Effects of beach replenishment on intertidal invertebrates: a 15-month, eight beach study.

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Abstract

Beach replenishment is an increasingly popular means to remediate coastal erosion, but no consensus exists regarding how long replenishment affects sandy beach intertidal invertebrates, key components of beach ecosystems. We monitored the intertidal invertebrate community for fifteen months following a replenishment project at eight beaches, each with replenished and control sections, across San Diego County. Nearly all taxa showed major declines in abundance immediately following replenishment. Populations of talitrid amphipods and the bean clam *Donax gouldii* recovered within one year, sooner than in previous studies. On some beaches, populations of the mole crab *Emerita analoga* bloomed four months after replenishment and were more numerous on replenished portions of beaches at that time. Mole crab populations subsequently declined and no longer differed by treatment. The polychaete community, composed of *Scolelepis* sp. and several other numerically important taxa, showed a strong replenishment-induced reduction in abundance that persisted through the end of the study. The large negative effect of replenishment on polychaetes, coupled with their overall importance to the invertebrate community, resulted in a more than twofold reduction in overall invertebrate abundance on replenished beaches at 15 months. Such reductions may have far reaching consequences for sandy beach ecosystems, as community declines can reduce prey availability for shorebirds and fish. As this and other recent studies have revealed longer times for the recovery of intertidal invertebrates than previously observed, longer study periods and more cautious estimates regarding the magnitude, variability, and duration of impacts of beach replenishment for management decision-making are warranted.

Keywords: Beach replenishment, Beach nourishment, Impact assessment, Community recovery, Polychaetes, Intertidal invertebrates

24

25 **Introduction**

26 Sandy beaches make up two-thirds of the Earth's shorelines, providing critical ecological,
27 commercial, and cultural resources for communities worldwide. As population growth and the
28 associated pressures of urbanization and climate change place further stress on sandy beaches,
29 the threat of degradation of these ecosystems increases (Brown & McLachlan, 2002; Peterson &
30 Bishop, 2005; Defeo et al., 2009). Because of their economic value, interest in preserving sandy
31 beach environments is growing, and a variety of practices to combat beach loss have been
32 implemented. Solutions range from constructing structures that maintain beach width, to
33 replenishment of beaches using offshore sand (McLachlan & Brown, 2006). Beach
34 replenishment, the loading of sand on depleted beaches, is viewed as an ecologically conscious
35 solution to erosion because it lacks the potential long-term impacts of hard solutions such as sea
36 walls (Hanson et al., 2002; McLachlan & Brown, 2006; Cooke et al., 2012). Nevertheless,
37 replenishment efforts often cite economic concerns such as coastal flooding risk or reduced
38 tourism as motivation for rebuilding beaches, while potential ecological consequences hold less
39 importance (Hanson et al., 2002; Lew & Larson, 2005; Sandag & U.S. Army Corps of
40 Engineers, 2011).

41 However, perturbations in the intertidal sandy beach community can have cascading
42 effects on higher trophic levels, reducing prey availability for shorebirds, juvenile fish, and a
43 host of other organisms (McLachlan & Brown, 2006). Reductions in foraging rates of shorebirds
44 and fish have been shown to follow human-induced reductions in benthic invertebrate
45 abundance, ranging from simple trampling to replenishment (Dugan et al., 2003; Neuman et al.,
46 2008; Peterson et al., 2006; Quammen, 1984; Wilber et al., 2003). Benthic invertebrates also

play an important role in nutrient cycling, breaking down both marine and terrestrial organic matter and providing coastal waters with the nutrient inputs essential for processes such as phytoplankton growth (Schlacher et al., 2008; Defeo et al., 2009; Cisneros et al., 2011; Dugan et al., 2011; Leewis et al., 2012). Accordingly, an ill-planned replenishment regime affecting beaches with high rates of shorebird use and nutrient cycling could have far reaching ecosystem consequences.

