Relationship of *Sphaeroma quoianum* to sediment characteristics and invertebrate community

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Abstract Many important wetland functions are tied to sediment dynamics, which are influenced by infaunal invertebrate communities. These communities are sensitive to changes in sediment structure and to colonization by non-native species. In a southern California salt marsh, the non-native isopod *Sphaeroma quoianum* has created dense networks of burrows within the marsh banks. Since this isopod increases erosion in many areas and can change local invertebrate communities, its possible contribution to habitat loss in this already-scarce southern California ecosystem is an important issue. To determine the relationship of *S. quoianum* to invertebrate community and sediment characteristics, three burrowed transects and one unburrowed transect were surveyed and sampled for invertebrate and sediment cores. This study tested the association between burrows and grain size distribution, sediment carbon content, respiration rates, and invertebrate community composition. *Sphaeroma quoianum* burrows were correlated with altered invertebrate community composition, decreased carbon content, and steep marsh bluffs. These results highlight the potential susceptibility of salt marsh habitat with steep edges to invasion by non-native species. These results also suggest that *S. quoianum* invasion of salt marsh habitats can alter native communities and ecosystem functions; thus, incipient invasions should be of concern to managers and ecologists alike.

Keywords *Sphaeroma quoianum* · Invertebrate community · Invasive isopod · Ecosystem engineers · Ecological impacts · Ecosystem functioning · Coastal salt marsh

Introduction

Invertebrates in estuarine sediments mediate vital ecosystem functions, including decomposition, food web dynamics, and carbon cycling (e.g. Dauwe et al. 1998; Nordhaus and Wolff 2007; Diaz Villanueva et al. 2012; Pulmanns et al. 2014). It is therefore important to understand the mechanisms behind...
factors that alter invertebrate communities, and subsequently, alter ecosystem functions. In particular, invertebrates that create physical habitat structures can act as ecosystem engineers, impacting habitats and functions disproportionately to their physical mass (Coleman and Hendrix 2000). By altering biotic or abiotic variables, they may influence the availability of resources in a given habitat (Jones et al. 1994; Crooks 2002). One important way benthic invertebrates alter habitat and ecosystem functions in estuarine environments is bioturbation via burrowing (Rosenberg et al. 2001; Reise 2002; Mermillod-Blondin and Rosenberg 2006).

Bioturbation via burrowing invertebrates have direct and indirect effects on ecosystem functions including impacts to vegetation communities and erosion. For example, in southeast England, the polychaete Hediste diversicolor (previously Neris diversicolor) decreased the spread of invasive grass Spartina anglica through passive seed grazing during burrowing (Emmerson 2000), while bioturbation and herbivory by this polychaete were connected to exacerbated creek erosion in the same region (Paramor and Hughes 2004). Erosion was also increased through burrowing by the native crab, Neohelice granulata (previously Chasmagnathus granulatus), causing accelerated tidal creek formation in a salt marsh in the southwest Atlantic (Escapa et al. 2007).

Bioturbation via burrowing invertebrates can also affect decomposition and carbon availability of the sediment. In mangroves in Brazil, burrows by the crab Ucides cordatus were found to increase sediment respiration, apparently by oxidizing sediment conditions (Pulmanns et al. 2014), and crab (Macrophthalmus japonicus) burrows increased carbon cycling in a tidal flat in Japan (Otani et al. 2010). In the Jadebusen Bay, Wadden Sea, Germany, the polychaete worm, Heteromastus filiformis, increased organic matter for sediment meiofauna by transporting deeper sediment to the surface during its burrowing activities (Neira and Hopner 1994).

Due to their potentially disproportionate ability to impact habitats and ecosystem functions, burrowing invertebrates cause concern when they colonize areas to which they are not native. For example, substrate alteration of soft mudflats to byssal mats by the invasive Asian mussel, Musculista senhousia, in San Diego, California increased species richness and densities of certain invertebrate species (Crooks 1998). In Newfoundland, Canada, the reduction of eelgrass biomass and associated impacts on fish communities were linked to the burrowing activities of the invasive European green crab, Carcinus maenas (Matheson et al. 2016). Burrowing activities of the isopod Sphaeroma quoianum (focus organism of our study) contributed to erosion rates of potentially more than 100 cm of marsh edge per year in San Francisco Bay, increasing habitat loss (Talley et al. 2001; Nichols and Pammatmat 1988) and altering the overall invertebrate community (Talley and Crooks 2007).

