THE INVASION OF THE AUSTRALASIAN BURROWING ISOPOD (*SPHAEROMA QUOIANUM*) IN COOS BAY, OREGON

by

TIMOTHY MATHIAS DAVIDSON

A THESIS

Presented to the Department of Biology
and the Graduate School of the University of Oregon
in partial fulfillment of the requirements
for the degree of
Master of Science

December 2006

"The Invasion of the Australasian Burrowing Isopod (*Sphaeroma quoianum*) in Coos Bay, Oregon," a thesis prepared by Timothy Mathias Davidson in partial fulfillment of the requirements for the Master of Science degree in the Department of Biology. This thesis has been approved and accepted by:

Dr. Alan Shanks, Chair of the Examining Committee

Date

Committee in Charge:	Dr. Alan Shanks, Chair Dr. Steven Rumrill Dr. Janet Hodder

Accepted by:

Dean of the Graduate School

An Abstract of the Thesis of

Timothy Mathias Davidson for the degree of Master of Science
in the Department of Biology to be taken December 2006
Title: THE INVASION OF THE AUSTRALASIAN BURROWING ISOPOD
(*SPHAEROMA QUOIANUM*) IN COOS BAY, OREGON

Approved: ______________________________
Dr. Alan Shanks

Approved: ______________________________
Dr. Steven Rumrill

The Australasian burrowing isopod (*Sphaeroma quoianum*) was discovered in Coos Bay, Oregon in 1995. After approximately ten years, *S. quoianum* has become a common member of the intertidal community and appears to be accelerating shoreline erosion. Surveys, density measurements, and a field experiment were conducted to determine the intertidal distribution, density, and substratum preference of this bioeroder within Coos Bay. Results were compared to two Australian embayments (Port Phillip Bay and the Tamar Estuary) to examine how the ecology of *S. quoianum* differs. In all bays examined, isopod presence was dependent upon salinity and densities varied between substrata (marsh bank, wood, and friable rock). Densities in marsh banks and friable rock were significantly higher within Coos Bay than the Australian embayments surveyed. In experimental trials, *S. quoianum* greatly preferred wood to other substrata. The wide distribution and high densities *S. quoianum* attains have clear environmental and economic implications.

CURRICULUM VITAE

NAME OF AUTHOR: Timothy M. Davidson

PLACE OF BIRTH: Tigard, Oregon

DATE OF BIRTH: March 2, 1979

GRADUATE AND UNDERGRADUATE SCHOOLS ATTENDED:

University of Oregon
Oregon State University

DEGREES AWARDED:

Master of Science in Biology, 2006, University of Oregon
Bachelor of Science in Environmental Science, 2002, Oregon State University

AREAS OF SPECIAL INTEREST:

Invasion Ecology
Marine Community Ecology
Crustacean Biology

PROFESSIONAL EXPERIENCE:

National Science Foundation EAPSI Fellow, Australian Maritime College, Summer 2006

National Science Foundation GK-12 Teaching Fellow, Oregon Institute of Marine Biology (University of Oregon), 2004-2006

Research Technician, David Lodge Laboratory, University of Notre Dame, 2003-2004

Research Assistant, Sylvia Behrens Yamada, Oregon State University, 2000-2004 (intermittently)

Research Assistant, Center for Water and Environmental Sustainability, Oregon State University, 2001-2002 (intermittently)

GRANTS, AWARDS AND HONORS:

NSF East Asia and Pacific Summer Institutes program, 2006

NSF GK-12 Fellowship, 2004-2006

Grant-in-aid of Research, Sigma Xi: The Scientific Research Society, 2006

General Scholarship, University of Oregon, 2006.

Neil Richmond Memorial Fellowship, Oregon Sea Grant, 2006.

Learner-Gray Research Grant, American Museum of Natural History, 2005.

PADI Project Aware Research Grant, 2005

Oregon Space Grant Scholarship, 2002.

Union of Classified Employees Scholarship, Portland Community College, 2001.

College of Science Scholarship, Oregon State University, 2000, 2001

PUBLICATIONS:

Davidson TM, Stefans R, Rumrill S (2006) Protecting Oregon's estuaries from invading species. A field guide to identifying and controlling invading species. Friends of the South Slough, Charleston, Oregon

Davidson TM, Behrens Yamada S (2004) The rate of prey consumption in two estuarine crab species: the introduced European green crab, *Carcinus maenas*, and the native Dungeness crab, *Cancer magister*. J Shellfish Res 23(2):653

ACKNOWLEDGMENTS

Many heartfelt thanks go to the entire Oregon Institute of Marine Biology and South Slough National Estuarine Research Reserve community. This research would not have been possible without the assistance, advice, and friendship everyone has offered. I would especially like to thank my advisors Dr. Alan Shanks and Dr. Steven Rumrill and my committee member Dr. Janet Hodder. Their support, guidance, and enthusiasm for my research was invigorating and always motivated me and to seek and create new opportunities. I thank my Australian host advisors Dr. Chad Hewitt and Dr. Marnie Campbell for their helpful advice, friendship, and many exotic dinners. I would also like to thank my field help, especially Ben Grupe, Mike Holmes, Jose Marin Jarrin, Scott Groth and Tracey Smart. Without your help, carrying cinder blocks across mudflats would have been a near impossible feat. My thanks also go to myriad others that have provided logistical support and technical advice including Barbara Butler, Jim Carlton, John Chapman, Christina Geierman, James Haddy, Robin High, Gary Poore, Theresa and Drew Talley, and Jim Trainer. Thanks go to Mr. Stan Sakai, Matt Groening, Zapp Brannigan, and Phillip J. Fry for reminding me to not take life too seriously. Finally, I thank my family and friends for their unwavering support and encouragement throughout the years.

This research was generously funded by the American Museum of Natural History Lerner-Gray grant, Sigma Xi Grants in Aid of Research, Neil Richmond Fellowship, PADI Project Aware grant, the National Science Foundation East Asia and South Pacific Summer Institutes Fellowship (under grant No. 0611556), and the NSF GK-12 Fellowship.

To those who enjoy, explore, and question the intricacies of the natural world.

TABLE OF CONTENTS

LIST OF FIGURES

CHAPTER II

CHAPTER III

CHAPTER IV

CHAPTER V

Figure Page

LIST OF TABLES

CHAPTER II

Table Page

CHAPTER III

CHAPTER IV

CHAPTER V

Table Page

CHAPTER I

GENERAL INTRODUCTION

The Australasian burrowing isopod, *Sphaeroma quoianum*, is introduced on the Pacific Coast of North America. *Sphaeroma* initially arrived in San Francisco and currently inhabits at least fourteen estuaries ranging from northern Baja California to Yaquina Bay, Oregon (Johnson and Snook 1927, Riegel 1959, Menzies 1962, Carlton 1979, Cohen and Carlton 1995, per. obs). *Sphaeroma* is native to mainland Australia, Tasmania, and New Zealand (Chilton 1912, Hurley and Jansen 1977) and was likely introduced via ship fouling or boring between the early 1850's and 1890's (concurrent with the arrival of Australian ships for the Gold Rush; Carlton 1979). *Sphaeroma* was discovered in Coos Bay, Oregon in 1995 (Carlton 1996) and has since spread to several locations throughout the estuary.

Sphaeroma creates networks of burrows in a variety of intertidal and subtidal substrata including marsh banks (composed of peat, mud, or clay), wood, friable rock (sandstone, mudstone, claystone), Styrofoam floats, and more. *Sphaeroma* is also a bioeroding species, capable of accelerating erosion and damaging maritime structures (Chilton 1919, Higgins 1956, Talley et al. 2001). In some heavily infested Californian marshes, erosion can exceed one meter per year (Talley et al. 2001).

The primary objective of this thesis was to determine the status and examine aspects of the autecology of this invasive species in Coos Bay, Oregon. Chapter II provides a review of the global and region distribution of *Sphaeroma* and provides baseline measurements of the distribution, prevalence, and the plausible factors limiting this invasive species within Coos Bay. Chapter III provides additional baseline data on the density of *Sphaeroma* within three of the most commonly invaded intertidal substrata (marsh banks, wood, and sandstone) and between three months (August, January, and April). Chapter III also examines the role of *Sphaeroma* as a physical ecosystem engineer whose burrow constructs are utilized by myriad fauna. The associated fauna present within these burrows were also determined as well as abundances of these species in different substrata. Chapter IV examines how the density, distribution, and habitat use of introduced *Sphaeroma* populations (Coos Bay) compare to two native populations within southeastern Australia. In this chapter, the distribution, prevalence, habitat use, and density of *Sphaeroma* in Coos Bay were compared to two Australian embayments: the Tamar estuary (Tasmania) and Port Phillip Bay (Victoria). Finally, Chapter V examines the substratum preference of *Sphaeroma* in four different intertidal substrata (marsh banks, wood, sandstone, and Styrofoam). Chapter V also examines how burrowing rate changes over time and the life stages that colonize intertidal substrata. This work provides important baseline data on a destructive invasive species, reveals aspects of the ecology of this relatively recently invader, and elucidates the potential effects this organism is having on the surrounding estuarine community.

CHAPTER II

DISTRIBUTION OF THE INTRODUCED BIOERODING ISOPOD *SPHAEROMA QUOIANUM* IN THE INTERTIDAL ZONE OF A TEMPERATE PACIFIC NORTHWEST ESTUARY

Introduction

The Australasian burrowing isopod *Sphaeroma quoianum* (H. Milne Edwards 1840; hereafter: *Sphaeroma*) was introduced to the Pacific Coast of North America during the late 19th century (Carlton 1979). The vector for this introduction was likely through ship boring or ship fouling. Arriving initially in San Francisco Bay, populations of *Sphaeroma* spread along the coast invading San Diego in 1927 (Johnson and Snook 1927) and Humboldt Bay in 1931 (Iverson 1974). Today, populations of *Sphaeroma* have been observed in at least fourteen estuarine embayments ranging from subtropical Bahia San Quintin (Baja California) to the temperate Yaquina Bay, Oregon (Menzies 1962, Iverson 1974, Carlton 1979, per. obs.; Figure 1). *Sphaeroma* are native to Australasia (Australia, Tasmania, New Zealand) and inhabit temperate to tropical regions of Australia (Chilton 1912, Hurley and Jansen 1977, Harrison and Holdich 1984). Individuals of *Sphaeroma* were also introduced to the Gulf of Tonkin in China (Kussakin and Malyutina 1993) and the species was observed, but failed to establish in Pearl Harbor, Hawaii (Bartsch 1916 as referenced in Eldredge and DeFelice 2002; Figure 2).

However, reports of *Sphaeroma* introductions in Alaska (Johnson and Snook 1927) and along the Atlantic coast of North America (Boyd et al. 2002) are erroneous (Iverson 1974, per. obs.). *Sphaeroma* has undergone a number of name changes and is synonymous with *S. quoyanum, S. pentodon, S. verrucauda, S. quoyana,* and *S. quoiana*.

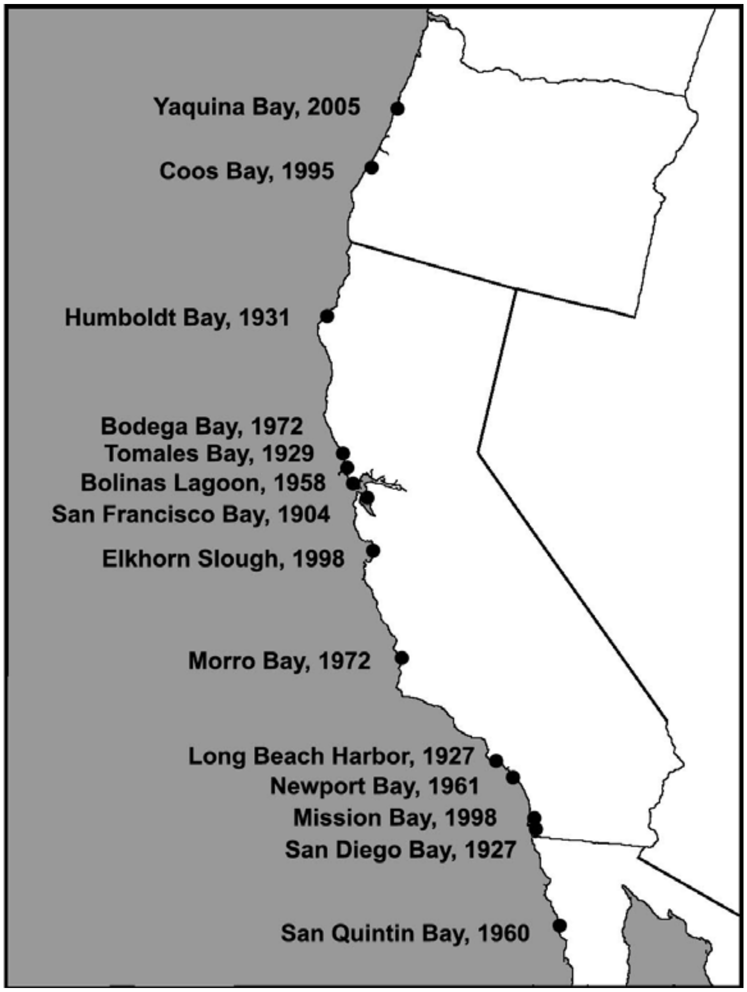


Figure 1. Regional distribution of *Sphaeroma* along the Pacific Coast of North America based on published data. The year of discovery is noted after the location.

