

PREVALENCE AND DISTRIBUTION OF THE INTRODUCED BURROWING
ISOPOD, *SPHAEROMA QUOIANUM*, IN THE INTERTIDAL ZONE
OF A TEMPERATE NORTHEAST PACIFIC ESTUARY
(ISOPODA, FLABELLIFERA)

BY

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ABSTRACT

The Australasian burrowing isopod, *Sphaeroma quoianum*, was introduced to San Francisco Bay, California in the late 19th century and is now found in fifteen estuaries ranging from San Quintin Bay, Baja California to Yaquina Bay, Oregon. In some estuaries, *S. quoianum* achieve high densities, accelerate shoreline erosion, and damage maritime structures. To determine the distribution, habitat use, and prevalence of this destructive bioeroder within the intertidal zone of Coos Bay, Oregon, a series of field surveys was conducted. Intertidal substrata at 373 haphazardly selected sites throughout the estuary were examined for the presence of *S. quoianum* and their burrows. Four intertidal substrata were suitable for *S. quoianum* burrowing: marsh banks, wood, friable rock, and Styrofoam. Isopods were found more frequently at sites with wood than sites with other substrata. *Sphaeroma quoianum* and burrows were present at approximately 50% and 76% of respective sites containing a substratum suitable for burrowing. Significantly more isopods and burrows were encountered in mesohaline (>5-18) and polyhaline (>18-30) salinities than euhaline (>30) or oligohaline salinities (0.5-5). Low salinity is likely the primary factor limiting isopod populations in the upper estuary. However, the factor(s) limiting lower estuarine distributions are unclear. Factors typically limiting intertidal organisms (salinity, water temperature, dispersal, substrata availability/quality, predation, and competition) do not adequately explain the absence of *S. quoianum* in the lower estuary.

RÉSUMÉ

L'isopode d'Australasie creusant des terriers, *Sphaeroma quoianum*, a été introduit dans la baie de San Francisco, Californie, à la fin du 19^{ème} siècle et est présent maintenant dans quinze estuaires allant de la baie de San Quintin, Basse-Californie à la baie de Yaquina, Orégon. Dans certains

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estuariers, *S. quoianum* présente des densités élevées, accélère l'érosion du rivage et endommage les structures maritimes. Afin de déterminer la répartition, l'utilisation de l'habitat et la prévalence de ce «bioérodeur» destructeur dans la zone intertidale de la baie de Coos, Oregon, une série d'enquêtes sur le terrain a été réalisée. Les substrats intertidaux de 373 sites choisis au hasard dans l'ensemble de l'estuaire ont été examinés quant à la présence de *S. quoianum* et de leurs terriers. Quatre substrats intertidaux convenaient à *S. quoianum* pour le creusement des terriers : bancs vaseux, bois, roche friable et polystyrène (Styrofoam). Les isopodes ont été trouvés plus fréquemment dans les sites avec bois que dans les sites avec d'autres substrats. *Sphaeroma quoianum* et ses terriers étaient présents dans approximativement 50% et 76% des sites respectifs contenant un substrat convenable pour le creusement du terrier. Les isopodes et les terriers ont été trouvés significativement plus nombreux aux salinités mésahalines (>5-18) et polyhalines (>18-30) qu'aux salinités euhalines (>30) ou oligohalines (0.5-5). Une salinité faible est probablement le premier facteur limitant les populations d'isopodes dans la partie supérieure de l'estuaire. Cependant, le (ou les) facteur(s) limitant les répartitions dans la partie inférieure de l'estuaire ne sont pas clairs. Les facteurs limitant typiquement les organismes intertidaux (salinité, température de l'eau, dispersion, disponibilité/qualité des substrats, prédation et compétition) n'expliquent pas suffisamment l'absence de *S. quoianum* dans la partie inférieure de l'estuaire.

INTRODUCTION

The Australasian burrowing isopod, *Sphaeroma quoianum* H. Milne Edwards, 1840 (also spelled *S. quoyanum*; for synonymy see Harrison & Holdich, 1984) was introduced to the Pacific coast of North America during the late 19th century (Carlton, 1979). *Sphaeroma quoianum* was likely introduced through ship boring or fouling from Australia, Tasmania, and New Zealand, where it is presumed to be native (Hurley & Jansen, 1977; Carlton, 1979). Arriving initially in San Francisco Bay, populations of *S. quoianum* spread along the coast invading San Diego sometime before 1927 (Johnson & Snook, 1927) and Humboldt Bay in 1931 (Iverson, 1974). Today, populations of *S. quoianum* have been reported in fifteen estuaries from subtropical San Quintin Bay, Baja California to temperate Yaquina Bay, Oregon (Menzies, 1962; Iverson, 1974; Carlton, 1979; Cohen et al., 2002; Davidson, 2006; fig. 1).