Sphaeroma quoianum (common names: burrowing isopod, Australian isopod, New Zealand pill-bug) is a bioturbator thought to be native to Australia, New Zealand, and Tasmania where it is often found with its commensal isopod, lalais californica (Rotramel 1972). Due in part to high tolerance to wide ranges of salinity and temperature (Davidson 2008), S. quoianum has spread well beyond its native range to harbors worldwide, with populations recorded along the west coast of the United States and in the Gulf of Tonkin in China and with occurrences recorded in Pearl Harbor in Hawai’i where it failed to establish (Davidson 2008). S. quoianum was likely introduced to California in the mid- to late 1800’s (Carlton 1979) and has been shown to have impacts on northeastern Pacific coastal ecosystems (Talley et al. 2001; Talley and Crooks 2007; Davidson 2010).

In its native range, S. quoianum has been recognized primarily as a woodborer (Hass and Knott 1998), but in its invaded range, it has been shown to bore into other substrata such as sandstone, friable mud, marsh banks, and even Styrofoam (Talley et al. 2001; Davidson et al. 2010). In California salt marshes, S. quoianum shows a strong preference for firm sediments under Salicornia spp. marsh as well as for vertical and undercut (rather than gently sloping) banks (Talley et al. 2001; Davidson 2008). Though past studies have revealed much about the natural history of S. quoianum, its geographic distributions, and its effects on erosion, few studies have investigated the impacts of this invasive species’ dense networks of burrows on invertebrate communities (but see Talley and Crooks 2007; Davidson et al. 2010), impacts on other ecosystem functions like carbon cycling, or how occupied and unoccupied sediment characteristics vary.
The objective of this study was to quantify the *S. quoianum* distribution in a southern California estuary and to investigate the potential impacts of *S. quoianum* and its burrow networks on carbon dynamics and infaunal macroinvertebrate communities. Since *S. quoianum* has been found to prefer steeper marsh banks (Davidson 2008) and to increase erosion in other west coast marshes (Talley et al. 2001), we hypothesized that *S. quoianum* and associated burrow networks would be found on steep marsh banks and burrow occurrence would correlate with altered sediment characteristics and lower shear strength than areas that did not have *S. quoianum*. Since burrowers increase the surface area of the oxic/anoxic interface and have been found to increase sediment respiration (Neira and Hopner 1994; Kristensen 2000; Otani et al. 2010; Pulmanns et al. 2014), we hypothesized that burrowed sediments would have higher respiration rates and lower carbon content than unburrowed sediments. Finally, since *S. quoianum* burrowing activity displaces sediment in which invertebrates live and creates altered habitat with burrow structures that are denser than those of native burrowers such as lined shore crabs (*Pachygrapsus crassipes*), fiddler crabs (*Uca crenulata*), or polychaetes, we hypothesized that *S. quoianum* presence would correlate with decreased invertebrate abundance and altered community composition.

**Methods**

**Study site**

The study was conducted at Bolsa Chica Ecological Reserve in Huntington Beach, California (33.41.59 N, 118.02.20 W; Fig. 1), roughly 30 km south of Los Angeles, California. Bolsa Chica Ecological Reserve is a coastal estuary of approximately 1300 acres including salt marsh, mudflat, open water, coastal dune, riparian, and brackish marsh habitats. Prior to its establishment as an ecological reserve in 1979, the natural ocean entrance was dammed by the Bolsa Chica Gun Club in 1899. The Bolsa Chica Lowlands Restoration Project reopened the inlet in 2006, restoring tidal flow to the estuary and its function to the ecosystem. The reserve includes the full tidal basin (which was not surveyed as part of this project) as well as Inner and Outer Bolsa Bays, which connect to the Pacific Ocean via Huntington Harbor. *S. quoianum* was absent from Bolsa Chica in prior surveys in the 1990s (Bolsa Chica Conservancy pers. comm.) and was observed in the channel edge at the north end of Bolsa Chica Wetlands in 2009 (Whitcraft pers. obs.). From aerial imagery in Google Earth Pro, the banks in this study (especially the West transect locations) appear to have become much steeper since 2001, and the authors have observed large chunks of bank sediment falling off since 2009 (Whitcraft pers. obs.).
Surveys were conducted in fall 2014 in Inner and Outer Bolsa Bays (Fig. 1) to determine the locations of *S. quoianum*. Since *S. quoianum* lives within the intertidal zone to filter feed on suspended particles and diatoms in the water column (Rotramel 1972), each bay was surveyed at low tide along the waterline, with careful attention to areas where vertical portions of mudflat or sediment occurred. When burrows were found, a hand spade was used to excavate a small amount of sediment around the burrow and the presence of *S. quoianum* was confirmed by visual inspection of the sediment. Evidence of invasion by *S. quoianum* was limited to the Outer Bolsa Bay (Fig. 1A).

