Title
Long-term effects of beach nourishment on intertidal invertebrates

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UNIVERSITY OF CALIFORNIA, SAN DIEGO

Long-term effects of beach nourishment on intertidal invertebrates

A Thesis submitted in partial satisfaction of the requirements for the degree
Master of Science
in
Biology

by

Tyler Brock Wooldridge

Committee in charge:
Professor Joshua Kohn, Chair
Professor David Holway
Professor Kaustuv Roy

2015
The Thesis of Tyler Brock Wooldridge is approved and it is acceptable in quality and form for publication on microfilm and electronically:

__________________________________________

__________________________________________

__________________________________________

Chair

University of California, San Diego

2015
DEDICATION

I dedicate this thesis to my parents, who don’t think it’s strange that I study worms.
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ABSTRACT OF THE THESIS

Long-term effects of beach nourishment on intertidal invertebrates

by

Tyler Brock Wooldridge

Master of Science in Biology
University of California, San Diego 2015
Professor Joshua Kohn, Chair

Although beach nourishment is an increasingly popular means to remediate coastal erosion, no consensus exists regarding how long nourishment affects sandy beach intertidal invertebrates, key components of sandy beach ecosystems. We monitored the intertidal invertebrate community for fifteen months following a nourishment project at eight beaches across San Diego County. Each beach was split into nourished and control sections. Nearly all taxa showed major declines in abundance immediately following nourishment. Populations of talitrid amphipods and the bean clam Donax gouldii recovered within one year, sooner than in previous studies. Populations of the mole crab Emerita
analoga bloomed at four months after nourishment, and were more numerous on nourished portions of beaches at that time. Mole crab populations subsequently declined and no longer differed by treatment. The polychaete community, composed of Scolelepis spp. and several other numerically important taxa, showed a strong nourishment-induced reduction in abundance that persisted through the end of the study. The large negative effect of nourishment on polychaetes, coupled with their overall importance to the invertebrate community, resulted in a more than twofold reduction in overall invertebrate abundance on nourished 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, more cautious estimates regarding the magnitude and duration of impacts of beach nourishment should be applied to management practices.
Chapter One

Introduction

Sandy beaches make up two-thirds of the Earth’s shorelines, providing critical ecological, commercial, and cultural resources for communities worldwide. As population growth and the associated pressures of urbanization and climate change place further stress on sandy beaches, the potential for degradation of these ecosystems increases (Brown & McLachlan 2002, Peterson & Bishop 2005, Defeo et al. 2009). Because of their economic value, interest in preserving sandy beach environments is growing, and a variety of practices to combat beach loss have been implemented. Solutions range from constructing protective, stabilizing structures that maintain beach width, to nourishment of beaches using offshore sand (Mclachlan & Brown 2006). Beach nourishment, the loading of sand on depleted beaches, is viewed as an ecologically conscious solution to erosion because it lacks the potential long-term impacts of hard solutions such as sea walls (Hanson et al. 2002, Mclachlan & Brown 2006, Cooke et al. 2012). Nevertheless, nourishment efforts often cite economic concerns such as coastal flooding risk or reduced tourism as motivation for rebuilding beaches, while potential ecological consequences hold less importance (Hanson et al. 2002, Lew & Larson 2005, Sandag & U.S. Army Corps of Engineers 2011). With beach nourishment becoming an increasingly widespread practice to combat coastal erosion, it is important to develop an understanding of how the process impacts sandy beach ecosystems, particularly in the intertidal zone where benthic invertebrates are abundant. While the initial disturbance of
adding sand is likely to have uniformly negative effects across taxa, the resulting
transformation of fundamental beach characteristics (e.g. slope, grain size) will interact
with the life histories and ecologies of intertidal invertebrates to shape community