The limited number of published beach replenishment (also called nourishment) studies show considerable variation in results (Table 1). Although certain taxa (e.g. haustoriid amphipods, *Emerita talpoida*, *Scolelepis squamata*) are repeatedly investigated, no single study has addressed the responses of all core intertidal taxa (Table 1). For most taxa, overall responses to replenishment are uniform; amphipods, mole crabs (*Emerita* sp.), and bean clams (*Donax* sp.) tend to respond negatively, while the polychaete *Scolelepis squamata* responds positively or is unaffected by replenishment. Most of the differences between studies are found in the time it took for organisms to recover; Schlacher et al. (2012) saw complete recovery of lower intertidal haustoriid amphipods within five months, while Peterson et al. (2014) failed to see a return to control levels after three years. *Emerita talpoida*, *Donax* sp., and *Scolelepis squamata* all show variability among studies in time to recovery (Table 1). Another feature of previous studies is that they sampled either a single beach (Schlacher et al., 2012), used a time series design consisting of sampling different beaches replenished at various times in the past (Leewis et al., 2012), or employed designs in which sampled replenished and control beaches were spatially segregated rather than interspersed (Peterson et al., 2006, 2014).

Southern California has a long history of implementing beach replenishment to combat continual erosion (Willis & Griggs, 2003). Sediment contributions from sea cliff erosion and

70 river runoff naturally rebuild the region's beaches (Young & Ashford, 2006) but controls on cliff
71 erosion, in conjunction with dams and jetties, now interrupt the input and flow of sediment in
72 coastal areas (Moore et al., 1999; Sherman et al., 2002; Willis & Griggs, 2003). In light of these
73 changes and the potential economic cost of beach erosion, the county of San Diego has
74 implemented two recent replenishment projects. The first, which occurred in 2001, was largely
75 successful in expanding target beaches for several years post-replenishment, though no study of
76 its impact on invertebrates was performed, and provided impetus for an additional project in
77 2012 (Sandag & U.S. Army Corps of Engineers, 2011). During the fall of 2012, eight beaches
78 across San Diego County were replenished with a total of 1.76 million cubic meters of sand as
79 part of the Regional Beach Sand Project II (RBSP II; Figure 1). Only portions of each beach
80 were replenished, leaving unreplenished control sections with the intent of leaving areas for
81 foraging birds and fish. Replenishment sediment was pulled from three offshore sites with fine-
82 medium sand, selected for best match to the grain size structure of recipient sites (Sandag & U.S.
83 Army Corps of Engineers, 2011).

84 No previous examination of replenishment had the opportunity to examine its effects on
85 the total invertebrate community across so many beaches, with control and treatment regions of
86 each beach. Such a design facilitates the understanding the general affects of replenishment as
87 well as the heterogeneity of responses among beaches. This study examines the effects of the
88 2012 replenishment in San Diego in order to: 1) Quantify initial impacts and recovery rates of
89 each component of the sandy beach invertebrate community. 2) Quantify variability among
90 beaches both in the invertebrates present and in taxon-specific responses to replenishment. 3)
91 Assess patterns of community diversity and structure following replenishment and the variability
92 of response to replenishment across replicate beaches within a region.

2. Methods

2.1 Study sites and sampling design

Sampling was conducted at four time periods to account for both seasonality and time since disturbance: 1 (Fall 2012), 4 (Winter 2013), 12 (Fall 2013), and 15 (Winter 2014) months after replenishment. Days with the lowest low tides for that season were chosen for sampling, permitting transects to extend from the low low tide line to the upper limit of the intertidal. During each sample period, two replicate transects were surveyed in both the replenished and unreplenished sections, totaling four transects per site. 10cm-wide sample cores were taken at 20cm depth and 5m intervals along each transect. Sediment cores were sifted through a 1mm sieve, and remaining organisms were transferred to 70% or 95% EtOH. Organisms were then identified to the lowest possible taxonomic rank using morphology.

2.2 Taxon-specific abundances

Transects varied in length due to differences in slope, producing unequal numbers of cores per transect. To account for this irregularity, as well as the patchy distribution of organisms in the intertidal, mean abundance of each taxon per core was calculated for each transect. Standard ANOVA was deemed problematic for testing the effects of replenishment on these values, due to the high number of zeroes, especially when analyzing particular taxonomic groups, causing extreme non-normality of the data (Shapiro's test, $p < 0.0001$ for all taxa; Underwood 1997).

