

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 largely governed 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 Australian 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 question. This study connected *S. quoianum* burrows to increased proportions of crustaceans, 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 and demonstrate that such invasion can correlate to key changes in ecosystem function. 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.

Introduction

Invertebrates that live within wetland sediments mediate vital ecosystem functions, including decomposition, food web dynamics, and carbon cycling (Dauwe et al. 1998; Nordhaus and Wolff 2007; Pulmanns et al. 2014). Often the physical structure created by one invertebrate species (e.g., burrows) can impact other biota, allowing invertebrates to act as keystone species, impacting habitats and functions disproportionately to their physical mass (Bertness 1985; Gerdol and Hughes 1994; Coleman and Hendrix 2000; Boyer and Fong 2005). These potentially disproportionate impacts of invertebrates can be of particular concern when non-native ecosystem-altering invertebrate species colonize new areas.

Burrowing invertebrates—both native and non-native—have been shown to alter sediment characteristics and functions through bioturbation. These changes have included increased organic matter availability (Niera and Hopner 1994), increased sediment respiration via more oxidized sediment conditions (Nordhaus and Wolff 2007; Pulmanns et al. 2014); decreased litter decomposition and altered microbial community composition (Boeker and Geist 2015); and increased sediment erosion associated with burrow formation (Paramor and Hughes 2004; Escapa et al. 2007). One such burrowing invertebrate *Sphaeroma quoianum* (common names: burrowing isopod, Australian isopod, New Zealand pillbug), is a bioturbator native to Australia, New Zealand, and Tasmania where it is often found with its commensal isopod, *lais californica* (Rotramel 1972). Due in part to high tolerance to wide ranges of salinity and temperature (Davidson 2006), *S. quoianum* has spread well beyond its native range and is now common in tropical and subtropical harbors worldwide, with populations recorded along the west coast of the United States, in the Gulf of Tonkin in China, and in Pearl Harbor in Hawai'i (Davidson 2006). *Sphaeroma quoianum* was likely introduced to California in the mid- to late 1800's (Carlton 1979) and has been shown to have impacts on California coastal ecosystems (Talley et al. 2001).

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. 2008). 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 2006). Burrowing activities in these marshes contributed to increased erosion rates of up to 100 cm of marsh edge per year (Talley et al. 2001), subsequently increasing habitat loss (Talley et al. 2001; Josselyn 1983; Nichols and Pamatamat 1998) and altering the overall invertebrate community (Talley and Crooks 2007).

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) or impacts on other ecosystem functions like carbon cycling. Further, only one study has looked at this in southern California estuaries, which are heavily invaded systems (Talley and Crooks 2007). In 2012, *S. quoianum* was observed in the channel edge at Bolsa Chica Wetlands, roughly 30 km south of Los Angeles, California. This study investigates the potential impacts of *S. quoianum* and its burrow networks on carbon dynamics and infaunal macroinvertebrate communities within an invaded southern California wetland habitat.

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). Bolsa Chica Ecological Reserve is a coastal estuary of approximately 1,300 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 Harbour.

Surveys were conducted in fall 2014 in Inner and Outer Bolsa Bays (Fig. 1B) to determine locations of *S. quoianum* colonization. Since *S. quoianum* lives within the intertidal zone in order to filter feed on suspended particles and diatoms in the water column (Rotramel 1972; Davidson 2006), 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 *S. quoianum* presence was confirmed by visual inspection of the sediment. Evidence of invasion by *S. quoianum* was limited to the Outer Bolsa Bay (Fig. 1C).

Within this invaded area, three transects were established (Fig. 1D) 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 (*Salicornia pacifica*), and *Ulva* spp. (green algae). 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 was similar to the South transect.