Individuals of *S. quoianum* were also found in the Gulf of Tonkin in China (Kussakin & Malyutina, 1993), but it is unclear whether this population is introduced or native. In addition, the species was introduced but failed to establish in Pearl Harbor, Hawaii (Bartsch, 1916 as referenced in Eldredge & DeFelice, 2002; fig. 2). However, reports of *S. quoianum* in Alaska (Johnson & Snook, 1927) and along the Atlantic coast of North America (Boyd, 2002) are erroneous (Iverson, 1974; pers. obs.).

Within estuaries, *S. quoianum* burrows into a variety of intertidal and shallow subtidal substrata including marsh banks (formed of mud, clay, or peat), friable rock (sandstone, mudstone, or claystone), concrete, Styrofoam floats, sponges, and wood (Hill & Kofoid, 1927; Rotramel, 1975). The isopods are also found

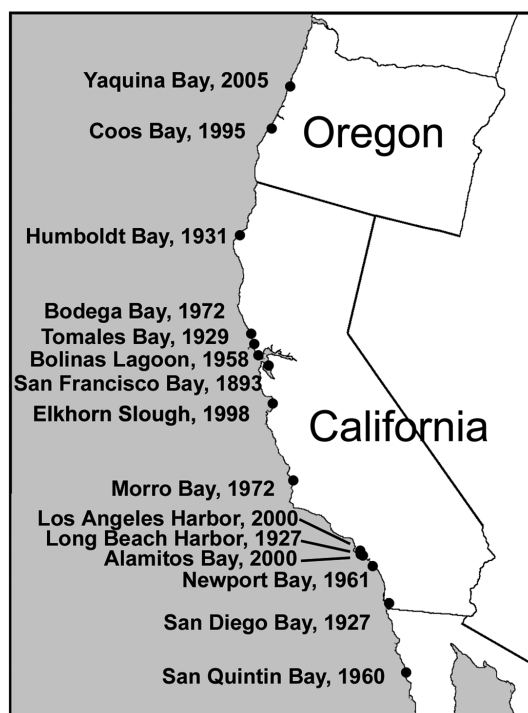


Fig. 1. Distribution of *Sphaeroma quoianum* H. Milne Edwards, 1840 along the Pacific coast of North America based on published sources. The year of discovery is noted after the location.

nestling amongst fouling organisms, within empty barnacle tests, and under rocks (Carlton, 1979; Hass & Knott, 1998). *Sphaeroma quoianum* do not consume the material excavated from burrows (Rotramel, 1975), but likely create burrows to be less vulnerable to epibenthic predators and to ameliorate environmental stress. Population densities in marsh banks in Pacific coast estuaries can reach thousands per 0.25 m² (Talley et al., 2001; T. M. Davidson, unpubl. data).

The creation of numerous interconnected burrows weakens substrata, accelerates erosion, and damages maritime structures (Higgins, 1956; Mills, 1978; Carlton, 1979; Cohen & Carlton, 1995; Talley et al., 2001; pers. obs.). Talley et al. (2001) found the burrowing of *S. quoianum* can increase the rate of sediment loss in saltmarsh banks by 240% and up to one meter of marsh shoreline could be lost in one year in infested areas. Their burrowing has also accelerated the rate of erosion of sandstone terraces in San Pablo Bay, California, (Higgins, 1956) and damaged Styrofoam floating docks (Cohen & Carlton, 1995; pers. obs.).

Sphaeroma quoianum was first discovered in the Isthmus Slough of Coos Bay, Oregon in 1995 (Carlton, 1996). The high abundances observed suggest the invasion likely started prior to 1995. Subsequent searches detected *S. quoianum* in abundance at multiple locations throughout Isthmus Slough in 1997, Haynes Inlet

