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Habitat utilization and alteration by the invasive burrowing isopod, *Sphaeroma quoyanum*, in California salt marshes

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Abstract In recent years the pace of exotic species introduction and invasion has accelerated, particularly in estuaries and wetlands. Species invasions may affect coastal ecosystems in many ways. Alteration of sedimentary environments, through structure formation and burrowing, has particularly dramatic effects on coastal habitats. This study examines modification of channel bank and marsh edge habitat by the burrowing Australasian isopod *Sphaeroma quoyanum* Milne Edwards, in created and natural salt marshes of San Diego Bay and San Francisco Bay. Abundance and distribution patterns of this isopod species, its relationships with habitat characteristics, and its effects on sediment properties and bank erosion were examined seasonally, and in several marsh microhabitats. Mean isopod densities were 1541 and 2936 individuals per 0.25 m^2 in San Francisco Bay, and 361 and 1153 individuals per 0.25 m^2 in San Diego Bay study sites during December and July 1998, respectively. This isopod forms dense, anastomosing burrow networks. *S. quoyanum* densities did not differ as a function of location within creeks or location in natural versus created marshes. Burrows, which are on average 6 mm wide and 2 cm long, were associated with firm sediments containing high detrital biomass. Although erosion is a natural process along salt marsh banks, enclosure experiments demonstrated that isopod activities can enhance sediment loss from banks. In areas infested with *S. quoyanum*, losses may exceed 100 cm of marsh edge per year. The effects of habitat alteration by this invading species are likely to increase in severity in the coastal zone as these ecosystems become degraded.

Introduction

Animal modification of sediments has long been recognized to influence the abiotic (McCall and Tevesz 1982) and biotic properties (Roads and Young 1970, 1971; Woodin 1976) of soft-substratum habitats. One of the most frequently encountered forms of animal influence is burrowing. Dwelling, feeding, movement, reproduction and predator avoidance often involve the formation of ephemeral or permanent burrows within sediments. Permanent burrows, which are maintained as lined, sediment-free habitat, are made by annelids, crustaceans, mollusks, echinoderms, cnidarians, echiurans, sipunculans and other invertebrate groups. They occur in both vegetated and unvegetated sediments throughout the world oceans (Bromley 1990).

Permanent burrows may extend a meter or more below the sediment surface, such as those formed by crabs, ghost shrimp or sipunculans, or may be much more surficial, as is the case with burrowing peracarid crustaceans. Permanent burrows alter habitat properties above and below ground (Jumars and Nowell 1984; Ray and Aller 1985; Ridd 1996) and influence both diffusive and advective exchange of oxygen and other porewater chemical constituents (Aller 1982). Both passive deposition of particles and organisms within burrows (DePatra and Levin 1989; Yager et al. 1993) and active feeding or subduction activities of burrowers (Graf 1989; Levin et al. 1997) can enhance organic matter content of burrowed sediments. Burrows can alter the water content, permeability, shear strength, and other geotechnical

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properties of the sediment matrix (Meadows and Meadows 1991).

Within vegetated wetland sediments, crabs generally form the most frequently encountered permanent burrow structures (e.g. Willason 1981; Bertness 1999). Other organisms found burrowing into vegetated coastal wetlands include isopods. Burrowing species in the genus *Sphaeroma* (family Sphaeromatidae), including *S. terebrans*, *S. peruvianum*, *S. serratum* and *S. quoyanum*, are known for their activities as bioeroders (e.g. Rehm and Humm 1973; Carlton 1979; Perry and Brusca 1989; El-Shanshoury et al. 1994). In Florida, the exotic *S. terebrans* is able to bore into the prop roots of the red mangrove (*Rhizopora mangle*) with potentially devastating effects (Carlton and Ruckelshaus 1997). Although the prop roots of the mangrove can undoubtedly be damaged by isopod burrowing (Rehm and Humm 1973; Ribi 1981, 1982; Perry and Brusca 1989), the mangrove may have compensatory mechanisms (i.e. stimulation of the production of root offshoots) that offset isopod-induced damage (Simberloff et al. 1978). This exotic habitat modifier, however, may set the lower distributional boundary for this important mangrove species, by overwhelmingly damaging prop roots (Carlton and Ruckelshaus 1997).

Because sphaeromatid isopods live in or on wood, many of these species (e.g. *S. terebrans*, *S. walkeri* and *S. quoyanum*) appear to have been spread anthropogenically around the world in or on the hulls of ships (Carlton and Iverson 1981; Morton 1987; Carlton and Ruckelshaus 1997). The Australasian isopod *S. quoyanum* Milne Edwards is believed to have first been introduced to western North America between the early 1850s and 1890s by ships from Australia coming to California during the Gold Rush (Carlton 1979). *S. quoyanum* was first reported in San Francisco Bay in 1893 (Carlton 1979), in San Diego Bay in the 1920s (Johnson and Snook 1927) and has also been reported from other western North American wetland systems.

Natural history of *S. quoyanum*

S. quoyanum is distinguished from other sphaeromatids by serrated outer uropods and two rows of tubercles on the telson (Hurley and Jansen 1977). Rotramel (1975) described both the burrowing and feeding behavior of *S. quoyanum* using direct observations and dye studies. Isopods form burrows using their pleopods. They orient head-first in the burrows and create a current that passes over the dorsum, down in front of the head, under the body towards the posterior end, under the telsons and out of the burrow. *S. quoyanum* breaks off substratum with its mandibles and releases the particles near the midline of the animal. Particles are washed out of the burrow by the current without being caught in the feeding brushes located on the first and third legs (Rotramel 1975). *S. quoyanum* is reported to be a filter feeder (Rotramel 1975) and likely does not eat the substratum into which it burrows (Talley et al., unpublished data). Using the same current created by the pleopods for burrowing, the isopod brings water into the burrow. The current passes through the brushes on the first and third pair of legs trapping particles. The pleopods occasionally stop beating, and the isopod cleans the brushes with its maxillipeds (Rotramel 1975).

S. quoyanum lives intertidally and is tolerant to (Riegel 1959; Morris et al. 1980) or may even prefer (Paradice 1926) brackish water pulses. Although this isopod can burrow into a variety of available substrata, including wood, soft rock and even Styrofoam (Barrows 1919; Miller 1926; Abbott 1940; Higgins 1956; Carlton 1979), its preferred habitats in California salt marshes are the peat and mud walls of tidal creek and marsh edge banks. The intensive burrowing activity of this species has been reported to weaken mud and clay banks of salt marsh edges, thus making them more susceptible to erosion by wave action or creek flow (Carlton 1979; Josselyn 1983; Nichols and Pamatmat 1988). This impact of *S. quoyanum* burrowing, however, has not been quantified previously.

This paper examines the natural history and habitat relationships of *S. quoyanum* in salt marshes of San Francisco Bay and San Diego Bay, and addresses the following questions: (1) What habitat associations does *S. quoyanum* exhibit in relation to marsh bank location, topography and sediment properties? (2) What aspects of the sediment matrix are altered by isopod burrowing, and what are the consequences of any isopod-induced sediment erosion? Ultimate goals of this work are to contribute to our understanding of the ecology of bioeroders and to generate information that may aid conservation of wetland resources potentially being damaged by *S. quoyanum*.

