

The composition and density of fauna utilizing burrow microhabitats created by a non-native burrowing crustacean (*Sphaeroma quoianum*)

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Abstract The non-native isopod, *Sphaeroma quoianum*, has invaded many estuaries of the Pacific coast of North America. It creates extensive burrow microhabitats in intertidal and subtidal substrata that provide habitat for estuarine organisms. We sampled burrows to determine the effects of substratum type on the community of inquilines (burrow inhabitants). The density of inquilines was higher in wood and sandstone than marsh banks. Inquilines, representing 58 species from seven phyla, were present in 86% of samples. Inquilines equaled or outnumbered *S. quoianum* in 49% of the samples. Non-native fauna comprised 29% of the species and 35% of the abundance of inquilines,

which is higher than other estuarine habitats in Coos Bay. Sessile non-native species were found living within burrows at tidal heights higher than their typical range. Thus, the novel habitat provided by burrows of *S. quoianum* may alter the densities and intertidal distribution of both native and non-native estuarine fauna.

Keywords Bioeroder · Ecosystem engineer · Facilitation · Habitat alteration · Inquilines · *Sphaeroma quoianum*

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Introduction

Non-native ecosystem engineers have profound impacts on communities. By modifying the abiotic environment, these species alter habitats or other resources and cause changes in the composition and abundances of the surrounding community (Jones et al. 1997; Crooks 2002). The magnitude of the impact is not only related to the per capita effects of the engineering, but also the density and prevalence of that engineer within its environment (Jones et al. 1994). Thus, engineering species with small per capita effects have large impacts on the physical environment where they occur at high densities and wide distributions. Within aquatic systems, there are abundant examples of non-native species with small per capita effects that, when aggregated in large numbers,

can have large cumulative effects on the structure of the habitat they invade (reviewed in Carlton 1992; Coleman and Williams 2002; Crooks 2002; Gutiérrez et al. 2003). While most studies have examined the negative aspects of non-native ecosystem engineers, others have documented increases in community diversity and abundance and other facilitative effects of non-native ecosystem engineers (Posey 1988; Crooks 1998; Simberloff and Von Holle 1999; Schwindt and Iribarne 2000; Castilla et al. 2004; Wonham et al. 2005; Buschbaum et al. 2006). Increases in community diversity and abundance, however, are sometimes due to facilitation of other non-native species (Heiman et al. 2008). Facilitations between non-native species have been documented in numerous aquatic systems including kelp forests (Levin et al. 2002), saltmarshes (Neira et al. 2006), estuarine mudflats (Grosholz 2005; Wonham et al. 2005), ponds and wetlands (Adams et al. 2003), and in numerous studies of the Great Lakes (Ricciardi 2001).

The facilitative effects of non-native ecosystem engineers on marine community diversity and abundance are often the result of an increase in the structural complexity of the habitats they invade (Jones et al. 1997). The serpulid polychaete *Ficopomatus enigmaticus* creates extensive reefs on invaded mudflats, which provide habitat for abundant fauna (Schwindt and Iribarne 2000; Heiman et al. 2008). Expansive fields of the non-native eelgrass *Zostera japonica* harbor significantly more infaunal invertebrates than adjacent unvegetated mudflats in Coos Bay, Oregon (Posey 1988). In Mission Bay, San Diego, California, the complex structure provided by mats of the non-native mussel *Musculista senhousia* host significantly more fauna (richness and abundances) than sediments without mats (Crooks 1998). Although these species increase structural complexity through their biogenic structures, ecosystem engineers can also increase complexity by altering the physical state of the habitat through their physical actions (known as *allogenic* engineers, Jones et al. 1994, 1997).