Within this invaded area, three transects were established (Fig. 1B) for subsequent sampling. The “West transect” was located on the west side of the channel with most of its banks facing southeast, and the “East transect” was across the channel from the West transect, with its banks facing west. Both West and East transects contained hard, friable sediment on tall, steep bluffs with no plant cover. The “South transect” was situated south of the East transect, with west facing banks, and more gently sloping banks of softer marsh sediment and vegetation including marsh Jaumea (*Jaumea carnosa*), alkali heath (*Frankenia salina*), sea lavender (*Limonium californicum*), Pacific pickleweed (*Saliicornia pacifica*), and *Ulva* spp. (green algae).

Compared to other marsh areas in the region, this invaded area was visibly steeper and appeared to have different grain size. Since it was not possible to determine whether this was the case before *S. quoianum* invasion or whether it had been changed due to *S. quoianum* invasion, we sampled the invertebrate community from a nearby marsh transect that more closely resembled other regional marshes. The “Natural transect”, where no *S. quoianum* were found, was chosen haphazardly at approximately the same tidal elevation to sample uninvaded “natural” marsh invertebrate community as a control for later comparisons with invaded areas. The Natural transect was situated south of the South transect, with southwest facing banks and gently sloping banks of softer marsh sediment and vegetation that were similar to the South transect.

Sediment and invertebrate sampling

For burrowed transects (West, East, and South), sampling quadrats were placed every 5 m along the length of the transect at low tide in September 2014. Transects were set horizontally at a consistent tidal elevation. Along these transects, an unburrowed quadrat was identified as close as possible (average distance of approximately 0.25 m) to each burrowed quadrat while sampling the same tidal elevation. Due to high densities of burrows, it was not possible to find an unburrowed quadrat to pair with each burrowed quadrat. Along the West transect, 9 burrowed (B) and 6 unburrowed (U) 0.125 m² quadrats were sampled; along the East transect, 3 B and 2 U quadrats were sampled; and along the South transect, 6 B and 4 U quadrats were sampled. In July 2015, 6 additional U quadrats were sampled from the Natural transect.

For all transects, burrow cover within each quadrat was assigned a numerical estimate (%) by visual assessment. At each quadrat on each burrowed transect, bluff angle and shear strength were measured, and cores for sediment characteristics and invertebrate community analysis were collected as described in the sections below. Only invertebrate cores were collected from the Natural transect.

Sediment characteristics

**Bluff angle and shear strength**

Bluff angle was determined in the field using Angle Meter PRO for iPhone, and shear strength of the sediment was measured using a Torvane shear device (Humboldt Manufacturing, Elgin, IL). Shear strength of sediments relates directly to how susceptible the sediment is to erosion by tide and wave induced currents (Tolhurst et al. 1999). The mean of three measurements was used to determine one data point for shear strength for each quadrat.

**Grain size distribution**

Samples for sediment grain size analysis were taken from sediment respiration cores (described below). Samples were dried for at least 48 h at 50 °C treated with hydrogen peroxide to remove organics, with hydrochloric acid to remove carbonates, and with sodium hydroxide to remove biogenic silica (Leeper
et al. 2017). Grain size analysis was performed using a Malvern Mastersizer 2000 laser diffraction grain size analyzer at California State University, Fullerton.

**Sediment respiration rate**

Small sediment cores (2 cm diameter by 2 cm deep) were taken from each quadrat along each transect, sealed into pre-weighed jars on site, transported back to the laboratory, and re-weighed. Carbon dioxide (CO₂) concentrations were measured from the sediment samples using an SRI Instruments gas chromatograph, equipped with a flame ionization detector and methanizer, at Chapman University in Orange, California immediately upon return to the laboratory. Samples were kept in the dark, and CO₂ concentrations were taken from each jar at three time points approximately 48 h apart to calculate rates of carbon mineralization (Keller and Takagi 2013). Six of 48 samples exhibited a non-linear (R² < 0.90) increase in CO₂ concentrations over time and were excluded from subsequent analyses. Sediment samples were dried at 50 °C in order to determine moisture content, and carbon respiration rates were calculated per gram dry weight of sediment.

