaling (nMDS) revealed large-scale spatial patterns that were similar to those based on abundance and biomass composition data for the total intertidal, lower beach, and wrack-associated assemblages (Fig. 5). These latitudinal patterns are apparent in the nMDS plots from north (left) to south (right) (Fig. 5). Overall, study beaches belonging to the same province, ecoregion (not grouped by symbol or color in figure), bioregion, or littoral cell clustered closely in nMDS plots with only a few exceptions (e.g. Ross Cove, Salmon Creek South, Montara, Dume Cove, and San Clemente). Those clusters differed significantly (PERMANOVA, $P \leq 0.0001$) in community assembly across provinces, ecoregions, bioregions, and littoral cells (Fig. 5).

The intertidal communities and assemblages of biogeographic provinces, ecoregions, and bioregions located north and south of Point Conception differed significantly in direct pairwise comparisons (Table 2). The intertidal communities of the largest biogeographic units we tested, the Cold and Warm Temperate Northeast Pacific (NEP) provinces differed significantly ($P = \leq 0.001$) (Table 2, Fig. 5). For comparisons between ecoregions, the intertidal communities of the Southern California Bight (= Warm Temperate NEP province in California) differed significantly ($P \leq 0.001$) from all others for all pairwise comparisons (Table 2, Fig. 5). We did not detect significant differences (ANOSIM, $P > 0.05$) in intertidal community assembly between the two ecoregions located in the Cold Temperate NEP province (includes OR, WA, & Vancouver and Northern California ecoregions) with the exception of the wrack-associated assemblage abundance-based composition data (Table 2). The intertidal community assembly of the Mendocinian bioregion differed significantly ($P \leq 0.05$) from that of all other bioregions including the Montereyan bioregion, which spans the coast from Monterey Bay to Point Conception. There were no significant ($P > 0.05$) differences in intertidal community assembly between the Southern Californian and

Ensenadian bioregions (= Warm Temperate NEP province in California) both located south of Point Conception (Table 2). We also did not detect significant ($P > 0.05$) differences between Montereyan (north of Point Conception) and Southern Californian (south of Point Conception) bioregions for the total community and lower beach assemblage composition and biomass (Table 2).

Beta diversity (expressed as turnover), estimated by the rate of change in community assembly along a gradient of distance alongshore, was greater for wrack-associated than lower beach assemblages. Community similarity (log transformed) and alongshore distance were significantly correlated for both lower beach ($r^2 = 0.17$, $P < 0.0001$) and wrack-associated ($r^2 = 0.30$, $P < 0.0001$) assemblages (Fig. 6). The slopes of those regressions differed significantly (ANCOVA, $F = 112.7$, $P < 0.0001$) with a steeper slope indicating a much shorter "halving distance" for the wrack-associated (1244 km) compared with the lower beach (4395 km) assemblage (Fig. 6). The intercept of the regressions also differed significantly and the initial similarity (small-scale beta diversity) was lower for the wrack-associated (1.66) than lower beach (1.68) assemblages.

Beach characteristics

We observed large-scale spatial patterns across the study region for more than half of the 14 environmental factors. In global scale comparisons, beaches with higher values of Dean's parameter (more dissipative morphodynamic type) have been associated with higher species richness and abundance (McLachlan 1990, Barboza & Defeo 2015). At the time of the surveys, observed values for Dean's parameter (Ω) ranged from 0.3 to 7.2 ($\bar{x} = 2.7 \pm 0.3$ SE; $n = 35$) and increased significantly with latitude ($\rho = 0.51$, $P = 0.002$, $n = 35$) (Table S3; Fig. 7). However, the majority of study beaches (91%) surveyed were of intermediate morphodynamic type ($1 \leq \Omega \leq 6$), with the exceptions of two reflective beaches (Ross Cove and Coal Oil Point; $\Omega < 1$) and one dissipative beach (Samoa Dunes; $\Omega > 6$) (Short & Wright 1983) (Table S3). Beach slope at the WTO (steepest on reflective beaches), a conservative estimate of beach morphodynamic type (Barboza & Defeo, 2015), was negatively correlated with latitude, though the relationship was not significant ($\rho = 0.51$, $P = 0.08$, $n = 35$) (Fig. 7).

Intertidal sediment characteristics (mean grain size and sediment sorting) were not correlated with latitude (Fig. 7) and ranged from fine (125 µm) to coarse (1000 µm) sand and well sorted (< 1.27 µm SD) to poorly sorted (2 – 4 µm SD) (Gallon & Fournier, 2013) across the study beaches (Table S3). Values for mean grain size were larger at the HTS ($\overline{x} = 319 \pm 18$ SE µm; $n = 35$) than the WTO level ($\overline{x} = 308 \pm 30$ SE µm; $n = 35$) for 70% of the study beaches. Grain size varied more than threefold (HTS: range = 182 – 654 µm) and fivefold (WTO: range = 174 – 899 µm), respectively across the study beaches. (Table S3; Fig. 7). Mean values for sediment sorting were similar at the HTS ($\overline{x} = 1.4 \pm 0.02$ SE µm SD; range = 1.2 – 1.8 µm SD; $n = 35$) and WTO ($\overline{x} = 1.5 \pm 0.06$ SE µm SD; range = 1.2 – 3.3 µm SD; $n = 35$) except for two study beaches (Tolowa Dunes and San Clemente) with poorly sorted sediment at the WTO (Table S3; Fig. 7).

Observed intertidal beach widths ($\overline{x} = 106 \pm 8$ SE m; range = 26 – 218 m; $n = 35$) varied over eightfold across the study beaches and increased significantly with latitude ($\rho = 0.49$, $P = 0.003$, $n = 35$) (Table S3; Fig. 7). Alongshore beach length was 21 km (± 4 SE km) on average and ranged from 1 km to 75 km with the longest beach lengths found south of Point Conception at the western edge of the Santa Barbara littoral cell (six study beaches) (Table S3; Fig. 7). Beach orientation was also significantly correlated with latitude ($\rho = 0.48$, $P =$

0.003, $n = 35$) with west facing beaches primarily located in the north and south facing beaches in the Santa Barbara littoral cell (Fig. 1). The majority of study beaches (89%) faced west (17 beaches; 47.5° – 292.5°), southwest (7 beaches; 202.5° – 247.5°), or south (7 beaches; 157.5° – 202.5°) (Table S3; Fig. 7). Of the remaining four study beaches, one faced east, two southeast, and one northwest (Table S3; Fig. 7).

Macroalgal wrack cover declined significantly with increasing latitude ($\rho = -0.63$, $P < 0.001$, $n = 35$), but total marine wrack cover was not correlated with latitude ($\rho = 0.054$, $P = 0.76$, $n = 35$) (Fig. 7). Macroalgal wrack cover was positively correlated with the number of species ($r^2 = 0.38$, $P < 0.001$, $n = 35$), abundance ($r^2 = 0.43$, $P < 0.001$, $n = 35$), and biomass ($r^2 = 0.52$, $P < 0.001$, $n = 35$) of wrack-associated species (Fig. 8). When recorded in our surveys, macroalgal (range: 0.001 – 15.4 $m^2\ m^{-1}$) and total (range: 0.03 – 17.3 $m^2\ m^{-1}$) marine wrack cover varied over six and two orders of magnitude, respectively (Table S3). The composition of stranded marine macroalgal wrack cover, an important food source for upper intertidal wrack-associated macroinvertebrates, shifted from south to north. Wrack was dominated by the kelps *Macrocystis pyrifera* and *Egregia menziesii* in the south and by *E. menziesii, Nereocystis luetkeana*, and *Postelsia palmaeformis* in the north. We did not measure *M. pyrifera* on study beaches north of Monterey Bay. By contrast, *N. luetkeana* and *P. palmaeformis*, which were only reported north of Point Conception, were restricted primarily to the study beaches in the Mendocinian bioregion.

The suite of oceanographic environmental factors we analyzed varied strongly with latitude. Monthly averages (15 years) for SST ($\rho = -0.99$, $P < 0.001$, $n = 35$) and salinity ($\rho = -0.71$, $P < 0.001$, $n = 35$) decreased significantly with latitude. Average chlorophyll concentrations ($\rho = 0.79$, $P < 0.001$, $n = 35$) increased significantly with latitude (Fig. 7).

Values of SST varied over ~7 °C across the study beaches from 10.8 °C in the north to 17.7 °C in the south (Table S3). Salinity ranged from 31.8 PSS to 33.4 PSS and was lowest for study beaches near the mouth of San Francisco Bay (Table S3). Chlorophyll concentrations varied over twofold across the study beaches ($\overline{x}$ = 1.7 ± 0.09 SE mg m^{-3}; range = 1.1 – 2.9 mg m^{-3}; n = 35) (Table S3).

Environmental drivers

Overall, a high percentage (>35%) of the variance in community assembly was explained by our distance based linear models (DistLM). Results from the DistLM predicted more variance in community assembly for the total community (abundance: five environmental factors, 52% of variance explained; biomass: six factors, 54%) and the lower beach assemblage (abundance: seven environmental factors, 59% of variance explained; biomass: seven factors, 57%) than for the wrack-associated assemblage (abundance: four environmental factors, 43% of variance explained; biomass: three factors, 37%) (Table 3).

Sea-surface temperature (SST) was the most important environmental factor explaining over 20% of variation in intertidal community assembly for all DistLMs (Table 3). Aspects of the habitat such as sediment characteristics (grain size and sorting) and food availability (macroalgal cover and chlorophyll concentration) were important (>7% of variance explained) predictors of community assembly for total intertidal, lower beach, and wrack-associated macroinvertebrates across all the DistLMs (Table 3). Mean grain size at the HTS and macroalgal cover were important (>11% and >15% of variance explained, respectively) factors explaining total intertidal community assembly (Table 3). Mean grain size at the HTS and chlorophyll concentration were important (>13% of variance explained) predictors explaining lower beach macroinvertebrate community assembly while macroalgal cover and sediment sorting at the HTS were important (>17% and >5% of variance explained, respectively) predictors of wrack-associated community assembly (Table 3). Dean's parameter, mean grain size at the WTO, sediment sorting at the WTO, wrack cover, beach length, and beach orientation were included in our DistLMs and independently explained significant ($P \leq 0.05$) percentages of variation in community assembly but were not important in building our models (Table 3).

Spatial autocorrelation can lead to inflated Type I errors in these types of associations, particularly for factors such as SST that are spatially structured (Borcard et al 1992, Lennon 2000, Telford & Birks 2005). Results of variance partitioning indicated that environmental factors selected for the DistLMs explained significant ($P \leq 0.05$) proportions of the variance in community assembly that were independent of spatial dynamics (Table 4). Although there was strong spatial autocorrelation ([*env*+*space*]) with oceanographic drivers (SST, chlorophyll concentration, and salinity), the oceanographic environmental factors explained a significant ($P \leq 0.05$) proportion of the variance in community assembly independent of space ([*env*]) (Table 4). Environmental factors that are influenced by processes acting at local spatial scales (e.g. grain size, slope, beach width, macroalgal wrack) explained a high proportion of the variation in community assembly independent of space ([*env*]) (Table 4).

Discussion

We found strong spatial patterns in the biodiversity, structure, and composition of intertidal macroinvertebrates of sandy beach ecosystems over nine degrees of latitude (32°N to 41°N) and >1800 km of temperate zone northeastern Pacific shoreline. The high biodiversity we found suggests that sandy beaches of central and southern California may represent a global biodiversity hotspot for intertidal macroinvertebrates. This high biodiversity also supports the uncommon finding of hemispheric asymmetry (higher species richness in northern than southern hemisphere) in species richness for sandy beach ecosystems (Defeo & McLachlan 2013) that has not been described for many other taxa or ecosystems (e.g. Chown et al 2004, Dunn et al 2009). By greatly improving the spatial coverage of sandy beach ecosystems including a new range of temperate northern hemisphere (35 beaches) beaches across latitudes that have never been represented in global analyses, the results of our study have generated new insights regarding the generality of widely accepted biogeographic patterns.