Burrowing sphaeromatid isopods are allogenic ecosystem engineers present in many temperate and tropical marine systems of the world (Harrison and Holdich 1984). These sphaeromatids burrow into a variety of substrata such as friable rock, woody debris, marsh banks (composed of peat, mud, or clay), mangroves, vegetative portions of marsh

plants, sponges, and maritime structures (Barrows 1919; Carlton 1979; Estevez 1994; Cragg et al. 1999; Talley et al. 2001; Murata and Wada 2002; Davidson 2008). Numerous studies have examined the detrimental impact of isopod burrowing on these substrata (Rehm and Humm 1973; Dharmaraj and Balakrishnan Nair 1982; Perry and Brusca 1989; Cragg et al. 1999; Talley et al. 2001). While a few studies have mentioned the presence of marine fauna in isopod burrows (Morton and Miller 1968; Estevez 1978; Talley and Crooks 2007; Davidson et al. 2008a), these studies did not adequately characterize the community in burrow microhabitats or examine if the community structure varies in different substrata.

In many estuaries of the Pacific coast of North America (PCNA), habitats are being altered by the non-native sphaeromatid isopod, *Sphaeroma quoianum* (= *S. quoyanum*; Milne Edwards 1840). This isopod creates dense burrow networks in a variety of habitats including marsh banks, decayed wood, friable rock cobble and ledges, and Styrofoam floats used in floating docks (Carlton 1979; Davidson et al. 2008b). In some bays, high densities of burrows of *S. quoianum* increase the rate of erosion of marsh banks (Talley et al. 2001) and friable rock (Higgins 1956) and damage some marine structures (Carlton 1979; Davidson 2008).

Sphaeroma quoianum is native to Australia, Tasmania, and New Zealand and likely was introduced to North America through ship fouling or by boring into ship hulls (Rotramel 1972; Carlton 1979). This species, introduced to San Francisco Bay during the late nineteenth century, has spread to numerous bays along the PCNA (reviewed by Davidson 2008), and reached Coos Bay, Oregon, sometime before 1995 (Carlton 1996). *Sphaeroma quoianum* occurs throughout Coos Bay (Davidson 2008) and has created extensive burrow networks in many areas that were previously uninhabited and often lacking obvious habitat heterogeneity (personal observation). Since many native and non-native organisms inhabit the novel habitats created by non-native engineers (Posey 1988; Crooks 1998; Schwindt and Iribarne 2000) including burrows of *S. quoianum* in Californian marsh bank systems (Talley and Crooks 2007), it is likely that the complex burrow habitat created by *S. quoianum* in marsh bank, wood, and sandstone substrata also provides novel habitat for other organisms in Coos Bay.

This study seeks to reveal how an estuarine community utilizes and is associated with the different burrow microhabitats created by a non-native allogenic engineer and elucidate aspects of the ecology of an understudied non-native crustacean. Specifically, our research seeks to answer the following questions: (1) What is the density, prevalence and identity of the faunal community utilizing the burrows of *S. quoianum* as habitat? (2) Does the density, prevalence, and composition of the burrow inhabitants (hereafter: *inquilines*) differ between substrata? (3) Does the population density and prevalence of *S. quoianum* differ in three substrata and across three months? and (4) How do the densities of *S. quoianum* relate to the density, richness, and diversity of the inquiline community?

Methods

Study location

Coos Bay is a small temperate drowned-river estuary (50 km²) located in southern Oregon, USA (43.35°N, 124.34°W). The estuary is heavily tidally influenced; salinity in the upper estuary can range from nearly fresh to full seawater during the same tidal cycle (Rumrill 2006). The shoreline is composed of sandy beaches, sloping marshes, extensive marsh banks, rocky riprap, and sandstone terraces and shelves. Abundant woody debris is present along the shore from past and present logging operations. Coos Bay also hosts at least 68 non-native species likely due to the long history of international shipping and commercial oyster cultivation (Ruiz et al. 2000; JT Carlton, unpublished data; personal observation).