Unsurprisingly, the limited number of published intertidal beach 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 nourishment are uniform; amphipods, mole crabs (Emerita spp.),
and bean clams (Donax spp.) tend to respond negatively, while the polychaete Scolelepis
squamata responds positively or is unaffected by nourishment. Most of the differences
between studies are found in the time it took for organisms to recover; Schlachler 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 spp., and Scolelepis squamata all show variability among studies in time
to recovery (Table 1).
Table 1. Summary of findings from peer-reviewed intertidal nourishment literature investigating the responses of macroinvertebrates. “Overall response” refers to the abundance of organisms at nourished sites when compared to control sites during the study; a “-” indicates reduced abundance, a “+” indicates increased abundance, and “=” indicates no significant difference. “Recovery time” is defined as the time at which control abundance was no longer significantly different from nourished abundance (when the overall response is no longer apparent). A “>” indicates that recovery had not occurred by the end of the study.
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<th>Emerita spp.</th>
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<th>Recovery Time</th>
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The effects of beach nourishment are not limited to benthic invertebrates. Perturbations in the intertidal sandy beach community can have cascading effects on higher trophic levels, reducing prey availability for shorebirds, juvenile fish, and a host of other organisms (Mclachlan & Brown 2006). Reductions in foraging rates of shorebirds and fish have been shown to follow human-induced reductions in benthic invertebrate abundance, ranging from simple trampling to nourishment (Dugan et al. 2003; Neuman et al. 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 nourishment regime affecting beaches with high rates of shorebird use and nutrient cycling could have far reaching ecosystem consequences.

More data are needed in order to achieve a comprehensive understanding of how beach nourishment affects intertidal macrofauna through time, so as to better inform future management decisions. Southern California has a long history of implementing beach nourishment to combat continual erosion (Willis & Griggs 2003). Sediment contributions from sea cliff erosion and river runoff naturally rebuild the region’s beaches (Young & Ashford 2006) but controls on cliff erosion, in conjunction with dams and jetties, now interrupt the input and flow of sediment in coastal areas (Moore et al. 1999, Sherman et al. 2002, Willis & Griggs 2003). In light of these changes and the potential economic cost of beach erosion, the county of San Diego has implemented two recent nourishment projects. The first, which occurred in 2001, was largely successful in expanding target beaches for
several years post-nourishment, providing a sound framework for an additional project in 2012 (Sandag & U.S. Army Corps of Engineers 2011). This study examines the effects of the 2012 nourishment in San Diego in order to quantify initial impacts and recovery rates of sandy beach invertebrates.
Methods

Study sites and sampling design

During the fall of 2012, eight beaches across San Diego County were replenished with a total of 1.76 million cubic meters of sand as part of the Regional Beach Sand Project II (RBSP II; Figure 1). Only portions of each beach were nourished, leaving unnourished (control) sections with the intent of sustaining foraging birds and fish. Nourishment sediment was pulled from three offshore sites with fine-medium sand, selected for best match to the grain size structure of recipient sites (Sandag & U.S. Army Corps of Engineers 2011).

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 nourishment. Days with low neap tides were chosen for sampling, permitting transects to extend from the lowest low tide line to the upper limit of the intertidal. During each sample period, two replicate transects were surveyed in both the nourished and unnourished 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.

**Data Analysis**

**Taxon-specific abundances**

Transects varied in length as a function of nourishment and natural beach width, 
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. An ANOVA was deemed inappropriate for testing 
the effects of nourishment on these values, due to the high number of zeroes 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). In order to test the effects of nourishment on 
taxon abundance at different times after nourishment, the data were analyzed separately 
for each of the four observation periods. Linear models were then constructed, treating 
nourishment status as a fixed effect and beach as a random effect, after which an F-statistic 
for the nourishment effect was calculated. 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. After permuting the data, the original 
linear model was re-fit and F-statistics for all factors recalculated. The process was 
repeated 5000 times, allowing construction of a null distribution of F-statistics. 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 all
invertebrates and for the five most abundant taxa (Table 2) separately: *Emerita analoga*,
talitrid amphipods, *Scolelepis spp.*, *Donax spp.*, and all polychaetes (including *Scolelepis
talitrid amphipods, Scolelepis spp., Donax spp.*, and all polychaetes (including *Scolelepis
talitrid amphipods, Scolelepis spp., Donax spp.*, and all polychaetes (including *Scolelepis
spp.*).