Sediment Sampling

Along each burrowed transect (West, East, and South), locations were identified and sampled 5 m apart at low tide in September 2014 along horizontal transects set at a consistent tidal elevation. 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 invertebrate community cores were taken from the Natural transect. Burrow cover within each quadrat was assigned a numerical estimate (%) as well as a burrow category (low: 0-33%, moderate: 34-66%, or high: 67-100%; as in Talley et al. 2001) by visual assessment. An unburrowed location was identified as close as possible (average distance of approximately 0.25 m) to each burrowed site. Due to high densities of burrows, it was not possible to find an unburrowed site to pair with each burrowed site. At each sampling location from each burrowed transect, bluff angle and shear strength were measured and sediment cores (for grain size distribution, carbon content analysis, and respiration rates) and sediment cores for invertebrate community analysis were collected as described below.

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 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 hours 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.

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 1M 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.

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 (CO_2) 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 CO_2 concentrations were taken from each jar at three time points approximately 48 hours apart to calculate rates of carbon mineralization (Keller and Takagi 2013). Six of 48 samples exhibited a non-linear ($R^2 < 0.90$) increase in CO_2 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.

Macrofaunal Invertebrate Community

To compare invertebrate abundance and biodiversity among sites with different densities of *S. quoianum* burrows, small sediment cores (7.62 cm diameter by 6 cm deep) were taken in September 2014 at each invasion intensity 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. *Sphaeroma quoianum* individuals from these invertebrate community cores were separated into small (< 4 mm) and large (> 4 mm) individuals, and counts were compared with visual assessment of burrow densities (%) from areas in which they were taken.

Statistical Analyses

All data were checked for normality and equal variances and transformed when appropriate. If no transformations were found to meet these assumptions, then nonparametric tests were used. Univariate statistical analyses were performed in Minitab®17, and multivariate analyses were performed using PRIMER 7 (Quest Research Limited, New Zealand).

Pearson's correlations were used to analyze the relationship between burrow cover and number of *S. quoianum*. 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 carbon and respiration rate.

Two-way ANOVAs, with burrow status and transect as factors, were used to analyze sediment shear strength, grain size distributions, and carbon content. Since bluff angle and respiration rate did not meet ANOVA assumptions, they were analyzed using PERMANOVA, which does not rely on the assumptions of normality and equal variances (Anderson 2001). 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. A two-way ANOVA, with burrow status and transect as factors, was used to analyze univariate invertebrate abundance and species richness, excluding the Natural transect since there were no burrowed samples there.

For multivariate environmental analyses, draftsman plots were used to determine which parameters were necessary to transform. 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 since it correlated negatively with percent sand, remaining environmental parameters (shear strength, percent clay, percent sand, carbon content, respiration rate, and bluff angle) were normalized, 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 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, 2-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 2-way PERMANOVA analyses were also run using summary taxonomic levels: Crustacea, Insecta, Mollusca, Oligochaeta, Polychaeta, and Other (Arachnida, Nemertea, Platyhelminthes).

Multivariate 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 proportion of clay because it did not have a skewed distribution.

Results

Sediment Characteristics

Bluff Angle and Shear Strength

Average (\pm SEM) bluff angle in burrowed sites was $62.89 \pm 6.97^\circ$, which was steeper than in unburrowed sites with an average of $15.94 \pm 1.98^\circ$ (pseudo- $F_{1,24} = 31.68$, $P = 0.001$). Average sediment shear strengths in burrowed and unburrowed sites were not significantly different (0.47 ± 0.041 and 0.67 ± 0.011 kg/cm², respectively).