The classical pattern of a negative association between taxonomic richness and latitude has been demonstrated for a wide range of ecosystems and taxa (Gaston 2000, Willig et al 2003). However, our results for intertidal macroinvertebrates of sandy beach ecosystems combined with others (Dexter 1974, 1976, 1979, McLachlan 1990) in the northeastern Pacific indicate these coastal communities do not follow this well-known biogeographic pattern (Fig. 9). The potential fit of that widely accepted trend of biodiversity with latitude has previously generated contrasting conclusions for sandy beach ecosystems. Dexter (1992) found no association between species richness and latitude in global comparisons of intertidal communities of 284 beaches using the results of a variety of studies including her own surveys. In contrast, Defeo & McLachlan (2013) and others argued that a classical relationship between diversity and latitude exists for beaches, but only when morphodynamic type (e.g. dissipative, intermediate, reflective) is factored into the analyses. However, the relationship of diversity with latitude presented by Defeo & McLachlan (2013) was weak and non-significant for the 18 northern hemisphere beaches (201 beaches globally) used in their analysis. Although our results for species richness of intertidal invertebrates appeared to match the classical pattern over a limited range of temperate latitudes (<10º latitude, 35 beaches), when a wider latitudinal range of northeastern Pacific beaches (>40º latitude, 59 beaches) is considered, a peak in species richness for mid-latitudes emerges (Fig. 9). This suggests sandy beaches of the northeastern Pacific represent a clear exception to the classical pattern of diversity increasing from temperate to tropical latitudes. The beaches used in our study are predominately of intermediate morphodynamic type, thus the latitudinal pattern we observed is unrelated to beach morphodynamic type. Importantly, biogeographic patterns in marine macroalgae also represent an important exception to the classical latitudinal pattern with a peak in diversity and biomass in temperate latitudes (Kerswell 2006). Macroalgae are a key source of trophic subsidies to intertidal beaches, which may help drive the peak in macroinvertebrate species richness we observed in temperate latitudes for California beaches. This in turn supports the key role of macroalgal wrack in influencing the biodiversity of beach ecosystems found here and elsewhere (Dugan et al 2003, Schooler et al 2017, *Chapter III*).

Our results for the diverse and important guild of wrack-associated macroinvertebrates in the study region revealed the importance of connectivity of beaches to donor ecosystems (Polis & Hurd 1996, Witman et al 2004) and the strong influence of subsidies, particularly drift macroalgae, on the composition, distribution, and abundance of intertidal macroinvertebrate communities of sandy beaches. Strongly influenced by bottom up processes, intertidal and subtidal macroinvertebrates from ecosystems with relatively high *in situ* primary production have often been shown to follow similar biogeographic structure to those exhibited by marine macroalgae (Blanchette et al 2008, Shears et al 2008, Claisse et al 2018). Monterey Bay is considered an important biogeographic boundary for marine macroalgae (Abbott & Hollenberg 1976, Murray et al 1980) and is where a compositional shift from perennial giant kelp (*Macrocystis pyrifera*) dominance to the south and to annual bull kelp (*Nereocystis luetkeana*) dominance to the north occurs (Bell et al 2015). The availability of macroalgal wrack subsidies is affected by the proximity to near-shore macroalgal biomass, macroalgal composition and its condition, transport and deposition by wind, waves, currents, and tides, and retention on beaches (Orr et al 2005, Revell et al 2011, Leibowitz et al 2016). The major shift in donor kelp forest communities at Monterey Bay from perennial giant kelp to the annual bull kelp affects the abundance, availability, and composition of marine macroalgal wrack subsidies to beaches. This shift in macroalgal wrack resources may contribute to the significance of the boundary between the Montereyan and Mendocinian bioregions and influence the biodiversity, structure, and composition of macroinvertebrates on beaches and other intertidal ecosystems (e.g. Blanchette et al 2008, Fenberg et al 2015). The coherence of peaks of macroalgal and sandy intertidal diversity in temperate latitudes and our findings that 1) the species richness, abundance, and biomass of the endemic guild of wrack-associated macroinvertebrates in temperate latitudes were positively correlated with macroalgal wrack abundance and 2) the assembly of these macroinvertebrates differed significantly between the Montereyan and Mendocinian bioregions where a major change in kelp forest composition occurs indicates the importance of macroalgal subsidies in structuring recipient ecosystems, such as sandy beaches.

The exclusion of many taxa of wrack-associated macroinvertebrates and of macroalgal wrack as a factor from the majority of existing biogeographic analyses of beaches has overlooked an important component of the biodiversity of sandy beaches (>40% of species on California beaches, Dugan et al 2003) and a potentially important driver of community assembly as well as vulnerability (Hubbard et al 2014, Schooler et al 2017, *Chapter III*). One key consequence of omitting many wrack-associated macroinvertebrate taxa from biogeographic analyses is the failure to provide information needed to adequately conserve and protect a critical element of unique intertidal biodiversity that contributes substantively to beach ecosystem function (nutrient cycling and wildlife support) (Lastra et al 2008, Dugan & Hubbard 2016). For example, the majority of marine protected areas (MPAs) do not protect habitats that are landward of mean high tide (Harris et al 2014, Dugan & Hubbard 2016) or account for the crucial connectivity between the donor ecosystems that supply wrack subsidies and recipient beach ecosystems that receive them (e.g. Dugan et al 2003, Liebowitz et al 2016). Compounding the critical oversight in conservation and protection of these vital ecosystems is the growing evidence that many of these wrack-associated upper beach species are the most vulnerable to anthropogenic and climatic impacts, some species of which could be considered endangered (Brown 2000, Harris et al 2014, Hubbard et al 2014, Schooler et al 2017, *Chapter III*). To address this knowledge gap, we suggest future analyses of the biodiversity and structure of intertidal communities of sandy beach ecosystems prioritize the inclusion of wrack-associated upper beach taxa (including insects) and the abundance and composition of macrophyte wrack. Information on the entire community of intertidal macroinvertebrates is needed to effectively achieve conservation of these threatened coastal ecosystems.

Ocean and land-based processes can strongly contribute to the biogeographic structure of marine ecological communities (e.g. Belanger et al 2012, Claisse et al 2018). For example, abrupt changes in oceanographic conditions (e.g. SST, upwelling, wave climate, currents) at important marine biogeographic features can influence the assembly of marine organisms at a range of spatial scales (Cowen et al 1993, Gaylord & Gaines 2000, Wares et al 2001, Spalding et al 2007). Considered more of a transition zone than a biogeographic boundary that blocks dispersal, the confluence of colder highly productive northern water with warmer less productive southern water at Point Conception strongly influences the biogeography of the region (Newman 1979, Dawson 2001, Blanchette et al 2007, Briggs & Bowen 2012). Our results of consistent and significant differences in the assembly of sandy beach macroinvertebrates at multiple spatial scales (province, ecoregion, bioregion) across Point Conception and a strong influence of SST on the assembly of intertidal sandy beach macroinvertebrates, match findings for an array of coastal and intertidal marine biota and ecosystems (e.g. Valentine 1966, Horn & Allen 1978, Murray et al 1980, Gaylord & Gaines 2000, Blanchette et al 2008, Belanger et al 2012, Fenberg et al 2015). The strong influence of SST on the spatial structuring of marine biota, including sandy beach macroinvertebrates, underlies some of the threats posed by a changing climate to intertidal and coastal marine ecosystems (Harley et al 2006).

Our results showed that assembly of macroinvertebrate communities of sandy beaches and the two trophic guilds were consistent with existing descriptions of biogeographic units (provinces, ecoregions, bioregions) for coastal marine ecosystems (Hall 1964, Valentine 1966, Briggs 1974, Spalding et al 2007, Tittensor et al 2010, Belanger 2012) for most comparisons. At Cape Mendocino, which has been identified as a biogeographic and phylogeographic break between two ecoregions (Spalding et al 2007) for many marine biota (reviewed in Haupt 2011), oceanographic conditions (e.g. currents, waves, wind, upwelling) can act as a barrier to dispersal for some groups of taxa but not for others by moving water and larvae offshore (Kelly & Palumbi 2010, Fenberg et al 2015). For groups of taxa, such as low dispersal direct developing rocky intertidal invertebrates, a life history trait that is prevalent in macroinvertebrates of sandy beaches (Grantham et al 2003), Cape Mendocino does not appear to block dispersal (Fenberg et al 2015). Our finding of no significant differences in the assembly of intertidal macroinvertebrates of sandy beaches between two ecoregions that share a boundary at Cape Mendocino is consistent with Fenberg et al (2015) and supports the findings of others that the effectiveness of biogeographic boundaries at impeding dispersal and contributing to the biogeographic structure of ecological communities may vary among groups of taxa with different life history traits (Wares 2001, Pelc et al 2009, Kelly & Palumbi 2010, Fenberg et al 2015).

However, our results for the two trophic guilds suggest that differences in functional traits, such as dispersal mode, for direct developing and other low dispersal taxa (e.g. crawling, hopping, flying, swimming, rafting), which can vary between the biota of lower beach and wrack-associated guilds, may influence the effectiveness of biogeographic barriers at blocking dispersal. Unlike lower beach macroinvertebrates and other intertidal taxa with direct development, we observed significant differences in the assembly of wrack-associated macroinvertebrates between ecoregions that share a boundary at Cape Mendocino. This finding suggest that variability in dispersal mode (e.g. rafting vs swimming) may influence biogeographic structure across biogeographic barriers. Furthermore, our comparisons of the distance decay of similarity relationships for sandy beaches, which reveal degrees of isolation across space, differed between the two trophic guilds showing higher degrees of isolation for wrack-associated macroinvertebrates. In concert, these results suggest that differences in functional traits, not just differences in life history, contribute to variability in the degrees of biogeographic structuring across taxa

(Soininen et al 2007). Our results illustrate how incorporating functional and life history traits into biogeographic analyses can enhance the understanding of interactions between dispersal and environmental processes in structuring communities and generating biogeographic structure.

For the California coast, oceanographic factors were important drivers associated with the assembly of lower beach and upper beach wrack-associated macroinvertebrates. Sea surface temperature (SST) is the most commonly identified and important driver of large-scale biogeographic patterns in coastal marine ecosystems (Belanger et al 2012), including sandy beaches (Barboza & Defeo 2015). As found for coastal (Roy et al 1998, Belanger et al 2012, Gooday & Jorissen 2012, Somero 2012, Payne et al 2012) and intertidal (Blanchette et al 2008, Shears et al 2008, Rodil et al 2012, 2014, 2018, Fenberg et al 2015,) ecosystems SST, salinity, and factors associated with primary productivity were significant predictors of lower beach macroinvertebrate assembly. Environmental factors that are influenced by ocean-based processes (SST, macroalgal wrack cover, and sediment characteristics) also drive the assembly of wrack-associated macroinvertebrates that burrow in the upper beach zone. Environmental factors, such as air temperature, wind, humidity, precipitation, and fog, that are associated with SST (van den Dool & Nap 1985, Rayner et al 2003, Kawai & Wada 2007, Tang 2012) could also potentially influence the distribution of wrack and upper beach macroinvertebrates via effects on desiccation that affect food and habitat quality (Colombini et al 2003). The close association of wrack-associated macroinvertebrates with the marine environment and their vulnerability to anthropogenic and climatic impacts suggests that these upper intertidal biota are worthy of inclusion in marine conservation and management efforts.