Isopod and community sampling methods

To evaluate the density of inquilines and individuals of *S. quoianum* within burrowed marsh bank, wood, and sandstone, intertidal stations were sampled between July 29–August 6, 2005, January 8–24, 2006 and April 3–14, 2006. Eight stations for each substratum type were haphazardly selected among areas with established *S. quoianum* populations. At marsh bank stations, ten cores (6.2 cm diameter × 10 cm depth) were randomly sampled along a 50 m transect in burrowed banks. At wood stations, four discrete pieces

of burrowed woody debris were randomly collected along a 50 m transect. At sandstone stations, either four pieces of burrowed cobble were randomly collected or burrowed sandstone terraces were randomly sampled along a 50 m transect (four cores) using a serrated steel corer (7.62 cm diameter × 6 cm depth). We were only able to collect four subsamples of wood and sandstone substrata due to logistical constraints. The depths of marsh bank and sandstone cores were selected to surpass the length of the deepest burrows created by *S. quoianum* in the respective substrata. The numbers of burrows within each subsample were counted in the field and the subsamples were brought to the lab for processing. The volumes of wood and sandstone cobble samples were calculated through a series of digital photographs taken at multiple angles and analyzed by Imagetool 3.0 image analysis software. All samples were physically sorted in the lab and all organisms were placed in 70% ethanol, enumerated, and identified to the lowest possible taxonomic level. To determine what fauna utilize unburrowed substrata, we also conducted qualitative surveys of the fauna inhabiting unburrowed substrata during April 2005 and June 2008.

Statistics

Three-way partially nested mixed-model repeated measures ANOVA was used to determine if the mean densities of inquilines, *S. quoianum*, and burrows differ between month (repeated factor) and substratum. The following factors were identified as fixed in this model: month, substratum, and the interaction between month and substratum. Station (nested within substratum) and the interaction between month and station were considered random factors. Assumptions of normality and homogenous variance were visually evaluated using residual and box plots. Isopod, burrow, and inquiline density data were $\log(x + 10^{-6})$ transformed to improve normality and the homogeneity of the variances. Transformations failed to normalize the data, but the homogeneity of variance was improved for most variables. To account for violations of the ANOVA, we set the significance level for all tests at $\alpha_{\text{crit}} \leq 0.025$ (Underwood 1981). We also used Greenhouse-Geisser corrected *P* values (for within subjects factors) to account for the violation of sphericity. All a posteriori comparisons were examined with Bonferroni pairwise contrasts.

We examined the relationship between the densities of *S. quoianum* and the density, richness, and Shannon diversity of inquilines in the stations using Pearson's correlations (log-transformed). The prevalence of *S. quoianum* and inquilines within samples in the different substrata during different months were analyzed using single classification goodness of fit *G*-tests with the Williams correction. We define prevalence as the number of samples with at least one specimen observed per the total number of samples examined. We examined the similarity of the communities of inquilines living in burrows of different substrata using non-metric multidimensional scaling with the Bray–Curtis dissimilarity measure (using *R*, version 2.4.1). Prior to the analysis, we pooled all subsamples at a given station per sampling month since many of the individual subsamples (cores, pieces) harbored few taxa. The relative abundances of inquilines were $\log(x + 1)$ transformed to down-weight the influence of dominant taxa. We did not include *S. quoianum* when calculating our measures of the inquiline community.

Results

Density, prevalence, and composition of inquilines

The mean densities of inquilines were significantly higher in sandstone and wood than marsh bank substrata (Fig. 1a; Table 1a). Nearly one half of samples (48.7%) harbored densities of inquilines greater than or equal to the densities of *S. quoianum*. Similar densities of inquilines across the three sampling months (Table 1a) suggested high year-round usage of burrows. Inquilines were present in 86.3% of all samples and we did not detect a significant difference in the prevalence of inquilines between substrata or month (Table 2).

Fifty-eight species from seven phyla were found within burrows of *S. quoianum* (see “Supplementary Materials”) including both estuarine and semi-terrestrial invertebrates (insect larvae, beetles, mites, and pseudoscorpians). The richness of the inquiline community varied between substrata (marsh bank: 40 species, wood: 36 species, sandstone: 44 species) but the mean Shannon diversity indices of inquilines (\pm SD) at stations were similar ($H_{\text{Marsh Bank}} = 1.13 \pm$