Grain Size Distribution

Sediment sand, silt, and clay contents ranged from 47.1 – 54.8%, 39.7 – 47.3%, and 4.6 – 7.4%, respectively. Sand and silt proportions were not different among transects or between burrow statuses. The proportion of clay was not different between burrowed and unburrowed samples, 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 ± 0.085 %C, than in the West and East transects, with 0.189 ± 0.035 %C and 0.124 ± 0.025 %C, respectively (log transformed, $F_{1,24} = 6.42$, $P = 0.006$; Fig. 2A). Unburrowed samples had higher sediment carbon content, averaging 0.308 ± 0.067 %C, than burrowed samples, averaging 0.158 ± 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 pattern to carbon content with the South transect averaging 168.38 ± 22.04 mg CO₂ gdw⁻¹ d⁻¹, and West and East transects averaging 79.12 ± 18.66 and 43.48 ± 3.14 mg CO₂ gdw⁻¹ d⁻¹, respectively (log transformed, pseudo- $F_{2,22} = 4.662$, $P(\text{perm}) = 0.076$; Fig. 2C). Respiration rates in the South transect were higher than in the West ($t = 2.630$, $P(\text{perm}) = 0.028$) or East ($t = 1.960$, $P(\text{perm}) = 0.053$) transects. Respiration rates averaged 105.51 ± 20.81 $\mu\text{g CO}_2$ gdw⁻¹ day⁻¹ in burrowed samples and 93.37 $\mu\text{g CO}_2$ gdw⁻¹ day⁻¹ in unburrowed samples but were not significantly different by burrow type alone. Sediment carbon content explained 52% of respiration rates ($\rho = 0.517$), and this correlation coefficient is statistically different from zero ($P = 0.006$; Fig. 2D).

Multivariate Analysis of Sediment Characteristics

Environmental parameters evaluated simultaneously differed among transects (pseudo- $F_{2,24} = 2.588$, $P = 0.014$) and between burrowed and unburrowed samples (pseudo- $F_{1,24} = 4.592$, $P = 0.001$), with no interaction effect (Fig. 3). Within transect, West and East were not different, but South was different from

West ($t = 1.744$, $P(\text{perm}) = 0.016$) and marginally different from East ($t = 1.634$, $P(\text{perm}) = 0.084$). 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 (Fig. 3), where respiration rate and carbon content were on average higher in the South transect as compared to West and East transects (Fig. 2A, 2C, 3).

Macrofaunal Invertebrate Community

The number of large *S. quoianum* ($R = 0.842$, $P < 0.001$) from invertebrate samples correlated more closely with burrow density estimates than total *S. quoianum* numbers ($R = 0.721$, $P = 0.001$). Excluding burrowed samples (as discussed in Methods), total macrofaunal invertebrate abundance was higher in the Natural transect than in the East and West transects (log transformed, $F_{3,14} = 8.76$, $P = 0.002$), but South was not different from any other area (Fig. 4A). Differences among transects in species richness followed this trend, but were only marginally significant ($F_{3,14} = 2.72$, $P = 0.084$; Fig. 4B).

Among West, East, and South transects, total abundance ($F_{1,24} = 52.49$, $P < 0.001$) and species richness ($F_{1,24} = 7.53$, $P = 0.011$) were higher in burrowed than unburrowed areas (Fig. 4C, 4D) when *S. quoianum* and *I. californica* were included, but were not different among transects. However, when these commensal isopods were excluded, there were no differences in abundance between burrowed and unburrowed samples, while differences emerged among transects with south being higher 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 in the West transect were characterized by an abundance of *Iais californica* (57%) and oligochaetes (28%); in the South transect unburrowed sites were characterized by white pill beetle larvae (53%) and oligochaetes (47%); in the Natural transect unburrowed sites were characterized by oligochaetes (82%), and in the East transect, the unburrowed sites had no invertebrates.

Species-level comparisons of samples from West, East, and South transects (excluding Natural), excluding *S. quoianum* and *I. californica* (as discussed in Methods), revealed marginal differences between burrowed and unburrowed samples (fourth root transformed, pseudo- $F_{1,24} = 1.9682$, $P(\text{perm}) = 0.082$), and among transects (pseudo- $F_{2,24} = 1.793$, $P(\text{perm}) = 0.078$) with no interaction effect. Among transects, West was not different from East or South, but South and East were marginally different from each other ($t = 1.661$, $P(\text{perm}) = 0.053$).