Instead of using classical ANOVA, we ran a series of restricted permutation significance tests (Anderson & Braak 2003). For permutations, transect values were sampled without replacement within each site, so as to break any existing associations between the explanatory

factors and the mean abundance data. Linear full factorial mixed models were then constructed treating replenishment status and time as fixed effects while beach and interactions with beach were random effects. We treated time as a nominal variable with four states (1, 4, 12, and 15 months after replenishment) because it simplified the model relative to treating year and season as separate factors. Inspection allowed assessment of whether time effects were due to seasonality, monotonic changes in abundance through time, or transient surges in abundance. A modified version of the PERMANOVA utility available in the R package *vegan* (Okansen et al., 2015) was used to rapidly permute the data. After each permutation, an F-statistic for each effect was calculated and the process was repeated 5000 times, allowing construction of a null distribution of F-statistics. F-statistics were calculated as appropriate for mixed models with balanced designs. Mean squares for fixed effects were tested over mean squares for interactions between that effect and the random effect beach. The effect of beach was tested over the composite mean square made up of the sum of the mean squares for the two two-way interactions involving the beach effect minus the mean square of the three-way interaction (Zar 1999). P-values were calculated from the proportion of permuted F-statistics greater than or equal to the observed values. This process was implemented to analyze mean abundance for the four most abundant taxa (Table 2) separately: *Emerita analoga*, talitrid amphipods, *Scoelelepis* sp., *Donax* sp., and for three groups of taxa: all polychaetes (including *Scoelelepis* sp.), all invertebrates, and all invertebrates except *Emerita analoga* (see below).

2.3 Community composition and recovery

In order to understand the effects of replenishment on community diversity, taxon richness was calculated for each transect. The mixed-model restricted permutation analysis described above was implemented analyzing richness values in place of abundance.

To visualize changes in community composition through time, non-metric multidimensional scaling (NMDS) was performed on the per-transect abundance data from the entire study as well as individual sampling periods, using the ordination tools available in the R package *vegan* for community ecology (Okansen et al., 2015). The data were log-transformed to reduce the weight of extremely abundant species (Anderson et al., 2011). A brief scan of the dataset revealed a high number of zeroes for abundance values, especially in the first month after disturbance. Zero-heavy datasets present challenges for many distance measures used in ordination. However, these zeroes might be informative, given that the common absence of an organism from samples could indicate an effect of disturbance. To include joint-absences in the ordination, a Euclidean dissimilarity matrix was constructed from the log-transformed community data (Anderson et al., 2011). Use of an adjusted Bray Curtis measure resulted in stress values greater than 0.20, indicating that the dissimilarity measure was not appropriate for ordination. To accompany each NMDS, PERMANOVAs were run on identical datasets to test the influence of replenishment, site, and their interaction on community structure using the same mixed model approach described above.

3. Results

3.1 Species surveyed and beach effects

For most specimens, taxonomy was resolved to genus or species level. Given our expertise, this was not possible for certain groups, such as Nemertea (ribbon worms) or amphipods of the family Talitridae (sand fleas) that are difficult to identify morphologically. A total of 20 different species or groups were recorded during the study (Table 2). Taxon abundances were highly variable, with the mole crab *Emerita analoga* accounting for 29% of all

collected organisms although its abundance varied greatly among beaches with 69.7% of all individuals coming from just two of the eight beaches. Only two individuals of the usually common pismo clam (*Tivela* sp.) were collected during the entire study (Dugan & Hubbard, 2000; Table 2). Several polychaetes were identified with no single species exceeding 12.7% of total invertebrate abundance. As a group, however, polychaetes accounted for 37.6% of all organisms sampled (Table 1).

High variability in abundance was observed across sediment cores, transects, and beaches. Only 12 taxa were sampled from all eight beaches. Even relatively abundant talitrid amphipods (16.2% of individuals) and the polychaete *Thoracophelia* sp. (5.4% of individuals) were completely absent from samples from certain beaches.