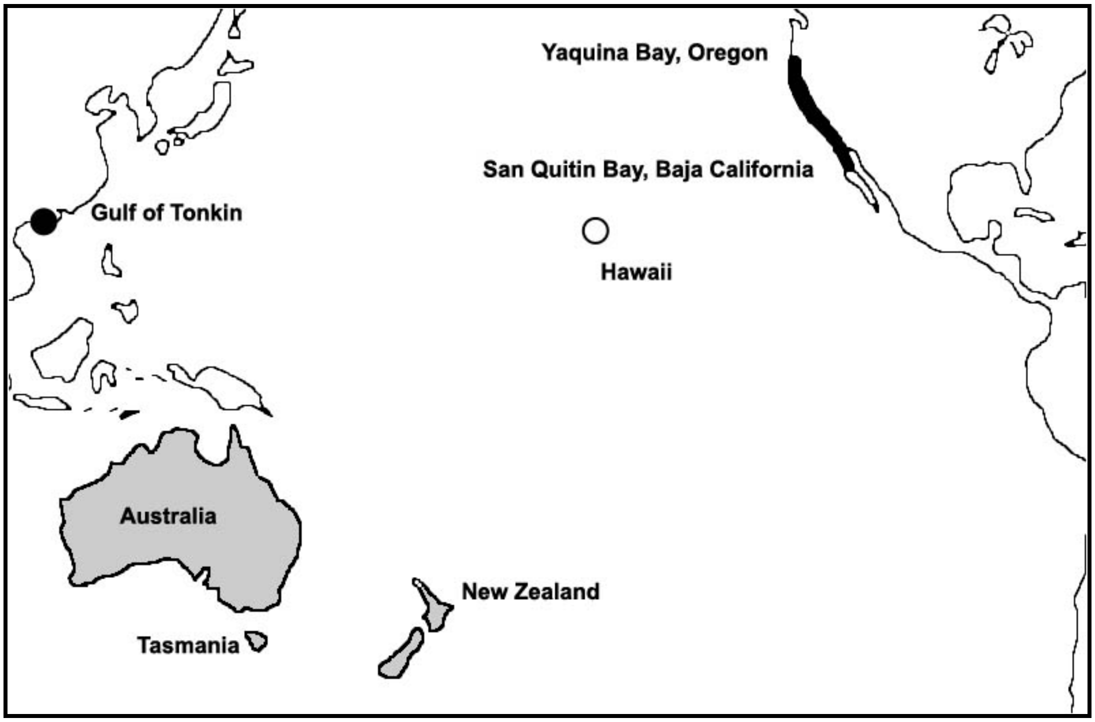


Figure 2. Global distribution of *Sphaeroma* based on published data. Native regions are noted by the light gray shading (Australia, Tasmania, New Zealand). Introduced regions are noted by the closed circle (●; Gulf of Tonkin) and the black shading (Oregon, California, Baja California). The open circle (○) represents a failed establishment in Hawaii.

Within estuaries, populations of *Sphaeroma* can burrow 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 and Kofoid 1927; Rotramel 1975). The isopods are also found nestling amongst dock fouling organisms, within empty barnacle tests, and under rocks (Carlton 1979, Hass and Knott 1998). Although *Sphaeroma* may inhabit myriad intertidal and shallow subtidal substrata, studies by Talley et al. (2001) have found that these sphaeromatids exhibit preferences within Californian marsh banks. Within these systems, *Sphaeroma* greatly prefer vertical and undercut marsh banks over sloped marsh banks. They also prefer firm, peaty soils directly under *Salicornia* spp. marsh (Talley et al. 2001). *Sphaeroma* do not consume the material excavated from burrows, but rather create a burrow likely for protection and to facilitate filter feeding. Beating pleopods generate a current of water that moves suspended particles and diatoms into the burrow (Rotramel 1975). The current passes through the dense setae on the front pereopods allowing food particles to be retained and consumed (Rotramel 1975).

Population densities and prevalence of *Sphaeroma* within Pacific Coast estuaries can be extremely high. During July 1998, Talley et al. (2001) measured the density of *Sphaeroma* within marsh banks and observed mean densities of 2936 individuals/ $0.25m^2$ in San Francisco Bay and 1153 individuals/ $0.25m^2$ in San Diego Bay at sites where *Sphaeroma* was abundant. *Sphaeroma* are also pervasive members of the intertidal community within San Diego Bay and San Francisco Bay. Approximately 71% of the marsh banks sampled in San Francisco Bay and 58% in San Diego Bay harbored burrows covering more than 34% of the marsh bank substratum (Talley et al. 2001). Similarly, in Elkhorn Slough, Wasson et al. (2001) report that nearly every bank examined was riddled with holes from this bioeroder.

The creation of numerous interconnected burrows serves to weaken substrata, accelerating the rate of shoreline erosion and damaging some maritime structures (Higgins 1956, Mills 1978, Carlton 1979, Cohen and Carlton 1995, Talley et al. 2001, per. obs.). Talley et al. (2001) examined the erosive abilities of *Sphaeroma* in a Californian marsh and found that burrowing activity within experimental enclosures can increase the rate of sediment loss in salt marsh banks by 240%. They further observed that up to one meter of marsh shoreline could be lost in one year in areas infested with *Sphaeroma* (Talley et al. 2001). Furthermore, Carlton (1979) suggested that tens to scores of meters of land over many kilometers might have been washed away in California bays over the last century, facilitated by this introduced species. The burrowing by this isopod has also greatly exacerbated the rate of erosion in the expansive sandstone terraces of San Pablo Bay, California (Higgins 1956). Researchers have even discovered populations of *Sphaeroma* burrowing into the Styrofoam floats used in floating docks (Rotramel 1975, Carlton 1979, Cohen and Carlton 1995). Similarly, many salt marsh banks in Coos Bay, Oregon harbor large populations of *Sphaeroma* and exhibit characteristics of intense erosion including undercut marsh banks and broken sections (per. obs.). Burrowing by *Sphaeroma* also appears to increase the rate of erosion of sandstone boulders and terraces and damages the Styrofoam floats in some floating docks (per. obs.).

Sphaeroma exhibits a wide tolerance to salinity and temperature. In San Francisco, *Sphaeroma* live in salinities between 3.8 and 33 (Riegel 1959). In the Swan River estuary in Western Australia, *Sphaeroma* live in areas with salinities between ~5-33, and on at least one occasion, they have also been found in waters with a salinity as high as 40 (Hass and Knott 1998). Laboratory experiments by Riegel (1959) corroborate these patterns. Riegel (1959) determined adult *Sphaeroma* could live in experimental salinities between 8.6-43 for 21 days without mortality, but when placed in freshwater for 11 days, *Sphaeroma* suffered 50% mortality. Adult *Sphaeroma* are also tolerant of extreme water temperatures. Jansen (1971) discovered *Sphaeroma* suffer zero mortality in water at 5ºC for 3 days, zero mortality at 20ºC for 1 day, and less than 20% mortality at 42º C for 1 day. The ability to withstand variable salinity and temperature may explain why the *Sphaeroma* invasion has been successful along the Pacific Coast of North America.

Current status

Sphaeroma was initially discovered in Coos Bay, Oregon in 1995 (Carlton 1996). The discovery of abundant specimens within Isthmus Slough, suggests the invasion likely started prior to 1995. Subsequent searches detected *Sphaeroma* in abundance within multiple locations throughout Isthmus Slough in 1997, Haynes Inlet in 1998, and in the South Slough in 1999 (Carlton 2005; Figure 3).

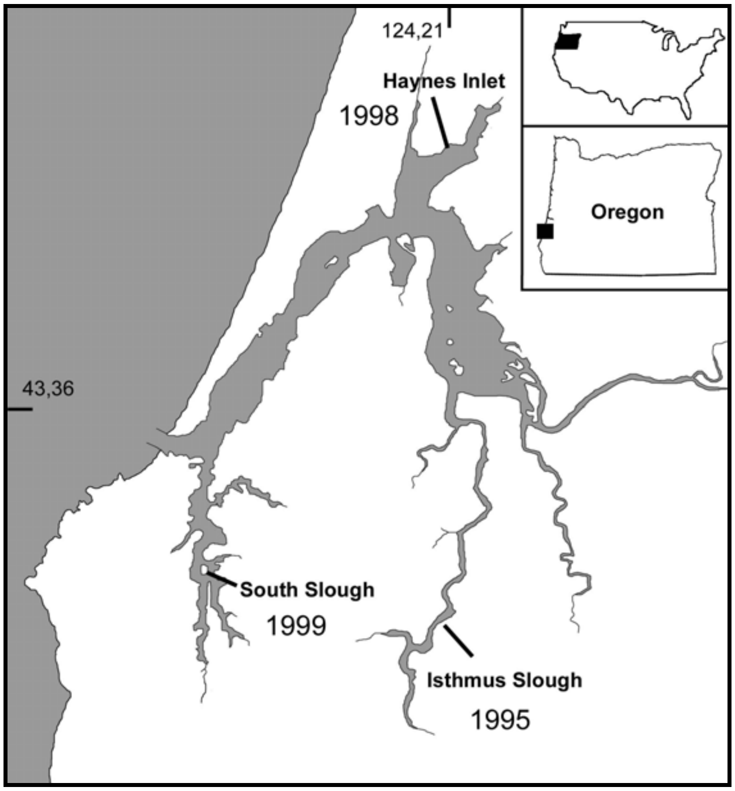


Figure 3. Initial reports of *Sphaeroma* in Coos Bay, Oregon, USA. *Sphaeroma* was first discovered in the Isthmus Slough in 1995. In 1997 populations were found in Haynes Inlet and in 1999 populations had spread to the South Slough (Carlton 2005).

Despite being present in numerous Pacific Coast embayments for almost 150 years and being abundant members of some estuarine communities, the distribution of this introduced species has not been adequately described within any estuary. Delineating the distribution of this isopod will help determine the pervasiveness and potential impacts of the *Sphaeroma* invasion and may help elucidate the factors that control the distribution of this destructive introduced species. This study: 1) determines the status and prevalence of *Sphaeroma* in the Coos Bay estuary, 2) determines what habitats *Sphaeroma* utilize within Coos Bay, and 3) identifies the possible factors that may limit intertidal populations of *Sphaeroma*.

Methods

Study location

Coos Bay is a relatively small drowned-river estuary (50 km^2) located along the coast of southern Oregon, USA (Figure 3). It is largely marine with significant freshwater input from the Coos River, Millicoma River, and numerous creeks (Rumrill 2006). Coos Bay is heavily tidally influenced; salinity in the upper regions of the estuary can range from nearly fresh to full seawater during the same tidal cycle. Coos Bay is also heavily influenced by winter and spring precipitation, which can reduce salinity in many parts of the bay to oligohaline (0.5-5) and mesohaline conditions (5-18) for several weeks (Queen and Burt 1955, Burt and McAllister 1959). The shoreline is composed primarily of sandy beaches, marsh, rocky riprap, sandstone, and abundant woody debris from past and present logging operations. Coos Bay is an active international shipping port and the tidal waters of the estuary are used for commercial cultivation of Pacific oysters (*Crassostrea gigas*). 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 to maximize effort. 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 ± 10m). At each site, intertidal substrata were characterized as: 1) marsh bank (marshes with an abrupt edge/vertical face), 2) wood (including debris, pilings, docks, etc.), 3) sandstone (terraces, shelves, cobble/boulders), 4) other friable rock (mudstone, claystone), 5) hard rock (non-friable rock, riprap, concrete), 6) sloping marsh (marsh without a vertical bank), 7) sandy beach, and/or 8) fouling (on docks or pilings). At sites that contained multiple substrata, each substratum type was noted and examined.

Each substratum type was examined for the presence of *Sphaeroma* individuals and burrows. Sites were characterized as burrowed if at least one substratum hosted shallow cylindrical burrows between 1mm and 10mm in diameter. As other estuarine fauna also create burrows in some of these substrata (i.e. grapsid crabs), the examination of burrow morphology was followed by a physical inspection of the interior of the burrows for specimens of *Sphaeroma*.

Site characterization and presence of *Sphaeroma*

Sites were characterized by the presence or absence of *Sphaeroma* and the presence or absence of *Sphaeroma* burrows (hereafter: burrows). Sites were also characterized by substratum type using two categories (Figure 4): a) suitable substrata, previously known to be burrowed by *Sphaeroma*, and b) unsuitable substrata, which are not burrowed by

Sphaeroma due to physical hardness (hard rock, riprap) or by their morphology (sandy beaches, sloping marshes, fouling). Because *Sphaeroma* have been observed living freely on the underside of hard rocks in Australia (Hass and Knott 1998, per. obs.), I examined these types of substrata for nestling *Sphaeroma*.

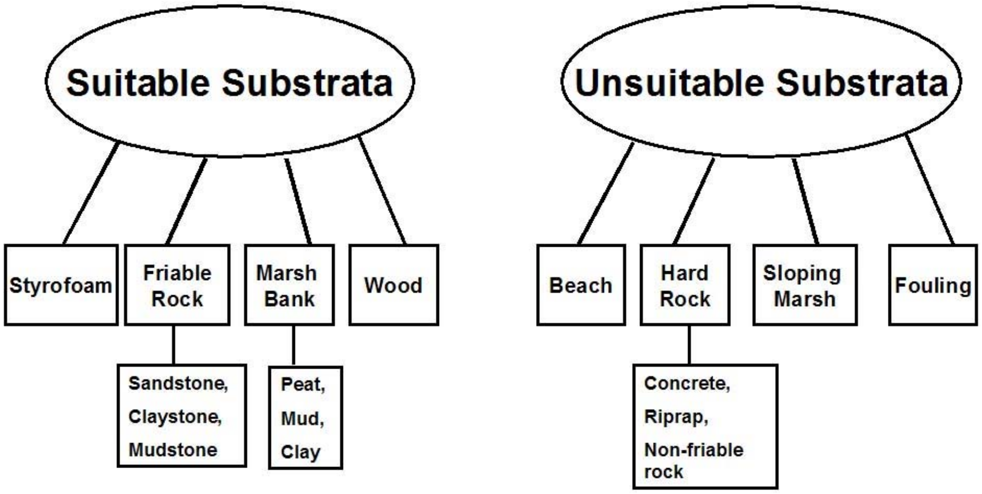


Figure 4. Classification of the intertidal substrata in Coos Bay, Oregon.