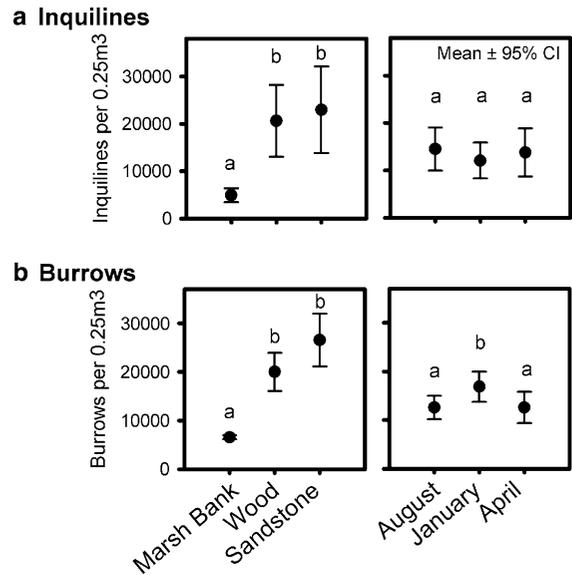


Fig. 1 Mean densities of **a** Inquilines and **b** Burrows (\pm 95% CI) in marsh bank, wood, and sandstone substrata and in August, January, and April samples; different letters denote a significant difference between means ($P < 0.025$). Inquiline densities do not include *S. quoianum*

0.40, $H_{\text{Wood}} = 1.22 \pm 0.50$, $H_{\text{Sand stone}} = 1.34 \pm 0.53$). However, our qualitative surveys of unburrowed substrata in 2005 and 2008 found few (and often zero) species living on or in the unburrowed substrata within our sampling stations and adjacent areas. In surveys of 2005, the cumulative richness of unburrowed marsh bank, wood, and sandstone substrata were 1, 4, and 3 species, respectively. Additional samples collected during June 2008 revealed a similar pattern, with only 6, 3, and 4 total species found on or within unburrowed marsh bank ($n = 40$), wood ($n = 22$), and sandstone samples ($n = 8$). The density, richness, and diversity of inquiline community were positively correlated with densities of *S. quoianum* in some substrata (Table 3). The inquiline communities in the three substrata overlap considerably in multidimensional space (Fig. 2) indicating the species composition of the inquiline community does not vary substantially between substrata.

Isopods and amphipods comprised the majority of all inquiline taxa (78.3%; Fig. 3). The native isopod *Gnorimosphaeroma oregonense*, the non-native isopod *Pseudosphaeroma campbellense* (= *P. campbellensis*), and the native amphipod *Eogammarus confervicolus* were the most numerically dominant

Table 1 Results of three-way mixed model partially nested repeated measures ANOVA tests for differences in mean density of a. Inquilines, b. Burrows, and c. *Sphaeroma quoianum* between substratum (marsh bank, wood, sandstone) and month (August, January, April)

Source of variation	df	MS	F	P
(a) Inquilines				
Between subjects				
Substratum	2	0.272	10.07	<0.001
Station (substratum)	21	0.027	2.80	<0.001
Residual	119	0.01		
Within subjects				
Month	2	0.002	0.13	0.726 (0.883)
Month × substratum	4	0.012	0.75	0.529 (0.564)
Month × station (substratum)	42	0.016	1.83	0.004 (0.003)
Residual	238	0.009		
Greenhouse-Geisser Epsilon	0.926			
(b) Burrows				
Between subjects				
Substratum	2	0.258	14.33	<0.001
Station (substratum)	21	0.018	6.54	<0.001
Residual	118	0.003		
Within subjects				
Month	2	0.022	5.50	0.024 (0.008)
Month × substratum	4	0.008	2.00	0.131 (0.112)
Month × station (substratum)	42	0.004	1.40	0.072 (0.063)
Residual	236	0.003		
Greenhouse-Geisser Epsilon	0.901			
(c) <i>Sphaeroma quoianum</i>				
Between subjects				
Substratum	2	0.331	18.39	<0.001
Station (substratum)	21	0.018	2.67	<0.001
Residual	119	0.007		
Within subjects				
Month	2	0.271	20.85	<0.001 (<0.001)
Month × substratum	4	0.088	6.77	0.001 (<0.001)
Month × station (substratum)	42	0.013	2.01	0.002 (0.001)
Residual	238	0.007		
Greenhouse-Geisser Epsilon	0.769			

Inquiline densities do not include *S. quoianum*

Boldface denotes statistical significance

P values for within subjects factors were adjusted with the Greenhouse-Geisser correction, uncorrected *P* values are presented in parentheses

species in all substrata. In marsh bank samples, these three species constituted 94.8% of the fauna, but they were also abundant in wood and sandstone burrows, comprising 47.8 and 63.9% of the inquilines,

respectively. Most inquilines were motile species (70.2%) and mesograzers (58.3%), although detritivores and predators were also relatively common (22.9 and 25%, respectively).