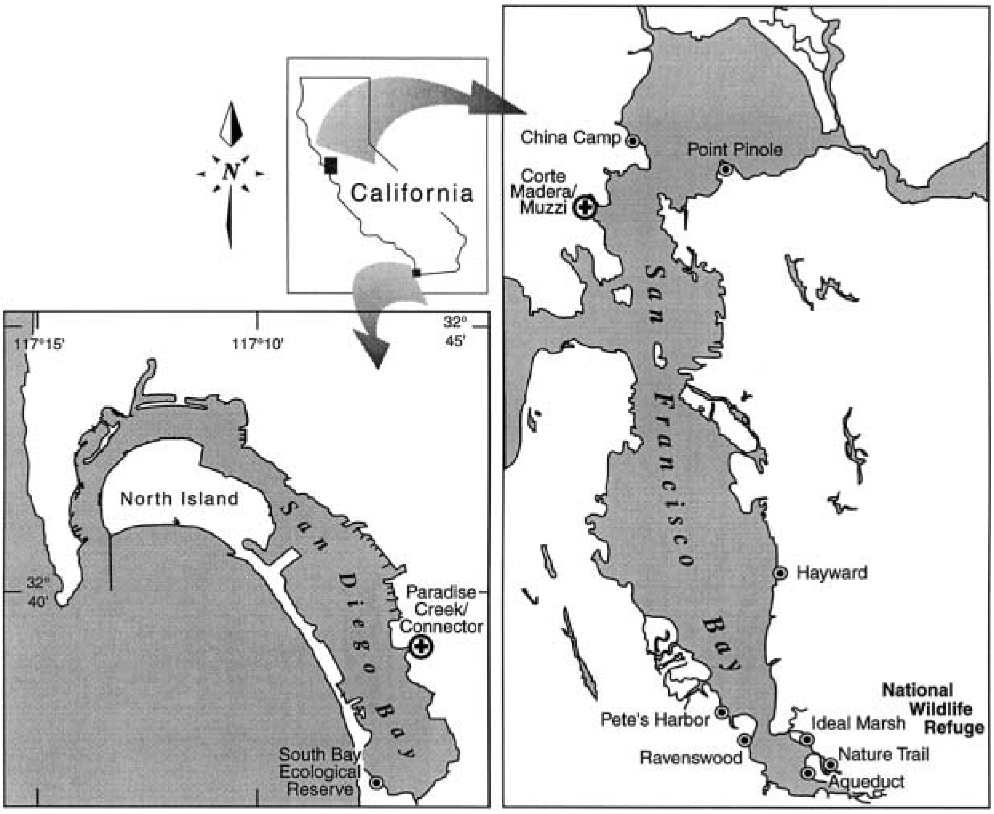
Materials and methods

Study sites

Research was carried out in San Diego and San Francisco Bays during 1998–1999. In San Diego Bay, National City, California, USA (32°39′N; 117°06′W), sampling and experimentation occurred in the natural Paradise Creek and adjacent created Connector Marshes (Fig. 1). Paradise Creek Marsh comprises 10 ha, and the 14-year-old Connector Marshes comprise 4.9 ha of intertidal salt marsh area. These marshes are bordered on the east by a highway (Interstate 5), to the north and west by industrial development and to the south by disturbed upland and remnant natural salt marsh.

In San Francisco Bay, investigations were carried out in the natural Corte Madera and created Muzzi Marshes, both located in the Corte Madera State Ecological Reserve, Corte Madera, California, USA (37°55′N; 122°30′W) (Fig. 1). Both Corte Madera and Muzzi Marshes are each traversed by tidal creeks. They are bordered to the west and south by disturbed upland habitat and urban development (retail and residential), to the north by a dredged channel and marina and to the east by the bay. Corte Madera Marsh contains 30 ha, and the 22-year-old Muzzi Marsh contains 55 ha of intertidal salt marsh habitat. Additional measurements of *Sphaeroma quoyanum* distribution and density were conducted at six other sites around San Francisco Bay and at one site in San

Fig. 1 Map of *Sphaeroma quoyanum* study sites in San Diego Bay and San Francisco Bay, California, USA (+, sites where extensive surveys and experiments were conducted; ●, sites where *S. quoyanum* density or presence/absence was determined on one occasion)



Diego Bay (Fig. 1) to provide a preliminary benchmark of *S. quoyanum* presence and density.

All marshes studied contain both Pacific cordgrass (*Spartina foliosa*, hereafter referred to as *Spartina*) habitat in the low marsh and pickleweed (*Salicornia* spp., hereafter referred to as *Salicornia*) habitat in the mid- to high marsh. In San Francisco Bay, the *Spartina* habitat may include hybrids of the native cordgrass (*S. foliosa*), and exotic, Atlantic cordgrass (*S. alterniflora*) (Anttila et al. 1998).

Field sampling

Stations were established along salt marsh edges either on banks of tidal creeks (San Diego and San Francisco Bays) or on exposed bay-front banks (San Francisco Bay) (Fig. 2). Sampling dates and measurements made at the primary sampling sites (Paradise Creek and the Connector Marsh in San Diego Bay and Corte Madera and Muzzi Marsh in San Francisco Bay) are listed in Table 1. Additionally, quantifications of water flow and sediment loss due to isopods, as well as an examination of burrow structure using X-radiographs and wax casts, were made during August and September 1999. In Paradise Creek, 12 stations were sampled along a 900 m stretch of creek, with each station alternately on a straightaway or creek bend. In the adjacent Connector Marsh, eight sampling stations were established along a 900 m length of straight creek (Fig. 2). In San Francisco Bay, six sampling stations each were established along the bay front (ca. 300 m in length) and main creeks (ca. 400 m length) of Corte Madera and Muzzi Marshes ($n = 24$ stations total) (Fig. 2).

On all sampling dates, burrow density at each station was visually assessed as either high (ca. 67–100% cover of burrows), medium (34–66%) or low (0–33%), because it was not possible to count the burrows or determine isopod densities for every measurement taken (see below). However, on selected dates (Table 1), visual evaluations were accompanied by determination of densities of *S. quoyanum*. These were assessed by collecting one sediment core (5.8 cm diameter × 10 cm deep) from each station. These

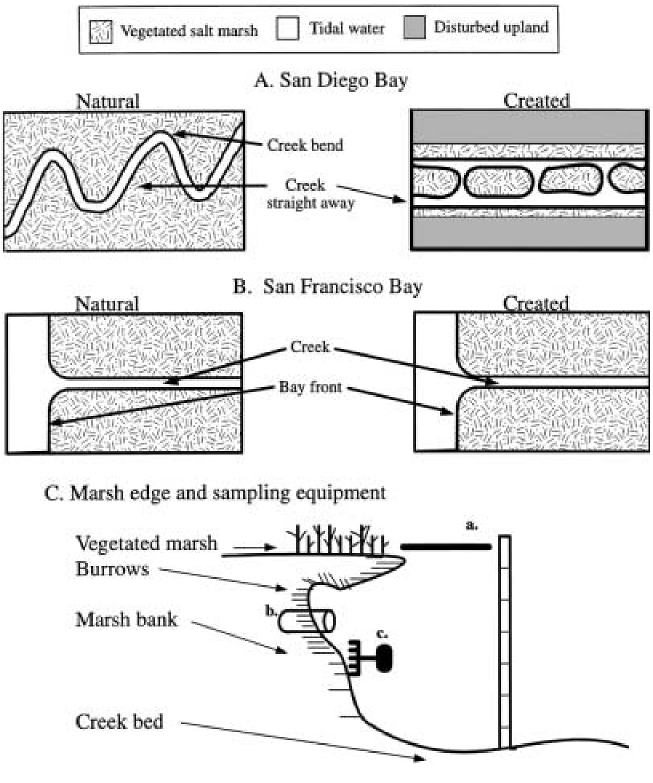


Fig. 2 Schematic diagrams of the microhabitats studied in **A** San Diego Bay and **B** San Francisco Bay. **C** Diagram of the marsh edge, illustrating the orientation of the poles used for measuring bank profiles (*a*), the cores, enclosures or X-ray slabs that were inserted into the bank (*b*), and the Torvane shear strength meter (*c*)