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 invaded transects not including the Natural transect, invertebrate community composition in the West transect was not different from that in the East or South transects, but communities were marginally different between East and South transects ($t = 1.839$, $P(\text{perm}) = 0.060$), driven by a lack of invertebrates in the East transect (excluding "NaturalU"; 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 transects, 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

Invertebrates play an important basal role in the food chain (Coleman and Hendrix 2000), and in decomposition by shredding organic material for microbial communities to consume and return nutrients back to the system (Diaz Villanueva et al. 2012). In particular, bioturbation by invertebrates has been shown to impact sediment biogeochemistry, overlying plant communities, organic matter, and nutrient cycling (Crooks 1998; Emmerson 2000; Mermillod-Blondin and Rosenberg 2006). Burrows by native bioturbators are important because they oxidize deeper sediments and create habitat (Rosenberg et al. 2001; Reise 2002), but the addition of a non-native burrower could have disproportionate effects on soft-sediment habitats, which are already particularly susceptible to invasion (Byers et al. 2006). Thus, we hypothesized that the ability of *S. quoianum* to create dense networks of burrows into salt marsh sediments outside its native range (Talley et al. 2001; Davidson et al. 2008) would have important implications for ecosystem functions such as respiration and habitat provisions for invertebrates.

Differences in Sediment Characteristics

Carbon content across invaded areas was low compared with surface carbon content in nearby Huntington Beach Wetlands (Keller et al. 2015). Similar to trends in invertebrate community characteristics among invaded transects, carbon content and respiration rates were higher in the South transect than in the West or East transects. Although burrows have been shown to increase respiration in soft-sediment habitats (Pulmanns et al. 2014; Sasaki et al. 2014), respiration rates in the invaded areas of Bolsa Chica Wetlands were not different between burrowed and unburrowed areas.

Low respiration rates were likely a result of low carbon content since sediment microbial communities had little organic matter to mineralize. However, it is interesting to note that carbon content was lower in burrowed samples as compared to unburrowed samples (Fig. 2A) while respiration was not. One

possibility is that the sediment in these areas, while inundated daily by tidal fluctuations, is not anoxic like typical soft-sediment habitats, possibly due to the high sand content. Grain size distributions in all three invaded areas surveyed in this study were approximately 50 – 55% sand, and less than 10% clay, while grain size distributions in nearby Huntington Beach Wetlands are closer to 22% sand, with higher clay content (Whitcraft et al. unpublished). As a result of higher proportions of sand, it is possible that the sediments in the surveyed areas of our study quickly drained between tidal flushing. If all soils were effectively aerobic, this could explain the lack of differences in sediment respiration between burrowed and unburrowed samples. Finally, burrowed and unburrowed samples in invaded areas could be subject to other sources of variation such as tidal height. Because unburrowed samples were extremely difficult to find due to high burrow densities along the intertidal zone, the closest unburrowed areas remaining for sampling were often slightly above or below this zone. This unavoidable variation in tidal height between burrowed and unburrowed samples could also explain the high variability in sediment shear strengths between those areas. However, the trend indicates that a higher sample size could reveal firmer sediment (higher shear strength) in unburrowed samples as compared with burrowed. This trend is consistent with the findings of Talley et al. (2001) that areas with high burrow densities had lower shear strengths, which leads to more erosion.

Though more research is needed to elucidate effects and habitat preferences 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. Davidson (2010) found that *S. quoianum* invaded marshes were typically taller than invaded sites. Talley et al. (2001) found firm sediments beneath vertical *Salicornia* marsh were more heavily invaded than softer, gently sloping *Spartina* habitats. While erosion is a characteristic inherent to areas that have steeper banks, which can result when water current is not slow enough 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 erosion. This strong association between *S. quoianum* and vertical banks should be considered when making management decisions.

Differences in Invertebrate Community Structure

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). While there is a temporal offset between the two invertebrate sampling periods, we believe the reduced abundance and species richness as well as the altered community composition seen in the study area in general is significantly greater than the year-to-year variation seen in similar southern California marshes (CRW will list some references – Whitcraft et al. 2012 HBW report).

Our analyses excluded the non-native isopod, *Iais 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. Interestingly, one of the species driving increased proportions of crustaceans in burrowed samples (after *S. quoianum* and *I. californica* were removed from analysis) was *Grandiderella japonica*, which is also non-native. *G. 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 Whitlatch 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 potentially as a facilitator for colonization by other non-native species in a habitat already highly susceptible to alteration by invasive species (Green et al. 2011).