3.2 Effects on abundance

Replenishment affected the taxa studied in different ways and over different time periods. All invertebrate groups showed reduced densities on replenished sites 1 month after replenishment (Fig. 2) except *Emerita analoga* which was rare on both treatment and control sites at this time. Throughout the study polychaete density was reduced by replenishment and remained at approximately one third of control levels after fifteen months (Fig. 2; Table 3, treatment effect, $P < 0.01$). Density of polychaetes also tended to increase through time (Fig. 1; Table 3, time effect, $P < 0.01$). For all polychaetes taken together, there was also a significant three-way interaction (Table 3, $P < 0.01$), reflecting variation in the magnitude of the effect of replenishment across time and beaches (Fig. 4a). In general, on beaches with substantial densities of polychaetes at control sites, lower densities were found on replenished portions of these same beaches. On beaches with low densities of polychaetes on control sites, differences between

control and replenished portions were small or reversed, at least for some time periods (e.g. North and South Carlsbad, Fig. 3a).

Not surprisingly, *Scolelepis* sp., which accounted for 27.5% of all polychaetes, followed the same trend (Fig. 2) but the main effect of replenishment was not statistically significant because of variation among beaches in the effects of replenishment (Table 3, site*treatment interaction, $P < 0.05$). As with all polychaetes analyzed together, on beaches with the highest abundance of *Scolelepis* (Solana Beach, Imperial Beach, Table 2) there was a substantial density reduction at replenished portions while on beaches with relatively low *Scolelepis* sp. densities, differences between control and replenished sites were small and sometimes reversed.

Emerita analoga underwent a population boom at four months after replenishment (Fig. 2), with specimens from this period accounting for 89% of all mole crabs, and 25.1% of all invertebrates collected throughout the study. This temporary flush accounts for the effect of time (Table 3, $P < 0.001$) on this taxon. This population boom was only observed at some beaches (Fig. 3b; Table 3, site*time interaction $P < 0.001$). At this time, and on these beaches, the densities of mole crabs at replenished sites surpassed those found at control sites (Fig. 3b; Table 2, three-way interaction, $P < 0.01$). After 4 months, densities of *Emerita analoga* declined and no further differences were seen between control and replenished portions for the remainder of the study (Figs. 2, 3b).

Densities of the bean clam *Donax gouldii* fluctuated across census periods (Fig. 2; Table 3, effect of time, $P < 0.01$). Initially, replenishment tended to reduce the density of this clam but when its populations peaked 12 months after replenishment, density tended to be higher on replenished than control sites, though not significantly so (Fig. 2). This temporary trend of higher

Donax density on replenished sites was restricted to beaches where *Donax* reached substantial population densities (Table 3, three-way interaction, $P < 0.01$).

For talitrid amphipods, populations tended to increase through time (Fig. 2; Table 3, effect of time, $P < 0.05$). On beaches where amphipods reached high density at some time during the study (e.g. Cardiff and Moonlight, Table 1), replenishment tended to negatively influence density while at beaches with lower amphipod densities, this trend was small or reversed (Table 2, three-way interaction, $P < 0.001$).

If *Emerita analoga*, which was both transiently very abundant and positively affected by replenishment on beaches where populations bloomed, is removed from the analysis, the density of all other invertebrates grouped together was negatively affected by replenishment (Fig. 2; Table 3, treatment effect, $P < 0.05$), was higher in the second year of the study (Fig. 2; Table 3, time effect, $P < 0.001$), and was affected in complicated ways by interactions between treatment, time, and site due to the combination of taxon-specific effects detailed earlier (Fig. 1; Table 3).

Due largely to the population flush and transient effects of replenishment on *Emerita analoga*, replenishment had no significant effect on overall invertebrate abundance (Table 3) although total invertebrate density on replenished transects averaged 48% that of control transects after 15 months (Fig. 2). The treatment by time interaction reflects primarily the increased abundance of invertebrates on replenished portions of beaches at 4 months, due to the flush of *Emerita analoga*, while reduced invertebrate densities on replenished sites were seen at all other time periods (Fig. 2). The treatment by site interaction reflects differences in the average effect of replenishment between beaches that exhibited high densities of *Emerita analoga* at four months and those that did not. Interactions involving time since disturbance also reflect transient, beach-specific, mole crab densities (Fig. 3).