Salinity gradients

Salinity gradients for Coos Bay were compiled from a variety of data sources. The primary sources were Queen and Burt (1955) who measured salinity approximately every two weeks between 1930-1932, Arneson (1975) who analyzed seasonal changes in tidal dynamics, water quality and sediments during 1971-1972, and NOAA (2004) which compiles multiyear data on several hydrographic parameters within the South Slough

National Estuarine Research Reserve. Additional data were supplied by Rumrill (2006) and by field measurements of salinity at high tide during February and May 2006. Since *Sphaeroma* 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 surveyed 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) salinity.

Statistical analysis

The relationship between the presence of *Sphaeroma* individuals and burrows in the salinity classes and in differing substrata were analyzed using single classification Chi-square goodness of fit tests with adjusted *G*-values. *G*-values were adjusted using Williams correction (Williams 1976) to compensate for the higher than intended type I error rate of *G*-tests (Sokal and Rohlf 1981).

Results

Distribution of *Sphaeroma*, burrows, and substrata

Sphaeroma burrows and individuals were found throughout the estuary. Burrows were found between 3.64 to 40 river kilometers from the estuary mouth and *Sphaeroma* individuals were found between 4.71 to 40 river kilometers from the estuary mouth

(Figure 5). *Sphaeroma* and burrows become very sparse just before the estuary mouth (euhaline), greatly increase in the middle and upper bays (mesohaline and polyhaline), and then drop sharply at the terminal ends of the estuary where salinities become increasingly influenced by riverine inputs. *Sphaeroma* burrows and individuals were found in salinities ranging from 5.5-30; however, burrows were occasionally found in salinities below 5 and above 30.

The presence of *Sphaeroma* individuals and burrows at a site with suitable substrata were dependent upon the salinity class ($G_{adj}= 28$, df=3, $P < 0.001$; $G_{adj}= 24$, df=3, $P < 0.001$; Table 1). Most *Sphaeroma* and their burrows were found within the polyhaline (salinity 18-30) and mesohaline (salinity 5-18) waters of Coos Bay including the South Slough and entire Isthmus Slough, and Coalbank Slough. *Sphaeroma* and burrow observations within the numerous creeks and sloughs appeared to decrease as the estuary became increasingly dominated by freshwater. *Sphaeroma* individuals and burrows were almost completely absent from the Coos River (which ranges from mesohaline to oligohaline salinity) and the mouth of the estuary (euhaline salinity).

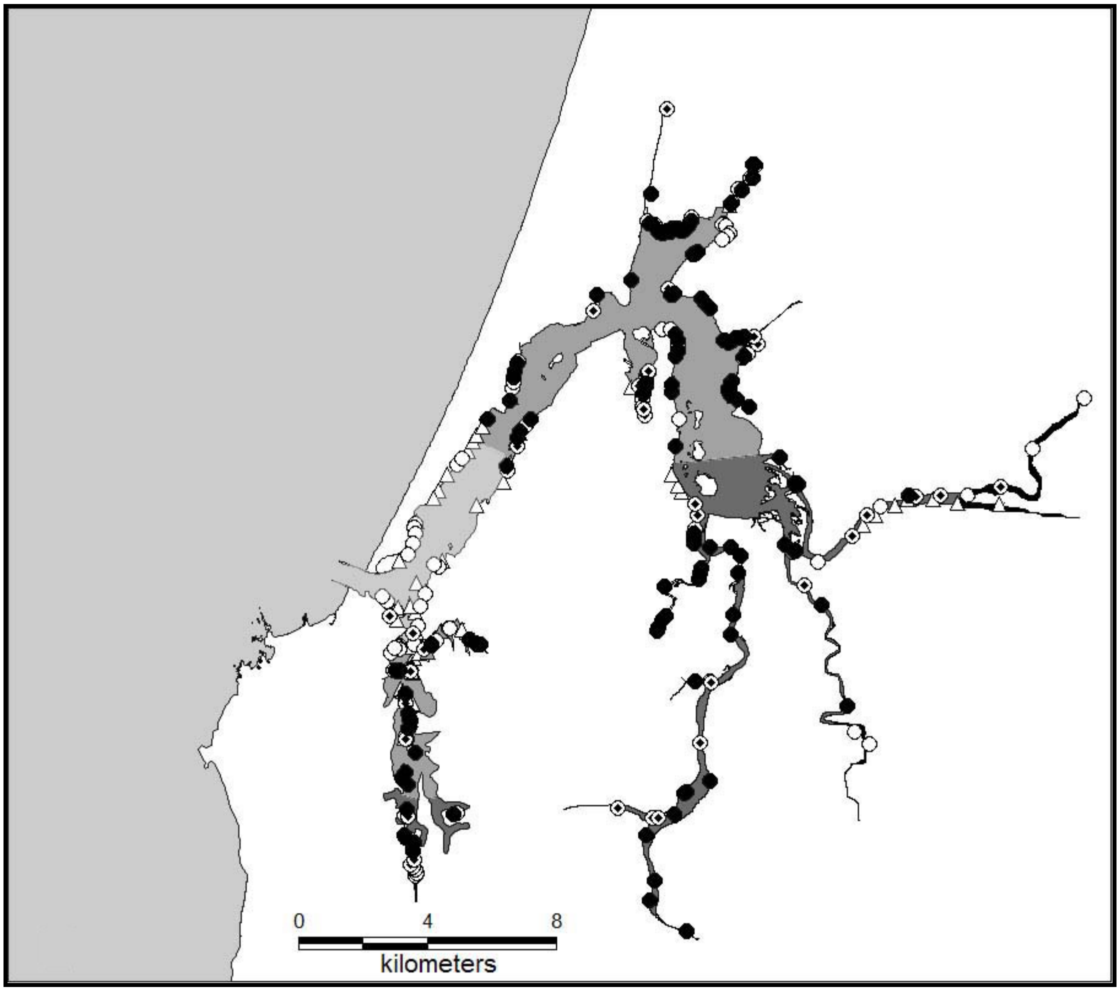


Figure 5. Surveyed sites in Coos Bay hosting suitable substrata. Closed circles (●) represent the presence of *Sphaeroma* individuals and burrows; open circles with a dot (⊙) represent the presence of *Sphaeroma* burrows and no individuals; open circles (○) represent suitable substrata lacking *Sphaeroma* individuals and burrows (○); (Δ) open triangles represent a site without a suitable substratum. The shades represent the following salinity classes: oligohaline (0.5-5; black), mesohaline (>5-18; dark gray), polyhaline (>18-30; light gray), and euhaline (>30; white). Note the absence of *Sphaeroma* from the Coos River (highly variable salinity) and presence of *Sphaeroma* through more lagoonal and less variable in salinity than Isthmus Slough and Catching Slough.

Table 1. The number and percentage of sites harboring *Sphaeroma* individuals (SQ) and burrows within suitable substrata (marsh bank, wood, sandstone, Styrofoam flotsam) in different salinity classes within the Coos Bay estuary; *n* = the number of sites examined in each salinity class.

	Sites with SQ	% sites with SQ	Sites with burrows	% sites with burrows	*n*
Oligohaline	**0**	0.0	6	42.9	14
Mesohaline	**51**	56.0	85	93.4	91
Polyhaline	**94**	53.1	143	80.8	177
Euhaline	**2**	8.0	4	16.0	25

***G*-adjusted**	27.0		23.0		
P	<<0.001		<<0.001		
df	3		3		

Presence of suitable substrata, *Sphaeroma* burrows, and *Sphaeroma* individuals

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 *Sphaeroma*, and 148 (39.7%) contained at least one living *Sphaeroma* (Table 2). Of the sites with suitable substrata, 236 (76.4%) had burrows and 148 (47.9%) contained *Sphaeroma*. Of the sites with burrowed substrata, 148 (62.7%) contained *Sphaeroma*.

Table 2. The presence of suitable and burrowed substrata and *Sphaeroma* individuals within all surveyed sites, within all sites with suitable substrata, and within sites containing burrowed substrata throughout Coos Bay. Classification of each site is as follows: *Suitable* - if at least one substrata previously known to be burrowed by *Sphaeroma* was present (includes mud, clay, peat, wood, sandstone, Styrofoam, claystone, and mudstone); *Burrowed* – if at least one substrata contains *Sphaeroma* burrows; *Sphaeroma* – if the site contains at least one *Sphaeroma* individual.

	Within all sites (%)	**Within sites with suitable substrata (%)**	**Within sites with burrowed substrata (%)**
Suitable	**82.8**	**-**	**-**
Burrowed	**63.3**	**76.4**	**-**
Sphaeroma	**39.7**	**47.9**	**62.7**

Distribution of *Sphaeroma* and burrows in marsh bank, wood, and sandstone habitat

Suitable substrata were found throughout the estuary, although the highest suitable substratum density was present near the mouth and in the upper estuary. The most common suitable substrata encountered during surveys were: marsh bank, wood, and sandstone. Substrata unsuitable for *Sphaeroma* burrowing were also found throughout the estuary. No individuals of *Sphaeroma* were observed nestling under rocks, among sloping marsh plants, or on sandy beach. *Sphaeroma* were found nestling amongst fouling organisms in only two locations. Most of the suitable substrata examined at each site contained burrows. The percentage of sites with burrowed marsh bank substratum was similar to the percentage of sites with burrowed wood and sandstone substrata (Table 3). The percentage of sites with *Sphaeroma* individuals was much lower than the percentage of sites with burrowed substrata. The presence of *Sphaeroma* was lowest in marsh bank substratum compared to wood and sandstone substrata.

Table 3. The number of sites harboring *Sphaeroma* individuals (SQ) and burrows within marsh bank, wood, and friable rock; *n* = the number of sites containing each of the different substratum types. Note: some sites contained more than one substratum.

	Sites with SQ	**% sites with SQ**	**Sites with burrows**	**% sites with burrows**	***n***
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
***G*-adjusted**	18.8		0.5		
P	<<0.001		NS		
df	2		2		

Discussion

Sphaeroma was discovered in the Isthmus Slough, Coos Bay in 1995 (Carlton 1996). Since the initial discovery approximately ten years ago, *Sphaeroma* individuals and burrows have been observed throughout nearly every part of Coos Bay where suitable intertidal substrata occur. Populations of *Sphaeroma* are found within natural substrata such as mud, peat, clay, sandstone, claystone, decaying wood, and fouling, as well as within maritime structures such as Styrofoam floating docks and wooden docks. Primarily, *Sphaeroma* populations inhabit marsh banks, wood, and sandstone. Although *Sphaeroma* have been found living under rocks in Australia (Hass and Knott 1998, per.

obs.), they were not observed living under rocks in Coos Bay. *Sphaeroma* and burrows were most frequently encountered within mesohaline and polyhaline waters of the Coos Bay estuary. *Sphaeroma* and burrows were absent near the mouth of the estuary (euhaline conditions: salinity >30 conditions) and in areas dominated by fresh water (oligohaline conditions: salinity 0.5-5).

Several factors may affect the distribution of *Sphaeroma* within Coos Bay including: salinity, temperature, substrata availability and quality, food supply, predation, competition, and dispersal limitations. In the upper regions of Coos Bay, the presence of *Sphaeroma* and burrows appear to be related to salinity. Nearly all *Sphaeroma* and burrows observations are located between mean annual salinities of ~5 and 30. This pattern aligns with observations that *Sphaeroma* individual and burrow densities in most rivers/creeks appear to decrease as the area becomes increasingly dominated by freshwater.

Interestingly, *Sphaeroma* and burrows are relatively absent within the mesohaline portions of the Coos River despite the abundance of friable sandstone and wood. The paucity of *Sphaeroma* and burrows within the Coos River may be attributed to the seasonal flux in salinity. The Coos River is the largest source of freshwater input into Coos Bay (Baptista 1989, Rumrill 2006). Salinity is highly variable (between 0 and 30) and substantially reduced by seasonal precipitation (Queen and Burt 1955, Rumrill 2006). During a two-year study of the hydrography of Coos Bay, Queen and Burt (1955) determined mean salinity at the mouth of the Coos River was under 5 in every measurement recorded during the months of December to mid-May in 1930 and 1931.

Similarly, a study by Arneson (1975) found high tide salinity in the Coos River during December and March can be as low as 0.7 and 0, respectively, but in September salinity exceeded 30. Although *Sphaeroma* can tolerate low salinities and freshwater conditions for several days, the seasonal influx of freshwater likely produces an unfavorable environment for a period of weeks. However, the presence of some burrows far up river indicate either *Sphaeroma* may be able to inhabit these areas seasonally or pieces of burrowed flotsam (wood, Styrofoam) were transported there via flood tides. In contrast, *Sphaeroma* is present far up river in the numerous other creeks and sloughs (Isthmus Slough, Coalbank Slough, Shinglehouse Slough, South Slough, etc.) that do not experience the large seasonal salinity flux like the Coos River.