Table 1 Number of replicates (*n*) for measurements and experiments conducted in San Diego Bay and San Francisco Bay, and the dates on which they were performed

Parameters	San Diego Bay				San Francisco Bay		
	1998		1999		1998		1999
	Jul	Dec	Mar	Jul	Jul	Dec	Jul
Mensurative							
Infaunal cores	20	32	32	–	24	24	–
Sediment grain size and organic matter	20	–	–	–	24	–	–
Profiles	32	32	32	32	24	24	24
Erosion measures	32	32	32	32	24	24	24
Vegetation cover	32	32	32	32	24	24	24
High and low burrows							
Porosity	–	6	–	–	–	–	–
Shear strength	32	32	32	32	24	24	24

samples were preserved in 8% buffered formalin and stained with Rose Bengal. Once preserved, the samples were sieved through a 1 mm mesh, and individuals of *S. quoyanum* were sorted and identified using a dissecting microscope, counted, and stored in 70% ethanol. These counts were used to provide spatial and temporal comparisons of abundance and to correlate visually assessed burrow density with density of isopods.

Burrow structure of *S. quoyanum* was quantified with X-radiography and wax casts. Slabs (3 cm × 12 cm × 18 cm deep) of isopod-burrowed mud were collected from Paradise Creek during September 1998 and X-rayed using a Kramex PX 20 N portable X-radiograph unit. For direct assessment of isopod burrow structure, five sediment cores (10.2 cm diameter × 20 cm deep) were collected from each burrow density class in Paradise Creek during September 1999. Melted wax was poured onto the surface of sediment in each core, and after hardening overnight, the core was rinsed clean of mud. The number, length and width of individual burrows, burrow openings and connections, and the total volume of burrows in each core (as water displacement) were measured.

Sediment analyses were conducted on one sediment core (4.8 cm diameter × 10 cm deep) collected from within 5 cm of each of the faunal samples in July 1998. Sediment cores were frozen at −20 °C and then analyzed for sediment particle size (percent sand) and percent combustible organic matter. To determine organic matter, sediments were sieved though a 2 mm mesh, thereby separating out most large plant (roots, rhizomes) and shell material. Organic matter content of both the ≥ 2 and < 2 mm fractions was determined by weight loss of dried sediments after combustion overnight at 550 °C. Particle size was analyzed by initially sieving wet sediments through a 2 mm mesh to remove large material and then digesting the < 2 mm fraction using hydrogen peroxide. The digested sediments were sieved wet through a 63 μm mesh, and both fractions (≥ 63 μm and < 63 μm) were dried and weighed to determine percent sand. Six sediment cores (4.8 cm diameter × 6 cm deep) were collected from sediments with both high and low burrow densities during December 1988 in Paradise Creek for analysis of sediment porosity (amount of interstitial water) based on water loss following oven drying at 65 °C overnight. One plaster of Paris clod card (29 ± 1 g) was set out for 4 days at each station in San Diego Bay during September 1999 to monitor relative flow regimes using dissolution rates of the cards. Below-ground plant biomass was assessed using the faunal cores. From each sample, roots, rhizomes and detritus ≥ 1 mm were dried and weighed to estimate below-ground biomass.

The shear strength (the amount of torsional force needed to shear the top 1 cm of sediment) of bank sediments was measured using a Torvane shear device (Zimbone et al. 1996), with six readings per station, three each in visually assessed high- and low-burrow-density areas. Vertical profiles of the marsh edge at each station were determined by measuring the distance between a vertical pole and the bank face every 10 cm from the marsh surface down to the creek bed. Measurements of 0 indicate a vertical face, > 0 indicate undercutting and < 0 indicate a sloped bank. Also, burrow density was visually assessed at each 10 cm interval. Temporal changes in the horizontal position of the edge of the marsh flat were evaluated at each sampling station by measuring the distance from the bank edge to stakes initially placed on the marsh surface 2 m from the edge. Percent cover of each plant species overlying the marsh bank was recorded at each station within a 0.25 m^2 quadrat in order to define vegetation habitat type.

Erosion experiment

Effects of *S. quoyanum* on bank sediment loss were tested by placing isopods and sediments in 1 mm mesh enclosures (10 cm diameter × 10 cm deep) during August 1999 in Paradise Creek. Each of 48 enclosures was filled with 800 g (wet weight) of sediment collected from Paradise Creek Marsh banks. Sediments were autoclaved and mixed to defaunate and homogenize the substratum. Twenty-five individuals of *S. quoyanum* collected from the same creek were placed in half (24) of the enclosures. The other half of the enclosures received no isopods and served as controls. Enclosures with and without isopods were paired (ca. 50 cm apart, same elevation) and inserted horizontally into vertical creek banks within the *S. quoyanum* burrow zone (1.0–1.3 m above MLLW). After 4 weeks, the enclosures were collected, the isopods removed and counted, and the sediments in the enclosures weighed wet and dry. The water content of sediments in all enclosures was determined by weighing sediments before and after overnight drying in an oven set at 65 °C.

Statistics

Densities and burrow densities of *S. quoyanum* were compared using Wilcoxon rank sum tests, and amounts of lateral marsh erosion were compared using *t*-tests for vertical versus sloped banks, bent versus straight creek segments, bay-front versus creek-bank habitat, natural versus created marshes and *Spartina* versus *Salicornia* habitat. Bonferroni-adjusted alphas corrected for the numbers of multiple comparisons are presented. One-way analysis of variance (ANOVA) and a posteriori multiple comparisons using Tukey–Kramer HSD-tests were used to test relationships between visually assessed burrow densities (high, medium, and low) and (1) isopod densities in sediments, (2) distance of bank undercutting and (3) burrow morphological parameters (as measured with wax casts). Loss of sediment in the isopod enclosure experiment was examined with paired *t*-tests. Comparisons of shear strength between sediments with high and low burrow densities were completed using paired signed rank tests. Relationships between sediment properties and *S. quoyanum* density were examined by simple linear correlations, as were relationships between burrow length and diameter as measured from wax casts. Relationships between sediment properties and burrow density were examined using Spearman's rho rank correlations.

Most numeric data were log(x + 1) transformed (exceptions were burrow density ranks, elevation data, shear strength) to normalize data and homogenize variances. Proportion data were arcsine, square-root transformed. If data were not normally distributed or variances were not homogenous after transformation, nonparametric tests were used. The mean ± 1 standard error of the mean is presented throughout the text and in the tables and graphs.