**Carbon content**

Small subsamples were taken from sediment respiration cores after respiration rates were measured. To remove inorganic carbon, soil samples were acidified with 50 μL of 1 M HCl and dried overnight at 50 °C twice (Craft et al. 1991). To determine organic carbon content, acidified and dried samples were weighed and analyzed with an elemental analyzer (Costech Analytical Technologies Inc., Valencia, CA) at Chapman University (Keller et al. 2015). Carbon content was calculated as percent carbon per mass.

**Macrofaunal invertebrate community**

To compare invertebrate abundance and community composition between burrowed and unburrowed quadrats, small sediment cores (7.62 cm diameter by 6 cm deep) were taken in September 2014 at each quadrat along each transect. Once back in the laboratory each sediment core was preserved in 8% formalin with Rose Bengal stain. Preserved samples were sieved through a 300 μm sieve, and all organisms present were identified to the lowest taxonomic level possible and then counted. To test whether the presence of burrows correlated with the presence of *S. quoianum*, individuals from these invertebrate community cores were separated into groups of small (<4 mm) and large (>4 mm) individuals and counted. Abundances of large and total *S. quoianum* were compared with visual assessment of burrow densities (%) from areas in which they were taken.

**Statistical analyses**

All univariate data were checked for normality and equal variances and transformed when appropriate. If data met assumptions, Type III ANOVAs were performed in Minitab®17. If the data could not meet these assumptions with any transformations, then we performed permutational ANOVAs, which do not rely on the assumptions of normality and equal variances (Anderson 2008). Following recent discussion about *p*-values and hypothesis testing (e.g. Wasserstein et al. 2019), we have presented results with *p*-values above 0.05 and discussed patterns in the data that appeared without a large sample size, while not overstating the conclusions. All multivariate analyses were performed Bray Curtis or Euclidean dissimilarity matrices in PRIMER 7 (Quest Research Limited, New Zealand).

**Sediment characteristics, respiration rate and carbon content**

Sediment characteristics (bluff angle, shear strength, grain size), sediment respiration rate, and carbon content were all analyzed with burrow status (burrowed or unburrowed) and transect as factors. Type III two-way ANOVAs were used to analyze sediment shear strength and grain size. Bluff angle and respiration rate did not meet ANOVA assumptions after transformation so were analyzed using permutational ANOVAs. Since no transformations were found to meet the assumption of normality for sediment respiration rate, a nonparametric Spearman Rho test was used to analyze the relationship between sediment respiration rate and carbon content.
Macrofaunal invertebrate community

Pearson’s correlations were used to analyze the relationship between burrow cover and number of *S. quoianum* individuals. A one-way ANOVA was used to analyze univariate invertebrate abundance and species richness in only unburrowed samples among West, East, South, and Natural marsh samples, since there were no burrowed samples in the Natural transect. Since only unburrowed samples were analyzed, *S. quoianum* and *I. californica* were excluded from analyses, but we note that four *I. californica* specimens were found in unburrowed samples from the West transect. Due to the degraded nature of these specimens at time of capture, we believe that they were left from nearby *S. quoianum* that were very abundant in areas adjacent to the unburrowed quadrats.

Two separate two-way ANOVAs, with burrow status and transect as factors, were used to analyze univariate invertebrate abundance and species richness with *S. quoianum* and *I. californica* (1) included, and (2) excluded (both excluding the Natural transect since there were no burrowed samples there) to reveal changes in the remaining invertebrate community (similar to Talley and Crooks 2007).

Multivariate analyses

For multivariate environmental analyses, draftsman plots were used to determine which parameters to transform to achieve normality before analysis. Bluff angle, shear strength, carbon content, and respiration rate were found to be right skewed and thus were log-transformed. Percent silt was removed from analysis due to multicollinearity (negatively correlated) with percent sand, remaining environmental parameters (shear strength, percent clay, percent sand, carbon content, respiration rate, and bluff angle) were normalized to compare among different scales, and multivariate two-way PERMANOVAs with transect and burrow as factors were run.