Sphaeroma and burrows are also absent near the mouth of Coos Bay. Although salinity may explain upper estuarine distributions of *Sphaeroma*, it is unclear what limits *Sphaeroma* distributions in the mouth of Coos Bay. Adult *Sphaeroma* are very tolerant of high salinities. Laboratory experiments by Riegel (1959) found *Sphaeroma* can survive at a salinity of 43 for 21 days without mortality. The highest recorded salinity near the Coos Bay estuary mouth was around 35 (NOAA 2004), which is well within the reported physiological tolerance of adult *Sphaeroma*. In addition, adult *Sphaeroma* are able to tolerate short-term exposure to very low temperatures (5°C; Jansen 1971). It is also possible that the effects of both low temperature and high salinity act synergistically to prevent the establishment of *Sphaeroma* populations at the estuary mouth. Riegel (1959) demonstrated that osmoregulation is depressed or inactivated when *Sphaeroma* are held in low temperatures. Likewise, Jansen (1970) demonstrated that the brackish congeners, *S. rugicauda* and *S. hookeri*, exhibit lower adult survivorship and reproductive output when exposed to low temperature and high salinities than when exposed to moderate temperature and high salinity and low temperature and moderate salinity.

The distribution of *Sphaeroma* may also be explained by decreased tolerance of juvenile isopods to high salinities and low temperatures. Juveniles in several isopod species exhibit higher mortality when exposed to high salinities and low temperatures than adults. Juvenile *S. rugicauda* and *S. hookeri* suffer greater mortality at high salinities and low temperatures than adults of the same species (Jansen 1970). In addition, juveniles of the isopod *Cyathura polita* are less able to osmoregulate than adults in high salinity (Kelly and Burbanck 1972). Reproduction may also be affected by high salinity. The brackish water isopod *S. hookeri* experiences decreased sexual activity in areas where the salinity is consistently high (Kouwenberg and Pinkster 1985). In Coos Bay, approximately 90% of all *Sphaeroma* colonizing experimental substrata are juveniles (Chapter V). If those juvenile colonizers are physiologically unable to inhabit regions of consistently high salinity/low temperature, then they may be avoiding the area around the estuary mouth. Likewise, adult isopods may be physiologically able to survive in high salinities/low temperature but choose not to inhabit the estuary mouth.

The other factors typically limiting intertidal organisms do not adequately explain the lack of *Sphaeroma* in the lower estuary. Along with salinity, water temperature may play a role in limiting these populations from the estuary mouth. Temperature, however, is unlikely to limit upper estuarine populations alone since *Sphaeroma* inhabits tropical and temperate zones and can live in waters considerably warmer than the maximum temperature experienced in Coos Bay. It is unlikely *Sphaeroma* are limited by dispersal since they are a rafting species (and at least one life stage disperses by swimming) that can be passively transported considerable distances during a flood tide. 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 now host *Sphaeroma* populations. Substrata availability and quality is also not likely a limiting factor since the lower estuary harbors large expanses of friable sandstone shelf, long stretches of marsh bank, thick accumulations of dock fouling, and numerous wood pilings and debris available for *Sphaeroma* inhabitation (per. obs.). The bay mouth is also a food rich environment with large concentrations of coastally derived chlorophyll-a (Roegner and Shanks 2001). The influence of predation is likely low since these isopods spend most of their time within burrows and thus are not susceptible to most predators. Similarly, epibenthic predators did not affect colonization rates of the burrowing congener, *S. terebrans* in Florida (Brooks and Bell 2001). Competition for space is also not likely a factor limiting *Sphaeroma* from the estuary mouth in Coos Bay. On a centimeter scale, *Sphaeroma* may compete with shipworms, barnacles, crabs, anemones, and other organisms for space; however, on a large scale, there are considerable substrata available for inhabitation.

The ubiquity of *Sphaeroma* within Coos Bay further illustrates the threat posed by this introduced bioeroding species. Individuals of *Sphaeroma* are currently present in one-third of marsh bank and over one-half of sandstone sites examined. In addition, *Sphaeroma* burrows are present in three-quarters of marsh bank and nearly three-quarters of sandstone sites surveyed. Thus, the prolific burrowing activity of *Sphaeroma* may be eroding many kilometers of Coos Bay shoreline. Of particular concern is the effect of *Sphaeroma* burrowing on the remaining salt marsh habitat of Coos Bay. Over 80% of Coos Bay salt marshes have been destroyed by diking, draining, filling, and development (Rumrill 2006). The destructive habitat of this invasive isopod is a major threat to the remaining salt marsh habitat. *Sphaeroma* populations have also been observed burrowing into several dikes. Dikes infested with *Sphaeroma* failed in Coalbank Slough during winter storms of 2005-06 causing tens of thousands of dollars of damage to several residences (S. Rumrill, per. comm.).

In addition to accelerating the rate of shoreline erosion, *Sphaeroma* can also damage some marine structures. *Sphaeroma* has been observed burrowing into wooden pilings and docks, Styrofoam floats, sea walls, and other marine structures (Chilton 1919, Miller 1926, Hill and Kofoid 1927, Carlton 1979). Although most damage appears minimal, occasionally *Sphaeroma* can be highly destructive (Miller 1926, Hill and Kofoid 1927, per. obs.). In Hawke's Bay, New Zealand, burrowing by *Sphaeroma* resulted in extensive damage to sea walls made from claystone and papa rock causing them to crumble away (Chilton 1919). Also in New Zealand, Mills (1978) reports *Sphaeroma* had burrowed into wooden transmission poles treated with copper-crome-aresenate. *Sphaeroma* can also damage Styrofoam floating docks. In Coos Bay, at least one floating dock had to be abandoned after *Sphaeroma* burrowing rendered it inoperable (J.T. Carlton, per. comm.). During the current study, numerous pieces of heavily burrowed Styrofoam were found throughout Coos Bay including a 10m section of dock. These observations suggest many floating docks have experienced extensive damage from *Sphaeroma* burrowing. Much of the damage sustained by this bioeroder is likely dependent on the density of the isopod, the local hydrography, and natural erosion rate. Future studies should examine the critical density at which *Sphaeroma* burrowing becomes a significant contributor to shoreline erosion and evaluate the potential impacts of *Sphaeroma* burrowing on the integrity of dikes and levees. In addition, future studies should examine how temperature and salinity affect juvenile and adult *Sphaeroma* survivorship and reproductive output.

Conclusion

This study examined the distribution of a detrimental introduced species in the temperate Coos Bay estuary. Approximately ten years following discovery, *Sphaeroma* is now a ubiquitous member of the intertidal community within most of Coos Bay. They inhabit a variety of substrata and pose a significant threat to the shoreline and maritime structures. *Sphaeroma* has been introduced to several other embayments along the Pacific coast. Since many Pacific coast estuaries also harbor substantial habitat suitable for *Sphaeroma* habitation, *Sphaeroma* populations may also be contributing to shoreline erosion in these estuaries and should be considered in future management plans.

BRIDGE I

Chapter II revealed the distribution and prevalence of *Sphaeroma* appear to vary greatly within various intertidal substrata. In some locations, *Sphaeroma* appears to be accelerating the rate of shoreline erosion and damaging some maritime structures. Through the creation of dense aggregations of burrows *Sphaeroma* may not only be contributing to erosion, but also creating a novel habitat within intertidal substrata in Coos Bay. The magnitude of these effects is likely related to the density of *Sphaeroma* in these areas. Chapter III examines the density of *Sphaeroma* within the three most commonly burrowed substrata (marsh bank, wood, and sandstone) and between three months (August, January, and April). This chapter also investigates the associated fauna of *Sphaeroma* burrows and determines how densities of these fauna change between substratum type and month. Furthermore, the chapter discusses the role of *Sphaeroma* burrows as habitat.

CHAPTER III

DENSITY AND THE ASSOCIATED FAUNA OF THE AUSTRALASIAN BURROWING ISOPOD *SPHAEROMA QUOIANUM* IN THREE INTERTIDAL SUBSTRATA IN COOS BAY, OREGON

Introduction

Biological invasions present one of the greatest challenges to maintaining the quality and health of marine ecosystems (Elton 1958, Carlton 1990, Vitousek et al. 1997). Invasive species impact marine organisms in a variety of ways ranging from direct impacts such as predation, competition, or parasitism, to indirect impacts such as altering ecosystem functioning or the availability of resources (Elton 1958, Ruiz et al. 1999, Crooks 2002, Grosholz 2002). Invasive species that can physically alter the availability of resources may have a greater per capita impact than those species that interact directly with native species. Species that physically alter the availability of resources (via their physical structures or by physical modification) are known as physical ecosystem engineers (*sensu* Jones et al. 1997). As Jones et al. (1994) indicate, the magnitude of impact of an ecosystem engineer is related to not only the per capita impact of the engineering, but the density and prevalence of that engineer within its environment. Thus, engineering species with very small per capita effects may have profound impacts on the physical environment if they occur at high densities and wide distributions. For example, burrowing earthworms (*Lumbricus terrestris*) have low individual effects in temperate North American forests, but due to their high abundance and wide distribution, they can impact the entire landscape (Meadows and Meadows 1991). By achieving high densities and consequently altering the quality and availability of habitat (habitat heterogeneity) of a system, invasive ecosystem engineers can have substantial effects on the abundance and richness of the surrounding communities (reviewed by Crooks 2002).

The species abundances and composition of many estuarine communities have been altered by invasive ecosystem engineers that create distinctive habitats. The expansive fields of the introduced eelgrass (*Zostera japonica*) provide a novel habitat within mid-high intertidal mudflats in many Pacific Coast estuaries. Significantly more infaunal invertebrates are associated with beds of *Z. japonica* than the adjacent unvegetated mudflat (Posey 1988) and *Z. japonica* can alter the composition of microbial communities (Hahn 2003). In Mission Bay, San Diego, California, the complex structures provided by mats of the introduced mussel *Musculista senhousia* harbor significantly more fauna (richness and abundances) than sediments without mats (Crooks 1998). Furthermore, extensive aggregations of the introduced ascidian *Pyura praeputialis* on some Chilean rocky shores provide a unique habitat that harbors greater species richness than rocky shores lacking this species (Castilla et al. 2004). The impact of an invasive engineering species is of particular concern when the creation of that habitat enhances the survivorship of other non-native species.

In Coos Bay, Oregon (USA), the introduction of a bioeroding and habitat altering invasive crustacean has raised concern. The invasive Australasian burrowing isopod

(*Sphaeroma quoianum*; H. Milne Edwards 1840) was discovered in Coos Bay, Oregon in 1995 and has spread to nearly every habitable area of the estuary (See Chapter II). *Sphaeroma quoianum* (= *S. quoyanum*; hereafter: *Sphaeroma*) creates extensive networks of shallow burrows primarily within marsh banks, woody debris and structures, and sandstone. These burrows create a novel habitat in many substrata and in some locations may be contributing to shoreline erosion.

Biology

Sphaeroma is a small, rotund sphaeromatid isopod reaching up to 16mm in length (Hurley and Jansen 1977). It may be distinguished from other common estuarine sphaeromatids by the presence of a double longitudinal row of four tubercles on the pleotelson, long dense setae on pereopod one, and serrated outer uropods (Hurley and Jansen 1977). Like other peracarids, *Sphaeroma* broods its young until they crawl away as fully formed juveniles. *Sphaeroma* grow at an average rate of about 0.64mm per month and are believed to become reproductive after six months (Schneider 1976). Gravid females and juveniles are found year round, suggesting that adults reproduce continuously (Hill and Kofoid 1927, Schneider 1976). The brood size of *Sphaeroma* varies between seasons with mean brood sizes of 64 in the spring and 19.5 in the fall and they live 1 ½ - 2 years (Schneider 1976). The introduced commensal isopod *Iais californica* is also present in *Sphaeroma* populations in Coos Bay and can be found clinging to the ventral surface of *Sphaeroma*.

Although *Sphaeroma* is primarily found in marsh banks, wood, and sandstone in Coos Bay, it is also found within other forms of friable rock such as claystone and mudstone and within the Styrofoam floats in floating docks. *Sphaeroma* is a filter feeder that excavates burrows primarily for living space (Rotramel 1975). These isopods are widely distributed throughout the intertidal but are most prevalent between salinities of 5-30 (See Chapter II). They primarily inhabit the shallow subtidal to the high tide mark, but *Sphaeroma* have also been found living amongst fouling communities in waters 7m deep (Cohen et al. 2001).

Through the creation of extensive burrow networks, *Sphaeroma* can significantly contribute to shoreline erosion (Higgins 1956, Carlton 1979, Talley et al. 2001) and damage maritime structures (Mills 1978, Carlton 1979, per. obs). Erosion is, however, most apparent within marsh edge systems. Talley et al. (2001) examined the erosive capabilities of *Sphaeroma* in marshes and found that *Sphaeroma* could increase the rate of sediment loss by as much as 240%. In addition, they found a positive correlation between the rate of lateral bank loss and density of *Sphaeroma* burrows. In some areas where *Sphaeroma* is abundant, lateral erosion can exceed one meter per year (Talley et al. 2001).