Results

Densities and burrows of *Sphaeroma quoyanum*

S. quoyanum was widely distributed in salt marsh habitats within both San Francisco and San Diego Bays (Table 2; Fig. 1), as indicated by direct counts of isopods and from observations of burrows. *S. quoyanum*, when present, had mean densities of 1541 (December) and 2936 (July) individuals per 0.25 m^2 in the study sites of San Francisco Bay, and 211 (March), 361 (December) and 1153 (July) individuals per 0.25 m^2 in the study sites of San Diego Bay. High and medium burrow densities occurred in 71% of the sites examined in San Francisco and 58% in San Diego Bay. Visual burrow-density class designations proved to be a reliable way to estimate densities of *S. quoyanum* (Table 3). The relationship between burrow density and *S. quoyanum* density was greatest in summer when *S. quoyanum* densities were highest. At other times, isopod densities in locations with high and medium burrow density were not significantly different, but they could be distinguished from isopod densities in locations with low burrow densities (Table 3).

Habitat relationships

Within San Francisco Bay, the bay-front habitat had higher *S. quoyanum* densities than the creek edges in the summer of 1998, but not in December 1998, when densities were lower (Fig. 3A). Bent and straight creek segments exhibited similar *S. quoyanum* densities in San Diego Bay (Fig. 3A). Natural marshes of San Diego and San Francisco bays exhibited *S. quoyanum* densities similar to created marshes on most dates, but had higher densities on at least one sampling date (Fig. 3B). The relative flow at each site in San Diego Bay, as measured with plaster clod cards, was not associated with *S. quoyanum* density.

Mean densities of *S. quoyanum* and its burrows were greater in *Salicornia*- than *Spartina*-vegetated habitats in both systems, particularly during summer when isopod densities were greatest (Fig. 4A, B). Summer 1998 *Salicornia* marsh isopod densities were 1987 ± 756 individuals per 0.25 m^2 and 3351 ± 800 individuals per 0.25 m^2 in the San Diego (Paradise Creek, Connector) and San Francisco Bay (Corte Madera, Muzzi) marshes, respectively. Mean *S. quoyanum* densities in the *Salicornia* marsh were much lower ($t_{74} = 2.1$, $P = 0.04$) in winter (455 ± 111 individuals per 0.25 m^2 in San Diego, 1703 ± 601 individuals per 0.25 m^2 in San Francisco). Burrows were more persistent than the isopods, and their visually assessed densities did not change ($t_{83} = 0.24$, $P = 0.81$) between summer and winter (Fig. 4B). *S. quoyanum* densities throughout the year in the *Spartina* habitats ranged from 42 to 214 individuals per 0.25 m^2 in San Diego Bay and from 31 to 410 individuals per 0.25 m^2 in San Francisco Bay (Fig. 4A).

In addition to overlying marsh type, densities of isopods and burrows were correlated with other habitat parameters. *Salicornia* marsh was generally at higher tidal elevations than *Spartina* habitats, and *S. quoyanum* burrow density (as measured in San Diego Bay) was found to increase with higher tidal elevations (Table 4). Also, *S. quoyanum* burrows were not always evenly distributed along the bank face. Most (67%) high and medium burrow densities occurred in the top half of the bank in San Diego Bay, but often were more widely

Table 2 *Sphaeroma quoyanum*. Density of this isopod in salt marsh habitats around San Diego Bay and San Francisco Bay. Values are mean ± 1 SE of the number of individuals per 0.25 m^2, with number of samples (n) shown in parentheses (+, presence noted, but no quantitative data; –, no data). Where two to four samples were collected, burrowed sediments were targeted, thus densities may be at the upper end of the range

Salt marsh habitats	1998			1999
	Mar	Jul	Dec	Mar
San Diego Bay				
Paradise Creek/Connector Marshes	3016 ± 895(4)	1153 ± 475(20)	361 ± 83(32)	211 ± 65(32)
South Bay Ecological Reserve	(+)	–	–	–
San Francisco Bay				
Corte Madera State Ecological Reserve	729 ± 298(4)	2936 ± 734(24)	1541 ± 534(24)	–
China Camp State Park	–	3148 ± 1922(2)	–	–
Hayward Regional Shoreline	(+)	–	–	–
Point Pinole Regional Shoreline	431 ± 254(4)	–	–	–
Pete's Harbor	555 ± 490(4)	–	–	–
Ravenswood Open Space Preserve	–	236 ± 236(2)	–	–
S.F. Bay National Wildlife Refuge				
Ideal Marsh	–	–	630 ± 99(2)	–
Nature Trail	–	–	265 ± 66(2)	–
Aqueduct	–	–	99 ± 0(2)	–

Table 3 *Sphaeroma quoyanum*. Density (individuals per 0.25 m^2) of this isopod within sediments containing high, medium and low density of burrows during each sampling date. Results of one-way ANOVAs and a posteriori Tukey–Kramer HSD-tests are shown. Different letter superscripts indicate significant differences in isopod density among burrow density classes (*n* number of replicates)

Burrow density	San Diego Bay			San Francisco Bay	
	Jul 1998	Dec 1998	Mar 1999	Jul 1998	Dec 1998
High	4352 ± 655^a	653 ± 151^a	454 ± 170^a	6120 ± 974^a	3216 ± 1523^a
Medium	899 ± 586^b	426 ± 151^{a,b}	246 ± 113^a	1315 ± 870^b	1882 ± 955^a
Low	246 ± 189^b	66 ± 57^b	28 ± 19^b	13 ± 13^c	265 ± 151^b
P	< 0.001	0.001	0.001	< 0.001	0.003
F	16.1	8.5	11.3	33.8	7.5
n	21	32	32	24	24

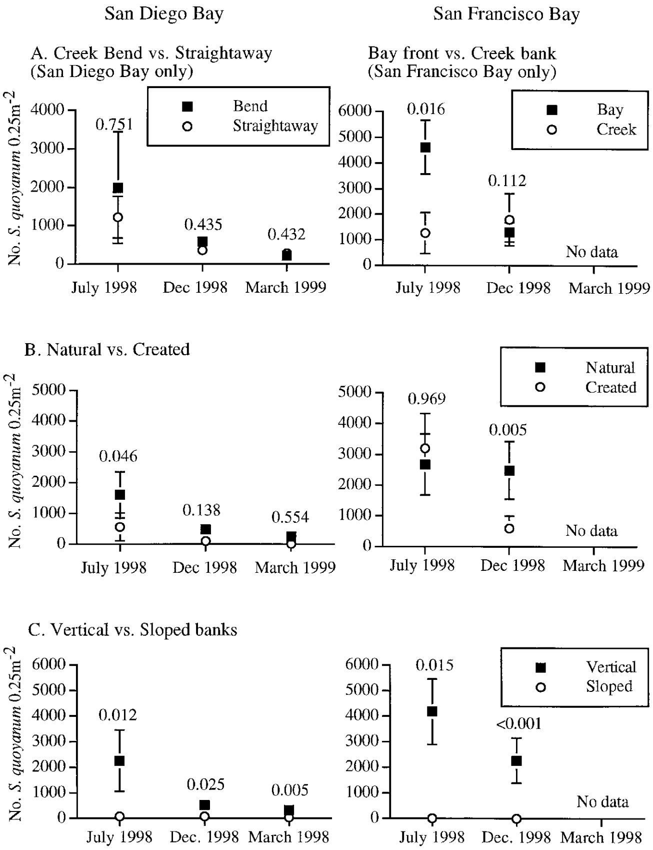


Fig. 3A–C *Sphaeroma quoyanum*. Mean (±1 SE) density of this isopod in the banks of **A** creek bends and straightaways (*n* = 6 cores, San Diego Bay only); bay front and creek edges (*n* = 12 cores, San Francisco Bay only). **B** Natural and created marshes (*n* = 6 for all except San Diego Bay created where *n* = 8 cores) of San Diego Bay and San Francisco Bay. Results (*P*-values) of Wilcoxon rank sum tests are shown. Bonferroni-adjusted alpha = 0.017 for San Diego Bay tests and 0.025 for San Francisco Bay tests. **C** Vertical and sloped edges (*n* = 11–12 sloped, 7–17 vertical edges in San Diego Bay; 7 sloped, 9–10 vertical edges in San Francisco Bay)