Table 2 The prevalence of inquilines, non-native species (non-natives), and individuals of *S. quoianum* in marsh bank, wood, and sandstone substrata and in August, January, and April samples

	Inquilines		Non-natives		<i>S. quoianum</i>	
	Obs/total	%	Obs/total	%	Obs/total	%
Marsh Bank	197/240	82.1	61/240	25.4	189/240	78.8
Wood	87/95	91.6	52/95	54.7	86/95	90.5
Sandstone	88/96	91.7	61/96	63.5	91/96	94.8
<i>G</i>	1.1		30.4		2.5	
<i>P</i>	0.57		<0.001		0.29	
August	120/143	83.9	59/143	41.3	115/143	80.4
January	122/144	84.7	68/144	47.2	126/144	87.5
April	130/144	90.3	47/144	32.6	125/144	86.8
<i>G</i>	0.40		3.88		0.52	
<i>P</i>	0.82		0.14		0.77	

Williams-corrected *G* statistics are displayed

Boldface denotes statistical significance

Obs/total = number of samples with at least one individual observed per total number of samples examined

Table 3 Results of Pearson’s correlations (r^2) between the density of *S. quoianum* and the density, richness (*S*), and Shannon diversity (*H*) of the inquiline community in marsh bank, wood, and sandstone substrata

	Marsh Bank	Wood	Sandstone
Density	$r^2 = 0.01$ (–) <i>P</i> = 0.65	$r^2 = 0.29$ (+) <i>P</i> = 0.007	$r^2 = 0.43$ (+) <i>P</i> < 0.001
Richness (<i>S</i>)	$r^2 = 0.21$ (+) <i>P</i> = 0.026	$r^2 = 0.01$ (+) <i>P</i> = 0.57	$r^2 = 0.01$ (+) <i>P</i> = 0.72
Diversity (<i>H</i>)	$r^2 = 0.34$ (+) <i>P</i> = 0.003	$r^2 = 0.02$ (+) <i>P</i> = 0.51	$r^2 = 0.09$ (–) <i>P</i> = 0.17

Data pooled from all sampling dates, *n* = 24

(+) positive correlation, (–) negative correlation

Boldface denotes statistical significance

Non-native inquilines

Non-native species comprised 28.9% of all identified species with a known origin. The percentage of non-native fauna varied between substrata (25.8, 29.0, and 31.4% in marsh bank, wood, and sandstone, respectively). By abundance, approximately 35% of the identifiable inquilines were non-native. The percentage of non-native fauna (by abundance) was lower

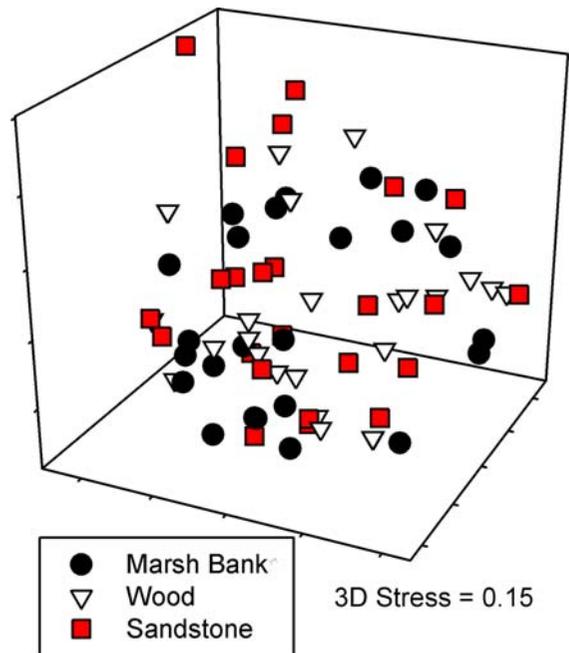


Fig. 2 Three-dimensional non-metric multidimensional scaling ordination plot showing the similarity (Bray–Curtis) of the inquiline communities in three different substrata (marsh bank, wood, sandstone). Spatial distance in the sites indicates the relative similarity of the communities