All multivariate infaunal invertebrate community data were fourth-root transformed to upweight the contribution of less abundant species. Because there were no burrowed samples in the Natural transect, only unburrowed West, East, South, and Natural marsh invertebrate community samples were compared using a 1-way ANOSIM, and SIMPER analyses were used to determine which species or taxonomic groups contributed to differences among transects. Since *S. quoianum* and *I. californica* dominate community composition in burrowed samples, they were removed from analyses of burrowed transects (West, East, and South) to reveal changes in the remaining invertebrate community. To compare community composition among invaded transects, a two-way PERMANOVA main test and pairwise tests were run on West, East, and South transects only, with transect and burrow status as factors, using a Bray–Curtis dissimilarity matrix with a dummy variable. These same two-way PERMANOVA analyses were also run using summary taxonomic levels: Crustacea, Insecta, Mollusca, Oligochaeta, Polychaeta, and Other (Arachnida, Nemertea, Plat�helminthes).

Canonical Analysis of Principal Coordinates (CAP) visualizations and PERMANOVAs were run to compare environmental parameters and invertebrate community composition to visualize differences between samples and determine the strength of the association (canonical correlations, δ) between the multivariate data cloud and the hypothesis of group differences. All environmental parameters in this analysis were log-transformed except for the proportion of clay because it did not have a skewed distribution.

Results

Sediment characteristics

Bluff angle and shear strength

Average (± SEM) bluff angle in burrowed sites was 62.89 ± 6.97°, which was steeper than in unburrowed sites (15.94 ± 1.98°) (pseudo-**F**1,24 = 31.68, *P* = 0.001). Sediment shear strength did not differ between burrowed and unburrowed sites (0.47 ± 0.041 and 0.67 ± 0.011 kg/cm², respectively; **F**1,24 = 1.76, *P* = 0.196).

Grain size distribution

Sediment sand, silt, and clay contents averaged (± SEM) 52.12 ± 2.11%, 42.0 ± 1.96%, and 5.86 ± 0.40%, respectively. Sand and silt proportions were not different among transects (sand: **F**2,24 = 2.32,
$P=0.12$; silt: $F_{2,24}=2.97$, $P=0.070$) or between burrow statuses (sand: $F_{1,24}=1.56$, $P=0.223$; silt: $F_{1,24}=1.55$, $P=0.244$). The proportion of clay was not different between burrowed and unburrowed samples ($F_{1,24}=0.66$, $P=0.423$), but was greater in the East transect than in the West or South transects ($F_{2,24}=3.48$, $P=0.047$).

**Carbon content**

Sediment carbon content was higher in the South transect, with an average of $0.320 \pm 0.085\%$C, than in the West and East transects, with $0.189 \pm 0.035\%$C and $0.124 \pm 0.025\%$C, respectively (log transformed, $F_{1,24}=6.42$, $P=0.006$; Fig. 2A). Regardless of location, unburrowed samples had higher sediment carbon content, averaging $0.308 \pm 0.067\%$C, than burrowed samples, averaging $0.158 \pm 0.028\%$C (log transformed, $F_{1,24}=11.97$, $P=0.002$; Fig. 2B).

**Sediment respiration rate**

Respiration rates among transects followed a similar spatial pattern to carbon content (significant at the $P(perm)=0.076$ level) with the South transect averaging $168.38 \pm 22.04 \text{ g CO}_2 \text{ gdw}^{-1} \text{ d}^{-1}$, and West and East transects averaging $79.12 \pm 18.66$ and $43.48 \pm 3.14 \text{ g CO}_2 \text{ gdw}^{-1} \text{ d}^{-1}$, respectively (log transformed, pseudo-$F_{2,22}=4.662$; Fig. 2C). Respiration rates in the South transect were higher than in the West transect ($t=2.630$, $P(perm)=0.028$), and were higher than the East transect at the $P(perm)=0.053$.
level \( (t = 1.960) \). Respiration rates averaged 105.51 ± 20.81 μg CO₂ g dw⁻¹ day⁻¹ in burrowed samples and 93.37 μg CO₂ g dw⁻¹ day⁻¹ in unburrowed samples, but were not significantly different by burrow status \( (F = 0.784, P = 0.363) \). The strength of the correlation between sediment carbon content and respiration rates was 52% \( (\rho = 0.517) \), and this correlation coefficient was statistically different from zero \( (P = 0.006; \text{Fig. 2D}) \).