**Community composition and recovery**

In order to understand the effects of nourishment over time on community diversity,
taxon richness and Shannon-Weaver index values were calculated for each transect. The
permutation tests described above were implemented for these diversity indices, analyzing
richness and Shannon 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. 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, we concluded that 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 community data (Anderson et al. 2011). To
accompany each NMDS, PERMANOVAs were run on identical datasets to test the
influence of nourishment and beach on community structure.
Results

Species surveyed and beach effects

A total of 20 different species or groups were recorded during the study (Table 2). 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) which are difficult to identify morphologically. Taxon abundances were highly variable, with the mole crab *Emerita analoga* accounting for 29% of all collected organisms, while only two individuals of the usually common pismo clam (*Tivela spp.*) were collected during the entire study (Dugan & Hubbard 2000; Table 2).

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 spp.* (5.4% of individuals) were completely absent from certain sites. Restricted permutation F-tests and PERMANOVAs showed sample beach to have a significant effect on total organismal abundance and community structure (p = 0.0446 and p = 0.001, respectively).
Table 2. Taxon abundance info, broken down by beach. Values are counts of each group over the course of the study. (C) = Crustacean, (P) = Polychaete, (B) = Bivalve, (G) = Gastropod, (N) = Nemertean

<table>
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<th>Batiquitos</th>
<th>Cardiff</th>
<th>Imperial Beach</th>
<th>Moonlight</th>
<th>North Carlsbad</th>
<th>Oceanside</th>
<th>Solana Beach</th>
<th>South Carlsbad</th>
<th>Total Abundance</th>
<th>Relative Abundance (%)</th>
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<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>1</td>
<td>0.04</td>
</tr>
</tbody>
</table>
**Effects on abundance**

The intertidal invertebrate community showed significantly reduced abundances at treatment sites one month after nourishment (Table 3, p < 0.001). Taxon-specific analyses confirmed that all common groups except the mole crab *E. analoga* were significantly reduced in nourished sites at one month. At four months, no effect was observed for talitrid amphipods and *Scolelepis spp.*, taxa with low abundance in both nourished and control sites during this time period, while the polychaete community and *D. gouldii* continued to show significantly reduced abundances at nourished sites. In contrast, *Emerita analoga* underwent a population boom at the four month mark that accounted for 89% of all mole crabs collected throughout the study. Numbers of mole crabs at nourished sites surpassed those of control sites (p < 0.01), a positive response to nourishment not seen in any other organism or time period for the duration of the study. The boom in *E. analoga*, accompanied by the positive effect of nourishment on this species during this time period, resulted in a non-significant increase in total invertebrate abundance in nourished sites at four months.