3.3 Effects on Diversity

Replenishment reduced taxon richness (Table 4, Fig. 4). The effect was strong at 1 month, where control sites had, on average, three-fold more taxa than replenished sites. By 15 months post-disturbance, effects of replenishment on this diversity measure had disappeared. The significant effect of time on diversity is largely due to seasonality, with higher diversity during fall than winter census periods. The strong treatment by time interaction reflects the diminished effect of replenishment over the course of study.

3.4 Community structure and recovery

Non-metric multidimensional scaling (NMDS) of the log-transformed community data across all time periods using a Euclidean distance measure showed clustering of the four most abundant polychaetes (*Scolelepis* sp., *Nephtys californiensis*, *Thoracophelia* sp., unknowns), indicating similarities in distribution and abundance across time and replenishment (Figure 5). Three less common polychaetes, *Naineris dendritica*, *Orbinia johnsoni*, and *Hemipodia borealis*, did not group with any other polychaete taxa. Separation of *Emerita analoga*, *Donax gouldii*, and talitrid amphipods suggest divergent patterns of abundance across time and treatment. A PERMANOVA revealed significant effects of replenishment ($P = 0.004$) and time since disturbance ($P = 0.001$) on community structure, as well as a strong interaction effect ($P = 0.013$).

This replenishment-by-time interaction is elucidated when NMDS and PERMANOVA analysis are applied to each time period (Figure 6). One month after replenishment transects were distinctly clustered by treatment ($P = 0.001$), with transects from replenished beaches being nearly identical to each other, and control transects showing considerable variability. However, no overall replenishment effect was observed for the remaining time periods. Rather, a strong replenishment-by-beach interaction persisted from four months on, indicating variability in the effect of replenishment across beach communities. Even at the end of the study, invertebrate

communities at some beaches were still strongly affected by replenishment ($P = 0.009$). The NMDS plot at 15 months showed clear separation of transects at Imperial Beach (IB), Moonlight (Moon), Cardiff (Car), and South Carlsbad (SC) according to replenishment status — indicating fundamental differences in the invertebrate communities — while no pattern was evident in the remaining four beaches.

Discussion

We found substantial effects of beach replenishment on sand-dwelling invertebrates such that replenished sections of beaches, on average, had only 48% as many invertebrates as controls after 15 months (Fig. 2). Beach replenishment had major impacts on community composition as well, initially lowering standard metrics of diversity, and affecting the structure of communities on some beaches through to the end of the study (Figure 5). A salient feature of this study's design was the assessment of variation across beaches in the effects of replenishment. Strong two and three way interactions involving site were found for all taxa or groups examined, and in community-wide analyses. This variation among beaches within a region may help explain variation among studies in the effects of replenishment summarized in Table 1 and caution against broad generalizations about the magnitude and duration of replenishment effects, even within a region. Nevertheless, the observed overall effects of replenishment on invertebrate abundance may have implications up the food chain for birds and fish known to feed on them.

The effects of replenishment on invertebrate abundance were primarily driven by the responses of polychaetes and the mole crab *Emerita analoga*. The response displayed by *E. analoga* — blooming at four months and becoming more common in replenished sites — had a major impact on total invertebrate densities, offsetting the decline in polychaetes such that no

overall effect of replenishment on total abundance of invertebrates was detected. After the *E. analoga* bloom subsided, polychaetes were the numerically dominant component of the community, and exhibited reduced densities on replenished portions of beaches throughout the study.

These results regarding *Emerita analoga* and polychaetes conflict with the findings of previous studies, which reported pronounced negative effects of replenishment on *Emerita talpoida* (Hayden & Dolan, 1974; Peterson et al., 2000a, 2006, 2014; Leewis et al., 2012; Manning et al., 2014) and positive or neutral effects on *Scolelepis* sp. and/or polychaetes in general (Menn et al., 2003; Peterson et al., 2006, 2014; Leewis et al., 2012; Manning et al., 2014; but see Schlacher and Thompson, 2012). The response of *E. analoga* may be explained in part by processes other than replenishment that produce boom-bust cycles. The long pelagic duration (3-6 months) of *E. analoga* larvae make it possible for beach populations to be sustained by long distance recruits (Efford, 1969; Dugan et al., 1991; Dugan & Hubbard, 1996; Dawson et al., 2011). Coastal currents may affect the spread of larvae and produce sudden, site-specific, population blooms (Dugan & Hubbard, 1996; Sorte et al., 2001; Diehl et al., 2007). The observed bloom of *E. analoga* at four months may have resulted from a significant recruitment event on certain beaches driven by changes in local ocean conditions, followed by mortality and population decline. What is less clear is why mole crabs were more abundant on replenished sites. Burrowing experiments show *E. analoga* to be a substrate generalist outside of very fine-textured sediment (Dugan et al., 2000; Viola et al., 2013) and previous studies have shown no correlation with environmental variables such as sediment structure and beach slope (Dugan & Hubbard, 1996). It is possible that replenishment changed swash zone characteristics which are known to affect settlement of *E. analoga* and other crustaceans (Cubit, 1969; Dugan et al., 1991,