Given the effects of *Sphaeroma* burrowing on shoreline erosion, evaluating the densities of this bioeroding species within different substrata may help indicate the threat posed by this species and elucidate some of the factors affecting densities in Coos Bay. Furthermore, identifying the fauna living within *Sphaeroma* burrows could reveal how the estuarine community is affected by this habitat creating isopod. The overall purposes of this study were to examine how month and substratum type affects densities of *Sphaeroma* and inquilines (burrow cohabitants) and to determine what fauna are utilizing *Sphaeroma* burrows as habitat. The four objectives are: 1) determine the mean and maximum densities of *Sphaeroma* and inquilines and the proportion of young in marsh banks, wood, and sandstone during August, January, and April; 2) examine the effects of month and substratum type on the densities of *Sphaeroma* and inquilines and the proportion of young; 3) determine the prevalence of *Sphaeroma*, inquilines, and young (% occurrence) in different substrata and months; and 4) examine the abundance and richness of introduced inquilines and describe any possible interactions with *Sphaeroma*.

Methods

Study location

Coos Bay is a small temperate drowned-river estuary (50 km^2) located in southern Oregon, USA (43.35º N, 124.34ºW; Figure 1). It is largely marine with significant freshwater input from the Coos River, Millicoma River, and numerous creeks (Rumrill 2006). Coos Bay is heavily tidally influenced; salinity in the upper regions of the estuary can range from nearly fresh to full seawater during the same tidal cycle. The shoreline is primarily composed of sandy beaches, sloping marshes, extensive marsh banks, rocky riprap, and sandstone terraces and shelves. Abundant woody debris is also present along the shore from past and present logging operations. Coos Bay is an international shipping port with extensive areas of commercial oyster cultivation (*Crassostrea gigas*) and hosts significant numbers of introduced species.

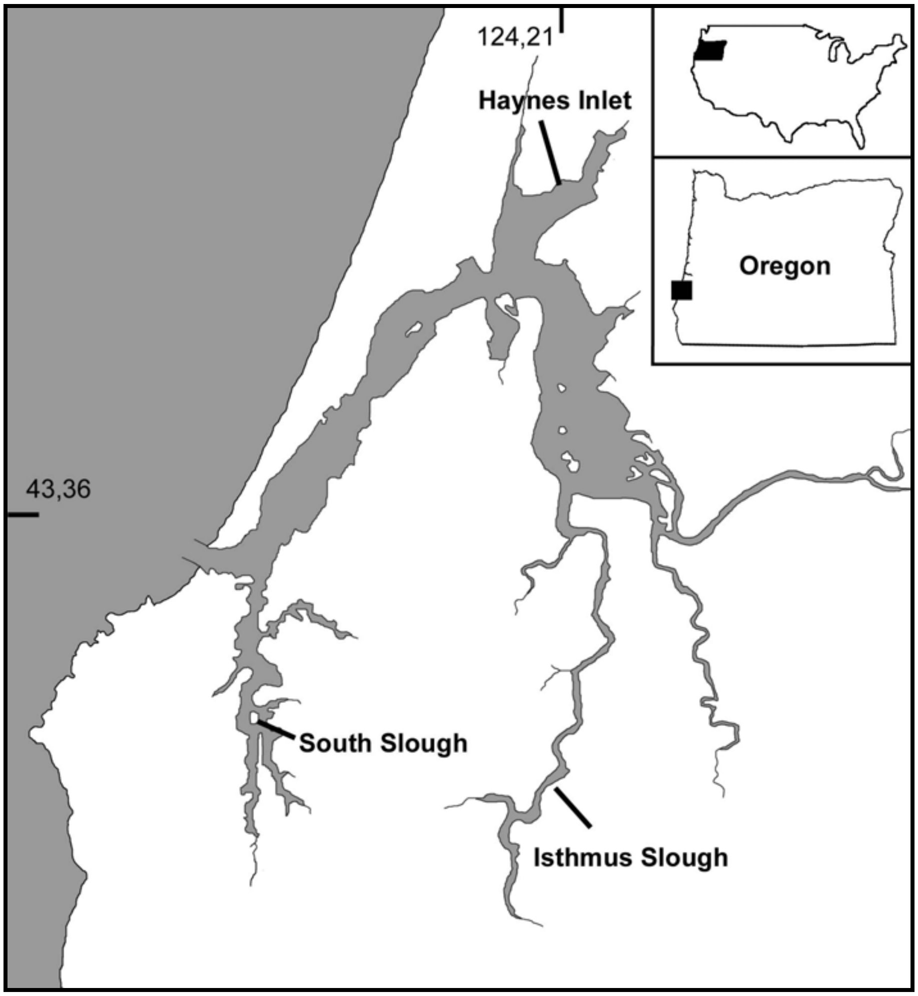


Figure 1. Coos Bay, Oregon (USA).

Density Measurements

To evaluate the density of *Sphaeroma* within burrowed marsh bank, wood, and sandstone, a series of representative intertidal sampling stations were selected in various locations within Coos Bay. Sampling occurred during or around the months of August (July 29-August 6, 2005), January (January 8-24, 2006), and April (April 3-14, 2006). Stations were selected in areas with established *Sphaeroma* populations between salinities of 11 and 24. Eight replicate stations were selected for each substratum. Different methods were employed to sample each of the substrata. At marsh bank stations, ten cores (6.2cm diameter x 10cm depth) were randomly sampled along a 50m transect. At wood stations, four discrete pieces of woody debris were randomly collected along a 50m transect. At sandstone stations, either cobble was randomly collected as discrete pieces or sandstone terrace or shelf was randomly sampled along a 50m transect. Sandstone terrace was sampled using a serrated steel corer (7.62 cm diameter) hammered to a depth of 6cm. The depths of marsh bank and sandstone cores sampled were selected to surpass the length of the deepest burrows created by *Sphaeroma*. The number of burrows within the core were counted in the field. All samples (both collected pieces and cores) were returned to the lab for processing. The volume and surface area of wood and sandstone samples were calculated through a series of digital photographs and analyzed by Imagetool 3.0 image analysis software. The area of the tops and sides of samples were measured with Imagetool 3.0 using a known size reference within the digital picture. Volume was determined by multiplying each respective area measurement by the mean depth or height of the other digital picture. All samples were physically sorted in the lab and all organisms were placed in 70% ethanol, enumerated, and identified to the lowest taxonomic level possible. All *Sphaeroma* under 5mm (representing instars 1-4 and a distinct cohort) were enumerated separately. These are referred to as *young* for the remainder of the analysis.

Statistics

The relationships between the occurrence of *Sphaeroma*, young, and inquilines within samples within the different substrata during different months were analyzed using single classification goodness of fit tests (Sokal and Rohlf 1981). The Williams correction was used on the *G*-values to account for higher than normal type I error associated with *G*-tests (Williams 1976).

Three-way partially nested mixed-model ANOVA was used to determine if the mean densities of *Sphaeroma*, burrows, and inquilines differ between month 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 scatterplots and box plots as recommended by Quinn and Keough (2002). Data were rank transformed to improve normality and homogeneity of the variance. The transformation was unsuccessful in normalizing the data, but variance was homogenized for most variables. Balanced ANOVA models, however, are robust to deviations from normality and homogenous variance (Box 1953, Underwood 1981). All *a posteriori* comparisons were tested using the Scheffe test to account for the increased family-wise type I error of multiple comparisons (Zar 1996, Quinn and Keough 2002).

Results

Sphaeroma Density

The mean and maximum densities of *Sphaeroma* were highest in wood and sandstone substrata (Table 1). The mean densities of *Sphaeroma* varied significantly between all factors and interactions (Table 2). The significant interactions between factors were examined first since they can lead to a misleading interpretation of main effects (Quinn and Keough 2002). The significant interaction between month and substratum indicates that mean density between months varied differently between each substratum. Within marsh banks, the mean densities of *Sphaeroma* vary relatively little across the surveyed months. In contrast, wood and sandstone substrata varied considerably between months. The interaction between month and station was also significant and likely reflected the normal variation these populations experienced between locations and during different times of the year. Seasonal effects often differ between areas in an estuary.

Table 1. Mean and maximum densities of *Sphaeroma*, burrows, and inquilines per $0.25m^3$ in marsh banks, wood, and sandstone substrata.

	Sphaeroma* per *0.25m³		**Burrows per 0.25m³**		**Inquilines per 0.25m³**	
	Mean	Maximum	Mean	Maximum	Mean	Maximum
Marsh Bank	4,383	30,136	6,566	17,579	4,942	49,473
Wood	23,556	128,543	20,142	82,737	20,654	180,504
Sandstone	24,324	86,989	26,568	120,919	22,997	145,021

The densities of *Sphaeroma* varied significantly between substrata (Figure 2). The densities of *Sphaeroma*, burrows, and inquilines were significantly lower within marsh bank substrata in comparison with wood $(P < 0.001)$ and sandstone $(P = 0.002)$. Mean *Sphaeroma* densities also varied by month (Figure 3). Pairwise contrasts revealed *Sphaeroma* densities were significantly different only between August and April $(P < 0.001)$ although the difference between August and January $(P = 0.053)$ and January and April were nearly significant $(P = 0.072)$.

Table 2. Results of ANOVA tests for differences in mean A) *Sphaeroma* density, B) Burrow density, C) Inquiline density and D) proportion of young between month (August, January, April) and substratum type (marsh bank, wood, sandstone). All data were rank transformed. Month, substratum, and the month-substratum interaction were fixed factors while station and station-month interaction were random factors. Degrees of freedom varied between tests due to missing values. Boldface denotes statistical significance.

A. *Sphaeroma*

Source of Variation	**df**	**MS**	***F***	**p**
Month	2	168,231	11.85	**< 0.001**
Substratum	2	783,991	17.94	**< 0.001**
Month X Substratum	4	45,296	5.14	**0.022**
Station (Substratum)	21	43,708	4.96	**< 0.001**
Month X Station (Substratum)	42	14,192	1.61	**0.012**
Residual	359	8,813		

B. Burrows

Source of Variation	**df**	**MS**	***F***	**p**
Month	2	29,773	3.58	**0.037**
Substratum	2	1,274,465	36.85	**< 0.001**
Month X Substratum	4	21,146	2.54	0.054
Station (Substratum)	21	34,587	4.38	**< 0.001**
Month X Station (Substratum)	42	8,322	1.05	0.388
Residual	358	7,905		

C. Inquilines

Source of Variation	**df**	**MS**	***F***	**p**
Month	2	34,898	2.02	0.145
Substratum	2	609,787	18.79	**< 0.001**
Month X Substratum	4	24,148	1.40	0.250
Station (Substratum)	21	32,459	3.00	**< 0.001**
Month X Station (Substratum)	42	17,238	1.59	**0.014**
Residual	359	10,818		

D. Proportion of young

Source of Variation	**df**	**MS**	***F***	**p**
Month	2	761,992	97.10	**< 0.001**
Substratum	2	18,528	2.43	0.112
Month X Substratum	4	10,165	1.30	0.287
Station (Substratum)	21	7,611	1.81	**0.017**
Month X Station (Substratum)	42	7,847	1.87	**0.002**
Residual	294	4,198		

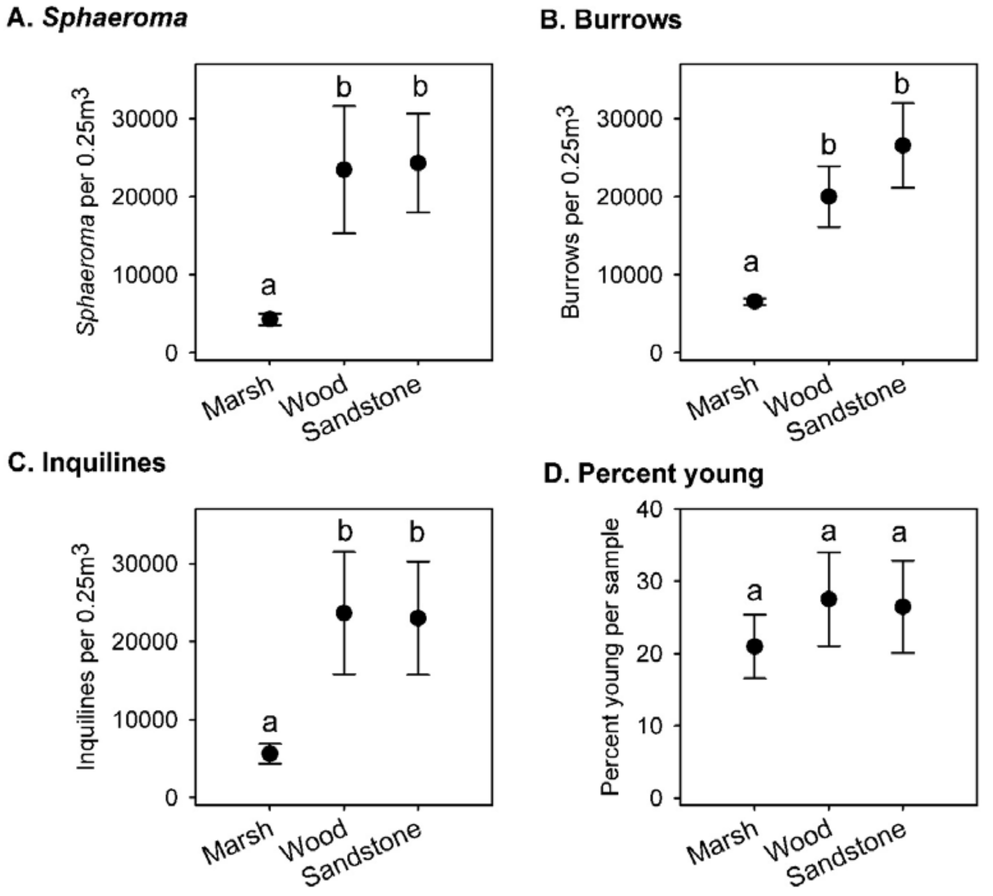


Figure 2. Mean *Sphaeroma*, burrow, and inquiline densities and the proportion of young (± 95% CI) within all three months combined in marsh bank (marsh), wood, and sandstone substrata; different letters denote a significant difference $(P \leq 0.05)$ between means; results of Scheffe tests are presented below. **A.** *Sphaeroma*; mean densities were significantly different between marsh and wood $(P = 0.002)$ and marsh and sandstone $(P < 0.001)$, wood and sandstone were not significantly different; **B.** Burrows; mean densities were significantly different between marsh and wood $(P < 0.001)$ and marsh and sandstone $(P < 0.001)$, wood and sandstone were not significantly different; **C.** Inquilines; mean densities were significantly different between marsh and wood $(P < 0.001)$ and marsh and sandstone $(P < 0.001)$, wood and sandstone were not significantly different; **D.** Percent young; the mean proportion of young were not statistically different between substrata.