At twelve months, nourishment had a weak effect on the whole community, which showed marginally lower mean abundance at treatment sites (p = 0.055). The polychaete community continued to show significantly reduced abundances at nourished sites. Talitrid amphipods, *D. gouldii*, and *Scolelepis spp.* showed no effects of nourishment at 12 months, as did *E. analoga*, which exhibited a marked decline in abundance from the previous sample period. By 15 months, total invertebrate abundance and polychaete abundance were significantly reduced in nourished sites relative to control sites (Table 3), while no significant difference was observed for the other groups.
Table 3. Mean number of organisms per core in nourished (N) and control (C) sites, for different taxa and sampling periods since disturbance: * p ≤ 0.05; ** p ≤ 0.01; *** p ≤ 0.001.
<table>
<thead>
<tr>
<th>Group</th>
<th>1 Month Nourished</th>
<th>1 Month Control</th>
<th>4 Months Nourished</th>
<th>4 Months Control</th>
<th>12 Months Nourished</th>
<th>12 Months Control</th>
<th>15 Months Nourished</th>
<th>15 Months Control</th>
</tr>
</thead>
<tbody>
<tr>
<td>All Organisms</td>
<td>0.136</td>
<td>1.174***</td>
<td>1.962</td>
<td>1.489</td>
<td>1.084</td>
<td>1.452</td>
<td>0.774</td>
<td>1.615*</td>
</tr>
<tr>
<td><em>Emerita analoga</em></td>
<td>0.016</td>
<td>0.040</td>
<td>1.886</td>
<td>0.863**</td>
<td>0.115</td>
<td>0.052</td>
<td>0.041</td>
<td>0.027</td>
</tr>
<tr>
<td>Talitrid amphipods</td>
<td>0.000</td>
<td>0.195***</td>
<td>0.004</td>
<td>0.020</td>
<td>0.219</td>
<td>0.272</td>
<td>0.225</td>
<td>0.453</td>
</tr>
<tr>
<td><em>Donax gouldii</em></td>
<td>0.012</td>
<td>0.139**</td>
<td>0.006</td>
<td>0.046*</td>
<td>0.277</td>
<td>0.178</td>
<td>0.087</td>
<td>0.078</td>
</tr>
<tr>
<td><em>Scolelepis spp.</em></td>
<td>0.007</td>
<td>0.118**</td>
<td>0.020</td>
<td>0.090</td>
<td>0.151</td>
<td>0.342</td>
<td>0.150</td>
<td>0.296</td>
</tr>
<tr>
<td>All Polychaetes</td>
<td>0.061</td>
<td>0.431***</td>
<td>0.057</td>
<td>0.381**</td>
<td>0.390</td>
<td>0.855**</td>
<td>0.345</td>
<td>0.979*</td>
</tr>
</tbody>
</table>
Effects on diversity

Mean taxon richness per transect was significantly higher in control than nourished sites up through 12 months after nourishment (Table 4). The effect was particularly strong at 1 month, where control sites had, on average, six more taxa than nourished sites. By 15 months post-disturbance, no effect was detected.

Mean Shannon-Weaver diversity was significantly higher in control sites up through four months after disturbance. For the remainder of the study, Shannon-Weaver diversity was not significantly different between nourished and control sites.

Table 4. Mean richness per transect and Shannon-Weaver index per transect, broken down by treatment and time since disturbance. Significance values: * p ≤ 0.05; ** p ≤ 0.01; *** p≤0.001.

<table>
<thead>
<tr>
<th>Time period</th>
<th>Mean richness per transect</th>
<th>Mean Shannon-Weaver index per transect</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Nourished</td>
<td>Control</td>
</tr>
<tr>
<td>1 Month</td>
<td>1.75</td>
<td>6.75***</td>
</tr>
<tr>
<td>4 Months</td>
<td>1.625</td>
<td>4.19***</td>
</tr>
<tr>
<td>12 Months</td>
<td>4.875</td>
<td>6.87***</td>
</tr>
<tr>
<td>15 Months</td>
<td>4.875</td>
<td>5.12</td>
</tr>
</tbody>
</table>

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* spp., *Nephtys californiensis*, *Thoracophelia* spp., unknowns), indicating similarities in distribution and abundance across time and nourishment (Figure 2).
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 nourishment. A PERMANOVA of the same dataset revealed significant effects of nourishment (p = 0.001) and time since disturbance (p = 0.001) on community structure, but no interaction effect. An identical analysis of the polychaete community showed a strong effect of time since disturbance (p = 0.001) and nourishment (p = 0.002) on community structure.

Breaking down the NMDS by sample period showed distinct clustering of transects by treatment in the first month after nourishment (Figure 3). Nourishment transects show nearly identical scores, while control transects are less similar to each other. Grouping of nourished samples, at least along axis 2, persisted through 4 months after nourishment,
followed by a more random distribution of samples with respect to treatment at 12 and 15 months.