1994, 2000; McLachlan, 1996; McLachlan & Brown, 2006; Speybroeck et al., 2006; Defeo & McLachlan, 2011). Another possibility is that recently replenished portions of beaches may have been less compacted than control sections facilitating burrowing and increasing residence times of mole crabs such that they were aggregated on replenished sites.

Previous studies of the effects of replenishment on polychaetes (Menn et al., 2003; Leewis et al., 2012; Manning et al., 2014; Peterson et al., 2006, 2014) often focused on a single species, *Scolelepis squamata*. None reported long-term negative effects and in some cases replenishment had a positive effect on the polychaete(s) studied (Menn et al., 2003; Leewis et al., 2012; Manning et al., 2014). In our study, *Thoracophelia* sp., *Nephtys californiensis*, *Hemipodia simplex*, *Naineris dendritica*, *Orbinia johnsoni*, and unknown polychaetes accounted for a large proportion (24%) of all collected invertebrates, were found in approximately equal numbers, and in aggregate were twice as abundant as *Scolelepis* sp. While analyzing *Scolelepis* sp. alone returned no significant effect of replenishment, mean densities were consistently lower in replenished than control sites (Fig. 2) while as a community (including *Scolelepis* sp.), polychaetes showed reduced numbers on replenished sites through the end of the study. Reasons for the conflict between our findings and previous studies are unknown. Sand churned up from offshore and thickly deposited on beaches is likely to be devoid of intertidal polychaetes and may have caused mortality of buried ones. Subsequent population growth will most likely occur via recruitment by planktonic larvae, due to the limited mobility of sandy beach polychaetes (Rouse & Pleijel, 2001). But in contrast to *E. analoga*, short times in the plankton (1-2 months for *T. mucronata* and *S. squamata*; Dales, 1952; Speybroeck et al., 2007) and long times until reproduction (2 years for *S. squamata*; Speybroeck et al., 2007) could delay recovery of denuded polychaete populations following replenishment. Interactions between regional variation in life

history (Speybroeck et al. 2007), recruitment, morphology (Williams, 2007; Rocha & Paiva, 2012) and beach and fill characteristics may explain divergent results between ours and previous replenishment studies.

One of the more striking results in this study was how strongly beach-specific idiosyncrasies influenced invertebrate abundance. Many beaches exhibited extreme asymmetry in community structure, often with one group dominating the intertidal macrofauna (Table 2). For instance, tailitrid amphipods were 36 times more abundant than the second most common group at North Carlsbad. In contrast, Batiquitos hosted a more evenly distributed, low-density intertidal community with similar numbers of mole crabs, amphipods, and polychaetes. All taxa examined were affected to some degree by significant interactions between sites and other factors. At half of the beaches, densities of *E. analoga* were near zero for the entire study, while beaches that accumulated appreciable numbers of mole crabs uniformly displayed increased densities on replenished sites. Polychaete responses were similarly variable. On beaches where polychaete populations increased substantially through the course of the study, population densities were higher on control portions (Fig 3). On beaches where polychaete densities were lowest at the end of the study, differences between replenished and control sites were small or reversed. Observed interactions between site and treatment effects in whole-community analyses were largely driven by these site-specific effects on *E. analoga* and polychaetes. Variability is characteristic of sandy beach communities (Dugan et al., 2000; Defeo & McLachlan, 2005; Schlacher et al., 2008) and complicates our ability to generalize replenishment affects. The necessity of examining multiple beaches to document the range of replenishment effects is clear.