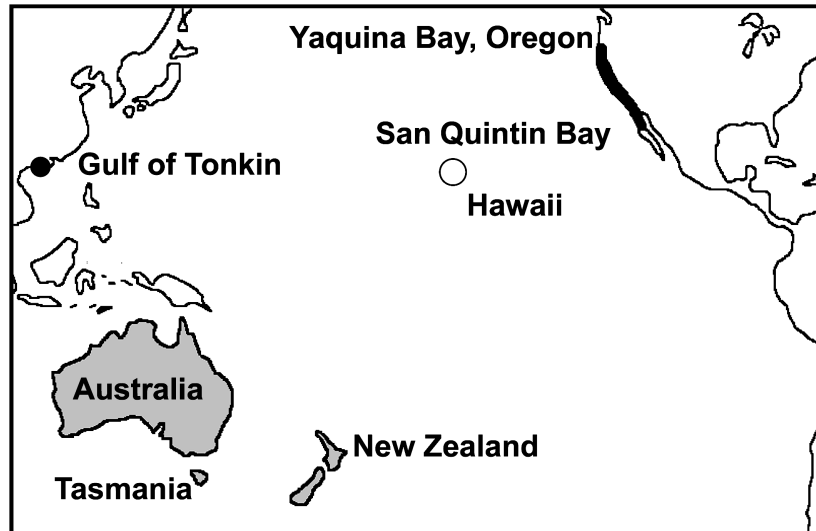


Fig. 2. Global distribution of *Sphaeroma quoianum* H. Milne Edwards, 1840 based on published data. Native regions are noted by the light gray shading (Australia, Tasmania, New Zealand). Introduced regions are noted by the black shading (Oregon, California, Baja California). The closed circle represents a cryptogenic population in the Gulf of Tonkin, China. The open circle represents a failed establishment in Hawaii.

in 1998, and in the South Slough in 1999 (J. T. Carlton, unpubl. data; fig. 3). Many saltmarsh banks and sandstone terraces in Coos Bay harbor large populations of *S. quoianum* and exhibit characteristics of intense erosion including undercutting and collapsed sections (Davidson, 2006).

Despite their abundance and presence in numerous Pacific coast embayments, the distribution of *S. quoianum* has not been adequately described within any estuary. Delineating their distribution will help determine the pervasiveness and potential impacts of invasions by *S. quoianum* and may help elucidate the factors controlling their distribution. This study assessed the prevalence, distribution, and habitats used by *S. quoianum* and identified the possible factors that may limit intertidal populations of *S. quoianum* within Coos Bay.

METHODS

Study location

Coos Bay is a small drowned-river estuary (50 km²) located along the southern-central coast of Oregon, U.S.A. (fig. 3). It is largely marine with significant seasonal freshwater input from the Coos River, Millicoma River, and numerous creeks (Rumrill, 2006). Coos Bay is heavily tidally influenced; salinity in the upper

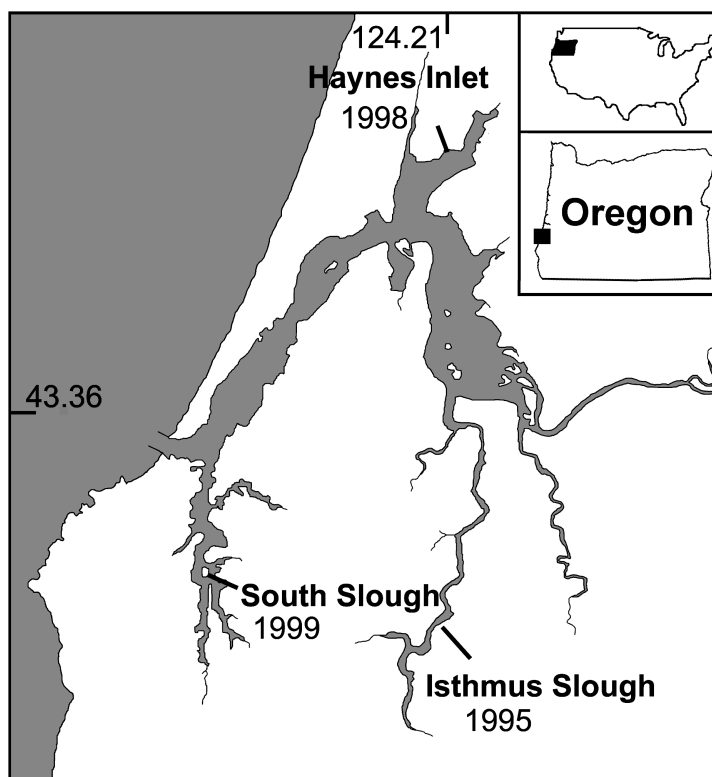


Fig. 3. Initial reports of *Sphaeroma quoianum* H. Milne Edwards, 1840 in Coos Bay, Oregon, U.S.A. *Sphaeroma quoianum* was first discovered in the Isthmus Slough in 1995. In 1998, populations were found in Haynes Inlet, and by 1999, populations had spread to the South Slough (J. T. Carlton, unpubl. data).

regions of the estuary can range from nearly fresh to full seawater during one tidal cycle. Coos Bay is an active international shipping port and is used for commercial cultivation of Pacific oysters (*Crassostrea gigas* (Thunberg, 1793)). Consequently, Coos Bay has experienced a substantial number of biological invasions.

Intertidal surveys

Shoreline surveys of all intertidal substrata located in 373 sites throughout Coos Bay were conducted between May 2005 and February 2006. Sites were haphazardly selected based upon accessibility by automobile, foot, or boat. Surveys ranged from the mouth to the terminal ends of the estuary. The geographic location of each site was determined using a handheld global positioning system (Garmin Geko 201, accuracy ± 3.4 m). At each site, intertidal substrata were characterized as: (1) marsh bank (marshes with an abrupt edge/vertical face); (2) wood (includ-

ing debris, pilings, docks, etc.); (3) sandstone (terraces, shelves, cobble/boulders); (4) other friable rock (mudstone, claystone); (5) Styrofoam (floats); (6) hard rock (non-friable rock, riprap, concrete); (7) sloping marsh (marsh without a vertical bank); (8) sandy beach; and/or (9) fouling communities. At sites that contained multiple substrata, each type of substratum was noted and examined.