**Multivariate analysis of sediment characteristics**

Environmental parameters evaluated simultaneously differed among transects \( (\text{pseudo-} F_{2,24} = 2.588, P = 0.014) \) and between burrowed and unburrowed samples \( (\text{pseudo-} F_{1,24} = 4.592, P = 0.001) \), with no interaction effect \( \text{(Fig. 3)} \). Within transects, West and East were not different, but South was different from West \( (t = 1.744, P(\text{perm}) = 0.016) \) and different from East at the \( P(\text{perm}) = 0.084 \) level \( (t = 1.634) \). For these data, CAP1 (bluff angle) separates the burrowed from the unburrowed samples, where bluff angle was on average steeper in burrowed areas, while CAP2 (respiration rate and carbon content) separates the South transect from West and East transects \( \text{(Fig. 3)} \), where respiration rate and carbon content were on average higher in the South transect as compared to West and East transects \( \text{(Fig. 2A, C, 3)} \).

**Macrofaunal invertebrate community**

Average \( (± \text{SEM}) \) total *S. quoianum* abundances per 18.1 cm² in the West, East, and South transects were 41 ± 8, 38 ± 6, and 27 ± 12, respectively. The number of large *S. quoianum* \( (R = 0.842, P < 0.001) \) and total *S. quoianum* numbers \( (R = 0.721, P = 0.001) \) from invertebrate samples correlated closely with burrow density cover (%) estimates, verifying that the presence of burrows indicated the presence of *S. quoianum*. Excluding burrowed samples \( \text{(as discussed in Methods)} \), total macrofaunal invertebrate abundance was higher in the Natural transect than in the East and West transects \( (\log \text{transformed}, F_{3,14} = 8.11, P = 0.002) \), but South was not different from any other area \( \text{(Fig. 4A)} \). Differences among transects in species richness followed this trend, differing at the \( P = 0.084 \) level \( (F_{3,14} = 2.72; \text{Fig. 4B}) \).

**Fig. 3** CAP analysis of sediment characteristics. Parameters include bluff angle, sediment shear strength, sediment grain size composition, sediment carbon content, and sediment respiration rates by transect \( \text{(West = triangles, East = circles, South = squares)} \) and burrow status \( \text{(burrowed (B) = open symbols, circled by dashed line; unburrowed (U) = solid symbols, circled by dotted line)} \), with environmental parameters as axes to separate groups. The first two canonical correlations are \( \delta_1 = 0.84 \) and \( \delta_2 = 0.69 \), indicating the strength of the association between the multivariate data cloud and the hypothesized groupings. For these data the first canonical axis \( \text{(CAP1, bluff angle)} \) separates burrowed from unburrowed samples and the second axis \( \text{(CAP2, respiration rate and carbon content)} \) separates the South transect from West and East transects.
Among West, East, and South transects, total abundance ($F_{1,24} = 54.23$, $P < 0.001$; Fig. 4C) and species richness ($F_{1,24} = 8.41$, $P = 0.008$; Fig. 4D) were higher in burrowed than unburrowed areas when *S. quoianum* and *I. californica* were included but were not different among transects (abundance—$F_{2,24} = 0.80$, $P = 0.460$; species richness—$F_{2,24} = 1.78$, $P = 0.190$). However, when these commensal isopods were excluded, there were no differences in abundance between burrowed and unburrowed samples ($F_{1,24} = 0.01$, $P = 0.917$), while differences emerged among transects with South having higher abundances than East and West ($F_{2,24} = 4.18$, $P = 0.028$).

**Multivariate analysis of invertebrate community**

With burrowed samples excluded (as discussed in Methods), the species-level community composition was different among transects (fourth-root transformed, $R = 0.337$, $P = 0.001$). West ($R = 0.397$, $P = 0.004$) and East ($R = 1.0$, $P = 0.036$) transects were both different from the Natural transect, the South transect was not different from the Natural transect, and West, East, and South transects were not different from each other (Fig. 5). Unburrowed sites with invertebrates present in the West transect contained mostly insects (beetle and fly larvae, 36%) and oligochaetes (29 ± 16%); in the South transect,
unburrowed sites contained mostly white pill beetle larvae (41%) and oligochaetes (27%); in the Natural transect, unburrowed sites were characterized by oligochaetes (73%), and in the East transect, the unburrowed sites had no invertebrates.

Species-level comparisons of samples from burrowed transects (West, East, and South) excluding *S. quoianum* and *I. californica* (as discussed in Methods), revealed differences at the $P=0.082$ level between burrowed and unburrowed samples (fourth root transformed, pseudo-$F_{1,24}=1.9682$, $P\text{(perm)}=0.082$), and among transects at the $P\text{(perm)}=0.078$ level (pseudo-$F_{2,24}=1.793$) with no interaction effect.