Reduction of average beach invertebrate densities by half, as observed here through 15 months, could seriously disrupt the sandy beach food web. Southern California beaches are host

to more than twenty five species of shorebirds that forage for benthic invertebrates (Dugan et al., 2000, 2003; Hubbard & Dugan, 2003). Common prey items include *Emerita analoga*, talitrid amphipods, isopods, and polychaetes (Stenzel et al., 1976; Quammen, 1984; Hubbard & Dugan, 2003; Neuman et al., 2008). Reductions in invertebrate abundance can cause decreased habitat use by shorebirds and fish (Peterson et al., 2006; Peterson et al., 2014; Quammen, 1984; Dugan et al., 2003; Speybroeck et al., 2006; Wilber et al., 2003; Peterson et al., 2000b; Dolbeth et al., 2008). Therefore, the observed decline in invertebrate abundance could negatively impact shorebird and fish feeding for at least fifteen months after replenishment. The timing of replenishment may exacerbate effects on shorebirds. Migrating species in Southern California account for a large increase in shorebird numbers during the winter and spring, putting extra pressure on invertebrate populations during these times (Hubbard & Dugan, 2003). Although the *E. analoga* bloom in winter 2013 likely favored foraging shorebirds, a winter decline—like that seen at 15 months—might put greater stress on shorebird populations than a similar effect in summer. This is especially relevant for areas like San Diego, where degradation of already limited mudflats force shorebirds to rely heavily on sandy beaches (Page et al., 1999; Hubbard & Dugan, 2003).

The environmental impact statement for this replenishment project (RBSP II) anticipated a complete recovery of the intertidal invertebrate community within one year of sand deposition (SANDAG & U.S. Army Corps of Engineers, 2011). Full recovery will clearly take longer. Because more recent studies show longer recovery times (this study; Peterson et al., 2014; Manning et al., 2014), longer estimates regarding the extent of replenishment's effects are warranted. Keeping in mind that our results for some taxa conflict with those of previous studies, further studies of replenishment affects are warranted in order to understand this variation. With

more data, longer studies, and greater attention to which physical features of beaches account for variation in replenishment effects, we may gain a deeper understanding of how replenishment impacts beach invertebrates. Our well-replicated study of the entire invertebrate community points to the need to understand and account for among-beach variation both as a research goal and management necessity.

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Summary of findings from peer-reviewed beach replenishment studies. Initial response (R) and time until replenishment effects are no longer observed (T) are listed for intertidal taxa when available. A “-” indicates reduced abundance, a “+” indicates increased abundance, and “=” indicates no significant difference. A “>” indicates that replenishment effects were still observable at the end of the study.

[illegible]

Table 2

Counts of all taxa collected during the study, organized by sample beach.

Organism	Batiquitos	Cardiff	Imperial Beach	Moonlight	North Carlsbad	Oceanside	Solana Beach	South Carlsbad	Total Abundance	Relative Abundance (%)
<i>Emerita analoga</i> (C)	65	19	16	14	289	24	212	80	719	28.20
Talitrid amphipods (C)	44	145	0	164	8	4	25	24	414	16.20
<i>Scolecipis</i> sp. (P)	31	23	101	41	7	19	88	14	324	12.70
<i>Donax</i> spp. (B)	25	25	4	70	4	31	55	17	231	9.04
Unknown polychaetes	17	15	51	23	5	8	19	7	145	5.68
<i>Thoracophelia</i> spp. (P)	4	44	83	4	2	1	0	0	138	5.40
<i>Nephtys californiensis</i> (P)	5	11	32	16	6	13	16	11	110	4.31
<i>Hemipodia simplex</i> (P)	7	0	6	17	8	10	32	4	84	3.29
<i>Naineris dendritica</i> (P)	13	14	1	22	1	1	20	1	73	2.86
<i>Orbinia johnsoni</i> (P)	9	11	1	9	5	1	30	5	71	2.78
Insects	0	0	0	2	0	0	51	0	53	2.08
<i>Excirolana</i> spp. (C)	2	7	14	14	1	2	2	7	49	1.92
Nemertea	5	7	9	10	2	1	5	10	49	1.92
Unknown (heavily damaged)	0	2	8	7	0	0	15	5	37	1.45
<i>Blepharipoda</i> spp. (C)	2	1	10	3	2	6	2	2	28	1.10
Spionidae (P)	0	3	2	2	0	0	4	3	14	0.55
<i>Olivella</i> spp. (G)	0	5	0	0	0	3	0	0	8	0.31
Unknown Crustaceans	0	0	4	0	0	0	0	0	4	0.16
<i>Tivela</i> spp. (B)	1	0	1	0	0	0	0	0	2	0.08
<i>Phialidium</i> spp. (N)	0	1	0	0	0	0	0	0	1	0.04