Each substratum type was examined for the presence of *Sphaeroma quoianum* and burrows. Up to five minutes of searching were devoted to each site. Sites were characterized as burrowed if at least one substratum hosted shallow cylindrical burrows 2-10 mm in diameter with a circular aperture. As other estuarine fauna also create burrows in some of these substrata (i.e., grapsid crabs, polychaetes, etc.), the examination of burrow morphology was followed by a physical inspection of the interior of the burrows for specimens of *S. quoianum*. Substrata were characterized using two categories: (a) suitable substrata, previously known to be burrowed by *S. quoianum*, and (b) unsuitable substrata, which are not burrowed by *S. quoianum* due to physical hardness (hard rock, riprap) or their morphology (sandy beaches, sloping marshes, fouling). Because *S. quoianum* have been observed living freely on the underside of hard rocks in Australia (Hass & Knott, 1998; pers. obs.), I examined these types of substrata for nestling *S. quoianum*.

Salinity gradients

Salinity gradients for Coos Bay were constructed from a variety of data sources. The primary sources were Queen & Burt (1955), Arneson (1975), and the National Oceanic and Atmospheric Administration (2004). Additional data were supplied by Rumrill (2006) and by field measurements of salinity at high tide during February and May 2006. Since *S. quoianum* primarily inhabits the mid and high intertidal, salinity measurements taken during mid tide were used to create gradients, when those data were available. Each site was assigned a salinity class based upon the salinity measurements in the sources listed previously. Salinity classes were designated as oligohaline (0.5-5), mesohaline (>5-18), polyhaline (>18-30), and euhaline (>30).

Single classification goodness-of-fit *G*-tests were used to examine the relationship between the presence of *S. quoianum* individuals and burrows in the salinity classes and in different substrata. The *G*-values were adjusted using Williams correction to compensate for the increased type I error rate of *G*-tests (Sokal & Rohlf, 1981).

RESULTS

Burrows and individuals of *Sphaeroma quoianum* were found throughout most of the estuary. Burrows were found between 3.64 and 40 river kilometers from the

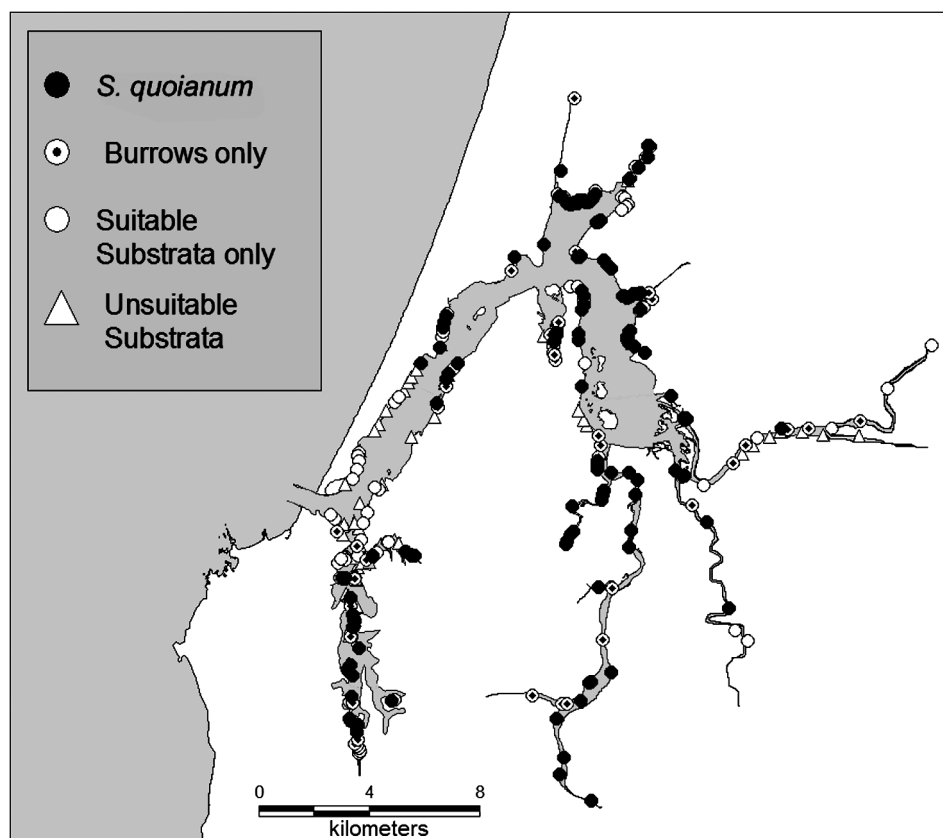


Fig. 4. Surveyed sites in Coos Bay. Closed circles represent the presence of *Sphaeroma quoianum* H. Milne Edwards, 1840 and burrows; dotted open circles represent the presence of burrows but no isopods; open circles represent suitable substrata lacking *S. quoianum* and burrows; open triangles represent a site without suitable substrata, isopods, or burrows.