Sediment characteristics and dynamics, which are known to strongly influence the community assembly of infaunal animals (e.g. Wieser 1952) by affecting habitat quality, are influenced by both ocean and land-based processes on beaches, including waves, currents, fluvial inputs, and wind (Komar 1976). To address these questions, we explored the responses of sandy intertidal community assembly to major coastal landscape features, such as littoral cells. Understanding the role of these geographically distinct compartments of the coast that contain a complete sediment budget including sources, transport paths, and sinks (Habel & Armstrong 1978, Patsch & Griggs 2006, Orme et al 2011) could provide valuable new insights into coastal marine biogeography. Based on results from beaches located in 13 of the 25 littoral cells in California, our analyses indicated the assembly of macroinvertebrate communities is strongly influenced by physical characteristics that can vary at a local scale (e.g. nearby beaches) or across littoral cells, such as grain size and sediment sorting. The significant differences we observed in community assembly across littoral cells (24 km to 230 km) suggest that features unique to littoral cells, such as the composition of sediment (e.g. quartz, feldspar, shell), the direction or seasonality of littoral transport, or effectiveness of littoral cell boundaries at blocking transport, may contribute substantively to the assembly of sandy beach macroinvertebrate communities. These results and those of others (Schooler et al *Chapter III*) suggest the alteration of sediment budgets (e.g. sediment fills, mining, damming of rivers) can have landscape-scale effects on the structure and composition of sandy beach macroinvertebrates. This first effort to link the biogeographic patterns in the assembly of intertidal biota to littoral cells highlights the need to further explore the influence of large-scale landscape features that are influenced by ocean and land-based processes on sandy beach and other coastal marine ecosystems.

In summary, our evaluation of biogeographic patterns in sandy beach macroinvertebrate communities revealed high biodiversity and biogeographic complexity along the coast of California. Our surveys provided the first quality baseline biogeographic-scale data on sandy beaches for the region. Our results showed that connectivity to sources of subsidies can strongly influence the structure and composition of recipient ecosystems, such as sandy beaches. Importantly, our results generated new insights regarding the generality of widely accepted biogeographic patterns of diversity with latitude and factors influencing community assembly can be used to inform the conserving of threatened coastal biodiversity.

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Figures

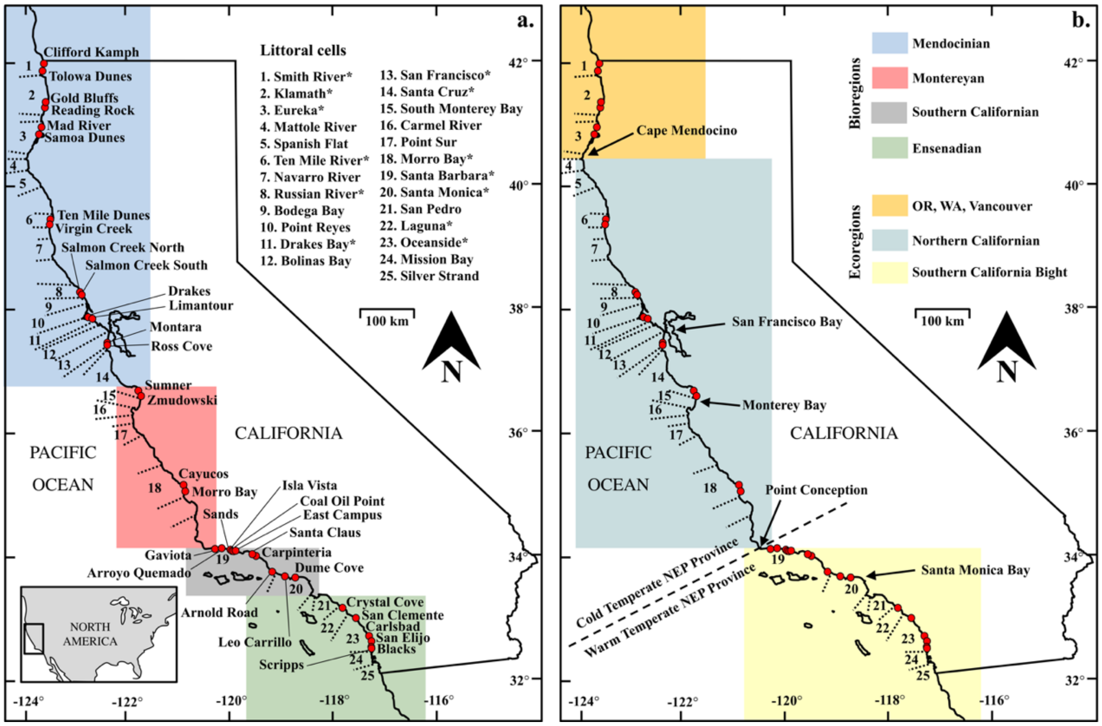

Figure 1. Maps of the study area with locations of the sandy beach study sites (red dots) and major littoral cell boundaries (dotted black lines), a) bioregions and b) ecoregions (colored boxes), and b) major biogeographic landscape features (black arrows) on the coast of California, USA. The numbers between littoral cell boundaries correspond with the littoral cell names numbered 1 through 25 from north to south listed in a above. In b. the major landscape feature, Point Conception, divides the Cold Temperate NEP and Warm Temperate NEP provinces with the boundary indicated by a dashed black line.

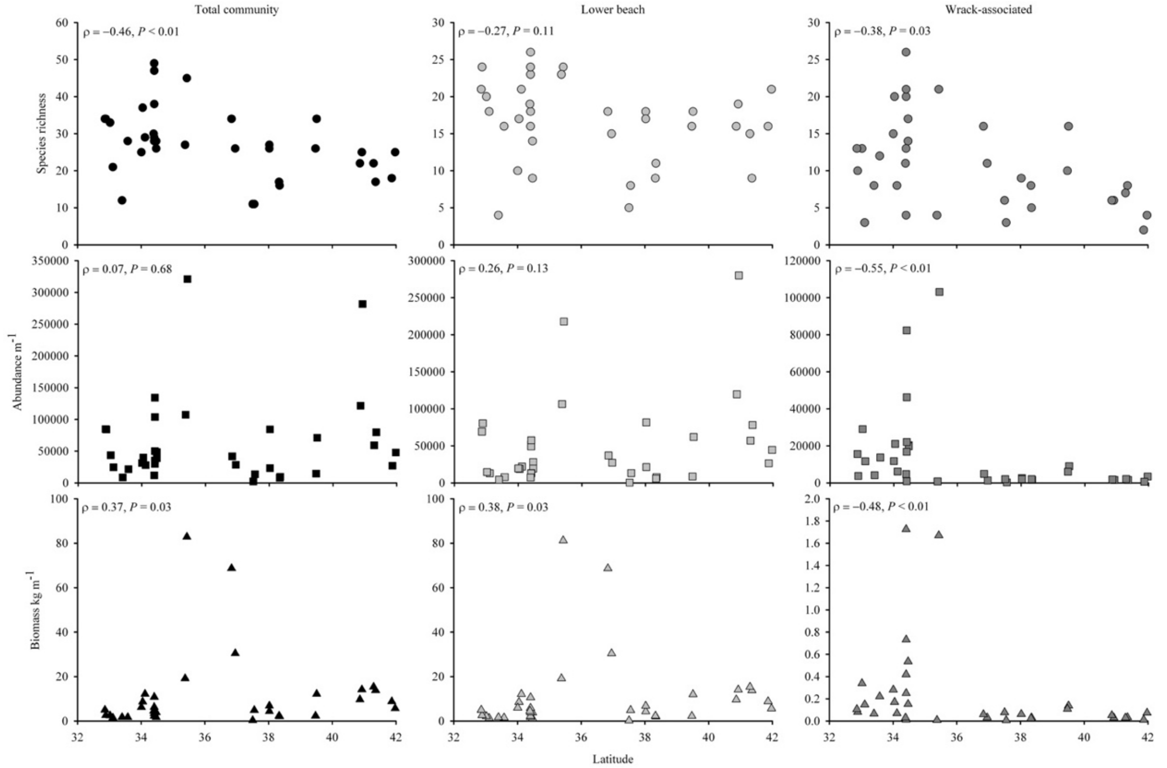

Figure 2. Scatterplots of (top to bottom) species richness, abundance, and biomass as a function of latitude of the study beach for (left to right) total intertidal community, lower beach, and wrack-associated macroinvertebrates. Rho (ρ) and *P*-values displayed for each plot were computed using Spearman's rank correlation.

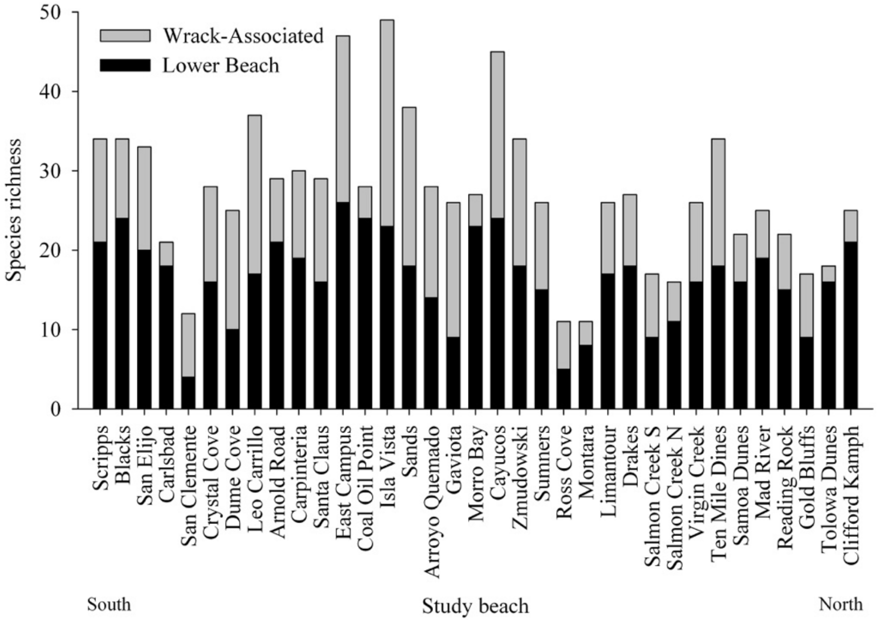

Figure 3. Values of observed species richness of intertidal macroinvertebrates at the study beaches. The black bars indicate the values of observed richness for lower beach species and grey bars indicated values for wrack-associated species. Study beaches are displayed from left to right in order of sequence alongshore from south to north.