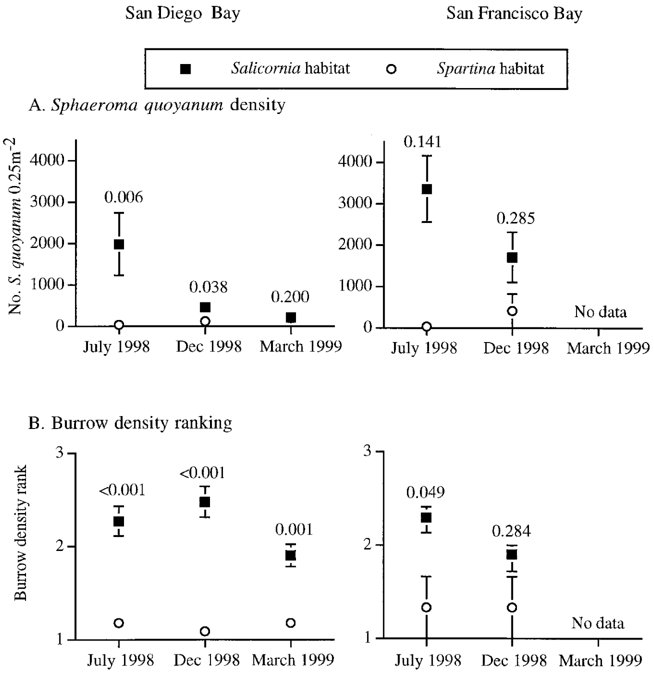


Fig. 4A, B *Sphaeroma quoyanum*. Mean (±1 SE) density of **A** *S. quoyanum* and **B** burrows (ranked) in the *Salicornia* and *Spartina* habitats of San Diego Bay and San Francisco Bay (*n* = 12 *Salicornia*, 9 *Spartina* in San Diego Bay; *n* = 21 *Salicornia*, 3 *Spartina* samples in San Francisco Bay). Burrow rankings are low (*1*), medium (*2*) and high (*3*) burrow density, with resolution to 0.5. Results (*P*-values) of Wilcoxon rank sum tests are shown. Bonferroni-adjusted alpha = 0.017 for San Diego Bay tests and 0.025 for San Francisco Bay tests

distributed in the banks of San Francisco Bay. Across all habitats, three general types of marsh bank topography were encountered: sloped, vertical and undercut marsh edges (Fig. 5). *S. quoyanum* densities in vertical and undercut banks, which typically occurred beneath *Salicornia* habitat, were 7–2200 times greater (314–4140 individuals per 0.25 m^2) than in sloped banks of both bays across all dates (Fig. 3C). Similarly, undercut and vertical banks were usually associated with high and medium burrow densities (Fig. 5). The amount each bank profile was undercut was greater in high- and often medium-burrow-density areas than in low-burrow-density areas (Table 5). Densities of *S. quoyanum* were correlated with amount of undercutting in July ($r^2 = 0.45$, $P < 0.001$) and December 1998 ($r^2 = 0.34$, $P < 0.003$) in San Francisco Bay and in July 1998 ($r^2 = 0.22$, $P < 0.036$) in San Diego Bay.

Table 4 Results of simple linear correlations between environmental properties and *Sphaeroma quoyanum* densities, and Spearman's rho rank correlations between environmental properties and rankings of the isopod burrow densities. Bonferroni-adjusted alpha = 0.017 for the San Diego Bay tests and 0.025 for the San Francisco Bay tests [(+) positive correlation; (–) negative correlation; –, P > 0.05]

	San Diego Bay			San Francisco Bay	
	Jul 1998	Dec 1998	Mar 1999	Jul 1998	Dec 1998
Sphaeroma quoyanum densities					
Below-ground plant biomass (g DW)	r^2 = 0.23(+) P = 0.031	–	r^2 = 0.15(+) P = 0.029	r^2 = 0.65(+) P < 0.001	r^2 = 0.26(+) P = 0.011
Sand content (%)	r^2 = 0.23(–) P = 0.034	–	–	–	r^2 = 0.27(–) P = 0.009
Organic matter (%, <2 mm)	–	–	r^2 = 0.13(+) P = 0.042	–	–
Organic matter (%, ≥2 mm)	–	–	–	–	–
Elevation (above MLLW)	–	r^2 = 0.26(+) P = 0.003	–	No data	
Burrow density ranking					
Below-ground plant biomass (g DW)	–	–	–	rho = 0.67(+) P < 0.001	rho = 0.63(+) P = 0.001
Sand content (%)	–	rho = 0.48(–) P = 0.006	rho = 0.48(–) P = 0.006	rho = 0.45(–) P = 0.028	–
Organic matter (%, <2 mm)	–	–	–	–	–
Organic matter (%, ≥2 mm)	–	–	–	–	–
Elevation (above MLLW)	rho = 0.46(+) P = 0.007	rho = 0.75(+) P < 0.001	rho = 0.64(+) P < 0.001	No data	

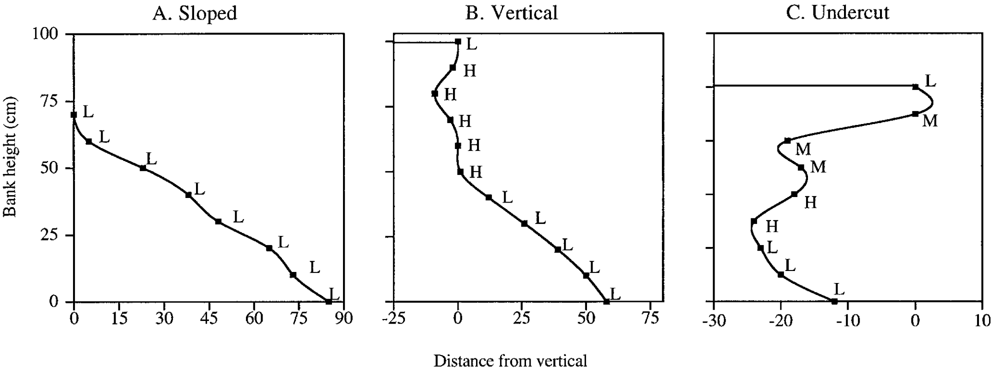


Fig. 5A–C Profiles exemplifying the three general topographic forms (sloped, vertical and undercut) of marsh banks and their associated *Sphaeroma quoyanum* burrow densities in San Diego Bay and San Francisco Bay (*L* low; *M* medium; *H* high burrow densities). Data are for actual profiles from July 1998, **A** Paradise Creek bend; **B** Paradise Creek straightaway; **C** Muzzi Marsh bay front

Banks beneath *Salicornia* habitats usually had firm, peaty sediments, and isopods displayed positive relationships with these sediment properties. High- and medium-density isopod burrows were generally associated with firm sediments (shear strength: San Diego 114 ± 5; San Francisco 91 ± 3 g cm^{-2}), whereas low burrow densities occurred in softer sediments (shear strength: San Diego 84 ± 6; San Francisco 50 ± 6 g cm^{-2}) (San Diego $t_{30} = 3.8$, $P \leq 0.001$; San Francisco $t_{22} = 6.7$, $P \leq 0.001$). The amount of below-ground plant biomass (roots, rhizomes and detritus, ≥1 mm) in bank sediments was positively correlated with *S. quoyanum* density in both bays, and with burrow density in San Francisco Bay (Table 4). Also, some negative relationships between *S. quoyanum* and burrow densities and percent sand content emerged in each bay (Table 4).