estuary mouth and individuals were found between 4.71 and 40 river kilometers from the estuary mouth (fig. 4). The presence of individuals and burrows at a site with suitable substrata was dependent upon the salinity class (table I). *S. quoianum* individuals and burrows were absent from the estuary mouth (euhaline salinity), greatly increased in the middle and upper bays (mesohaline and polyhaline salinities), and then dropped sharply at the terminal end(s) of the estuary where salinities become increasingly influenced by riverine inputs (oligohaline salinities). Most burrows and individuals were found in salinities ranging from 5.5 to 30; however, burrows were found in salinities below 5 and above 30, though rarely.

Of the 373 intertidal sites examined, 309 (82.8%) contained at least one suitable substratum, 236 (63.3%) contained at least one substratum burrowed by *S. quoianum*, and 148 (39.7%) contained at least one living *S. quoianum*. Of

TABLE I

The number and percentage of sites harboring individuals of *Sphaeroma quoianum* H. Milne Edwards, 1840 and burrows within suitable substrata (marsh bank, wood, sandstone) in different salinity classes within the Coos Bay estuary; *n*, number of sites examined in each salinity class

	Sites with <i>S. quoianum</i>	% sites with <i>S. quoianum</i>	Sites with burrows	% sites with burrows	<i>n</i>
Oligohaline	0	0.0	6	42.9	14
Mesohaline	51	56.0	85	93.4	91
Polyhaline	95	53.7	143	80.8	177
Euhaline	1	4.0	4	16.0	25
<i>G</i> -adjusted	32.6		23.7		
<i>P</i>	<0.001		<0.001		
Df	3		3		

the sites with suitable substrata, 236 (76.4%) had burrows and 148 (47.9%) contained *S. quoianum*. Of the sites with burrowed substrata, 148 (62.7%) contained *S. quoianum*. Suitable substrata were found throughout the entire estuary. The most common suitable substrata encountered during surveys were marsh bank, wood, and sandstone. Substrata unsuitable for burrowing were also found throughout the estuary. *S. quoianum* were not found nestling under rocks, among sloping marsh plants, or on sandy beaches but were found nestling amongst fouling organisms in two locations. *S. quoianum* were primarily found within marsh banks, wood, and sandstone; rarely were they found in claystone or Styrofoam. The percentage of sites with burrowed marsh banks was similar to the percentage of sites with burrowed wood and sandstone substrata (table II). The percentage of sites with *S. quoianum* was lower than the percentage of sites with burrowed substrata. *Sphaeroma quoianum* occurred less frequently in marsh bank substratum than in wood or sandstone substrata.

TABLE II

The number of sites harboring individuals of *Sphaeroma quoianum* H. Milne Edwards, 1840 and burrows within marsh bank, wood, and friable rock; *n*, number of sites containing each of the different substratum types; NS, non-significant result. Note: some sites contained more than one substratum

	Sites with <i>S. quoianum</i>	% sites with <i>S. quoianum</i>	Sites with burrows	% sites with burrows	<i>n</i>
Marsh Bank	57	32.4	138	75.8	182
Wood	94	65.3	116	77.9	149
Sandstone	44	56.4	55	69.6	79
<i>G</i> -adjusted	18.8		0.5		
<i>P</i>	<0.001		NS		
Df	2		2		

DISCUSSION

In 1995, *Sphaeroma quoianum* was discovered in the Isthmus Slough, Coos Bay (Carlton, 1996) and in the ensuing 12 years, has spread throughout the bay. Populations of *S. quoianum* are found within natural substrata such as mud, peat, clay, sandstone, claystone, decaying wood, and amongst fouling communities, as well as within maritime structures such as Styrofoam floats and wooden docks. Primarily, populations of *S. quoianum* inhabit marsh banks, wood, and sandstone. Although *S. quoianum* are found living under rocks in Australia (Hass & Knott, 1998; pers. obs.), they were not found in this habitat in Coos Bay. *Sphaeroma quoianum* and its burrows are mostly absent from euhaline areas (salinity > 30) and from areas dominated by fresh water (salinity 0.5-5). Burrowed flotsam (wood, Styrofoam) was occasionally found in oligohaline and euhaline areas, but it was likely transported there via tidal action.