Analysis of summary taxonomic levels (Crustacea, Insecta, Mollusca, Oligochaeta, Polychaeta, and Other) across invaded transects revealed differences between burrowed and unburrowed samples (pseudo-$F_{1,24}=3.286$, $P\text{(perm)}=0.043$) where burrowed samples had higher numbers of crustaceans, and unburrowed samples had more oligochaetes and insects (Fig. 5). Among burrowed transects, invertebrate community composition in the West transect was not different from that in the East or South transects, but communities were different between East and South transects at the $P\text{(perm)}=0.060$ level ($t=1.839$), driven by a lack of invertebrates in the East transect (excluding “Natural”; pseudo-$F_{2,24}=1.974$, $P=0.097$; Fig. 5). For these data, the first canonical axis (insects and oligochaetes) separates the Natural and South transects from the East transect, while the second canonical axis (crustaceans and polychaetes) separates the burrowed and unburrowed samples (Fig. 5). There were more oligochaetes and insects in the Natural and South transects, and more crustaceans and polychaetes in burrowed samples. With regard to environmental parameters, CAP1 (carbon content and bluff angle) separates burrowed and unburrowed samples, where burrowed samples had steeper bluff angles and unburrowed samples had higher carbon content (Fig. 6).
Discussion

Understanding the context of this invasion relative to others in the region is important to contextualize our findings. Talley et al. 2001 reported seasonally variable densities, but overall their study presented results from much higher density invasion sites in San Francisco (1540–2900 S. quoianum per 0.25 m²) and slightly higher density sites in San Diego Bay (200–1150 S. quoianum per 0.25 m²). Davidson et al. 2010 reported burrow densities (which correlate with S. quoianum densities) of 1000–3000 per 0.25 m², which are also much higher than the burrow densities observed in our study. Thus, our study might represent a less severe invasion and lower impacts than those seen in other studies.

Despite lower S. quoianum densities than prior studies and high variability in environmental parameters and invertebrate community among transects, differences between burrowed and unburrowed areas were still apparent with slope, carbon content, and invertebrate community composition in this study. The burrowed slopes were steeper but of similar grain size to the unburrowed areas. We correctly hypothesized that sediment carbon content would be lower in burrowed areas; however, inconsistent with our hypothesis, respiration rates were not different between burrowed and unburrowed areas. Also, contrary to our hypothesis, invertebrate abundance (with S. quoianum and I. californica excluded) was not different between burrowed and unburrowed areas, but community composition did differ between them. These community composition differences were correlated with differences in the slope and carbon content between burrowed and unburrowed areas, and were most pronounced in the South transect, which more closely resembled typical marsh habitat. Thus, seeing patterns in spite of the spatial variability among transects suggests that S. quoianum colonization and burrows could have effects on respiration rates and native invertebrate communities in southern California marsh habitats that are more similar to our southernmost transect.

Differences in sediment characteristics and processes

Though more research is needed to elucidate habitat preferences versus impacts of S. quoianum, bluff angle is one environmental parameter clearly associated with S. quoianum burrows in this study as well.
as others, where burrows are consistently found on steep or undercut marsh banks. Talley et al. (2001) found that firm sediments beneath vertical Salicornia marsh were more heavily invaded than softer, gently sloping Spartina habitats. Davidson et al. 2010 found that S. quoianum burrow densities in hard substrates (e.g., wood, sandstone) were much higher than in the softer marsh banks. We also observed that sediment in the invaded area was much harder and more friable than most areas of the marsh, possibly due to their location relatively low on the profile of tall, steep banks beneath a bridge where the channel narrows. Davidson (2010) found that S. quoianum-burrowed marsh banks were typically taller than unininvaded banks, and though we did not measure bank height, the banks of the burrowed transects appeared significantly taller and steeper than most areas of the marsh.

While erosion is a characteristic inherent to areas that have steeper banks, which can result when water current is too fast to allow for settling of fine particles, S. quoianum has been linked to significantly decreased shear strength of the sediment and increased erosion rates (Talley et al. 2001; Davidson 2010). If these isopods are indeed preferentially located on steeper marsh banks, then they are likely to increase erosion in microhabitats that are already prone to it.