Table 3

Restricted permutation analysis of variance of density (animals per core) of individual taxa and groups of taxa. Factors are treatment (Tr), time since disturbance (TSD), and beach (Be): * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.

Factor	df	Total		<i>Emerita analoga</i>		Amphipods		<i>Donax gouldii</i>		<i>Scolecipis</i> spp.		All Polychaetes		No <i>Emerita analoga</i>	
		MS	F	MS	F	MS	F	MS	F	MS	F	MS	F	MS	F
Tr	1	5.72	1.93	2.32	6.71**	0.48	1.65	0.01	0.16	0.54	2.96	6.43	7.18**	15.33	9.15*
TSD	3	5.73	1.43	14.08	4.48***	0.69	2.65*	0.24	4.20**	0.33	2.93*	1.80	3.47*	5.81	6.42***
Be	7	6.06	0.96	2.87	0.93	0.66	1.94	0.12	1.79	0.26	1.08	1.44	1.32	3.57	1.71
Tr x TSD	3	4.02	5.80**	2.03	5.00**	0.09	0.42	0.07	1.78	0.02	0.37	0.15	0.47	0.66	1.34
Tr x Be	7	2.97	4.27*	0.35	0.85	0.29	1.39	0.04	1.06	0.18	3.13*	0.90	2.77	1.68	3.39
TSD x Be	7	4.02	5.79**	3.14	7.74**	0.26	1.24	0.06	1.43	0.11	1.98	0.52	1.61	0.90	1.83
Tr x TSD x Be	21	0.69	2.00*	0.41	2.43*	0.21	5.18**	0.04	4.83**	0.06	0.75	0.32	3.44*	0.49	2.72*
Residuals	64	0.35		0.17		0.04		0.01		0.08		0.09		0.18	

Table 4

Restricted permutation analysis of variance in taxon richness. Factors and significance levels as in Table 3.

Taxon Richness			
Factor	df	MS	F
Tr	1	182.88	10.33*
TSD	3	51.40	6.74**
Be	7	18.11	0.87
Tr x TSD	3	27.55	5.98**
Tr x Be	7	17.70	3.84*
TSD x Be	21	7.63	1.66
Tr x TSD x Be	21	4.61	1.65
Residuals	64	2.79	

Figure 1

Project map for Regional Beach Sand Project III (RBSP II), with recipient sites indicated by green circles.

Figure 2

Abundance of common taxa through time at nourished and control beaches, represented by the mean number of individuals per core. The time since nourishment in months is plotted on the x axis. 95% confidence intervals are shown for each census period.

Figure 3

Density of the two most common groups, *Emerita analoga* and Polychaetes, through time and by beach.

Figure 4

Taxon richness through time at nourished and control beaches. 95% confidence intervals are displayed for each time period.

Figure 5

NMDS of log-transformed abundance data using a Euclidean distance measure. Species scores for the most abundant taxa and all polychaetes included. Stress = 0.167.

Figure 6

Euclidean distance based-NMDS of log-transformed community data, partitioned by time since disturbance. Transects are labeled as abbreviations of source beach. Red labels indicate the transect is from the control portion of that beach, while green labels indicate it is from the nourished portion. PERMANOVA p-values for nourishment, site, and the nourishment-by-site interaction are located in the top right.

Figure 1 **Figure 2**

Figure 3

Figure 4

Figure 5

Figure 6

Graphical Abstract

No sand (control)

Sand added to improve beach

X 8 beaches

Individuals per core

Mole crabs
(*Emerita analoga*)

Months after treatment

All other invertebrates

Months after treatment