However, the seemingly random distribution of samples with respect to treatment at 12 and 15 months begins to show a pattern when taking source beach into account. Transects within a given treatment and from the same beach show greater similarity to each other than to transects from the same treatment from another beach (e.g. Moonlight, Cardiff, Imperial Beach, and South Carlsbad at 15 months). PERMANOVAs confirmed this, showing a significant effect of nourishment on community composition at all sampling periods except twelve months, and a significant interaction between beach and nourishment for all sample periods.
Figure 3. 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.
Discussion

We found substantial and long-lasting effects of beach nourishment on the community of sand-dwelling invertebrates. Nourishment resulted in rapid and pronounced reductions in the abundance of most invertebrate groups. While such a major loss of invertebrate abundance is expected to immediately follow nourishment, we also found that overall invertebrate abundance remained substantially depressed 15 months after nourishment, with treated beaches having only 48% as many invertebrates as controls. Beach nourishment had major impacts on community composition, determining what invertebrates occurred in the sandy intertidal (Table 3) and the relative abundances with which they were found (Figure 3). The strong nourishment-by-site effect on community composition throughout the study also indicates that nourishment affected each beach differently. So while nourishment continued to structure intertidal invertebrate communities at the end of the study, not every community showed the same changes. These effects of nourishment on taxon abundance and community structure have broad implications for organisms feeding on sandy beach invertebrates.

Effects of nourishment were both time and taxon dependent. One month after nourishment, the intertidal invertebrate community displayed abundances at control sites that were an order of magnitude greater than those for nourished sites. This disparity was significant for all common invertebrate taxa with the exception of the mole crab *E. analoga*. At four months the *E. analoga* population bloomed, becoming most pronounced in nourished sites and offsetting the continued lower abundances of *Donax gouldii* and polychaetes such that no overall effect of nourishment on invertebrate abundance was detected. As time went on, the *E. analoga* bloom subsided and numbers of *Donax gouldii*
recovered, but polychaete abundance continued to be depressed. Even after 15 months, polychaete abundance in nourished sites was only 35% that of controls. While no other invertebrate groups showed a nourishment effect at this time period, reduced polychaete numbers drove the observed two-fold reduction in overall invertebrate abundance at nourished sites.

Both Donax gouldii and talitrid amphipods showed no effects of nourishment from one year onwards. This recovery time frame is shorter than the minimum times for Donax spp. and haustoriid amphipods found by Manning et al. (2014) and Peterson et al. (2014), the latter of which saw reduced abundances for both groups through the end of a 3-year study period. Only Leewis et al. (2012) observed a complete recovery of Donax spp. from an initial nourishment-induced decline, but this result was obtained via a study design in which beaches that were nourished at various times in the past were compared; this approach did not permit observation of the same beach community through time. Haustoriid amphipods have shown comparable recovery times to our study, from five months (Schlacher & Thompson 2012) to one year (Jones et al. 2008), although talitrids have previously shown no effect of nourishment (Fanini et al. 2009). In general, nourishment in San Diego affected Donax gouldii for a shorter time—less than one year—than previously observed. And while the literature is more variable regarding amphipods, they also recovered more quickly in our study than in other recent reports (Peterson et al. 2014, Manning et al. 2014). However, a departure from previous research is unsurprising, given that fundamental differences in the ecologies of haustoriid amphipods and talitrid amphipods likely contribute to differences in nourishment response (Defeo & Mclachlan 2005, Mclachlan & Brown 2006).
Unexpected results were not limited to those taxa; *Emerita analoga* underwent a population boom at four months which lead to its accounting for 25% of all collected organisms. At four months *E. analoga* was more common in nourished sites, but these crabs were found in approximately equal and scarce abundances at control and nourished sites during all other time periods. In contrast, previous studies found a clear negative response for the mole crab *Emerita talpoida* following nourishment, despite variation in length of recovery times (Hayden & Dolan 1974, Peterson et al. 2006, 2014, Manning et al. 2014).