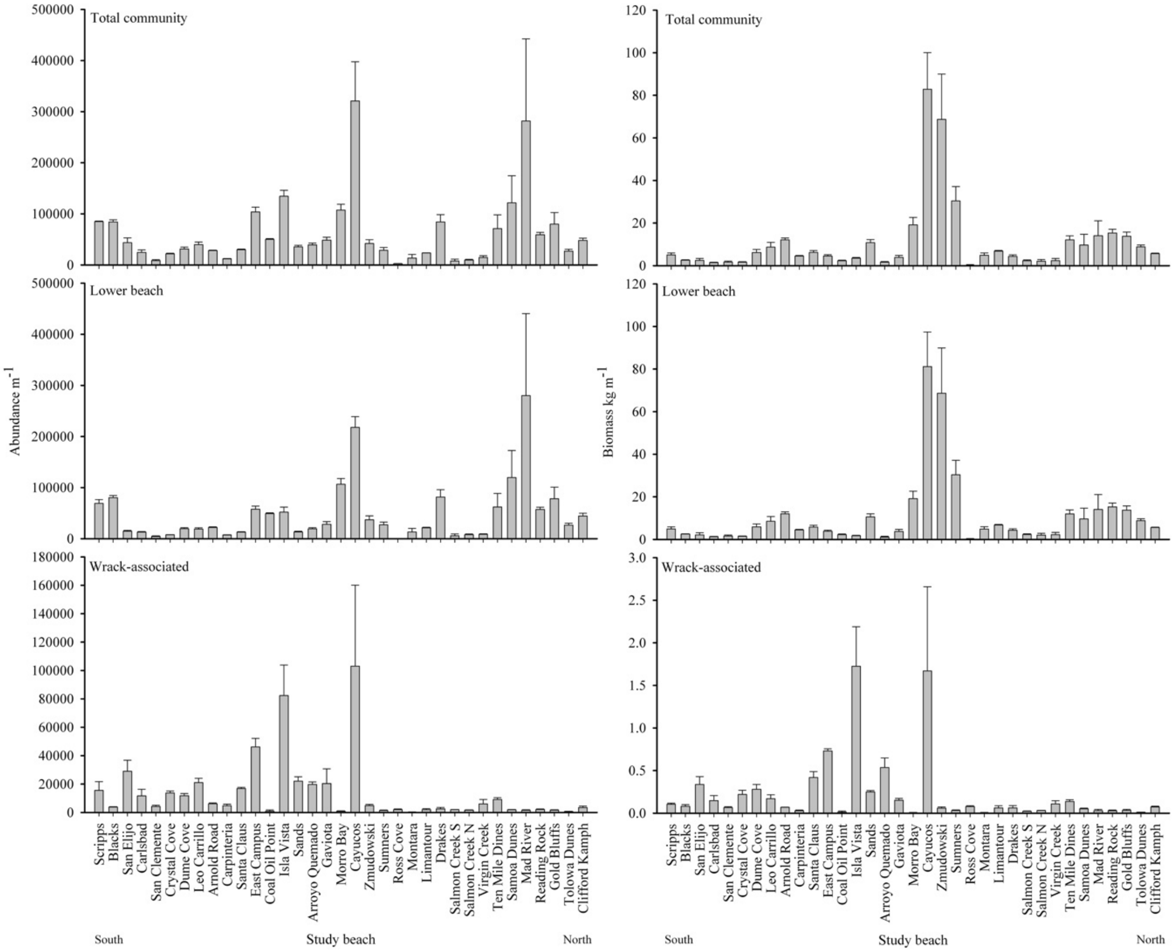

Figure 4. Mean (± SE) values of abundance and biomass for (top to bottom) total intertidal community, lower beach, and wrack-associated macroinvertebrates for each study beach displayed from left to right in order of sequence alongshore from south to north.

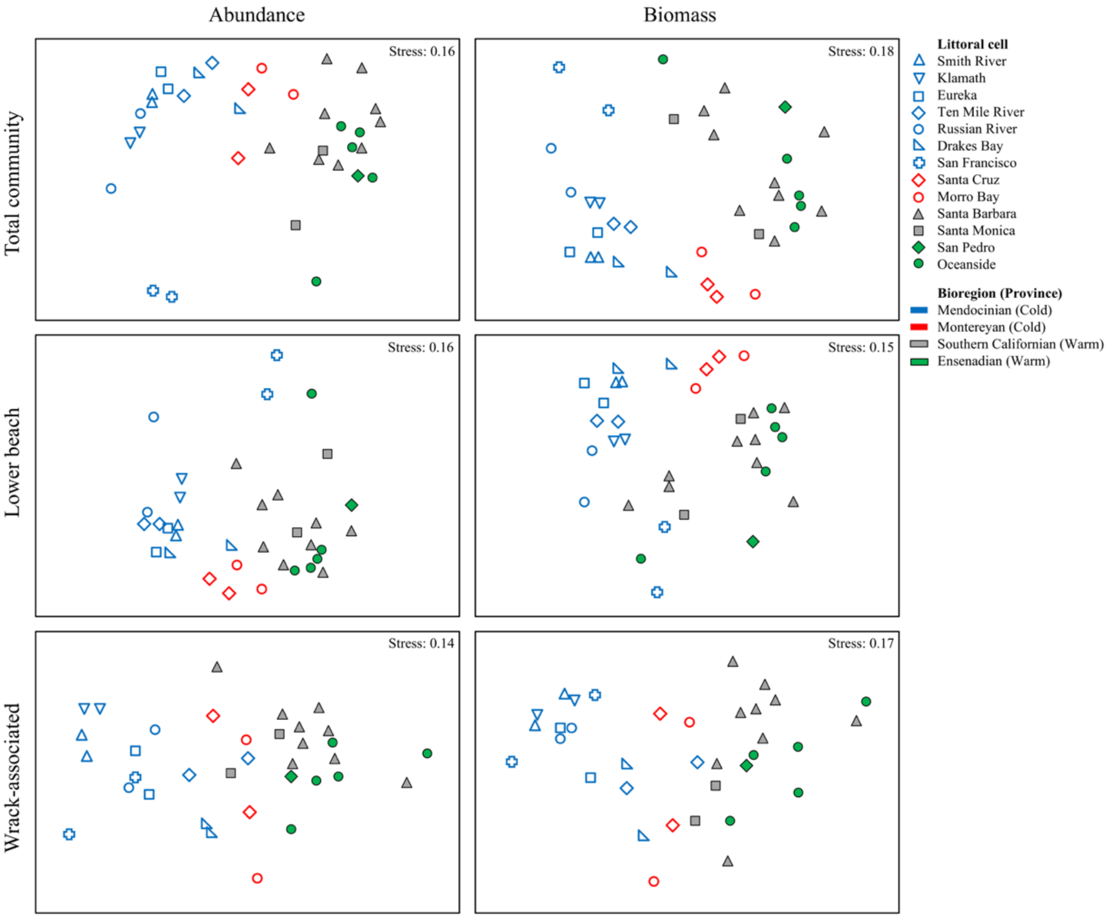

Figure 5. Results of non-metric multidimensional scaling (nMDS) analysis comparing macroinvertebrate assemblages of study beaches grouped by province, bioregion, ecoregion (not displayed), and littoral cell for the total community, lower beach, and wrack-associated macroinvertebrates using log (x+1) transformed abundance and biomass data. All groupings based on province, ecoregion (not displayed), bioregion, or littoral cell as the factor differed significantly (PERMANOVA, $P < 0.0001$).

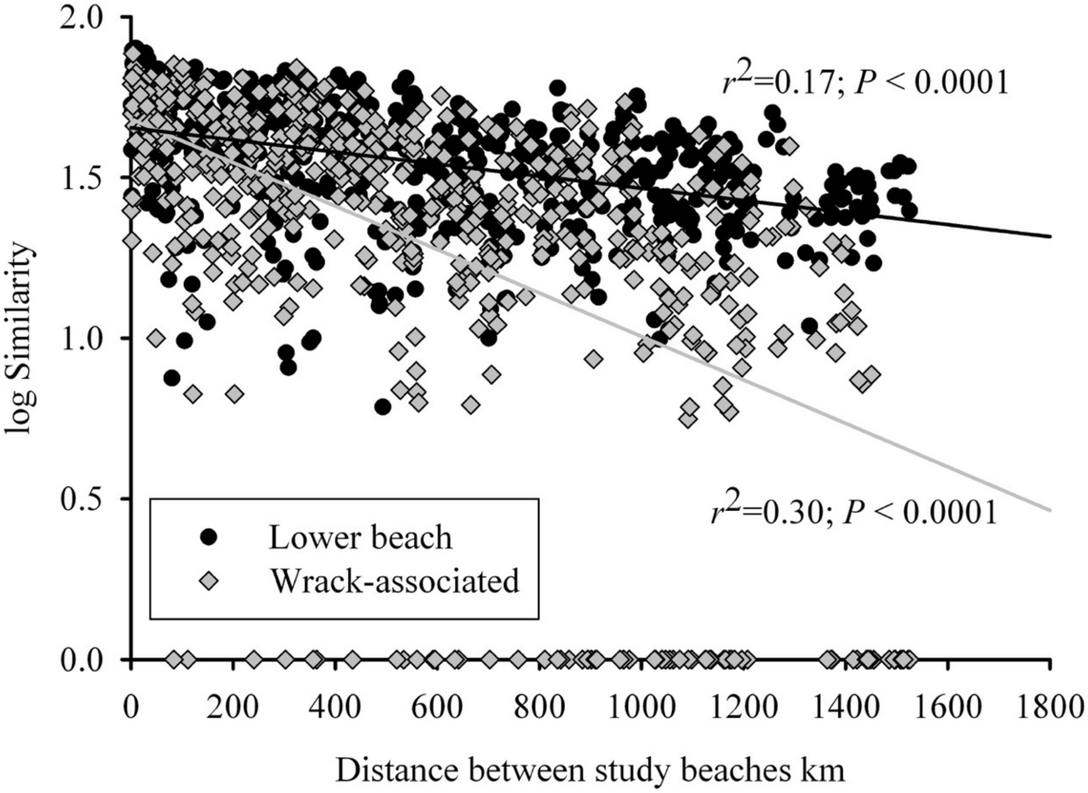

Figure 6. Relationships of distance decay of similarity for lower beach (black) and wrack-associated (grey) macroinvertebrates as a function of alongshore distance and the log of similarity (Bray-Curtis) between study beaches. Regression correlation coefficients and *P*-values are displayed adjacent to the corresponding lines.