Burrow characteristics

S. quoyanum burrows in San Diego Bay were on average 2.2 cm long, with a maximum depth of 5.6 cm, and 0.5–0.7 cm wide (Table 6; Figs. 6, 7). Occasionally a large isopod blocked the flow of wax into the burrows, so these may be conservative estimates of length. Burrow diameter increased with burrow-density class (Table 6), and with increased burrow length ($r^2 = 0.25$–0.36, $P < 0.001$) (Table 6). Burrows occupied 3–15% of the volume within the outer 5 cm of marsh bank sediments and increased with burrow-density class (Table 6). Most (88%) of the burrows were horizontal (1800 ± 100), while the rest were angled, either up (≤160°) or down (≥200°) (Figs. 6, 7). Almost all of the burrows were connected to at least one other burrow (Figs. 6, 7), and

Table 5 Amount of undercutting, measured as the largest distance (cm) from vertical (0 cm), of each profile within each burrow-density class. Results of one-way ANOVAs (within date) and a posteriori Tukey–Kramer tests are shown. Different letter superscripts indicate significant differences among density classes within each date. Negative numbers indicate an outward sloped bank; positive numbers indicate undercuttting

Burrow density	San Diego Bay				San Francisco Bay		
	Jul 1998	Dec 1998	Mar 1999	Jul 1999	Jul 1998	Dec 1998	Jul 1999
High	9.8 ± 2.5^{a}	10.3 ± 2.3^{a}	7.0 ± 6.6^{a}	8.3 ± 2.8^{a}	27.2 ± 5.4^{a}	34.2 ± 7.8^{a}	21.9 ± 6.0^{a}
Medium	9.1 ± 2.7^{a}	$1.8 \pm 3.4^{a,b}$	4.3 ± 2.9^{a}	1.6 ± 2.3^{a}	9.9 ± 6.5^{a}	$12.4 \pm 6.8^{a,b}$	16.3 ± 4.2^{a}
Low	-4.2 ± 2.1^{b}	-3.2 ± 2.3^{b}	-11.9 ± 3.0^{b}	-12.6 ± 3.3^{b}	-19.4 ± 6.5^{b}	-9.9 ± 6.0^{b}	-6.1 ± 5.7^{b}
P	< 0.001	0.001	0.001	< 0.001	< 0.001	< 0.001	0.003
F	11.6	8.5	8.5	13.0	15.2	10.2	7.5
n	33	32	32	32	24	24	24

Table 6 *Sphaeroma quoyanum* burrow characteristics. Data are means (per core) ± 1 SE of the mean. A range of values taken from within cores are shown *in parentheses*. Where one-way ANOVAs revealed significant differences among density classes, results of a posteriori Tukey–Kramer tests are shown. Different letter superscripts indicate significance at $P < 0.05$ (*NS* not significant). Results of simple linear correlations are also shown. Data are from September 1999 (n number of burrows measured; +, positive correlation)

Burrow characteristic	Burrow-density class					
	High	Medium	Low	P	F	*df*
No. cores (81 cm^2)	6	5	5			
Volume (cm^3)	60.8 ± 2.3^{a} (51–66)	24.8 ± 2.3^{b} (20–33)	10.4 ± 2.5^{c} (2–17)	< 0.001	28.0	2.13
Percent of total volume (81 cm^2 × 5 cm depth)	15.0 ± 0.6^{a} (12.6–16.2)	6.1 ± 0.6^{b} (5.0–8.2)	2.6 ± 0.6^{c} (0.4–4.2)	< 0.001	28.0	2.13
Burrow density (no. isopods per 81 cm^2)	50.2 ± 7.3^{a} (33–73)	28.8 ± 3.1^{a} (19–38)	13.2 ± 2.7^{b} (3–19)	< 0.001	13.0	2.13
No. of burrow openings (per 81 cm^2)	36.2 ± 5.7^{a} (21–52)	20.4 ± 2.1^{a} (13–26)	8.6 ± 1.9^{b} (2–13)	< 0.001	14.1	2.13
Burrow length (mm)	21.3 ± 0.5 (4.1–55.9)	22.2 ± 0.7 (6.8–51.0)	22.8 ± 1.6 (5.6–56.1)	NS		
Burrow diameter (mm)	6.9 ± 0.1^{a} (3.0–16.0)	5.8 ± 0.1^{b} (2.1–7.4)	5.4 ± 0.2^{b} (1.9–9.5)	0.002	10.8	2.13
No. of separate groups	1.8 ± 0.3^{a} (1–3)	$2.4 \pm 0.4^{a,b}$ (1–3)	3.2 ± 0.4^{b} (2–4)	NS		
Percent horizontal burrows (vs. angled)	93.2 ± 1.1 (88.7–97.0)	76.1 ± 4.5 (61.9–85.0)	82.0 ± 11.1 (40–100)	NS		
Burrow length × diameter – simple linear correlations (relationship)						
r^2	0.25 (+)	0.36 (+)	0.25 (+)			
P	< 0.001	< 0.001	< 0.001			
n	302	173	66			

the branching occurred at any point along the burrow, from just inside the opening to the back end. Groups of inter-connected burrows ranged from 1.8 ± 0.3 groups per 81 cm^2 core in the high-density sediments to 3.2 ± 0.4 units core^{-1} in the low-burrow-density sediments (Table 6). Most (71%) of the burrows opened at the sediment–water interface; the remainder had primary openings off existing burrows (Figs. 6, 7).

Erosion of marsh habitat

The presence of collapsed, burrow-riddled blocks of marsh (Fig. 8A, B) and the positive relationship between isopod burrow density and the degree of undercutting (Table 5) suggest that isopods contribute to marsh habitat loss. Further direct measurements and experimental manipulations demonstrated effects of *S. quoyanum* burrowing activities on bank sediment properties. On centimeter scales (i.e. within stations), shear strength of banks was 1.3–2.6 times higher in low- than high-burrow-density areas (Fig. 9A, B). Sediment water content was not affected by burrow density. Water content of sediment in San Diego Bay (December 1998) was 43 ± 1.4% and 45 ± 1.3% in high- and low-burrow-density sediments, respectively.