The boom-bust pattern of mole crab abundance found here suggests the importance of factors and processes other than nourishment in shaping temporal fluctuations in their populations. The long pelagic duration (3-6 months) of *E. analoga* larvae makes it possible for sandy beach populations to be sustained by recruits from distant beaches (Efford 1969, Dugan et al. 1991, Dugan & Hubbard 1996, Dawson et al. 2011). Despite this high dispersal capability, changes in coastal currents affect the spread of larvae and have been shown to produce sporadic recruitment events, resulting in sudden population blooms (Dugan & Hubbard 1996, Sorte et al. 2001, Diehl et al. 2007). This would suggest that the observed bloom of *E. analoga* at four months was the result of a significant recruitment event driven by changes in local ocean conditions. It is less clear why mole crabs would have a preference for, or survive better in, nourished 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 distributions on Southern California’s beaches have previously shown no correlation with environmental variables such as sediment structure and beach slope (Dugan & Hubbard 1996). Nevertheless, changes in the swash zone, the
primary habitat of *E. analoga*, might have driven the increased abundances observed at nourished sites. There is a strong empirical and theoretical evidence for changes in the swash zone affecting crustacean communities (McLachlan 1996, Melachlan & Brown 2006, Speybroeck et al. 2006, Defeo & McLachlan 2011), and key swash zone features have been shown to influence the life history and fine scale aggregation of *E. analoga* (Cubit 1969, Dugan et al. 1991, 1994, 2000). Changes in sediment size, sorting, or beach slope may have reshaped the swash zone at nourished sites to encourage aggregations of *E. analoga*.

*Scolelepis* *spp.* was significantly impacted by nourishment in the first month, and continued to show non-significant, but nevertheless two-fold or greater reductions in mean abundance at nourished sites through the end of the study. This contradicts the common perception of *Scolelepis squamata* as a nourishment opportunist (Eede et al. 2014, Greene 2002). Previous studies had found either no effect of nourishment on *S. squamata* (Peterson et al. 2006, 2014) or a positive response to nourishment events occurring at various times in the reproductive cycle (Leewis et al. 2012, Manning et al. 2014). These results make sense given that *S. squamata* appears to be a successful generalist with a cosmopolitan distribution and broad preferences for fundamental beach characteristics such as grain size (Mclachlan & Brown 2006, Peterson et al. 2006, Van Tomme et al. 2013). However, our results—indicating a negative impact of nourishment in the short term—conflict with previous literature and add a layer of uncertainty regarding how generalizable the effects of nourishment are on various beach dwelling organisms. Explanations for the variation in responses of *Scolelepis* *spp.* could lie in geographic differences in life history, or uncertainty over whether various studies are observing the same species (Speybroeck et al.
2007, Defeo et al. 2009). Subtle interactions related to differences between populations (or species) and nourishment characteristics (e.g. timing, sand quality) could cause variation in responses.

In spite of the recognized diversity of sandy intertidal polychaetes (Viola et al. 2013; Mclachlan & Brown 2006), few nourishment studies differentiate between taxa, describing the general polychaete response in terms of the *Scolelepis squamata* response (Peterson et al. 2006, 2014). In our study, *Thoracophelia spp.*, *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 spp.* Analyzed as a community (including *Scolelepis spp.*), polychaetes showed significantly reduced numbers at nourished sites for all sampling periods. This persistent negative effect of nourishment again conflicts with previous literature, which showed polychaetes responding neutrally (Peterson et al. 2006, 2014), positively (Menn et al. 2003), or negatively in the very short term only (Schlacher & Thompson 2012). Despite being the only dominant taxon still showing reductions at 15 months, polychaetes were a large enough component of the community to affect total organismal abundance, which showed a significant two-fold decrease at nourished sites.

Understanding the ecology of sandy beach polychaetes might help explain the observed long-term effect of nourishment. *Scolelepis spp.*, *Thoracophelia spp.*, *Naineris dendritica*, and *Orbinia johnsoni* are all deposit feeders, which should be significantly affected by sediment characteristics (Fauchald & Jumars 1979, Rouse & Pleijel 2001, Defeo & McLachlan 2011). Decreases in grain size and beach slope—and associated
changes in organic matter and moisture content—have shown positive correlations with abundance and diversity of intertidal polychaetes (Omena & Amaral 2003, Mattos et al. 2013). Burrowing ability is also affected by sediment characteristics; *N. dendritica*, *O. johnsoni*, and *Hemipodia borealis* all have distinct behavioral and morphological adaptations to burrowing in the sandy intertidal (Murphy & Dorgan 2011, Francoeur & Dorgan 2014), and Viola *et al.* (2013) demonstrated declines in the burrowing ability of *Thoracophilinia mucronata* in fine-grained sands. Changes in beach morphodynamics through nourishment could have impaired the feeding and burrowing ability of these polychaetes, slowing down population growth in nourished sites. 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 polychaete populations following nourishment.