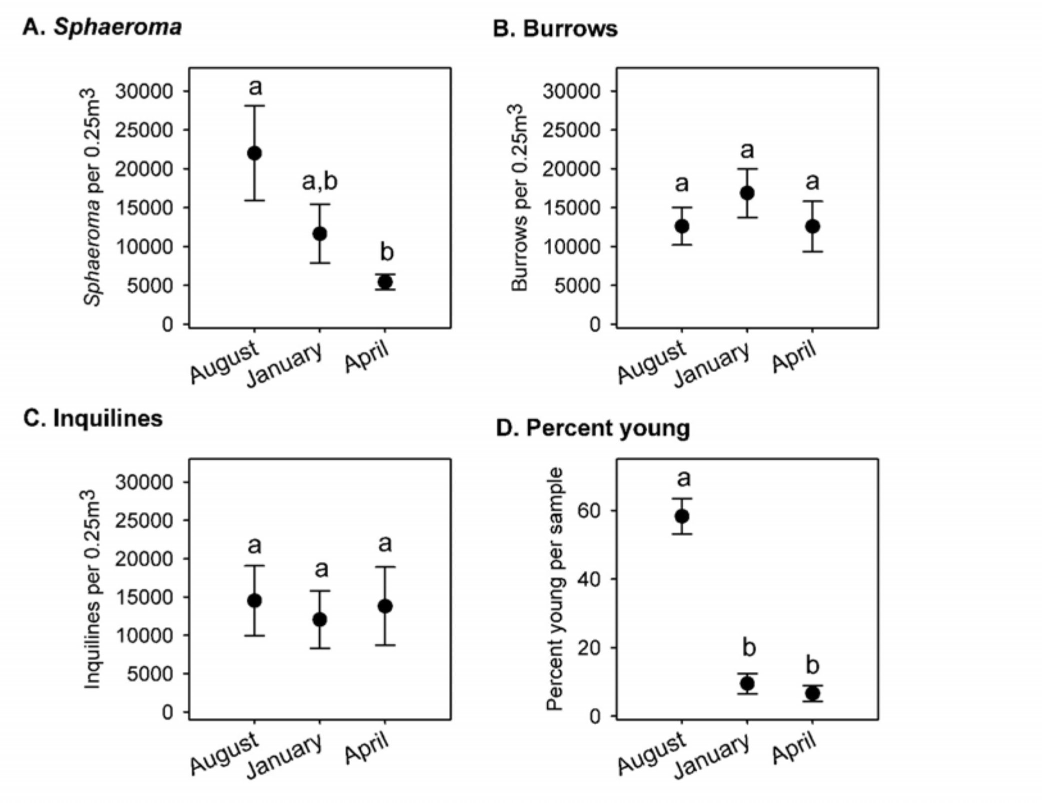


Figure 3. Mean *Sphaeroma*, burrow, inquiline densities and the proportion of young (± 95% CI) within all three intertidal substrata combined in August, January, and April; different letters denote a significant difference $(P \leq 0.05)$ between means; results of Scheffe tests are presented below. **A.** *Sphaeroma*; mean densities were significantly greater between August and April $(P < 0.001)$, differences between August and January $(P = 0.053)$ and between January and April $(P = 0.072)$ were not significant; **B.** Burrows; mean densities were not significant between any month; **C.** Inquilines; mean densities were not significant between any month; **D.** Percent young; the mean proportion of young (expressed as a percentage) were significantly greater between August and April $(P < 0.001)$ and between August and January $(P < 0.001)$, January and April $(P = 0.082)$ did not differ significantly.

Burrow Density

The mean and maximum densities of burrows were highest in sandstone followed by wood and marsh bank substrata (Table 1). Within wood, the mean burrow density was lower than the mean *Sphaeroma* density. The mean densities of *Sphaeroma* burrows varied significantly between month, substratum, and station (Table 2). When the main effects were analyzed, a significant difference between burrow densities across months was detected. However, pairwise contrasts did not detect a significant difference in burrow densities across any month. Burrow densities were significantly lower within marsh bank substrata than both wood $(P < 0.001)$ and sandstone $(P < 0.001)$.

Inquiline Density

Similar to *Sphaeroma* and burrow densities, the mean and maximum densities of inquilines were highest in sandstone followed by wood and then marsh bank substrata (Table 1). The densities of inquilines appear equivalent to *Sphaeroma* densities. Inquiline density varied only by substratum, station, and by the month-station interaction. The interaction between month and station likely reflected the differing effects of season on the various sampling stations. Inquiline densities varied significantly between substrata (Figure 2). Pairwise contrasts indicated inquiline densities were significantly lower within marsh bank substrata than both wood $(P < 0.001)$ and sandstone $(P < 0.001)$.

Proportion of young

The proportion of young differed significantly between month, station, and by the month-station interaction (Table 2). Like *Sphaeroma* and inquiline densities, the interaction between month and station likely reflected the differing effects of season on the various sampling stations. This likely represents the normal variation between stations as well as the differing effect month has on the abiotic and biotic factors at those stations.

The mean proportion of young per sample in August was significantly different than both January $(P < 0.001)$ and April $(P < 0.001)$.

Prevalence

Sphaeroma, young, and inquilines were present in approximately 85%, 39%, and 86% of all samples taken, respectively. In addition, *Sphaeroma*, young, and inquilines were found less often in marsh bank samples than wood and sandstone but the difference was only significant for young (Table 3). The prevalence of *Sphaeroma* and inquilines in samples were relatively similar between months but young were most prevalent during August (Table 4).

Table 3. The prevalence of *Sphaeroma*, young, and inquilines in marsh bank, wood, and sandstone samples; *obs/total* = observations per total samples; results of a single classification goodness of fit with adjusted G statistics (G_{adj}) are displayed. Bold face denotes statistical significance.

	Sphaeroma		Young		Inquilines	
	obs/total	(%)	obs/total	(%)	obs/total	(%)
Marsh Bank	189/240	78.8	83/240	34.6	197/240	82.1
Wood	86/95	90.5	57/95	60.0	87/95	91.6
Friable Rock	91/96	94.8	55/96	57.3	88/96	91.7

	Sphaeroma	Young	Inquilines
G_{adj}	2.5	13.5	1.1
P	0.286	**0.001**	0.572

Table 4. The prevalence of *Sphaeroma*, young, and inquilines in August, January, and April samples; *obs/total* = observations per total samples; results of a single classification goodness of fit with adjusted G statistics (G_{adj}) are displayed. Bold face denotes statistical significance.

	Sphaeroma		Young		Inquilines	
	obs/total	(%)	obs/total	(%)	obs/total	(%)
August	115/143	80.4	106/143	74.1	120/143	83.9
January	126/144	87.5	52/144	36.1	122/144	84.7
April	125/144	86.8	37/144	25.7	130/144	90.3

	Sphaeroma	Young	Inquilines
G_{adj}	0.5179	39.2	0.3961
P	0.7719	**<<0.001**	0.8203

Inquiline composition

In total, 56 species from seven phyla were found within *Sphaeroma* burrows (Table 5). The inquiline community was divided into the following taxa: isopods, amphipods, tanaids, decapods, barnacles, bivalves, gastropods, bryozoans, polychaetes, nemerteans, platyhelminths, anthozoans, and other invertebrates (including arachnids and insects). Isopods and amphipods constituted an overwhelming majority of the inquilines living within *Sphaeroma* burrows across all substrata (Figure 4) and comprised 78.3% of the inquilines. Gastropods, however, were a relatively abundant taxon in marsh banks, and the encrusting bryozoan, *Conopeum tenuissimum*, was relatively abundant within wood and sandstone burrows.

Table 5. List of all species found in burrows within marsh banks, wood, and sandstone. The taxonomic identity is classified as native, introduced (a.k.a. non-native, non-indigenous, exotic, invasive, etc.), both (if the taxon includes both native and introduced species), or unknown (if the taxonomic identity is not known).

Taxon	Species	Taxonomic identity	Marsh Banks	Wood	Sandstone
Isopoda					
	Gnorimosphaeroma insulare	Native	x	x	x
	Gnorimosphaeroma oregonese	Native	x		x
	Pseudosphaeroma campbellense	Introduced	x	x	x
	Limnoria sp.	Both		x	
	Idotea schmitti	Native		x	x
	I. Wosnesenskii	Native		x	x
Amphipoda					
	Allochestes angusta	Native	x	x	x
	Ampithoe sp.	Both	x	x	x
	Corophium spp.	Both	x	x	x
	Eogammarus confervicolus	Native	x	x	x
	Grandiderella japonica	Introduced	x	x	x
	Hyale plumulosa	Native	x	x	x
	Hyale sp.	Native	x	x	x
	Melita nitida	Introduced	x	x	
	Traskorchestia traskiana	Native	x	x	
	Unknown amphipod A	Unknown	x	x	x
	Unknown amphipod B	Unknown			x

Table 5. (continued)

Taxon	Species	Taxonomic identity	Marsh Banks	Wood	Sandstone
Tanaidacea					
	Unknown tanaid	Unknown	X	X	
Cirripedia					
	Balanus glandula	Native		X	X
	B. improvisus	Introduced		X	X
Decapoda					
	Cancer magister	Natve			X
	Hemigrapsus nudus	Natve	X		
	H. oregonensis	Natve	X	X	X
	Pachygrapsus crassipes	Natve	X		X
	Pagurus sp.	Natve	X	X	
Bivalvia					
	Crassostrea gigas	Introduced			X
	Macoma balthica	Introduced		X	
	Mya arenaria	Introduced	X	X	X
	Mytilus trossulus	Natve	X	X	X
Gastropoda					
	Assiminea californica	Native	X	X	X
	Littorina scutulata	Native	X	X	X
	L. sitkana	Native	X	X	X
	Myosotella myosotis	Introduced	X	X	X
	Onchidella borealis	Native			X
	*Potamopygrus antipodarum**	Introduced			X
	Unknown gastropod	Unknown			X
Bryozoa					
	*Bowerbankia gracilis**	Introduced			X
	Conopeum tenuissimum	Introduced	X	X	X
Polychaeta					
	Nereidae	Unknown	X		X
	Unknown polychaete A	Unknown	X	X	
	Unknown polychaete B	Unknown	X		X
Nemertea					
	Unknown nemertean	Unknown	X		
Platyhelminthes					
	Notoplana acticola	Native			X
	Unknown Platyhelminth	Unknown			X
Anthozoa					
	Diadumene lineata	Introduced		X	X
Insecta					
	Limonia marmorata	Native	X	X	X
	Diaulota densissima	Native	X	X	X
	Coelopa vanduzeei	Native	X		X
	Cercyon fimbriatus	Native	X	X	
	Ochthebius vandykei	Native	X		
	Tethymyia aptena	Native			X
	Unknown Staphylinid	Unknown	X		X
	Unknown Coleopteran	Unknown	X		
Arachnida					
	Halobisium occidentale	Native		X	X
	Neomolgus littoralis	Native	X		
	Unknown Araneomorph	Unknown	X		X

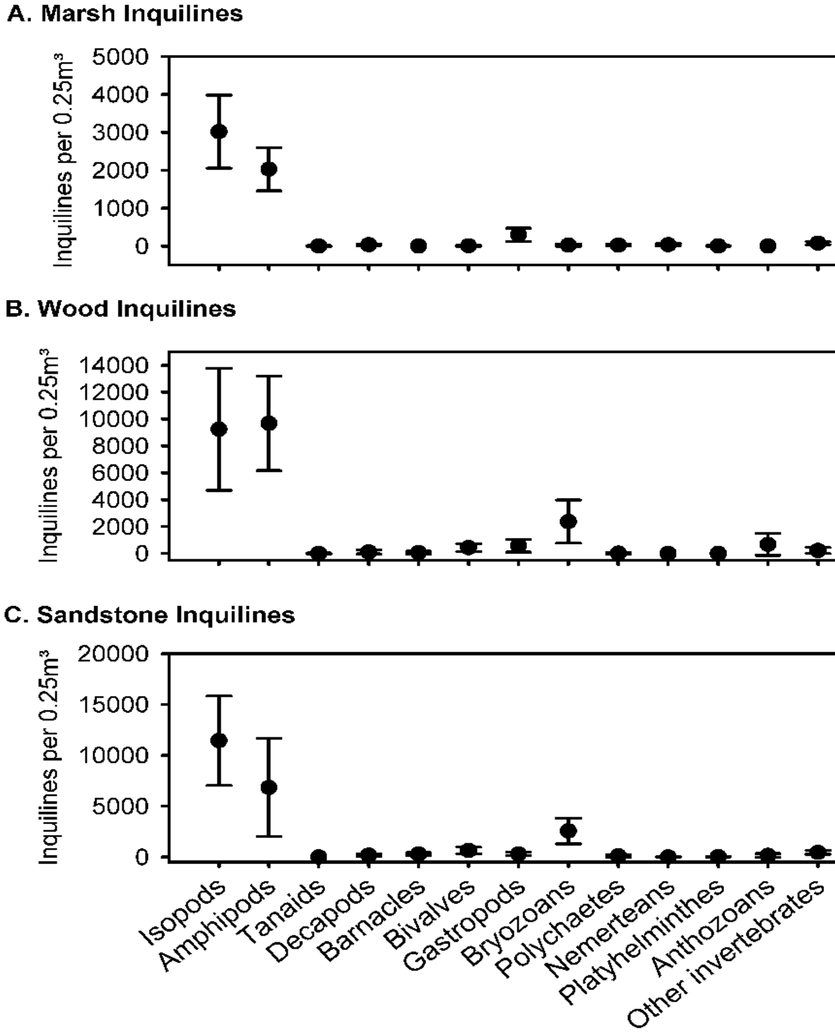


Figure 4. The mean abundances per 0.25m³ (± 95% CI) of the various inquiline taxa found within **A.** marsh banks, **B.** wood, and **C.** sandstone substrata. Other invertebrates include insects and arachnids.