This study also revealed differences in invertebrate community structure among transects. The Natural transect had the highest invertebrate abundance, as compared with unburrowed samples in West, East, and South transects. Among invaded transects, South had the highest invertebrate abundance. One explanation for this finding could be the proximity of the South transect to the Natural transect. In our study, the unvegetated, sandier West and East transects were situated further from the relatively well vegetated Natural transect, while the South transect was closest to it and occupied an area transitioning from the narrow channel and steep sandy banks to the wider, more gently sloping marsh. Indeed, Natural and South transects had higher proportions of oligochaetes, with the largest proportion of oligochaetes found in the Natural transect, while the highest proportions of insects were found in the West and South transects. Prior studies have connected oligochaetes to more vegetated areas since oligochaetes are detrital grazers (Whitcraft and Levin 2007), which could explain why there are more oligochaetes in the Natural transect, which had higher vegetation cover than the invaded transects (pers. obs.). 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.

Total abundances in all invaded areas (West, East, and South transects) of Bolsa Chica were very low. However, differences were still found between burrowed and unburrowed samples, particularly in the South transect which resembled natural marsh conditions more closely than other areas. This suggests the potential for *S. quoianum* to have large impacts on associated macroinvertebrates in more natural settings. Similar to our study, Dauwe et al. (1998) found very low macrofaunal biomass in a site with low organic matter and coarse-grained, sandy sediment. This points to the potential importance of environmental factors to the microhabitats of invertebrate communities.

Management Recommendations

Since *S. quoianum* is known for accelerating erosion of marsh banks, managers with the goal of creating or restoring coastal salt marshes should avoid creating tall vertical marsh bluffs, and consider the importance of sediment characteristics such as grain size, organic matter content, bluff angle, and shear strength. Furthermore, since this isopod undergoes direct development and does not have a larval stage, efforts can be made to reduce spread through sediment fouling by ensuring that construction equipment used during restoration activities or near susceptible habitat is cleaned thoroughly. This may be particularly important in Bolsa Chica Wetlands, where other portions of the salt marsh could be vulnerable. Although our study was conducted in a small section of mid-marsh unvegetated habitat within Bolsa Chica, the area is representative of some additional habitat within Bolsa Chica (~10%) as well as an important habitat regionally in southern California. Bolsa Chica shares important features with numerous regional estuaries (disturbance from surrounding land use, erosion) indicating that additional estuaries in southern California are susceptible to invasion by *S. quoianum*. Our results demonstrate that *S. quoianum* has the potential to alter the habitat and environmental conditions of the mid intertidal habitats within these marshes. Thus, vigilant monitoring for incipient invasions and rapid, coordinated responses in southern California marshes will be essential to effective management.

Declarations

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Conflicts of interest/Competing interests: Not applicable

Availability of data and material: Sediment parameters (carbon content, respiration rates) and invertebrate parameters (including species list) will be available on a specific DOI link once accepted for publication.

Code availability: Not applicable

Authors' contributions:

Morgan Brown was responsible for project conceptualization, data collection and curation, formal analysis, funding acquisition, investigation, development of methodology, writing the original draft, and revising the subsequent drafts.

Jason Keller was responsible for project conceptualization, supervision of data collection and curation, assistance with formal analysis, development of methodology, writing the original draft, and subsequent drafts.

Christine R. Whitcraft was responsible for project conceptualization, supervision of data collection and curation, assistance with formal analysis, funding acquisition, investigation, development of methodology, project administration, supervision, writing the original draft, and subsequent drafts.