Several factors may affect the distribution of *S. quoianum* within Coos Bay including: salinity, water temperature, dispersal of juveniles and adults, substratum availability and quality, predation, and competition. Populations of *S. quoianum* disappear around mean salinities less than 5 and above 30, suggesting salinity (or a salinity correlate) as the primary controlling factor. The hypothesis that low salinity limits the upper-estuary distribution of *S. quoianum* is corroborated by laboratory studies indicating that *S. quoianum* are tolerant of salinities down to 8 but suffer 50% mortality when exposed to fresh water for 11 days (Riegel, 1959). However, laboratory experiments have shown adult *S. quoianum* can tolerate a salinity of 43 for 21 days (Riegel, 1959), which is considerably higher than the highest recorded salinity near the Coos Bay estuary mouth (NOAA, 2004). Furthermore, assuming their introduction into San Francisco Bay around the 1850-1890's was due to transit from Australia on the hulls of wooden sailing ships, then *S. quoianum* would have been exposed to full strength seawater for a period of weeks. *Sphaeroma quoianum* are tolerant of high salinities, but may not be tolerant of long-term exposure to the salinities experienced in the lower estuary. The distribution pattern may also indicate preference for mesohaline and polyhaline salinities.

Although present, *S. quoianum* and burrows are relatively uncommon within the mesohaline portions of the Coos River despite the abundance of friable sandstone and wood. The paucity of *S. quoianum* and burrows within this section of the Coos River may be attributed to seasonally low salinity. The Coos River is the largest source of freshwater input into Coos Bay (Baptista, 1989), salinity is highly variable (between 0 and 30), and substantially reduced by seasonal precipitation (Queen & Burt, 1955). Mean salinity at the mouth of the Coos River was below 5 in every measurement recorded during the months of December to mid-May in 1930 and 1931 (Queen & Burt, 1955). Although *S. quoianum* can tolerate low

salinities and freshwater conditions for many days (Riegel, 1959), the seasonal influx of freshwater likely produces an unfavorable environment for a period of weeks. In contrast, *S. quoianum* is present throughout numerous other creeks and sloughs in Coos Bay that do not experience low seasonal salinity.

The other factors typically limiting intertidal organisms do not adequately explain the absence of *S. quoianum* in the upper and lower estuary. Water temperature does not likely limit *S. quoianum* since they are indigenous to waters substantially warmer than the maximum temperature observed in Coos Bay (Harrison & Holdich, 1984) and can tolerate low temperatures (5°C) for several days (Jansen, 1971). It is unlikely that the current distribution of *S. quoianum* is related to dispersal limitation. Adults and juveniles disperse by rafting (pers. obs.) and likely by swimming; hence, they can be passively transported over considerable distances during a single tidal cycle. This assertion is supported by the fact that nearly every part of Coos Bay, including remote creeks and sloughs kilometers from the plausible invasion sources (ports, marinas), now host populations of *S. quoianum*. Substratum availability and quality are also not likely limiting factors since the upper and lower estuary harbors large expanses of friable sandstone shelf, long stretches of marsh bank, thick accumulations of dock fouling, numerous wood pilings, and woody debris available to *S. quoianum*. The influence of predation on their distribution is likely low since they spend most of their time inside their burrows (pers. obs.) and thus are less susceptible to most predators. In concordance, epibenthic predators did not affect colonization rates of the burrowing congener, *S. terebrans* Bate, 1866 in Florida (Brooks & Bell, 2001). Competition for space is also not likely a factor limiting the distribution of *S. quoianum* in Coos Bay. On a very small scale (cm), *S. quoianum* may compete with numerous organisms for space; however, on a large scale (m to tens of m), there are considerable substrata available for inhabitation. Temperature, dispersal, substratum availability/quality, predation, and competition probably have a limited effect on the distribution of *S. quoianum* in Coos Bay. Salinity, particularly low salinity, is likely the major factor limiting *S. quoianum*. Clearly, more studies are needed to investigate the long-term effects of varying salinity and to elucidate the role of other factors in limiting *S. quoianum*.

The ubiquity of *Sphaeroma quoianum* within Coos Bay illustrates the threat posed by this introduced species. *S. quoianum* is currently present in one-third of marsh bank and over one-half of the sandstone sites in Coos Bay and their burrows are present in three-quarters of marsh bank and sandstone sites surveyed. Thus, the burrowing activity of *S. quoianum* may be eroding many kilometers of Coos Bay shoreline including critical saltmarsh habitat. Over 80% of Coos Bay saltmarshes have been destroyed by diking, draining, filling, and development (Rumrill, 2006). The destructive burrowing of this invasive isopod is a significant threat to the

remaining saltmarsh habitat. Populations of *S. quoianum* have also been observed burrowing into dikes. Dikes infested with *S. quoianum* failed in Coalbank Slough, Coos Bay during winter storms of 2005-06 causing tens of thousands of dollars of damage to several residences (S. Rumrill, pers. comm.). The role of *S. quoianum* in reducing the integrity of dikes is an important concern and should be addressed in future studies.