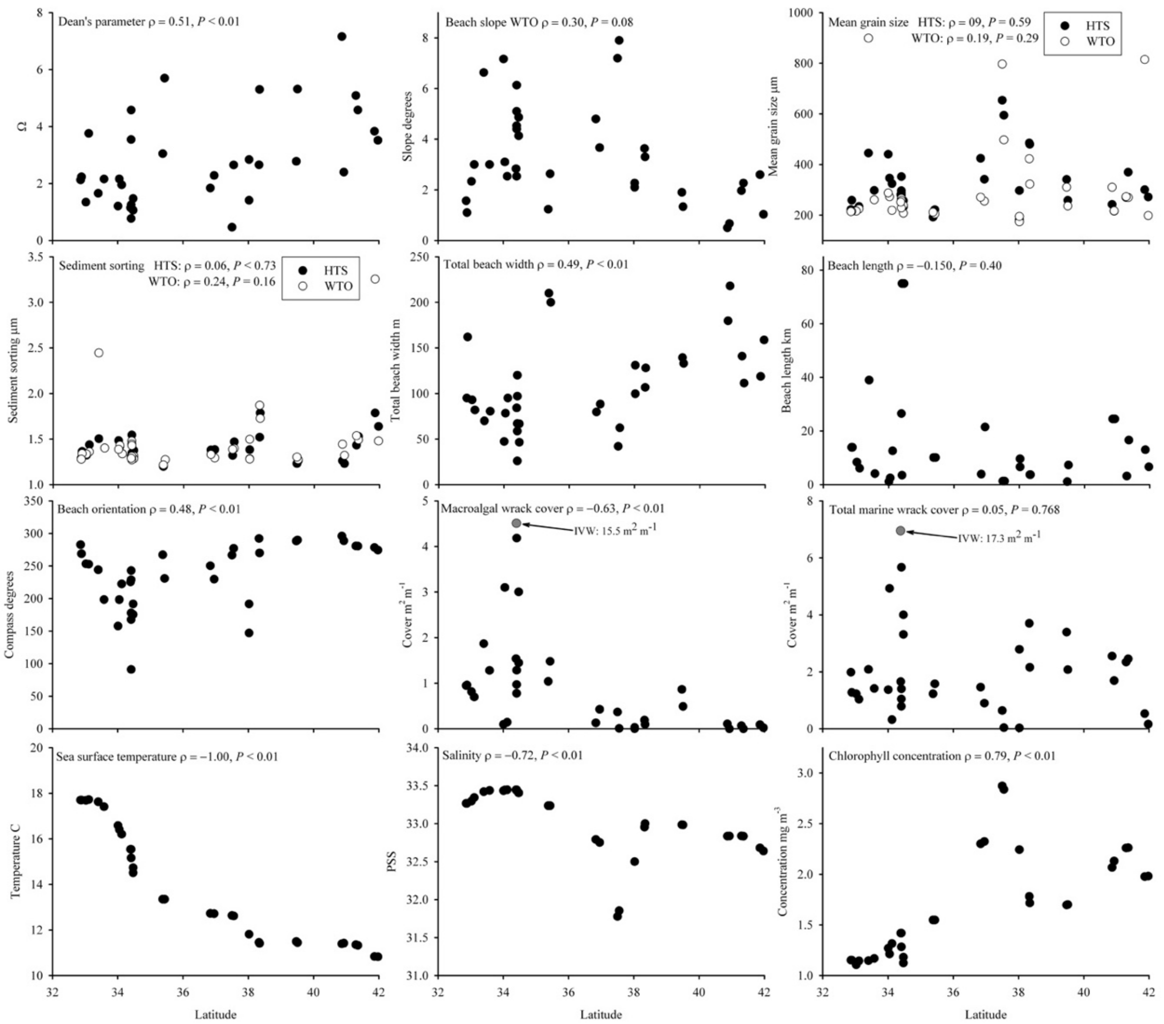

Figure 7. Scatterplots of environmental characteristics as a function of the latitude of the study beaches. Rho (ρ) and *P*-values displayed for each plot were computed using Spearman's rank correlation. Outliers are included and indicated by grey circles.

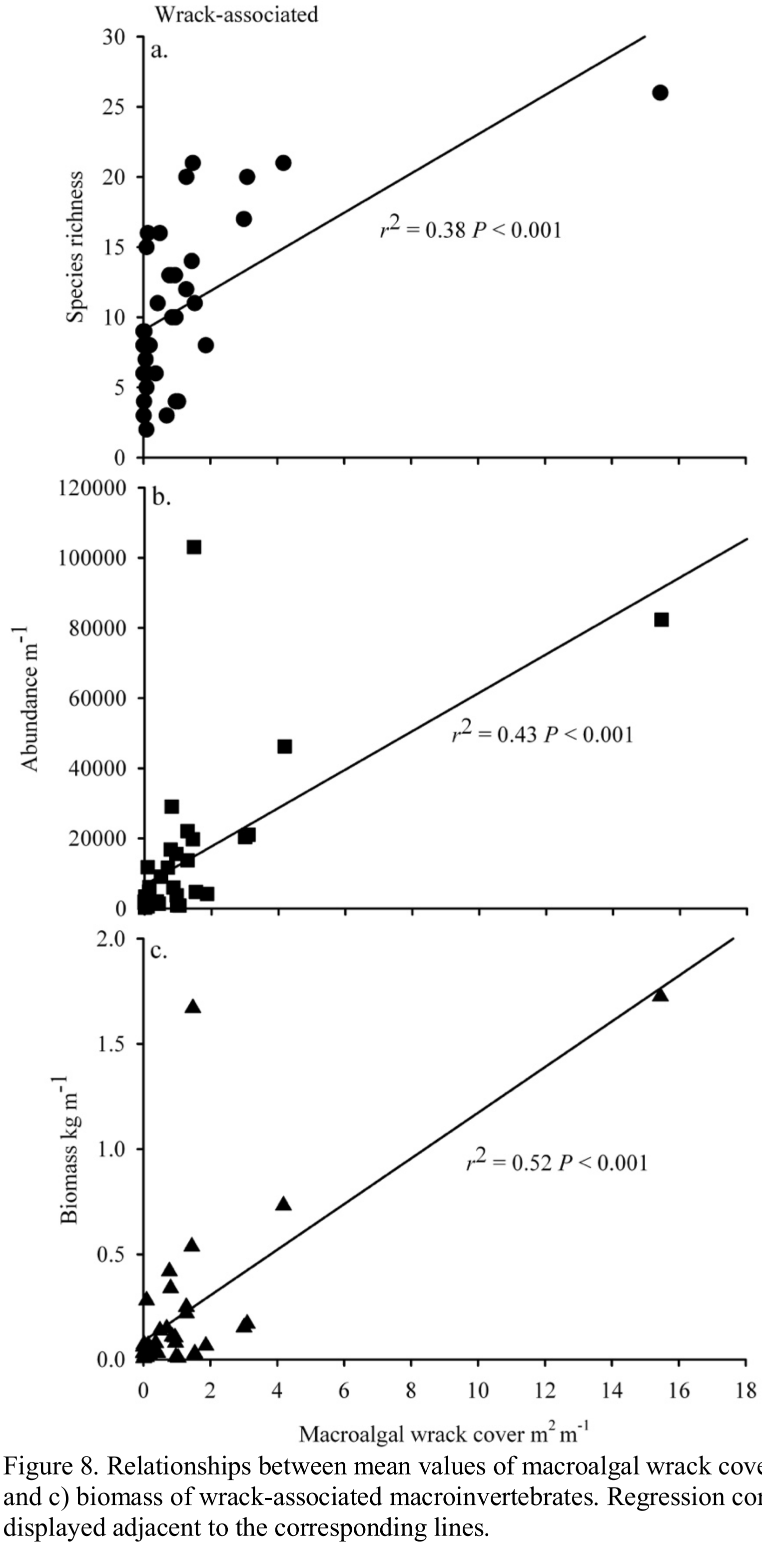

Figure 8. Relationships between mean values of macroalgal wrack cover and a) species richness, b) abundance, and c) biomass of wrack-associated macroinvertebrates. Regression correlation coefficients and *P*-values are displayed adjacent to the corresponding lines.

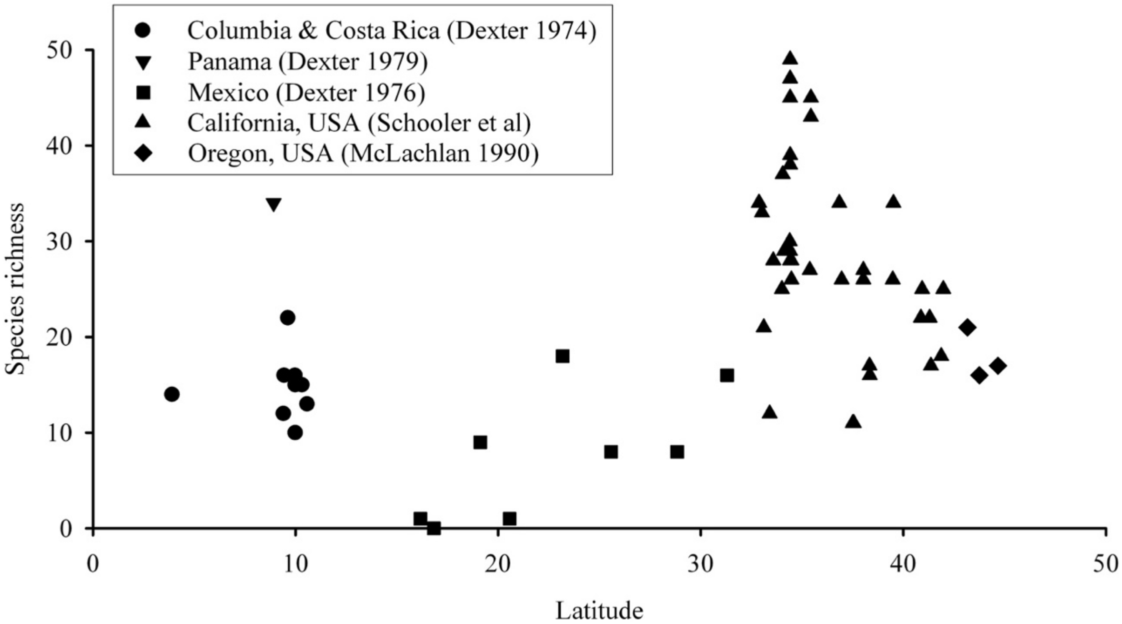

Figure 9. The relationship between total intertidal species richness as a function of latitude for all available intertidal surveys of sandy beach macroinvertebrates from the northeastern Pacific including our study beaches.

Tables

Table 1. The study site names and codes, coordinates, survey date, biogeographic unit (province, ecoregion, bioregion), littroal cell, and status within marine protected areas (MPA) for the 35 study beaches arranged from top to bottom in order of site sequence from north to south.