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Figures

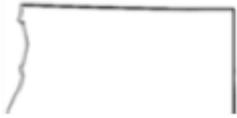


Figure 1

Map of the study area. (A) Location of study in southern California. (B) Google Earth image of Bolsa Chica Ecological Reserve, showing Outer Bolsa Bay (solid), and Inner Bolsa Bay (dashed). (C) North portion of Outer Bolsa Bay where *Sphaeroma quoianum* burrows were found and where West, East, South and Natural transects were designated. (D) Map of West, East, South, and Natural transects. Map data: ©2019 Google

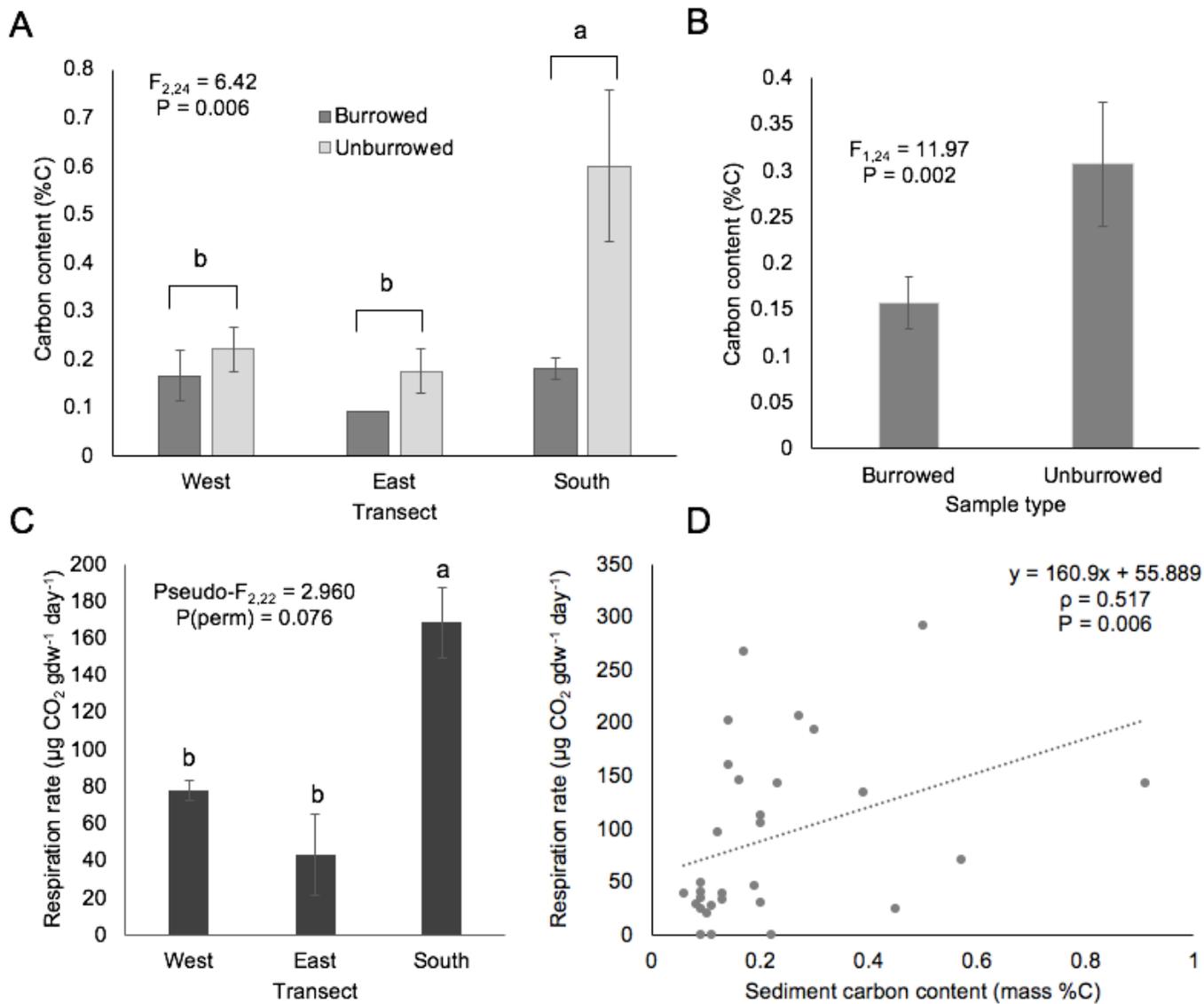


Figure 2

Carbon content. (A) Carbon content (% C) \pm SEM of burrowed (dark) and unburrowed (light) sediment samples among West, East, and South transects. (B) Carbon content (% C) \pm SEM of burrowed and unburrowed sediment samples including West, East, and South transects. (C) Respiration rates. Average respiration rates \pm SEM in West, East, and South transects. (D) Carbon content versus sediment respiration. Relationship between sediment carbon content (mass %C) and sediment respiration ($\mu\text{g CO}_2 \text{gdw}^{-1} \text{day}^{-1}$) across West, East, and South transects.