Reduced invertebrate abundance up to 15 months after nourishment may cause serious disruption of the sandy beach food web. Exposed sandy beaches of Southern California are host to more than twenty five species of shorebirds that forage for benthic invertebrates in intertidal sediments and macrophyte wrack (Dugan & Hubbard 2000, Dugan *et al.* 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). While the conditions under which shorebirds exhibit preferences for certain prey need to be resolved, there is evidence that reductions in invertebrate abundance cause decreased habitat use by shorebirds as well as 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. 2000; Dolbeth et al. 2008). Therefore, the significant decline in total invertebrate abundance, driven primarily by polychaetes, suggests a potential to negatively impact shorebird feeding for at least fifteen months after a nourishment event. The timing of nourishment may have further effects on shorebirds, as many populations are seasonal. 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* boom in the winter of 2013 likely favored foraging shorebirds, a winter decline—like that seen at 15 months—might be expected to put greater stress on shorebird populations than a similar effect in the summer. This is especially relevant for areas like San Diego, where degradation of already limited mudflats force shorebird populations to rely heavily on sandy beaches (Page et al. 1999, Hubbard & Dugan 2003).

The environmental impact statement for this beach nourishment 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). While some taxa (e.g. talitrid amphipods, *Donax gouldii*) recovered within one year, the polychaete community showed a lasting effect of nourishment that significantly reduced total invertebrate abundance for at least fifteen months. Given that the environmental impact statement was itself informed by earlier sandy beach and nourishment literature, and keeping in mind that our results disagree in some aspects with the findings of all previous intertidal nourishment studies, it’s clear that further study of how beach nourishment affects intertidal invertebrate communities is warranted.
Differences in study design and nourishment characteristics might explain discrepancies between results of this study and those reported elsewhere (Table 1). Few studies extend beyond one year (but see Manning et al. 2014; Peterson et al. 2014), perhaps preventing convergence on a clear time-to-recovery for organisms that repeatedly show nourishment effects through the last observation period (Donax spp., Table 1). Additionally, intertidal macroinvertebrates show high variability both between and within beaches (Defeo & Mclachlan 2005) that few studies account for in their sampling design (Peterson & Bishop 2005, Schlacher & Thompson 2012, Leewis et al. 2012). Donor sand quality and recipient beach morphodynamics are other sources of variability in the literature. The match of donor grain size to recipient grain size is predicted to have the largest impact on how beach morphodynamics change following nourishment, and as a result the range in donor sand from much finer (Peterson et al. 2000) to much coarser (Peterson et al. 2006) than recipient beach sand might be associated with the range in recovery times. (McLachlan 1996, Defeo & Mclachlan 2005, Mclachlan & Brown 2006, Van Tomme et al. 2013). A host of other factors, such as the timing of nourishment relative to reproductive cycles (Manning et al. 2014) or the distribution of fill sand along the beach (Schlacher & Thompson 2012) weakens the strength of any conclusions drawn from this limited body of research.

With more data and longer studies, patterns may emerge to help explain how intertidal invertebrates respond to beach nourishment. Because more recent studies show longer recovery times (this study; Peterson et al. 2014; Manning et al. 2014), conservative estimates regarding the extent of nourishment’s effects are warranted. More research investigating the duration of nourishment’s effects on sandy beach invertebrates, as well
as the mechanisms by which nourishment affects invertebrates, is needed to create better models of community recovery and inform the sound management of beach ecosystems.

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