Study site name	Site code	Coordinates	Survey date	Province	Ecoregion	Bioregion	Littoral Cell	MPA
Clifford Kamph	CKMP	41°58'21"N, 124°12'21"W	August 10, 2014	Cold Temperate NEP	OR, WA, Vancouver	Mendocinian	Smith River	Yes
Tolowa Dunes	TDSP	41°52'01"N, 124°12'50"W	August 11, 2014	Cold Temperate NEP	OR, WA, Vancouver	Mendocinian	Smith River	No
Gold Bluffs	GBB	41°21'34"N, 124°04'37"W	August 13, 2014	Cold Temperate NEP	OR, WA, Vancouver	Mendocinian	Klamath	No
Reading Rock	RRB	41°17'51"N, 124°05'29"W	August 12, 2014	Cold Temperate NEP	OR, WA, Vancouver	Mendocinian	Klamath	Yes
Mad River	MRB	40°55'45"N, 124°08'10"W	June 27, 2014	Cold Temperate NEP	OR, WA, Vancouver	Mendocinian	Eureka	No
Samoa Dunes	SMD	40°51'60"N, 124°09'51"W	June 26, 2014	Cold Temperate NEP	OR, WA, Vancouver	Mendocinian	Eureka	Yes
Ten Mile Dunes	TMD	39°30'29"N, 123°47'06"W	July 14, 2014	Cold Temperate NEP	Northern California	Mendocinian	Ten Mile River	No
Virgin Creek	VC	39°28'21"N, 123°48'18"W	July 13, 2014	Cold Temperate NEP	Northern California	Mendocinian	Ten Mile River	Yes
Salmon Creek North	SCBN	38°20'43"N, 123°04'06"W	July 2, 2011	Cold Temperate NEP	Northern California	Mendocinian	Russian River	No
Salmon Creek South	SCBS	38°19'45"N, 123°04'17"W	July 3, 2011	Cold Temperate NEP	Northern California	Mendocinian	Russian River	Yes
Drakes	DB	38°01'33"N, 122°57'46"W	July 17, 2011	Cold Temperate NEP	Northern California	Mendocinian	Drakes Bay	Yes
Limantour	LB	38°01'30"N, 122°52'51"W	July 4, 2011	Cold Temperate NEP	Northern California	Mendocinian	Drakes Bay	No
Montara	MB	37°33'02"N, 122°30'51"W	July 6, 2011	Cold Temperate NEP	Northern California	Mendocinian	San Francisco	No
Ross Cove	RC	37°30'03"N, 122°29'55"W	July 19, 2011	Cold Temperate NEP	Northern California	Mendocinian	San Francisco	Yes
Sumner	SUM	36°57'10"N, 121°52'57"W	September 26, 2015	Cold Temperate NEP	Northern California	Montereyan	Santa Cruz	No
Zmudowski	ZB	36°50'11"N, 121°48'10"W	September 27, 2015	Cold Temperate NEP	Northern California	Montereyan	Santa Cruz	No
Cayucos	CAY	35°26'06"N, 120°53'18"W	November 5, 2010	Cold Temperate NEP	Northern California	Montereyan	Morro Bay	No
Morro Bay	MOR	35°22'44"N, 120°51'50"W	November 15, 2009	Cold Temperate NEP	Northern California	Montereyan	Morro Bay	No
Gaviota	GAV	34°28'16"N, 120°13'40"W	September 26, 2011	Warm Temperate NEP	Southern California Bight	Southern Californian	Santa Barbara	Yes
Arroyo Quemado	AQB	34°28'13"N, 120°07'10"W	October 10, 2011	Warm Temperate NEP	Southern California Bight	Southern Californian	Santa Barbara	No
Sands	SNDS	34°24'41"N, 119°52'57"W	November 6, 2010	Warm Temperate NEP	Southern California Bight	Southern Californian	Santa Barbara	Yes
Isla Vista	IVW	34°24'33"N, 119°52'26"W	October 7, 2010	Warm Temperate NEP	Southern California Bight	Southern Californian	Santa Barbara	Yes
Coal Oil Point	COP	34°24'33"N, 119°52'10"W	August 23, 2009	Warm Temperate NEP	Southern California Bight	Southern Californian	Santa Barbara	Yes
East Campus	EUC	34°24'38"N, 119°50'32"W	October 8, 2010	Warm Temperate NEP	Southern California Bight	Southern Californian	Santa Barbara	No
Santa Claus	SCL	34°24'31"N, 119°33'06"W	October 6, 2010	Warm Temperate NEP	Southern California Bight	Southern Californian	Santa Barbara	No
Carpinteria	CARP	34°23'29"N, 119°31'18"W	August 21, 2009	Warm Temperate NEP	Southern California Bight	Southern Californian	Santa Barbara	No
Arnold Road	ARN	34°07'18"N, 119°09'38"W	October 21, 2010	Warm Temperate NEP	Southern California Bight	Southern Californian	Santa Barbara	No
Leo Carrillo	LEO	34°02'49"N, 118°56'51"W	September 29, 2011	Warm Temperate NEP	Southern California Bight	Southern Californian	Santa Monica	No
Dume Cove	DUM	34°00'22"N, 118°48'07"W	October 11, 2011	Warm Temperate NEP	Southern California Bight	Southern Californian	Santa Monica	Yes
Crystal Cove	CRY	33°34'41"N, 117°50'52"W	September 29, 2011	Warm Temperate NEP	Southern California Bight	Ensenadian	Laguna	Yes
San Clemente	CLM	33°24'04"N, 117°36'13"W	September 27, 2011	Warm Temperate NEP	Southern California Bight	Ensenadian	Oceanside	No
Carlsbad	CAR	33°06'38"N, 117°19'23"W	October 12, 2011	Warm Temperate NEP	Southern California Bight	Ensenadian	Oceanside	No
San Elijo	ELJ	33°01'31"N, 117°17'13"W	October 28, 2011	Warm Temperate NEP	Southern California Bight	Ensenadian	Oceanside	Yes
Blacks	BLK	32°53'23"N, 117°15'12"W	October 26, 2011	Warm Temperate NEP	Southern California Bight	Ensenadian	Oceanside	No
Scripps	SCR	32°51'49"N, 117°15'17"W	August 31, 2011	Warm Temperate NEP	Southern California Bight	Ensenadian	Oceanside	Yes

Table 2. Analysis of similarity (ANOSIM) results for abundance and biomass based multivariate analyses (see Fig. 5). Testing for significant differences ($p \leq 0.05$) in community assemblages by making direct pairwise comparisons between biogeographic units (provinces, ecoregions, and bioregions).

			Abundance		**Biomass**	
Biogeographic unit	**Assemblage**	**Group**	**R statistic**	***p***	**R statistic**	***p***
Province	Total community	Cold Temperate NEP, Warm Temperate NEP	0.667	< 0.01	0.616	< 0.01
	Lower beach	Cold Temperate NEP, Warm Temperate NEP	0.534	< 0.01	0.467	< 0.01
	Wrack-associated	Cold Temperate NEP, Warm Temperate NEP	0.603	< 0.01	0.617	< 0.01
Ecoregion	Total community	OR, WA, & Vancouver, Northern CA	0.084	0.20	-0.047	0.58
		OR, WA, & Vancouver, Southern CA Bight	0.925	< 0.01	0.827	< 0.01
		Northern CA, Southern CA Bight	0.594	< 0.01	0.49	< 0.01
	Lower beach	OR, WA, & Vancouver, Northern CA	-0.046	0.59	-0.074	0.71
		OR, WA, & Vancouver, Southern CA Bight	0.735	< 0.01	0.661	< 0.01
		Northern CA, Southern CA Bight	0.454	< 0.01	0.353	< 0.01
	Wrack-associated	OR, WA, & Vancouver, Northern CA	0.335	< 0.01	0.14	0.10
		OR, WA, & Vancouver, Southern CA Bight	0.907	< 0.01	0.883	< 0.01
		Northern CA, Southern CA Bight	0.554	< 0.01	0.516	< 0.01
Bioregion	Total community	Mendocinian, Montereyan	0.375	0.029	0.597	0.003
		Mendocinian, Southern Californian	0.762	0.0001	0.592	0.0001
		Mendocinian, Ensenadian	0.786	0.0001	0.685	0.0001
		Montereyan, Southern Californian	0.498	0.004	0.174	0.095
		Montereyan, Ensenadian	0.587	0.005	0.456	0.014
		Southern Californian, Ensenadian	0.119	0.155	0.007	0.361
	Lower beach	Mendocinian, Montereyan	0.375	0.03	0.636	< 0.01
		Mendocinian, Southern Californian	0.632	< 0.01	0.74	< 0.01
		Mendocinian, Ensenadian	0.602	< 0.01	0.835	< 0.01
		Montereyan, Southern Californian	0.334	0.02	0.227	0.06
		Montereyan, Ensenadian	0.464	< 0.01	0.579	0.01
		Southern Californian, Ensenadian	0.075	0.21	-0.006	0.44
	Wrack-associated	Mendocinian, Montereyan	0.394	< 0.01	0.539	< 0.01
		Mendocinian, Southern Californian	0.709	< 0.01	0.722	< 0.01
		Mendocinian, Ensenadian	0.804	< 0.01	0.791	< 0.01
		Montereyan, Southern Californian	0.378	0.03	0.325	0.03
		Montereyan, Ensenadian	0.464	0.01	0.603	< 0.01
		Southern Californian, Ensenadian	0.091	0.20	0.014	0.41

Table 3. 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 a) abundance-based and b) biomass-based data . Asterisk specifies log transformed data.

a. Abundance

Assemblage	**Environmental driver**	**AIC**	**Pseudo-F**	**Variance**	***p***
Total community	SST	262.3	11.6	0.26	< 0.01
	Mean grain size - HTS*	258.9	5.4	0.37	< 0.01
	Macroalgae*	257.2	3.4	0.43	< 0.01
	Salinity*	256.1	2.8	0.48	< 0.01
	Total beach width*	255.2	2.5	0.52	0.00
Lower beach	SST	260.5	10.8	0.25	< 0.01
	Mean grain size - HTS*	255.7	6.9	0.38	< 0.01
	Total beach width*	254.4	3.0	0.44	< 0.01
	Salinity*	253.1	3.0	0.49	< 0.01
	Macroalgae*	252.2	2.5	0.53	< 0.01
	Chl A*	251.5	2.2	0.56	< 0.01
	Mean grain size - WTO*	251.2	1.9	0.59	0.05
Wrack-associated	SST	269.2	12.2	0.27	< 0.01
	Macroalgae*	267.6	3.4	0.34	< 0.01
	Grain size SD - HTS*	267.2	2.3	0.39	0.02
	Salinity*	266.6	2.3	0.43	0.02

b. Biomass

Assemblage	**Environmental driver**	**AIC**	**Pseudo-F**	**Variance**	***p***
Total community	SST	260.7	11.0	0.25	< 0.01
	Mean grain size - HTS*	257.2	5.4	0.36	< 0.01
	Macroalgae*	255.8	3.2	0.42	< 0.01
	Total beach width*	255.1	2.5	0.46	< 0.01
	Chl A*	254.8	1.9	0.50	0.03
	Salinity*	253.8	2.5	0.54	< 0.01
Lower beach	SST	257.4	10.4	0.24	< 0.01
	Mean grain size - HTS*	252.7	6.8	0.37	< 0.01
	WTO slope*	251.6	2.8	0.43	< 0.01
	Chl A*	251.5	1.9	0.46	0.06
	Salinity*	250.3	2.8	0.51	0.01
	Macroalgae*	249.7	2.1	0.54	0.03
	Total beach width*	249.2	2.1	0.57	0.04
Wrack-associated	SST	274.6	11.3	0.26	< 0.01
	Macroalgae*	273.1	3.4	0.33	< 0.01
	Grain size SD - HTS*	272.9	2.1	0.37	0.04

* log transformed

Table 4. Results of variance partitioning for the environmental drivers included in the DistLM (see Table S3) showing the influence of the pure environmental component independent of spatial structure ([*env*]) on the assembly of total, lower beach, and wrack-associated macroinvertebrates. Adjusted r^2 values are shown for [*env*], [*env* + *space*], and [*space*]. The *F* and *P*-values are the result of an ANOVA for [*env*].

	Total community					**Lower beach**					**Wrack-associated**				
Environmental driver	**[*env*]**	**[*env + space*]**	**[*space*]**	***F***	***P***	**[*env*]**	**[*env + space*]**	**[*space*]**	***F***	***P***	**[*env*]**	**[*env + space*]**	**[*space*]**	***F***	***P***
Dean's parameter	0.01	0.01	0.18	1.42	0.11	0.02	0.07	0.16	1.94	0.03	0.00	0.00	0.19	0.75	0.73
WTO slope	0.06	0.06	0.23	3.95	0.00	0.09	0.11	0.20	4.97	0.00	0.02	0.02	0.25	1.82	0.05
Mean grain size - HTS	0.08	0.08	0.23	4.95	0.00	0.11	0.11	0.22	5.93	0.00	0.03	0.03	0.23	2.14	0.01
Grain size SD - HTS	0.01	0.01	0.22	1.30	0.17	0.01	0.02	0.21	1.41	0.13	0.02	0.02	0.22	0.17	0.06
Mean grain size - WTO	0.06	0.06	0.23	3.56	0.00	0.10	0.10	0.22	5.42	0.00	0.01	0.01	0.22	1.28	0.19
Grain size SD - WTO	0.00	0.00	0.21	0.98	0.45	0.01	0.03	0.20	1.29	0.22	0.00	0.00	0.21	0.78	0.69
Total beach width	0.05	0.05	0.20	3.07	0.00	0.06	0.10	0.17	3.73	0.00	0.03	0.03	0.22	2.12	0.02
Beach length	0.03	0.03	0.22	2.39	0.00	0.02	0.02	0.21	1.84	0.04	0.03	0.03	0.21	2.10	0.01
Orientation	0.01	0.01	0.18	1.52	0.07	0.02	0.06	0.17	1.64	0.10	0.00	0.00	0.18	1.13	0.33
Macroalgae	0.03	0.03	0.13	2.36	0.01	0.01	0.09	0.13	1.62	0.08	0.03	0.03	0.12	2.31	0.02
Wrack	0.02	0.02	0.23	1.72	0.04	0.00	0.00	0.21	1.09	0.34	0.02	0.02	0.23	1.80	0.05
SST	0.02	0.02	0.03	1.82	0.02	0.02	0.21	0.02	1.79	0.05	0.03	0.03	0.05	2.41	0.05
Salinity	0.05	0.05	0.14	3.19	0.00	0.05	0.10	0.16	3.24	0.00	0.04	0.04	0.10	2.56	0.01
Chl A	0.03	0.03	0.09	2.41	0.00	0.03	0.12	0.12	2.43	0.01	0.02	0.02	0.05	1.86	0.03

env = adjusted r2 pure environmental variable (independent of spatial structure)

env + *space* = adjusted r2 spatial component of environmental influence (spatial structuring that is shared by environmental data)

space = adjusted r2 pure spatial component (independent of environment - eg dispersal)