within marsh banks (22.4%) than wood (36%) and sandstone (36.8%). Non-native species were present in 40% of all samples and occurred more frequently in burrows in wood and sandstone substrata than marsh banks (Table 2). Several non-native sessile and sedentary taxa (*Crassostrea gigas*, *Diadumene lineata*, *Conopeum tenuissimum*, *Mya arenaria*) were found within sandstone or wood burrows at tidal heights higher than they normally occur in (≈ 0.5 m below the high tide mark). This pattern of higher distribution was also found for the native clam *Macoma balthica*.

Densities of *S. quoianum* and burrows

The mean densities of *S. quoianum* were significantly higher in wood and sandstone substrata than marsh banks and densities decreased from August through April (Table 1; Fig. 4). We did not detect a difference in the prevalence of isopods in the substrata or across months (Table 2). Most samples (85%) harbored at least one individual of *S. quoianum*. The mean densities of burrows of *S. quoianum* were

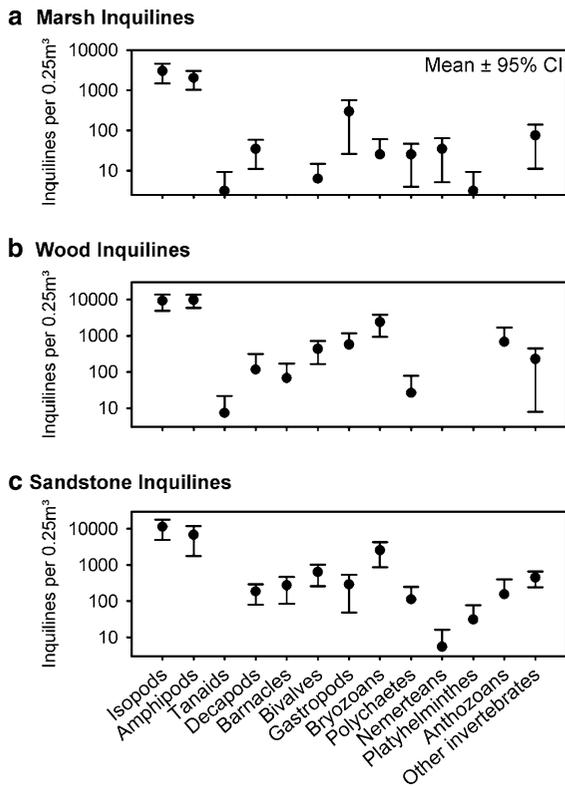


Fig. 3 The mean abundances per 0.25 m³ ($\pm 95\%$ CI) of inquiline taxa found within **a** marsh bank, **b** wood, and **c** sandstone substrata. Other invertebrates include insects, spiders, mites, and pseudoscorpions. Inquiline densities do not include *S. quoianum*. Note the log scaling on the y-axis

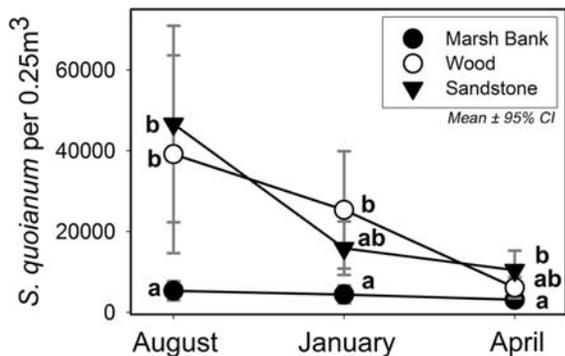


Fig. 4 Mean density of *S. quoianum* ($\pm 95\%$ CI) in three substrata (marsh bank, wood, sandstone) and across 3 months (August, January, April); different letters denote a significant difference in mean isopod densities between substrata ($P < 0.01$)

significantly higher in sandstone and wood than marsh bank substrata and varied significantly between months (Table 1; Fig. 1).