Overall, carbon content across invaded areas was low compared with surface carbon content in nearby regional wetlands (Keller et al. 2015). In addition, within the invaded area, carbon content and respiration rates were variable among sampling locations, showing higher values in the South transect, where sediment was more similar to other marshes, than in the West or East transects. Despite this variability by location, carbon content was lower in burrowed samples as compared to unburrowed samples (Fig. 2A). Literature often shows that burrows increase respiration in soft-sediment habitats (Kristensen 2000; Pulmanns et al. 2014; Sasaki et al. 2014), but since respiration depends on the availability of organic carbon for microbial communities in the sediment (Pulmanns et al. 2014), it is likely that low respiration rates measured in Bolsa Chica were related to their low carbon content. Another possibility is that the sediment in these areas, while inundated daily by tidal fluctuations, is not anoxic like typical soft-sediment habitats since they have a relatively high sand content and are potentially well-drained between tidal flushing. Since oxygen enters only a few millimeters into saturated marine sediments (Kristensen 2000; Michaels and Zieman 2013), it is also possible that our respiration cores were too shallow (2 cm) to reveal differences resulting from sediment aeration by burrows.

Differences in invertebrate community structure

Location-specific differences were found in both sediment characteristics and invertebrate community structure among transects. The Natural transect had the highest invertebrate abundance, as compared with unburrowed samples from invaded transects. Among invaded transects, South had the highest invertebrate abundance. Natural and South transects had higher proportions of oligochaetes, with the largest proportion of oligochaetes found in the Natural transect, likely because these areas were more vegetated (pers. obs.) and oligochaetes are detrital grazers (Whitecraft and Levin 2007). Our findings that invertebrate community structure is different between burrowed and unburrowed areas, in addition to the finding that differences were stronger in the South transect that seems to be more like the typical softer-sediment marsh, indicate that S. quoianum colonization could have even larger impacts if it expands into the rest of the marsh.

Burrowed transects contained very few invertebrates overall compared with the Natural transect. While samples in burrowed transects were temporally offset from samples in the Natural transect, the community differences between the areas was greater than the year-to-year variation seen in similar southern California marshes (e.g., McClain et al. 2020; McAtee et al. 2020). Despite the paucity of invertebrates in burrowed transects, differences were found between burrowed and unburrowed samples at the higher taxonomic level, which suggests the potential for S. quoianum to have larger impacts on associated macroinvertebrates in more natural settings.

Our analyses excluded the non-native isopod, I. californica since they are commensal to S. quoianum (Rotramel 1972) and, with hundreds of individuals found in some samples, would have strongly driven invertebrate community composition in burrowed areas. If S. quoianum and I. californica were included in our analyses, the total abundance of invertebrates in invaded areas was higher. This is one clear example of the potential for S. quoianum to impact community composition. The finding of higher proportions
of crustaceans in burrowed samples suggest that *S. quoianum* may facilitate the colonization of others in this taxon. These findings are consistent with other studies which have found increased crustaceans and fewer deposit feeders (e.g., oligochaetes) in association with *S. quoianum* burrows (Talley and Crooks 2007; Davidson et al. 2010). Interestingly, one of the species driving increased proportions of crustaceans in burrowed samples (after *S. quoianum* and *I. californica* were removed from analysis) was *Grandidierella japonica*, which is also non-native. *Grandidierella japonica* is an exotic corophiid amphipod first reported in the United States in San Francisco Bay, California in 1966 (Chapman and Dorman 1975). Rapidly reproducing, opportunistic species like *G. japonica* are capable of taking advantage of expanded resources such as expanded habitat (Zajac and Whitlach 1982; West et al. 2003). *Musculista senhousia*, a non-native Asian mussel, was also found only in burrowed samples. These findings point to *S. quoianum* burrows as a mode for changes in community composition, and are consistent with the findings of Davidson et al. 2010 of their potential to facilitate colonization by other non-native species in a habitat already highly susceptible to alteration by invasive species (Green et al. 2011).

Though overall invertebrate abundance was low in invaded areas, differences in community composition highlight the potential impact that *S. quoianum* burrows could have on invertebrate communities in areas that represent more typical salt marsh habitat. The ability of these ecosystem engineers to alter sediment structure and habitat could change invertebrate community composition and facilitate colonization by other invasive species (Talley and Crooks 2007; Davidson et al. 2010). Changes in invertebrate community composition could have cascading effects on marsh functions such as decomposition, nutrient cycling, and food web dynamics.

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**Declarations**

**Conflict of interest** Not applicable.

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