Supplementary material

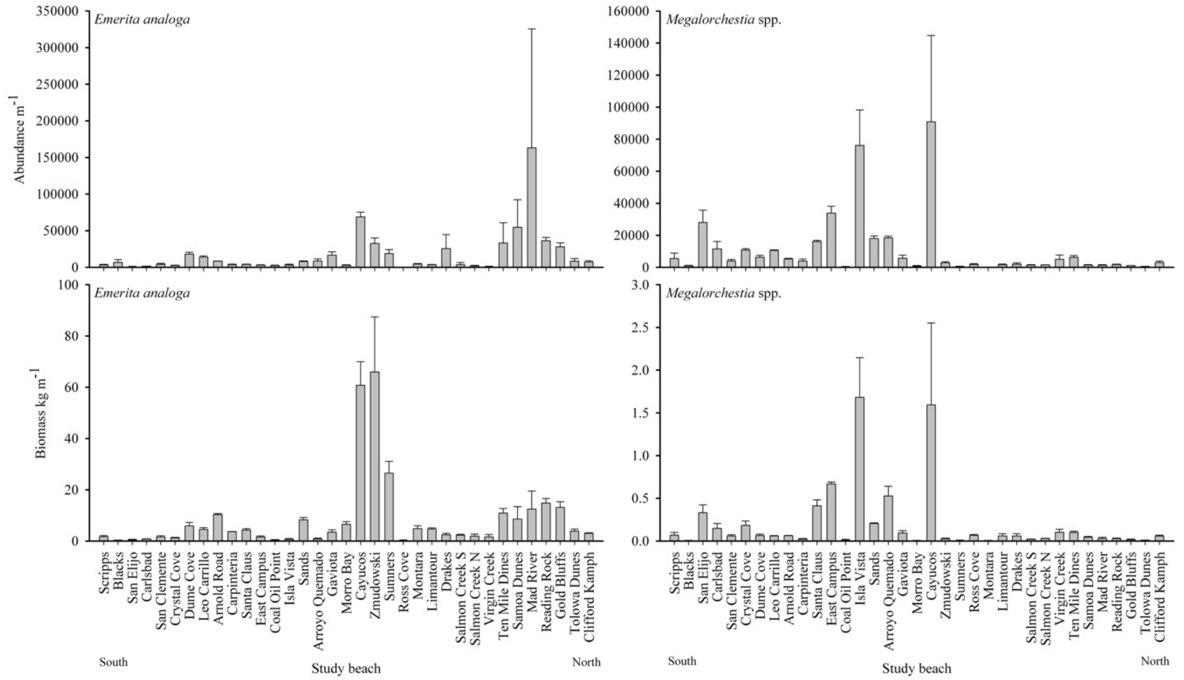

Figure S1. Mean (± SE) values of abundance and biomass for the sand crab *Emerita analoga* and the talitrid amphipods *Megalorchestia* spp. for each study beach displayed from left to right in order of site sequence from south to north.

Table S1. Beach characteristics for each study site arranged from top to bottom in order of site sequence from north to south.

Study site	Dean's parameter Ω	Slope (WTO)	Mean grain size (HTS) µm	Sediment sorting (HTS) µm	Mean grain size (WTO) µm	Sediment sorting (WTO) µm	Macroalgal cover m2 m-1	Total wrack cover m2 m-1	Beach width m	Beach length km	Orientation compass °	SST °C	Salinity PSS	Chlorophyll concentration mg m-3
Clifford Kamph	3.5	1.0	271.7	1.6	198.3	1.5	0.021	0.16	158.7	7	274.5	10.8	32.6	2.0
Tolowa Dunes	3.8	2.6	300.3	1.8	814.8	3.3	0.090	0.53	118.7	13	278.4	10.8	32.7	2.0
Gold Bluffs	4.6	2.3	369.6	1.5	269.6	1.5	0	2.45	111.3	17	280.5	11.3	32.8	2.3
Reading Rock	5.1	2.0	269.9	1.4	273.0	1.5	0.067	2.34	140.9	3	280.7	11.4	32.8	2.3
Mad River	2.4	0.7	215.9	1.2	216.8	1.3	0	1.69	218.0	25	288.7	11.4	32.8	2.1
Samoa Dunes	7.2	0.5	242.3	1.3	310.3	1.4	0.107	2.55	179.7	25	296.0	11.4	32.8	2.1
Ten Mile Dunes	5.3	1.3	258.5	1.3	236.2	1.3	0.490	2.07	133.0	7	289.9	11.4	33.0	1.7
Virgin Creek	2.8	1.9	341.0	1.2	310.5	1.3	0.863	3.39	139.3	1	288.4	11.5	33.0	1.7
Salmon Creek North	5.3	3.3	480.0	1.8	322.7	1.7	0.097	2.16	128.0	4	270.0	11.4	33.0	1.7
Salmon Creek South	2.7	3.6	484.7	1.5	422.7	1.9	0.189	3.70	106.7	4	292.3	11.5	33.0	1.8
Drakes	2.8	2.1	182.3	1.3	173.7	1.3	0.030	2.79	131.0	7	147.1	11.8	32.5	2.2
Limantour	1.4	2.3	297.0	1.4	195.0	1.5	0.001	0.03	99.7	10	191.7	11.8	32.5	2.2
Montara	2.6	7.9	594.3	1.5	497.3	1.4	0.008	0.04	62.3	1	277.1	12.6	31.9	2.8
Ross Cove	0.5	7.2	653.7	1.3	796.7	1.4	0.367	0.64	42.0	1	266.7	12.6	31.8	2.9
Sumner	2.3	3.7	341.5	1.4	255.4	1.3	0.427	0.90	88.3	21	229.8	12.7	32.8	2.3
Zmudowski	1.8	4.8	424.5	1.4	270.5	1.3	0.130	1.46	79.7	4	250.4	12.7	32.8	2.3
Cayucos	5.7	2.6	221.5	1.3	204.9	1.3	1.479	1.58	200.0	10	230.9	13.3	33.2	1.5
Morro Bay	3.0	1.2	191.8	1.2	211.4	1.2	1.040	1.23	210.0	10	267.2	13.3	33.2	1.5
Gaviota	1.5	4.9	256.9	1.4	239.3	1.3	3.003	4.00	66.7	75	175.5	14.5	33.4	1.1
Arroyo Quemado	1.1	4.1	232.2	1.3	207.7	1.3	1.447	3.31	46.5	75	191.7	14.7	33.4	1.2
Sands	4.6	6.1	352.1	1.5	267.7	1.3	1.283	1.40	120.0	75	243.0	15.2	33.4	1.3
Isla Vista	1.1	5.1	287.5	1.4	263.5	1.5	15.450	17.30	67.0	75	167.7	15.2	33.4	1.3
Coal Oil Point	0.8	4.5	279.3	1.4	265.7	1.4	0.970	1.04	26.0	75	177.9	15.2	33.4	1.3
East Campus	1.3	4.4	249.0	1.3	258.1	1.4	4.183	5.67	97.0	75	91.1	15.2	33.4	1.3
Santa Claus	3.5	2.5	296.7	1.3	228.6	1.3	0.777	0.79	58.7	4	228.9	15.5	33.4	1.4
Carpinteria	1.1	2.8	280.9	1.3	251.5	1.3	1.537	1.65	84.2	27	225.5	15.5	33.4	1.4
Arnold Road	2.0	2.5	324.2	1.3	218.9	1.3	0.143	0.32	95.0	13	222.5	16.2	33.4	1.3
Leo Carrillo	2.2	3.1	346.2	1.4	272.7	1.4	3.100	4.93	78.3	3	198.4	16.4	33.4	1.2
Dume Cove	1.2	7.2	440.5	1.5	287.5	1.4	0.097	1.37	47.3	1	157.8	16.6	33.4	1.3
Crystal Cove	2.2	3.0	297.6	1.4	260.6	1.4	1.280	1.41	80.5	4	198.5	17.4	33.4	1.2
San Clemente	1.7	6.6	445.2	1.5	899.1	2.4	1.867	2.08	70.0	39	244.2	17.6	33.4	1.1
Carlsbad	3.8	3.0	234.0	1.4	224.5	1.4	0.697	1.03	81.8	6	252.8	17.7	33.3	1.1
San Elijo	1.3	2.3	220.9	1.3	215.9	1.3	0.813	1.23	93.0	8	253.4	17.7	33.3	1.1
Blacks	2.2	1.1	258.9	1.4	214.9	1.3	0.960	1.27	162.0	14	268.8	17.7	33.3	1.2
Scripps	2.1	1.6	222.2	1.3	213.8	1.3	0.947	1.98	95.0	14	282.8	17.7	33.3	1.2

Table S2. Macroinvertebrate species list . Province, ecoregion, bioregion, littoral cell and study beaches are arranged from left to right in order of site sequence from north to south. An "X" indicates that the species was present. Taxa identified to lowest taxonomic level.