In addition to accelerating the rate of shoreline erosion, *S. quoianum* can also damage some marine structures. *Sphaeroma quoianum* has been observed burrowing into wooden pilings and docks, Styrofoam floats, sea walls, and other marine structures (Chilton, 1919; Carlton, 1979). Although most damage appears minimal, occasionally, *S. quoianum* can be highly destructive (Miller, 1926). In New Zealand, burrowing by *S. quoianum* resulted in extensive damage to claystone and papa rock sea walls (Chilton, 1919) and wooden transmission poles (Mills, 1978). Wooden docks have also been extensively damaged in Port Phillip Bay, Australia (pers. obs.). In Coos Bay, extensive burrowing severely damaged a Styrofoam floating dock, rendering it inoperable (J. T. Carlton, pers. comm.). During the current study, numerous pieces of heavily bored Styrofoam were found throughout Coos Bay including the Styrofoam billets under a 10 m section of an abandoned dock. These observations suggest many floating docks have experienced extensive damage from *S. quoianum*.

CONCLUSIONS

This study examined the distribution of a detrimental introduced species in the temperate Coos Bay estuary. Approximately ten years following discovery, *S. quoianum* is now a ubiquitous member of the intertidal community within the mesohaline and polyhaline portions of Coos Bay. They inhabit a variety of substrata and pose a significant threat to the shoreline and maritime structures. Since many other Pacific coast estuaries harbor populations of *S. quoianum*, these isopods may also be contributing to shoreline erosion in these estuaries and should be considered in future management plans.

ACKNOWLEDGEMENTS

I would like to thank James T. Carlton, Janet Hodder, Steven Rumrill, and Alan Shanks for advice and suggestions. I would also like to thank Benjamin Grupe, Holly Keammerer, Tracey Smart, and the reviewers for their helpful comments on previous versions of this manuscript. The author was supported by a National Science Foundation GK-12 Graduate Fellowship (DGE-0338153 to A. Shanks and J. Hodder). The research was also supported by PADI Project Aware and the American Museum of Natural History Lerner Gray grant for marine research.

REFERENCES

- ARNESON, R. J., 1975. Seasonal variations in tidal dynamics, water quality, and sediments in the Coos Bay estuary: 1-250. (Ph.D. Thesis, Oregon State University, Corvallis, Oregon).
- BAPTISTA, A. M., 1989. Salinity in Coos Bay, Oregon. Review of historical data (1930-1989). Army Corps of Engineers Technical Report, **ESE-89-001**: 1-40. (Portland, Oregon).
- BARTSCH, P., 1916. Marine borers, Naval Station, Pearl Harbor, Hawaii. Public Works Navy Bulletin, **22**: 27-28.
- BOYD, M. J., T. J. MULLIGAN & F. J. SHAUGHNESSY, 2002. Non-indigenous marine species of Humboldt Bay, California: 1-118. (Technical Report, Humboldt State University, Arcata, California).
- BROOKS, R. A. & S. S. BELL, 2001. Colonization of a dynamic substrate: factors influencing recruitment of the wood-boring isopod, *Sphaeroma terebrans*, onto red mangrove (*Rhizophora mangle*) prop roots. *Oecologia*, **127**: 522-532.
- CARLTON, J. T., 1979. History, biogeography, and ecology of the introduced marine and estuarine invertebrates of the Pacific coast of North America: 1-904. (Ph.D. Thesis, University of California, Davis).
- — —, 1996. Marine bioinvasions: the alteration of marine ecosystems by nonindigenous species. *Oceanography*, **9**: 36-43.
- CHILTON, C., 1919. Destructive boring Crustacea in New Zealand. *New Zealand Journ. Sci. Techn.*, **2**: 1-15.
- COHEN, A. N. & J. T. CARLTON, 1995. Nonindigenous aquatic species in a United States estuary: a case study of the biological invasion of San Francisco Bay and Delta. Biological study. Final report no. NOAA-NA36RG0467, FWS -14-48-0009-93-9 61: 1-246. (University of California, Berkeley).
- COHEN, A. N., L. H. HARRIS, B. L. BINGHAM, J. T. CARLTON, J. W. CHAPMAN, C. C. LAMBERT, G. LAMBERT, J. C. LJUBENKOV, S. N. MURRAY, L. C. RAO, K. REARDON & E. SCHWINDT, 2002. Project report for the Southern California exotics expedition 2000: a rapid assessment survey of exotic species in sheltered coastal waters: 1-23. (Final report for: California Department of Fish and Game, Sacramento, CA; State Water Resources Control Board, Sacramento, CA; and National Fish and Wildlife Foundation, San Francisco, CA).
- DAVIDSON, T. M., 2006. The invasion of the Australasian burrowing isopod, *Sphaeroma quoianum*, in Coos Bay, Oregon: 1-158. (M.Sc. Thesis, University of Oregon, Eugene).
- ELDREDGE, L. & R. C. DEFELICE, 2002. Checklist of the marine invertebrates of the Hawaiian Islands. Hawaii Biological Survey, Bishop Museum, Honolulu, Hawaii. http://www2.bishopmuseum.org/HBS/invert/list_home.htm [Accessed 17 Feb 2007.]
- HARRISON, K. & D. M. HOLDICH, 1984. Hemibranchiate sphaeromatids (Crustacea: Isopoda) from Queensland, Australia, with a world-wide review of the genera discussed. *Zool. Journ. Linn. Soc. London*, **81**: 275-387.
- HASS, C. G. & B. KNOTT, 1998. Sphaeromatid isopods from the Swan River, Western Australia: diversity, distribution, and geographic sources. *Crustaceana*, **71**: 36-46.
- HIGGINS, C. G., 1956. Rock-boring isopod. *Bulletin of the Geological Society of America*, **67**: 1770.
- HILL, C. & C. A. KOFOID, 1927. Marine borers and their relation to marine construction on the Pacific coast: 1-357. (Final Report of the San Francisco Bay Marine Piling Committee, San Francisco, CA).
- HURLEY, D. & K. P. JANSEN, 1977. The marine fauna of New Zealand: family Sphaeromatidae (Crustacea: Isopoda: Flabellifera). *Memoirs of the New Zealand Oceanographic Institute*, **63**: 1-95.
- IVERSON, E. W., 1974. Range extensions for some California marine isopod crustaceans. *Bull. Southern California Acad. Sci.*, **73**: 164-169.