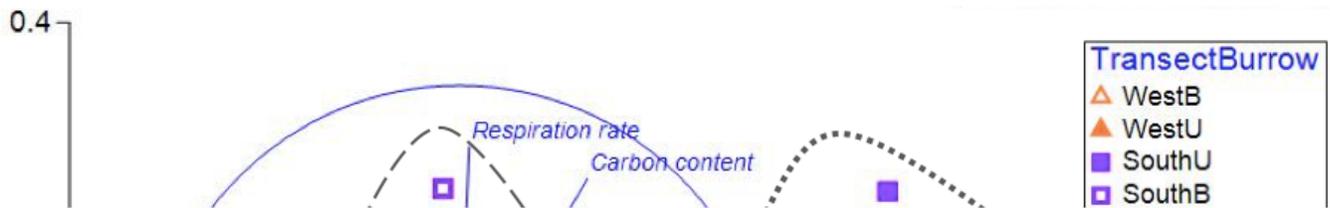


Figure 3

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 (West = triangles, East = circles, South = squares) and burrow status (burrowed (B) = open symbols, circled by dashed line; unburrowed (U) = solid symbols, circled by dotted line) with environmental parameters as axes to separate groups ($\delta 1 = 0.84$, $\delta 2 = 0.69$).

Figure 4

Abundance and species richness by transect and burrow status. (A) Invertebrate community total abundance (N) \pm SEM and (B) species richness (S) \pm SEM of invertebrate communities in unburrowed samples among transects. (C) Total abundance (N) \pm SEM and (D) species richness (S) \pm SEM in burrowed and unburrowed samples, shown with *S. quoianum* and *I. californica* included (dark gray) and excluded (light gray) from analysis.

Figure 5

Invertebrate community CAP. CAP analysis of summary invertebrate levels by transect (West = triangles, East = circles, South = squares, Natural = crosses) and burrow status (burrowed [B] = open symbols, circled by dashed line; unburrowed [U] = solid symbols, circled by dotted line) with summary levels as axes to separate groups ($\delta_1 = 0.69$, $\delta_2 = 0.51$).

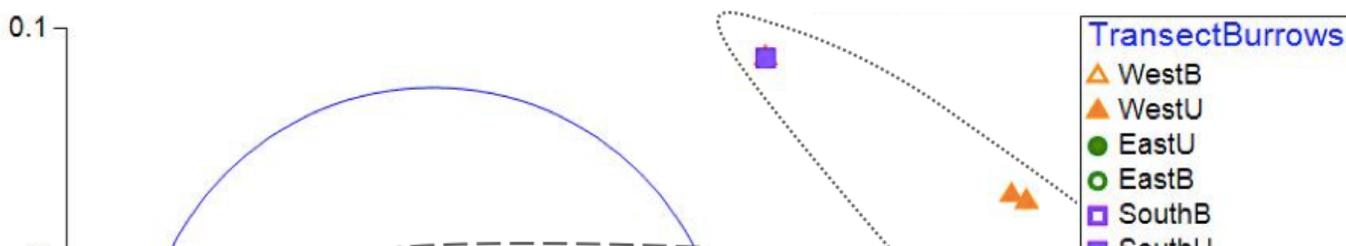


Figure 6

Invertebrate community CAP with environmental parameters. CAP analysis of summary invertebrate community by transect (West = triangles, East = circles, South = squares) and burrow status (burrowed [B] = open symbols, circled by dashed line; unburrowed [U] = solid symbols, circled by dotted line) with environmental parameters as axes to separate groups ($\delta_1 = 0.62$, $\delta_2 = 0.42$).