Province:	Cold Temperate NEP																		Warm Temperate NEP																
Ecoregion:	OR, WA, Vancouver						Northern California												Southern California Bight																
Bioregion:	Mendocinian														Montereyan				Southern Californian											Ensenadian					
Littoral cell:	Smith River		Klamath		Eureka		Ten Mile River		Russian River		Drakes Bay		San Francisco		Santa Cruz		Morro Bay						Santa Barbara					Santa Monica		Laguna			Oceanside		
Study beach: Lowest taxonomic level	CKMP	TDSP	GBB	RRB	MRB	SMD	TMD	VC	SCBN	SCBS	DB	LB	MB	RC	SUM	ZB	CAY	MOR	GAV	AQB	SNDS	IVW	COP	EUC	SCL	CARP	ARN	LEO	DUM	CRY	CLM	CAR	ELJ	BLK	SCR
Saccocirrus_sp	X			X						X			X	X																					
Scoletoma_zonata				X			X	X	X						X		X	X		X	X	X		X	X	X		X	X	X		X	X	X	X
Arabella_iricolor																			X			X	X	X				X	X	X		X			
Glycera_dibranchiata				X							X																								
Glycera_macrobranchia																		X				X		X											
Hemipodia_simplex	X		X	X							X		X	X						X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X
Nephtys_caecoides																		X														X	X		X
Nephtys_californiensis	X	X	X	X	X	X	X	X	X		X	X	X		X	X	X	X	X	X	X	X	X	X	X	X	X	X	X			X	X	X	X
Eteone_dilatae		X	X	X	X	X	X									X	X	X					X												
Pisione_hermansi	X	X	X	X						X			X	X																					
Syllis_sp																						X													
Owenia_collaris										X																									
Paraonella_platybranchia	X	X			X	X	X		X		X							X			X						X	X		X					
Magelona_pitelkai																		X																	
Dispio_sp.											X	X					X	X			X	X		X	X		X	X				X	X	X	X
Pygospio_californica	X			X	X	X	X	X			X	X				X	X	X					X			X									
Pygospio_elegans					X																														
Scolelepis_bullibranchia											X					X	X			X	X		X		X	X	X	X	X	X		X	X	X	X
Scolelepis_squamata	X				X	X														X		X	X	X			X		X	X			X		
Aphelochaeta_elongata							X																												
Cirriformia_sp																						X		X						X					
Arenicola_sp																						X		X											
Amastigos_acutus																							X			X									
Heteromastus_sp																							X												
Notomastus_spp_D																														X					
Notomastus_sp																							X												
Capitellidae										X			X											X										X	
Thoracophelia_dillonensis											X	X			X	X	X	X					X			X			X					X	X
Thoracophelia_mucronata											X	X					X	X	X	X		X	X	X				X				X		X	X
Thoracophelia_williamsi	X	X	X	X	X	X		X				X																							
Leitoscoloplos_pugettensis											X	X					X	X																	
Orbinia_johnsoni								X																											X
Scoloplos_armiger																				X		X		X		X		X		X		X	X	X	X
Stygocapitella_sp													X																						
Atylus_tridens							X															X	X			X	X								
Allorchestes_bellabella							X	X																											
Allorchestes_rickeri							X	X																											
Proboscinotus_loquax					X																														
Eohaustorius_sawyeri	X	X			X												X	X	X	X			X	X	X	X	X	X							
Eohaustorius_washingtonianus	X	X		X	X	X	X	X	X		X	X			X	X		X					X				X			X		X	X	X	X
Parallorchestes_sp																						X	X												
Gibberosus_devaneyi																																X		X	X
Gibberosus_myersi																								X	X		X						X	X	
Americhelidium_micropleon	X						X	X							X			X	X	X		X	X	X		X	X			X			X	X	
Hartmanodes_hartmanae	X						X																												
Pacifoculodes_spinipes	X	X			X	X			X			X																							
Grandifoxus_grandis				X	X	X	X	X	X	X		X																							
Heterophoxus_sp																X																			
Mandibulophoxus_gilesi	X				X	X	X	X	X	X		X					X				X			X			X			X					
Paraphoxus_sp																	X					X	X	X						X			X	X	X
Amphipoda I									X												X														
Lepidopa_californica																	X	X			X			X	X	X	X	X				X	X	X	X
Blepharipoda_occidentalis											X				X	X	X				X			X	X			X					X		X
Lissocrangon_stylirostris	X	X					X	X				X																							
Isocheles_pilosus																	X																		
Emerita_analoga	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X
Excirolana_chiltoni	X	X	X	X	X	X		X			X	X			X	X	X	X	X	X	X	X	X	X	X	X	X						X	X	X	X
Excirolana_linguifrons	X	X	X	X	X	X	X	X	X	X	X	X			X	X		X	X	X			X					X	X						
Gnorimosphaeroma_noblei																	X		X	X		X	X							X	X					
Archaeomysis_grebnitzki	X	X	X	X	X	X	X	X	X	X	X	X			X		X	X			X							X							X	
Archaeomysis_maculata																					X				X	X	X		X					X	
Archaeomysis_spp																															X				
Siliqua_sp															X		X																		
Donax_gouldii																					X			X	X	X	X					X	X	X	X
Tivela_stultorum															X	X	X	X			X	X		X	X	X	X							X	X
Neverita_lewisii															X																				
Nassarius_fossatus																X																			
Callianax_biplicata	X	X									X	X			X	X	X				X			X				X				X	X	X	
Callianax_pycna															X	X																			
Cerebratulus_californiensis																X																			
Paranemertes_californica					X											X	X	X			X	X	X	X	X	X	X	X		X		X	X	X	X
Paranemertes_peregrina																						X													
Carinoma_mutabilis	X	X			X	X																													
Nemertea		X				X					X		X	X		X	X	X		X		X	X	X	X	X		X			X	X	X	X	X
Eutichuridae			X																																
Lutica_sp																					X														
Araneae			X	X																	X			X											
Garypus_californicus																																			
Neomolgus_littoralis												X																	X						
Amblyderus_parviceps			X				X									X																			
Amblyderus_parvicollis																					X														
Akephorus_marinus								X								X	X			X		X					X								
Akephorus_obesus				X			X	X																											
Carabidae A	X																																		
Emphyastes_fucicola						X	X				X	X			X		X		X	X	X	X		X	X			X	X	X			X	X	X
Sitona_sp																						X		X											
Trigonoscuta_cruzi															X																				
Euspilotus_scissus																X						X			X										
Hypocaccus_bigemmeus																X																			
Hypocaccus_gaudens					X		X									X	X					X		X						X					X
Neopachylopus_aeneipunctatus																			X			X			X			X							X
Neopachylopus_sulcifrons							X	X								X						X		X	X	X		X					X		
Neopachylopus_spp																				X									X						
Histeridae			X			X								X																	X				
Cercyon_fimbriatus										X							X	X	X	X	X	X	X	X	X	X		X		X	X		X	X	X
Oedemeridae																											X								
Aleochara_sulcicollis												X			X		X		X	X	X	X		X		X				X			X	X	
Bledius_fenyesi																			X	X	X	X	X	X	X	X		X		X		X	X		X
Bledius_monstratus							X	X		X	X					X	X	X																	
Bledius_ornatus											X	X																							
Cafius_canescens							X	X			X	X			X	X	X		X		X	X		X		X		X							
Cafius_lithocharinus																				X		X													
Cafius_luteipennis																						X		X				X							
Cafius_seminitens							X										X		X		X	X		X		X		X							
Cafius_sulcicollis																												X							
Cafius_spp																													X						X
Hadrotes_crassus																						X		X											
Pontamalota_opaca																	X		X									X	X						
Pontamalota_terminalia										X																									
Tarphiota_fucicola					X					X							X							X											
Tarphiota_geniculata								X					X				X		X		X	X		X			X	X							
Thinopinus_pictus							X							X		X	X		X	X	X	X				X		X						X	
Staphylinidae			X	X													X																		
Coelus_ciliatus									X										X		X							X	X						
Coelus_globosus															X														X		X				
Coelus_spp																X																	X		
Epantius_obscurus																						X		X									X		
Phalaria_rotundata																X	X				X	X					X		X	X	X		X	X	X
Phaleromela_globosa															X																				
Tenebrionidae					X	X					X																								
Coleoptera A				X																															
Fucellia_costalis															X		X																		
Fucellia_rufitibia															X		X				X	X	X	X	X	X									
Fucellia_sp							X							X					X	X								X	X	X		X	X	X	X
Coelopa_vanduzeei																			X	X		X		X				X							
Dolichopodidae							X												X																
Empididae																X			X	X				X		X							X	X	X
Thoracochaeta_johnsoni																	X				X				X										X
Therevidae	X		X	X																	X														
Diptera A							X			X																									
Megalorchestia_benedicti					X		X	X	X	X	X	X			X	X	X	X	X	X	X	X		X	X	X	X	X	X	X			X	X	X
Megalorchestia_californiana						X	X	X			X	X			X		X	X			X	X			X			X	X	X	X		X		
Megalorchestia_columbiana	X	X	X	X	X	X		X	X	X		X	X	X		X	X												X						
Megalorchestia_corniculata																			X	X		X	X	X	X	X				X	X	X	X	X	X
Megalorchestia_minor							X									X					X	X		X	X		X	X	X		X				
Megalorchestia_pugettensis									X		X	X	X	X																					
Alloniscus_perconvexus	X	X	X	X	X	X	X	X	X	X	X			X	X	X	X			X	X	X			X		X	X	X	X					
Tylos_punctatus																											X	X	X	X				X	X

Table S3. Species richness, abundance, and biomass of the total community, lower beach, and wrack-associated macroinvertebrates for each study site arranged from top to bottom in order of site sequence from north to south.

			Richness			Mean abundance m-1			Mean biomass kg m-1	
Study site name	**Site code**	**Total community**	**Lower beach**	**Wrack-associated**	**Total community**	**Lower beach**	**Wrack-associated**	**Total community**	**Lower beach**	**Wrack-associated**
Clifford Kamph	CKMP	25	21	4	47946	44491	3455	5.68	5.60	0.07
Tolowa Dunes	TDSP	18	16	2	27120	26483	637	8.79	8.78	0.01
Gold Bluffs	GBB	17	9	8	79756	78160	1596	13.81	13.78	0.03
Reading Rock	RRB	22	15	7	59248	57168	2080	15.33	15.30	0.03
Mad River	MRB	25	19	6	281640	280048	1592	14.11	14.08	0.03
Samoa Dunes	SMD	22	16	6	121518	119633	1884	9.67	9.62	0.05
Ten Mile Dunes	TMD	34	18	16	71008	61956	9053	12.13	12.00	0.14
Virgin Creek	VC	26	16	10	14685	8658	6027	2.34	2.23	0.11
Salmon Creek North	SCBN	16	11	5	9609	7966	1642	2.06	2.03	0.03
Salmon Creek South	SCBS	17	9	8	7813	5823	1990	2.32	2.30	0.02
Drakes	DB	27	18	9	84263	81704	2559	4.36	4.30	0.06
Limantour	LB	26	17	9	23292	21289	2003	6.83	6.77	0.06
Montara	MB	11	8	3	13537	13263	274	4.87	4.87	0.01
Ross Cove	RC	11	5	6	2409	365	2044	0.29	0.21	0.08
Sumner	SUM	26	15	11	28639	27273	1367	30.41	30.38	0.03
Zmudowski	ZB	34	18	16	41858	36977	4881	68.70	68.64	0.06
Cayucos	CAY	45	24	21	320915	217825	103090	82.85	81.18	1.67
Morro Bay	MOR	27	23	4	107334	106485	849	19.16	19.15	0.01
Gaviota	GAV	26	9	17	48570	28181	20389	3.90	3.75	0.15
Arroyo Quemado	AQB	28	14	14	39180	19408	19771	1.67	1.13	0.54
Sands	SNDS	38	18	20	35209	13140	22069	10.83	10.58	0.25
Isla Vista	IVW	49	23	26	134301	51948	82353	3.47	1.75	1.73
Coal Oil Point	COP	28	24	4	50106	49206	900	2.27	2.25	0.01
East Campus	EUC	47	26	21	103801	57578	46223	4.55	3.82	0.73
Santa Claus	SCL	29	16	13	29821	12993	16828	6.23	5.81	0.42
Carpinteria	CARP	30	19	11	11934	7181	4753	4.51	4.48	0.03
Arnold Road	ARN	29	21	8	28045	21925	6120	12.13	12.06	0.07
Leo Carrillo	LEO	37	17	20	39937	18865	21072	8.68	8.51	0.17
Dume Cove	DUM	25	10	15	31309	19531	11777	6.20	5.92	0.28
Crystal Cove	CRY	28	16	12	21581	7830	13751	1.70	1.48	0.22
San Clemente	CLM	12	4	8	8537	4354	4183	1.70	1.63	0.07
Carlsbad	CAR	21	18	3	24595	12923	11671	1.45	1.30	0.15
San Elijo	ELJ	33	20	13	43697	14642	29055	2.45	2.11	0.34
Blacks	BLK	34	24	10	84135	80367	3769	2.60	2.52	0.08
Scripps	SCR	34	21	13	84819	69251	15567	5.05	4.95	0.11