The manipulative experiment demonstrated the ability of the isopod to increase erosion rates. The presence of *S. quoyanum* in enclosures resulted in the loss of 2.4 times more wet sediment (55 ± 4 g) than in the enclosures without isopods (29 ± 5 g) ($t_{23} = 3.6$, $P = 0.002$). Also, final dry weights of sediments were

Fig. 6 Wax cast of *Sphaeroma quoyanum* burrows taken from bank sediments in Paradise Creek Marsh in San Diego Bay, during September 1999

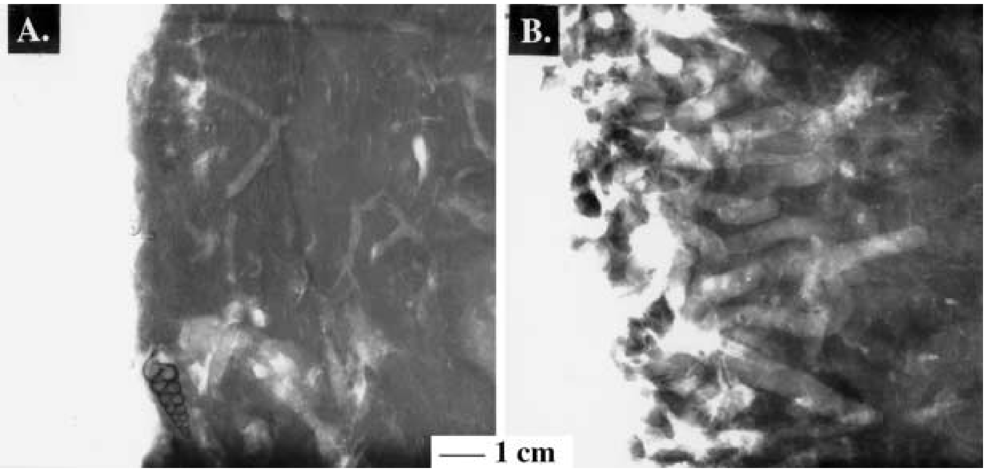
lower in treatments with isopods (431 ± 2.9 g) compared with those without (452 ± 3 g) ($t_{23} = 4.4$, $P \leq 0.001$). Sediments from both treatments had identical water contents (42 ± 0.4%).

Loss of marsh edge in all habitats studied generally ranged from 0 to 40 cm within each 3- to 6-month period. *S. quoyanum* density was positively correlated with marsh edge erosion only for the period between the summer and winter 1998 in San Diego Bay ($r^2 = 0.46$, $P = 0.02$). Because some stakes were lost during portions of the year, annual estimates of marsh loss were based on extrapolation of loss during 3- to 6-month periods. Overall erosion of edge habitat averaged 15 ± 3 and 27 ± 7 cm year^{-1} at San Diego and San Francisco Bay sites, respectively, but marsh edge loss was as high as 112 cm year^{-1} at sites where actual loss per year was measured. Lateral erosion of edge habitat was not significantly different in creek bend (17 ± 3 cm year^{-1}) versus straight (9 ± 3 cm year^{-1}) segments of San Diego Bay channels ($t_{22} = 1.4$, $P = 0.169$) or in bay-front (36 ± 12 cm year^{-1}) versus creek (18 ± 6 cm year^{-1}) habitats of San Francisco Bay ($t_{22} = 1.1$, $P = 0.263$). Lateral erosion in the natural versus created marshes of San Diego (natural 13 ± 2, created 22 ± 11 cm year^{-1}) ($t_{18} = 0.6$, $P = 0.535$) and San Francisco (natural 33 ± 12, created 21 ± 7 cm year^{-1}) ($t_{22} = 0.7$, $P = 0.507$) Bays also did not differ. Losses of over 60 cm occurred when whole sections of marsh edge (overhangs) fell to the surface below (see Fig. 9B). This happened along the bay-front marsh edge in San Francisco Bay with two slumps during the year causing the loss of 62 and 90 cm, and in the created marsh in San Diego Bay with one slump during the year causing the loss of 80 cm of marsh edge.

Discussion

Management of *Sphaeroma quoyanum* impacts may be aided by understanding the habitat requirements of this species. *S. quoyanum* appears to have fairly specific microhabitat preferences within marsh edge and channel bank systems. Burrow collapse in softer sediments may limit the distribution of this species (Josselyn 1983). In the present study, firm, vertical, and peaty sediments beneath *Salicornia* marsh were more heavily colonized than gently sloping, softer sediments associated with the lower *Spartina* habitats. Difficulties arise when assessing which inherent characteristics of these habitats (e.g. tidal height, bank morphology, peat content) are most strongly correlated with *S. quoyanum* density, as well as teasing apart the extent to which these relationships are due to cause versus effect of *S. quoyanum* presence. The observation of a strong relationship between *Salicornia* habitat and *S. quoyanum* presence explains the positive relationship found between below-ground biomass and isopod densities. Experiments are required to determine the extent to which the isopod “chooses” this peaty substratum (e.g. for substratum stability) or creates this substrate (e.g. facilitation of root growth through aeration by burrows). While some combination of these processes is probably occurring, it seems that this isopod

Fig. 7 X-radiographs of sediments containing **A** low and **B** high densities of *Sphaeroma quoyanum* burrows. Sediments were collected during December 1998 from Paradise Creek Marsh in San Diego Bay. *White or light areas* are plant roots and rhizomes (**A**) or burrows (**B**)



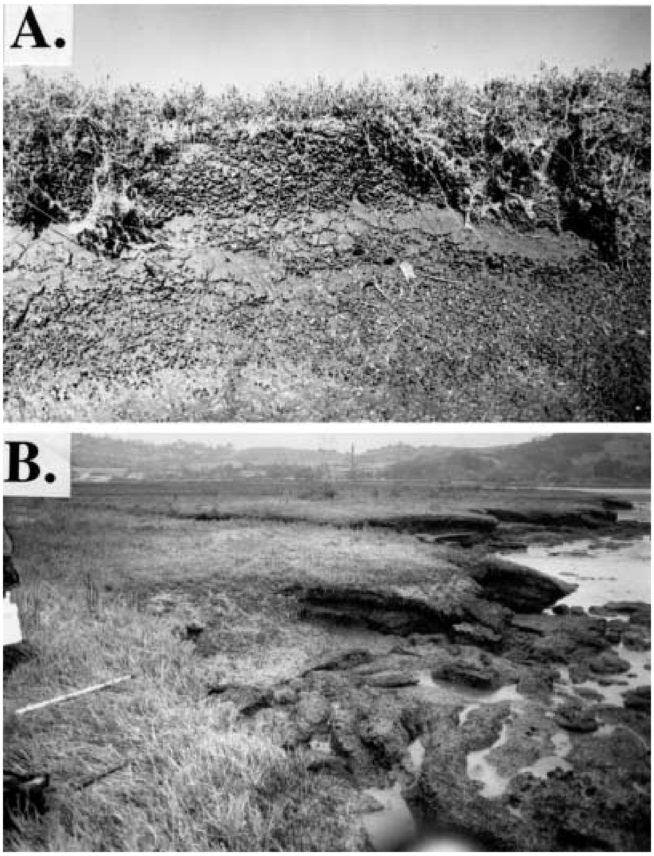


Fig. 8 **A** Paradise Creek, San Diego Bay, November 1998. The extensive burrowing activity of *Sphaeroma quoyanum* in vertical marsh banks loosens sediments causing increased localized erosion and undercutting. **B** Bay front, Corte Madera Marsh, San Francisco Bay, December 1998. Extensive undercutting leads to release of large chunks of the marsh surface and a subsequent loss of marsh habitat