Discussion

Density, prevalence, and composition of inquilines

Through the creation of an extensive network of burrows, *S. quoianum* physically engineers a novel habitat in invaded substrata. A variety of estuarine and semi-terrestrial species utilize this burrow habitat in densities that can equal or exceed the densities of *S. quoianum* (thousands to tens of thousands of individuals per 0.25 m³). Fauna were prevalent within burrow habitat; over 82% of marsh bank samples and nearly 92% of wood and sandstone samples harbored inquilines. In contrast, our qualitative surveys and samples of unburrowed substrata were largely depauperate of fauna. Surveys detected only 1, 4, and 3 total species living on or within marsh bank, wood, and sandstone substrata, respectively. Likewise, unburrowed marsh bank, wood, and sandstone samples collected during 2008 only harbored 6, 3, and 4 total species, respectively. The dense and species-rich community found within burrows compared to relatively uninhabited unburrowed substrata indicates that populations of *S. quoianum* could alter the abundance and composition of the local estuarine community.

The positive associations between the density, richness, and diversity of the inquiline community and densities of *S. quoianum* in some substrata suggest populations of *S. quoianum* may facilitate a variety of fauna. Similarly, Talley and Crooks (2007) found the richness and abundance of benthic macrofauna inhabiting marsh banks in San Francisco bay were weakly associated ($R^2 = 0.21$ and 0.15 , respectively) with densities of *S. quoianum*. While we did not detect an association between inquiline and isopod densities in marsh bank substrata, we did detect a positive association in wood and sandstone substrata. In addition, we found the richness and diversity of the inquiline community is positively correlated to isopod densities in marsh banks.

Although many organisms utilize *S. quoianum* burrows, the duration and benefits of this use are unknown. Inquilines could be using the burrows temporarily to escape the physical stresses encountered at low tide, as with gastropods utilizing crevices (Garrity 1984; Jones and Boulding 1999), or they could be semi-permanent residents of these burrow

networks. The increased habitat heterogeneity of burrow habitat likely provides cover from predators (as with organisms utilizing cracks and holes, Menge and Lubchenco 1981; Menge et al. 1983) and ameliorates environmental stresses (temperatures, desiccation, UV exposure). In addition, burrows can harbor an interior surface lined with a fine layer of organic matter (personal observation) and possibly biofilm, fungi, and microalgae (as with burrows of *S. serratum*, El-Shanshoury et al. 1994) that many mesograzers and detritivores might feed upon. Thus, the habitat created by *S. quoianum* may be providing a nutritive benefit as well as a favorable microhabitat for the inquiline community. In all three substrata, a majority of the inquiline community was composed of mesograzers; we hypothesize that these taxa are most likely to benefit from the conversion of bare substrata to heterogeneous burrow habitats. If burrows of *S. quoianum* enhance the survivorship of mesograzers, there may be a cascade of community effects resulting from increased grazing by these taxa (Duffy and Hay 2000; Davenport and Anderson 2007; Moksnes et al. 2008). Furthermore, burrows provided habitat for a variety of semi-terrestrial invertebrates including pseudoscorpions, mites, spiders, and the larval or adult stages of insects. Although they were not numerically dominant, occupation of isopod burrows by semi-terrestrial organisms may present new opportunities for competitive and trophic interactions at the interface between the estuarine and terrestrial environments.

In addition to providing a more complex habitat for numerous species, burrows of *S. quoianum* may extend the tidal range of some fauna. The Pacific oyster, *Crassostrea gigas*, anemone *Diadumene lineata*, and bryozoan *Conopeum tenuissimum* (all non-native species) are typically found in low and mid intertidal areas in Coos Bay (Rudy and Rudy 1983; personal observation) and other estuaries (Ricketts et al. 1985; Morris et al. 1980), but within burrows, they were found inhabiting the upper-mid to high intertidal zone. Two infaunal species, the non-native clam *Mya arenaria* and native clam *Macoma balthica*, typically associated with sand or mudflats in the mid to low intertidal (Rudy and Rudy 1983; Morris et al. 1980; personal observation) were also found within burrows. This suggests that isopod burrows may extend the intertidal distribution of these species, perhaps by providing a habitat in the high intertidal