The native isopod *Gnorimosphaeroma insulare*, the introduced isopod *Pseudosphaeroma campbellense* (= *P. campbellensis*), and the native amphipod *Eogammarus confervicolus* were the most numerically dominant species in all substrata (Table 6). In marsh bank samples, these three species constituted 95% of the fauna.

They were also abundant in wood and sandstone burrows, comprising ~48% and ~64% of the inquilines, respectively.

Table 6. The percentages of the three most abundant species in marsh bank, wood, and sandstone samples.

	***Gnorimosphaeroma* (%)**	***Pseudosphaeroma* (%)**	***Eogammarus* (%)**	**Total (%)**
Marsh Bank	39.2	15.0	40.6	94.8
Wood	26.4	12.3	9.1	47.8
Sandstone	31.7	18.0	14.2	63.9
All substrata	30.1	15.1	14.7	59.9

The richness of the inquilines appears to be relatively similar between substrata (Table 7) although not all species occurred in each substratum (Table 5). There were a number of introduced organisms found living in *Sphaeroma* burrows. Approximately 28% of the species with a recognizable taxonomic identity and geographic origin were introduced species, which comprised approximately 35% of the abundance of all samples (Table 7). The percentage of introduced species was lower within marsh banks than wood and sandstone and varied according to month. Introduced species accounted for only 14% of the fauna inhabiting marsh bank burrows, but made up 62% of the species in wood and 50% of the species in sandstone during August.

Table 7. The richness and the percentages of species (spp.) and abundance of introduced species in marsh banks, wood, and sandstone samples.

	Richness	Introduced (% spp.)	Introduced (% abundance)
Marsh Bank	38	20.7	22.4
Wood	34	32.1	36.0
Sandstone	43	29.4	36.8
All substrata	56	27.9	35.0

Discussion

After little more than ten years in Coos Bay, *Sphaeroma* has attained high densities within marsh banks, woody debris, and sandstone rock. The highest densities of *Sphaeroma* and highest proportion of young were found in August, results consistent with other studies of the genus *Sphaeroma* (Schneider 1976, Thiel 1999e, Murata and Wada 2002). Similarly, the prevalence of young within samples was also greatest during August. Schneider (1976) studied the population biology of *Sphaeroma* in San Francisco Bay and found 27% of females collected during March were gravid, but by May, this number had increased to 60%. In addition, she found the growth rate of *Sphaeroma* was highest in spring (~1.5mm per month). Thus, the high densities of young in August observed in this study suggest peak reproduction in *Sphaeroma* occurs during late spring to early summer. Young *Sphaeroma* were found on all sampling dates in the current study and in past studies (Hill and Kofoid 1927, Schneider 1976), so *Sphaeroma* likely reproduces year round. The occurrence of *Sphaeroma* did not appear to vary much across the months sampled, but densities were lowest during April. This result suggests that while populations of *Sphaeroma* may decrease seasonally, there are either enough surviving isopods to maintain the local population and prevent local extinction or isopods are immigrating from other areas.

Densities of *Sphaeroma*, burrows, and inquilines also varied significantly between substrata. The high densities of *Sphaeroma* and burrows within wood and sandstone substrata are likely related to the physical characteristics of these substrata since the other plausible factors influencing the creation of burrows (tidal height, salinity, temperature, predators) are similar between stations. Wood and sandstone are substantially stronger and more resistant to erosion than marsh banks. Thus, more burrows could perforate these substrata before succumbing to erosion. *Sphaeroma* may also prefer these stronger wood and sandstone substrata to marsh banks (See Chapter V). There are also more inquilines in wood and sandstone, which is likely explained by the higher density of burrows in those substrata. Furthermore, the lower occurrence and proportion of young within burrowed marsh bank samples could have several possible explanations. Young *Sphaeroma* may either prefer other substrata or experience a higher rate of mortality, or adult *Sphaeroma* may experience lower reproductive success in marsh banks.

Alternatively, differences in densities between substrata may be explained by the relative amount of each substratum within Coos Bay. Coos Bay has many kilometers of vertical marsh banks and tidal channels available to *Sphaeroma*. While there are also several kilometers of sandstone terrace and abundant cobble and woody debris, there appears to be much more marsh bank (per. obs.). Therefore, *Sphaeroma* has much more space to exploit in marsh banks compared to the sandstone cobble and woody debris scattered around Coos Bay. *Sphaeroma* are prevalent throughout Coos Bay (Chapter II), but densities vary greatly between stations and there appears to be an abundance of unexploited marsh bank, wood, and sandstone in even the most heavily invaded sites. The discontinuous distribution of *Sphaeroma* within sites, absence of *Sphaeroma* in areas that appear hospitable, and the abundance of available substrata suggest they are not limited by space. The exception may be within wood substrata, where mean *Sphaeroma* densities exceeded burrow densities. This indicates multiple *Sphaeroma* are using the same burrows in wood and may be experiencing intraspecific competition, and that wood may be preferred over other substrata.

Implications

The high densities of *Sphaeroma* within marsh banks, sandstone terraces, and wood threaten shoreline integrity and maritime structures in Coos Bay. Within the mesohaline and polyhaline areas of Coos Bay, *Sphaeroma* has been observed boring into a nearly every maritime structure examined (per. obs.). Even relatively new structures were attacked. Fortunately, most of the damage attributed to *Sphaeroma* appears minor and significant damage appears to be limited to wooden structures that are old and already decayed. However, *Sphaeroma* can completely riddle the Styrofoam floats often used in floating docks, causing irreparable damage. At least one dock in Coos Bay had to be abandoned after *Sphaeroma* burrowing rendered it inoperable (J.T. Carlton, per. comm.). During the course of this study, numerous pieces of broken Styrofoam dock were found, often heavily burrowed by *Sphaeroma*. The burrow densities of these pieces were very high (mean 32,814 burrows/0.25m^3, maximum 104,167/0.25m^3) and exceeded the mean densities of all three substrata sampled. Furthermore, during sampling, a ~10m section of dock washed onshore with all nine Styrofoam billets completely covered in *Sphaeroma* burrows. There is no doubt the extensive burrowing by *Sphaeroma* reduced the integrity of those floats.

Sphaeroma populations also appear to be facilitating the rate of erosion within burrowed sandstone terraces and boulders. In some areas, *Sphaeroma* are able to completely riddle and erode sandstone boulders leaving nothing but a flat surface. Many of the sandstone terraces of Haynes Inlet (northern Coos Bay) are experiencing undercutting and in some areas, collapse. Although quantitative measurements were not taken, *Sphaeroma* appears to have a distinct impact on the rate of sandstone erosion in this area.

The most pronounced erosive effects appear within vertical marsh banks. There appear to be significant undercutting and loss of marsh bank shoreline where *Sphaeroma* occur in high numbers. During this study, numerous large sections of marsh within the sampling stations have broken off the main marsh body and since been eroded away. Likewise, *Sphaeroma* appear to facilitate erosion in some Californian marshes (Talley et al. 2001). Studies by Talley et al. (2001) determined *Sphaeroma* within experimental enclosures could increase sediment loss by 240% compared to experimental controls. In that study, experimental enclosures were stocked with a *Sphaeroma* density of approximately 19,900 isopods/0.25m^3, which suggests that *Sphaeroma* in this density can remove substantial amounts of sediment and increase erosion rate. Where isopods occur, the mean density of *Sphaeroma* in August in Coos Bay marsh banks was considerably lower (7,818 isopods/0.25m^3) than the experimental densities used in erosion studies in California. Mean densities at some stations, however, were over 19,500 isopods/0.25m^3, and maximum densities were over 34,000 isopods/0.25m^3. Based on field observations and the measured densities, it seems plausible that *Sphaeroma* is accelerating marsh bank erosion in Coos Bay.

In comparison, the mean densities of *Sphaeroma* (where they occur) in San Diego and San Francisco marsh banks during July were 11,530 and 29,360 isopods/0.25m^3, respectively (modified from Talley et al. 2001). Coos Bay densities appear to be considerably lower, which suggests the impact of *Sphaeroma* may not be as severe as the study sites in San Diego and San Francisco. *Sphaeroma* is a relatively recent invader to Coos Bay while populations in San Francisco and San Diego have been present for several decades. It is possible *Sphaeroma* populations in Coos Bay have not yet attained maximum population levels. Also, the mean density values presented in those studies were all within the same stretch of marsh, thus those values are not necessarily representative of the entire bay. Results from this work indicate that *Sphaeroma* density is highly variable according to location in the estuary, and it is possible that the sample sites in Talley et al. (2001) happen to harbor higher *Sphaeroma* densities than other locations. Regardless of the differences in mean density, *Sphaeroma* still occurs in very dense aggregations and appears to be accelerating erosion rates in some Coos Bay marshes.

Physical changes

The burrows created by *Sphaeroma* likely alter many physical properties of the substratum such as surface area, water content, organic content, and integrity. Burrows increase the surface area available for sedentary organisms and bacteria, fungi, and microalgal growth. In addition, wood and sandstone burrows often capture water and thus may be increasing the water content. Within marsh banks, however, there was not a difference in water content between burrowed and unburrowed samples (Talley et al. 2001). The feeding activity of *Sphaeroma* may also be depositing significantly more organic matter within the substrata. Levin et al. (1997) found burrowing maldanid polychaetes subduct organic matter into burrows, making that material available to other burrow inhabitants. In addition, Talley et al. (2001) found a positive relationship between percent organic matter content $(< 2mm)$ and *Sphaeroma* density in marsh banks. The occurrence of fine organic matter in sandstone and wood burrows suggest *Sphaeroma* are also increasing organic matter in these substrata. The increased surface area for algal-bacterial films to grow on as well the active transport (feeding) and deposition (feces) of organic matter into the burrows is enriching the substratum and likely providing a food source for other organisms. Finally, the creation of numerous burrows reduces the integrity of these substrata, making them more susceptible to erosion (Talley et al. 2001, per. obs.).

Novel habitat

Through the creation of an extensive network of burrows, *Sphaeroma* physically engineers a novel habitat in invaded substrata. These burrow constructs are frequently utilized by numerous estuarine fauna. Of all marsh bank samples, over 82% contained inquilines, whereas in wood and sandstone inquilines were present in nearly 92% of samples. Similarly, the numbers of inquilines were often equal to or exceeded the densities of *Sphaeroma* in these habitats. Although many organisms are utilizing *Sphaeroma* habitat, the extent of this use is unknown. Inquilines could be using the burrows temporarily to escape the physical stresses incurred at low tide or they could be semi-permanent residents of these burrow networks. Burrows likely provide a host of ecological benefits for an intertidal organism including cover from many epibenthic predators, amelioration of environmental stresses (temperatures, desiccation, UV exposure), and an enriched interior surface, which may enhance the growth of microbial/algal film on which many organisms feed. Thus, the creation of burrows may be facilitating and increasing survivorship of various intertidal estuarine fauna.

The extent of any facilitative effect is likely a function of the density of burrows, the heterogeneity of the surrounding area, and the biology of the inquiline. Habitat complexity in the intertidal estuarine environment can vary considerably. In some heterogeneous areas there are any number of possible refuges for epifauna including marsh plants, rocks, woody debris, algae, fouling, and more. In other areas, the intertidal surface is composed of homogenous bare mud or sand. Thus, in some areas, an increase of structural complexity would be readily exploited and may affect the abundances of the local community. For example, sandstone terraces within the brackish areas of Coos Bay were relatively bare, only marked occasionally with algae, barnacles, and crevices. However, the addition of the extensive galleries of *Sphaeroma* burrows has dramatically increased the amount of habitat available to intertidal organisms in these areas. In contrast, marsh banks often have many natural contours, complex topography, and an abundance of marsh plants. In this instance, burrows do not necessary increase the amount of habitat available. However marsh bank burrows do alter the type of habitat available to organisms. By burrowing into marsh banks, *Sphaeroma* is altering the habitat available for infaunal animals and creating habitat for epibenthic organisms. In wood, *Sphaeroma* is joining the niche of other wood-borers such as shipworms (*Teredo navalis* and *Bankia setacea*) and the isopods of the genus *Limnoria*. The magnitude and effects of burrows vary according to substratum type. But in all substrata, burrows add another possible refuge choice, even if others are available.