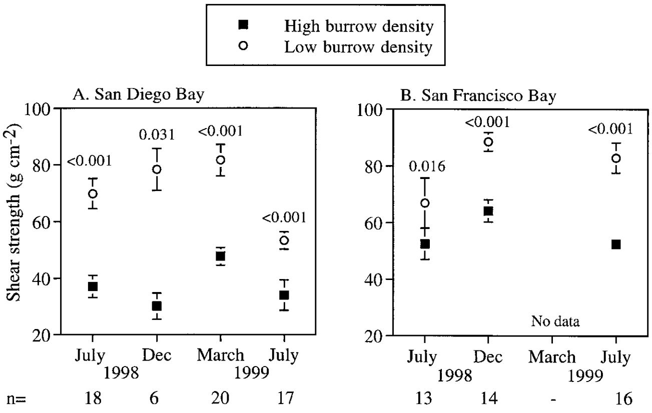


Fig. 9 Shear strength of sediments in high- and low-burrow-density areas within **A** San Diego Bay and **B** San Francisco Bay. Numbers of pairs (*n*) are shown below panels. Results (*P*-values) of paired signed rank tests are shown above data points. Bonferroni-adjusted alpha = 0.013 for San Diego Bay tests and 0.017 for San Francisco Bay tests

is actually more detrimental than beneficial in these systems. Perhaps if there were fewer burrows, facilitation through root zone aeration (e.g. Bertness 1985) would be more likely. However, there are many, densely packed burrows that cause the sediments (often centimeter-sized chunks) to dislodge and wash away. Once undercutting occurs, the plant roots dangle, exposed to the air, and die.

Although the burrowing activities of *S. quoyanum* may contribute to erosion of the vertical banks associated with the *Salicornia* habitat, we acknowledge that steep marsh banks characteristically experience greater erosion than sloping banks, which generally contain few or no *S. quoyanum*, and are depositional environments (Atwater et al. 1979). Quantification of isopod-induced lateral erosion against background erosion caused by other physical and biological factors is complicated and will require long-term monitoring of marsh and isopod dynamics. A variety of interacting forces, both natural and anthropogenic, can lead to net loss of marsh habitat (Redfield 1972; Atwater et al. 1979; Josselyn 1983; Webb et al. 1995). Bioerosion by native (e.g. Letzsch and Frey 1980) or exotic (e.g. Rehm and Humm 1973) species may combine with dredging or filling, or altered hydrodynamic and wave energy regimes to cause marsh destruction. Decreased sedimentation within marshes, caused by diversion of water sources or reduction in suspended sediment loads, can limit the ability of marsh systems to replenish eroded sediments. Also, sea-level rise (or local land subsidence) can serve to increase erosion and inundate marsh habitat, especially where upland transition zones have been lost to development.

Carlton (1979) estimated that, in some areas of San Francisco Bay, tens of meters or more of marsh edge have been lost since the introduction of the isopod at the end of the nineteenth century and that this species is one of the most important agents in shoreline erosion. At Corte Madera, both increased wave energy from ferry traffic as well as erosion due to *S. quoyanum* were suggested as causes of marsh retreat measured at 95 cm year^{-1} (Josselyn 1983). Recently, marsh erosion within tidal creeks at China Camp, San Francisco Bay, has been measured at 2.3 ± 0.3 cm year^{-1} (Gabet 1998). Our data for San Francisco Bay indicate average erosion rates of almost ten times this value (but lower than that previously measured by Josselyn 1983), and maximum marsh erosion of over 1 m year^{-1}. The small fraction of original marsh habitat remaining, the altered hydrodynamic and sedimentation regimes within these systems, and the marsh destruction by isopods, may contribute to large losses of salt marsh habitat in this century.

Our studies demonstrate that *S. quoyanum* can exacerbate marsh erosion. Excavation of burrows loosens sediment that is then removed by water motion and tidal currents. Isopod burrowing and filter feeding activities also reduce stability of bank sediments, as indicated by decreases in shear strengths of burrowed mud. Also, burrows are more persistent features of the marsh banks than the isopods themselves, so erosion may continue despite low isopod densities. Although marsh banks are naturally eroded by tidal action, enclosure experiments suggest that sediment loss can potentially occur more than twice as rapidly with isopods present. However, the sediment loss rates observed in the enclosure experiments may be artificially enhanced above natural effects because of altered structure in the experimental substratum. Water motion coupled with small-scale, isopod-induced erosion appears eventually to cause the undercut topography. As undercutting continues (to a maximum distance of approximately 0.7 m; Gabet 1998), the overhanging slope breaks off and falls to the creek bed or tidal flat surface. This process leads to an appreciable but uneven pattern of marsh loss and makes it difficult to directly correlate isopod or burrow density with marsh retreat.

S. quoyanum typifies one of the most serious and continuing threats to the integrity of California's remaining coastal wetlands, the introduction of nonindigenous species (Cohen and Carlton 1998). As do all peracarid crustaceans, *S. quoyanum* has direct development and lacks a larval stage. Dispersal along the coast of California may be slow and is probably mediated by movement of adults on fouling surfaces, such as boats or floats, in floating wood or Styrofoam, or in transplants of marsh flora (Cohen and Carlton 1995; B. Collins, personal communication). On the Pacific coast of North America, *S. quoyanum* has been recorded as far north as Coos Bay, Oregon (Carlton 1996) and as far south as Bahia de San Quintín, northern Baja California, Mexico (Carlton 1979). There are embayments between infested areas, such as Estero de Punta Banda, Tijuana Estuary, Mission Bay and Upper Newport Bay, where *S. quoyanum* has not appeared (Crooks and Talley, personal observations). Invasibility of marsh habitat may depend upon isopod habitat preferences, the proximity of donor sites and available vectors of transport among embayments.

Created wetland habitats have proven particularly susceptible to invasion by exotic species (Scatolini and Zedler 1996; Crooks 1998). The created systems we studied in San Francisco and San Diego Bays had *S. quoyanum* densities equal to the natural marshes on several dates. Created marsh creeks, formed by bulldozing, often are formed with vertical banks. The above information about microhabitat preferences suggests that *S. quoyanum* invasion may be less likely where edge and bank faces are sloped and emphasizes the importance of having an intact zone of native *Spartina foliosa* and a source of sedimentation to counteract marsh erosion.

Salt marshes are critical habitat within North America, valued for their high productivity and their roles as shoreline stabilizers, land builders, water purifiers and nursery habitat (Mitsch and Gosselink 1993). In California, where between 75% and 90% of original salt marsh habitat has been lost, these fragmented ecosystems now provide habitat support for endangered plant and animal species, and for migratory birds (Schoenherr 1992; Murray and Bray 1993). Loss of remaining salt marsh habitat through erosional processes, as was observed in this study, is occurring and is of serious concern regardless of the contribution of *S. quoyanum*. It is clear that careful study and management of these wetland ecosystems are required to remedy ecological problems associated with anthropogenic impacts, including modifications that alter sediment deposition and hydrodynamic regimes, and the introduction of invasive substratum modifiers. Particularly important is the observation that invasive species are not only capable of altering community structure through interspecific competition or predation (Race 1982; Brenchley and Carlton 1983; Grosholz and Ruiz 1995), but through habitat alteration (often referred to as ecosystem engineering, sensu Jones et al. 1997) that may have a variety of cascading, ecosystem-level consequences (Crooks 1998). Further research is needed to learn how *S. quoyanum* interacts with other sediment-dwelling species, such as crustaceans, bivalves, anemones, polychaetes and gastropods, which have been observed inhabiting *S. quoyanum* burrows (Morton and Miller 1968; Levin et al., unpublished data), and how its burrows affect marsh plant communities, such as above- and below-ground productivity (e.g. Bertness 1985; Perry and Brusca 1989) and community structure.

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