- JANSEN, K. P., 1971. Ecological studies on intertidal New Zealand Sphaeromatidae (Isopoda: Flabellifera). *Mar. Biol.*, Berlin, **11**: 262-285.
- JOHNSON, M. E. & H. J. SNOOK, 1927. Seashore animals of the Pacific coast: 1-659. (Dover Publications, New York).
- KUSSAKIN, O. F. & M. V. MALYUTINA, 1993. Sphaeromatidae (Crustacea: Isopoda: Flabellifera) from the South China Sea. *Invertebr. Taxon.*, **7**: 1167-1203.
- MENZIES, R. J., 1962. The marine isopod fauna of Bahia De San Quintin, Baja California, Mexico. *Pacific Naturalist*, **3**: 337-348.
- MILLER, R. C., 1926. Ecological relations of marine wood-boring organisms in San Francisco Bay. *Ecology*, **7**: 247-254.
- MILLS, P. E., 1978. *Sphaeroma quoyana* on treated poles in New Zealand. *Int. Biodeterior. Bull.* **14**: 35-36.
- NATIONAL OCEANIC AND ATMOSPHERIC ADMINISTRATION, NATIONAL ESTUARINE RESEARCH RESERVE SYSTEM-WIDE MONITORING PROGRAM, 2004. South Slough Estuarine Research Reserve monitoring data. Centralized Data Management Office, Baruch Marine Field Lab, University of South Carolina. <http://cdmo.baruch.sc.edu> [Accessed 15 Feb 2007.]
- QUEEN, J. & W. V. BURT, 1955. Hydrography of Coos Bay: 1-16. (School of Science, Oregon State College, Data Report No. 1, Corvallis, Oregon).
- RIEGEL, J. A., 1959. Some aspects of osmoregulation in two species of sphaeromatid isopod Crustacea. *Biological Bulletin*, Woods Hole, **116**: 272-284.
- ROTRAMEL, G., 1975. Filter-feeding by the marine boring isopod, *Sphaeroma quoyanum* H. Milne Edwards, 1840 (Isopoda, Sphaeromatidae). *Crustaceana*, **28**: 7-10.
- RUMRILL, S., 2006. Site profile of the South Slough Estuary, Oregon: a National Estuarine Research Reserve: 1-240. (National Oceanic and Atmospheric Administration, National Ocean Service, Estuarine Reserves Division, Charleston, Oregon).
- SOKAL, R. & F. J. ROHLF, 1981. *Biometry*: 1-859. (W.H. Freeman and Company, New York).
- TALLEY, T. S., J. A. CROOKS & L. A. LEVIN, 2001. Habitat utilization and alteration by the invasive burrowing isopod, *Sphaeroma quoyanum*, in California salt marshes. *Mar. Biol.*, Berlin, **138**: 561-573.

First received 12 April 2007.

Final version accepted 16 May 2007.