that is buffered from environmental stressors (desiccation, temperature, etc.). Burrow use by highly mobile estuarine taxa, such as isopods and gammarid amphipods, may only be incidental. While some amphipod species have specific microhabitat preferences (*Eogammarus confervicolus*, Stanhope et al. 1992), many isopod and amphipod taxa utilize habitats opportunistically (Edgar 1991; Aikins and Kikuchi 2001).

Non-native inquilines

Burrow microhabitats appear to harbor greater proportions of non-native fauna than other habitats in Coos Bay. Non-native fauna comprise ~29% of the species and 35% of the total abundance of inquilines living within the three substrata. In contrast, Hewitt (1993) and de Rivera et al. (2005) found non-native taxa comprised ~12 and 23% of the total fouling species within Coos Bay, respectively. Approximately 18% of the species and 26% of the abundance of fauna with a recognizable invasion status (non-native or native) were non-native in *Z. japonica* and the adjacent mudflats of Coos Bay (calculated from Posey and Rudy 1987). Compared to burrowed habitat, several other habitats in Coos Bay also exhibit lower percentages of non-native species including: eelgrass beds (13.9%), unvegetated mudflats (14.3%), burrowing shrimp beds (23.5%), and mixed oyster and eelgrass beds (10.8%; calculated from Rumrill 2006). By providing habitat for a greater proportion of non-native fauna than other habitats within Coos Bay, burrow microhabitats created by *S. quoianum* could be important sources for the establishment and spread of non-native species. Given the wide distribution of *S. quoianum* along the PCNA (Davidson 2008), populations of isopods in other temperate embayments may also facilitate the non-native fauna present in those estuaries. Thus, by reducing the population levels of this non-native ecosystem engineer, managers may reduce the abundances and prevent the facilitation of other non-native species. Future studies should determine if population levels are reduced by different management strategies such as: the physical removal of invaded substrata, filling in burrows and smothering isopods, or application of the pesticide carbaryl (Sevin). However, the difficulty and feasibility of implementing these management strategies

further underscores the importance of preventing the spread of *S. quoianum* to other estuaries on the PCNA.

Density of *S. quoianum* and burrows

Approximately 10 years following the discovery of *S. quoianum* in Coos Bay, populations have attained densities in the thousands to tens of thousands of individuals per 0.25 m³ within marsh banks, woody debris, and sandstone rock. The higher densities of *S. quoianum*, burrows, and inquilines found in wood and sandstone than marsh bank substrata, are likely related to the physical characteristics of these substrata. More burrows could perforate wood and sandstone than marsh bank substrata before the substrata succumb to erosion, thus providing more habitat for *S. quoianum* and inquilines. Other plausible factors influencing the density of isopod burrows (tidal height, salinity, temperature, predators) appear similar between stations. Burrow networks created by *S. quoianum* in marsh bank, sandstone, and wood substrata persist in the intertidal and can outlive the engineer that created them (Talley et al. 2001; personal observation). Thus, as isopod populations continue to colonize these substrata, burrows may become a semi-permanent shoreline feature with possible long-term influences on the estuarine community.

Conclusions

Sphaeroma quoianum has converted many estuarine areas into heterogeneous burrow habitats in Coos Bay and other invaded estuaries on the PCNA (Carlton 1979). In areas that lack habitat heterogeneity, the structure associated with *S. quoianum* burrows may increase the abundances of estuarine fauna and allow some species to live at higher tidal elevations than normal. However, the possible facilitative effect of burrows on estuarine fauna should be evaluated with manipulative studies. In particular, studies should investigate the facilitative effects of burrows on the abundances of mesograzers and non-native species. While this non-native allogenic engineer creates burrows used by other estuarine fauna, the possible facilitative effects on community diversity and abundance are negated by the direct and indirect

effects of the erosive burrowing by *S. quoianum* on estuarine shorelines and maritime structures.

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