Any possible facilitative effect is also dependent on the biology of the inquilines. The most abundant taxa inhabiting these burrows are isopods and gammarid amphipods. Nearly all of these species are highly mobile and are not obligate burrow dwellers. Many free living gammarid amphipods and isopods act opportunistically in their selection of habitat and will select any manner of artificial or natural habitat providing complex structure (Aikins and Kikuchi 2001). However, other amphipod species select specific habitat. For example, subpopulations of *Eogammarus confervicolus* select habitats based on where they were raised (Stanhope et al. 1992). Thus, the benefits and use of burrows is variable. In contrast, certain sedentary inquilines (anemones, bivalves and bryozoans) that utilize burrows are now able to live higher in the intertidal than they normally would perhaps due to the increased moisture content within burrows. Therefore, sedentary species may be dependant on this habitat to live in the high intertidal whereas most mobile species are likely incidental burrow inhabitants.

Burrow use in native vs. introduced species

Introduced fauna comprise approximately 28% of the species and 35% of the total abundance of inquilines living within the three substrata. This value is considerably higher than the composition of introduced species present in fouling communities as determined by Rumrill (2006). Approximately 12% of epifouling species within Coos Bay were introduced. Similarly, Hewitt (1993) reports approximately 21% of encrusting species within Coos Bay fouling communities are introduced or cryptogenic. Thus, *Sphaeroma* burrows may be providing habitat for a greater proportion of introduced fauna than other habitats.

The communities living within marsh bank burrows appear to have fewer species and a lower abundance of introduced fauna than the communities within wood and sandstone substrata. This may be explained by the physical characteristics of wood and sandstone. These firm substrata can harbor sedentary epibenthic organisms (most of which were introduced species) as well as the motile epifauna present in marsh banks. However, the presence of sedentary epifauna is limited within the softer marsh banks.

Although burrow use by many of the inquilines is likely incidental, some species may be dependent on the microhabitat created by *Sphaeroma* burrows. The burrows may provide a more suitable microclimate that could allow some organisms to live higher in the intertidal than they normally could. For example, the Pacific oyster, *C. gigas*, anemone *Diadumene lineata*, and bryozoan *Conopeum tenuissimum* are typically limited to low and mid intertidal areas (Ricketts et al. 1968) but were found living in moist sandstone burrows in the high mid to high intertidal. The species that appear to be utilizing the novel habitat are not only mostly sedentary but are also introduced from various locations around the world. This suggests that *Sphaeroma* burrows may actually be extending the intertidal distribution of these particular introduced species by providing a moist habitat in the high intertidal. Some infaunal species typically associated with sand or mudflats were also found within burrows. These species, the introduced clams *Mya arenaria* and *Macoma balthica*, were found inhabiting empty *Sphaeroma* burrows on several occasions. Thus *Sphaeroma* burrows are altering both the vertical distributions and the habitat use of some fauna.

Inquiline interactions

The most distinct interaction between *Sphaeroma* and inquilines was with the introduced bryozoan *Conopeum tenuissimum*. During August, this thin encrusting bryozoan was a frequent burrow inhabitant within wood and sandstone substratum. When both *Sphaeroma* and *Conopeum* inhabited the same burrow, *Conopeum* cover was limited to the areas near the aperture of the burrow. A distinct line of bare space separated *Sphaeroma* and the *Conopeum* colony, suggesting *Conopeum* growth is being inhibited perhaps through *Sphaeroma* removal (i.e. scrapping) or filtering activities. When *Sphaeroma* is absent, *Conopeum* colonies were often observed growing throughout the entire burrow. The nature of the *Sphaeroma-Conopeum* relationship may be competitive. As *Sphaeroma* actively brings water into the burrow, *Conopeum* may be removing food from the water column before *Sphaeroma* can obtain access to it. The zooids feeding on the periphery of the burrow may be enhanced by *Sphaeroma* feeding, while zooids growing towards the bottom of the burrow may be being inhibited.

Summary

Sphaeroma occurs in dense aggregations within marsh banks, woody debris, and sandstone substrata within Coos Bay. In some locations, *Sphaeroma* densities are high enough to damage maritime structures and possibly even facilitate shoreline erosion. Although mean *Sphaeroma* densities within marsh banks are lower than other Pacific Coast estuaries, population densities surpass the empirically-determined densities responsible for significant sediment loss (Talley et al. 2001). The creation of anastomizing burrow networks likely alter physical characteristics of the substrata, provide a more suitable microclimate than the surrounding areas, and may act as a refuge from predation. Although *Sphaeroma* burrows increase the amount of habitat available to species, the effect of burrow creation likely only impacts communities in areas that lack habitat heterogeneity. In those areas, the structure associated with *Sphaeroma* burrows may increase the abundances of epibenthic fauna and may allow some species to live at higher tidal heights than normal.

BRIDGE II

Previous chapters indicated how widely distributed and dense populations of *Sphaeroma* are within Coos Bay and suggested that *Sphaeroma* is contributing to shoreline erosion in some areas. While *Sphaeroma* has been linked to erosion in some estuaries on the Pacific Coast of North America, an examination of historical and current literature of this species within its native range indicate that the ecology of Australian *Sphaeroma* populations may differ from the populations along the Pacific Coast of North America. Chapter IV examines how the distribution, prevalence, habitat use, and density differ between the introduced populations within Coos Bay and native populations within two southeastern Australian embayments: the Tamar estuary (Tasmania) and Port Phillip Bay (Victoria). This chapter then explores the possible factors that may be responsible for the observed ecological differences between *Sphaeroma* populations.

CHAPTER IV

DISTRIBUTION, DENSITY, AND HABITAT USE AMONG NATIVE AND INTRODUCED POPULATIONS OF THE AUSTRALASIAN BURROWING ISOPOD (*SPHAEROMA QUOIANUM*)

Introduction

Biological invasions are one of the premier threats to the biodiversity and integrity of marine systems (Elton 1958, Vitousek et al. 1997, Cohen and Carlton 1998). Invading organisms may affect marine systems by altering ecosystem processes, trophic dynamics, physically disturbing and degrading habitat, or by directly competing, parasitizing, or preying upon native species (reviewed by Ruiz et al. 1999). While some introduced species are relatively benign, others negatively impact the ecology and economics of a region. These disruptions are often attributed to or exacerbated by the high densities these organisms attain within their introduced range (Carlton 1990, Lodge et al. 1994, Ruiz et al. 1999). For example, the Asian clam *Potomocorbula amurensis* attain densities exceeding 16,000/m^2 and can filter the entire water column of San Francisco Bay in just one day (Carlton 1990). In New England, high densities of the European green crab (*Carcinus maenas*) have been implicated in the decline of the soft-shelled clam (*Mya arenaria*) fishery (Glude 1955). Furthermore, in Midwest lakes, the non-indigenous Rusty crayfish (*Orconectes rusticus*) achieves extremely high densities and removes nearly all native macrophytes, crayfish, and mollusks (Lodge et al. 1994, per. obs.).

Current invasion theory suggests introduced species may be more successful in a new range because the ecological factors normally controlling the distribution and abundances of the introduced organisms (competition, predation, parasites, disease, etc.) are absent (Wilson 1961). This phenomenon, known as ecological release (Wilson 1961), may allow introduced species to attain higher densities, larger body sizes, higher fecundity, and exploit habitats/ranges beyond what they could in their native regions (Behrens-Yamada 2001, Grosholz and Ruiz 2003, Torchin et al. 2003).

Many sphaeromatid isopod species have been dispersed throughout the world, presumably via ship fouling or by boring into ship hulls. (Carlton and Iverson 1981, Morton 1987). These introductions often occurred before accurate biological record keeping, thus the native distribution of some sphaeromatids remains uncertain (Carlton and Iverson 1981, Hass and Knott 1998). In Coos Bay, Oregon (USA), a destructive sphaeromatid, the Australasian burrowing isopod (*Sphaeroma quoianum*), has been recently introduced (1995; Carlton 1996) and subsequently spread throughout the shoreline.

Identification

Sphaeroma quoianum (H. Milne Edwards, 1840; hereafter: *Sphaeroma*) is a small, rotund sphaeromatid reaching up to 16mm in length (Hurley and Jansen 1977). Coloration can vary from solid black to sandy brown with mottled brown/black and reddish markings (Hill and Kofoid 1927, per. obs). It may be distinguished from other common estuarine sphaeromatid isopods by the presence of a double longitudinal row of 4-5 tubercles on the pleotelson, long dense setae on pereopod 1, and serrated outer uropods (Hurley and Jansen 1977). *Sphaeroma* has undergone a number of name changes and is synonymous with the following species: *S. quoyanum, S. pentodon, S. verrucauda, S. quoyana,* and *S. quoiana* (Chilton 1912, Baker 1926, Hurley and Jansen 1977, Harrison and Holdich 1984, J. T. Carlton and G. Poore, per. comm.).

Life history and natural history

Sphaeroma is gonochoric and undergoes direct development. Female isopods carry fertilized eggs within a marsupium and the young crawl away as fully formed juveniles (Hill and Kofoid 1927, Schneider 1976). *Sphaeroma* grow at a rate of about 0.64mm per month and are believed to become reproductive after 6 months (Schneider 1976). Gravid females and juveniles are found year round, suggesting that adults reproduce continuously (Hill and Kofoid 1927). The brood size of *Sphaeroma* varies between seasons with an average brood size of 64 in the spring and 19.5 in the fall (Schneider 1976). The life span is estimated to be about 1 ½ - 2 years (Schneider 1976). *Sphaeroma* primarily inhabit the shallow subtidal intertidal to the high tide mark. However, *Sphaeroma* has been found living amongst fouling organisms in waters 7m deep (Cohen et al. 2001). *Sphaeroma* create burrows within a variety of firm substrata including: peat, mud, clay, decaying wood, friable rock and Styrofoam floats (Hill and Kofoid 1927, Rotramel 1975, Carlton 1979). *Sphaeroma* is a filter feeder and does not consume the material it excavates (Rotramel 1975). Using its pleopods to generate a current of water, *Sphaeroma* moves particles into the burrow, which are then captured by the setal brushes and are cleaned off by the mandibles (Rotramel 1975). *Sphaeroma* usually are found within the brackish regions of estuaries but are known to tolerate extreme temperatures and a wide range of salinities (Riegel 1959, Jensen 1971, Chapter II).

Invasion

Sphaeroma has become a common member of the estuarine community in many Pacific Coast embayments. *Sphaeroma* was initially introduced to San Francisco Bay via ship fouling/boring in the mid-19th century and now inhabits at least fourteen embayments ranging from northern Baja California to Yaquina Bay, Oregon (Menzies 1962, Carlton 1979, Cohen and Carlton 1995, per. obs.). *Sphaeroma* is native to New Zealand, Australia, and Tasmania and was first discovered in Coos Bay, Oregon in 1995. After approximately ten years, this destructive species is now present in approximately one-half of 373 surveyed intertidal sites and can reach densities of 4,383, 23,556, and 24,324 individuals per $0.25m^3$ within marsh bank, wood, and friable rock substrata, respectively (Chapters II and III). When abundant, *Sphaeroma* create anastomizing burrow networks, which can exacerbate shoreline erosion and may damage Styrofoam floating docks and wooden structures (Higgins 1956, Carlton 1979, Talley et al. 2001, per. obs.). The extirpation of tidal wetland habitat, loss of estuarine shoreline, and damage to maritime structures may deleteriously affect both the ecology and economy of the Pacific Coast.

After an extensive literature search and consulting Australian and New Zealand isopod experts and estuarine biologists, I determined that the distribution, density, and ecology of *Sphaeroma* within its native range of Australia and New Zealand remains largely unknown. Interestingly, there are no reports of *Sphaeroma* achieving extremely high densities or exacerbating shoreline erosion in Australia, despite extensive research in Australian saltmarshes and estuaries. The rarity of *Sphaeroma* in Australian estuarine studies suggests population densities are lower than on the Pacific Coast of North America. This paper compares the population densities, distribution, and habitat use, and identifies the possible factors that may be limiting *Sphaeroma* within the Tamar Estuary, (Tasmania, Australia), Port Phillip Bay (Victoria, Australia) and Coos Bay (Oregon, USA). The following questions will be addressed:

1) What is the estuarine distribution of intertidal *Sphaeroma* within the Tamar Estuary, Port Phillip Bay, and Coos Bay?
2) Is presence of *Sphaeroma* related to salinity?
3) What abiotic or biotic factors may be limiting *Sphaeroma* distributions in Tamar Estuary, Port Phillip Bay, and Coos Bay?
4) Does habitat use differ in *Sphaeroma* populations in the Tamar Estuary, Port Phillip Bay, and Coos Bay?
5) What is the mean and maximum density of *Sphaeroma*, burrows, and inquilines (fauna inhabiting the burrows) in marsh banks, wood debris, and friable rock substrata in the Tamar Estuary, Port Phillip Bay, and Coos Bay?
6) Does the mean density of *Sphaeroma* and inquilines differ between embayments?
7) Does the mean density of *Sphaeroma* and inquilines differ between substrata?

Understanding the ecology and factors affecting the distribution and density of this common introduced bioeroder within their native range may elucidate the reasons this introduced species has attained such high and destructive densities within estuaries along the Pacific Coast of North America.

Methods

Study sites

Port Phillip Bay (PPB) is a large (1930km^2) marine embayment in southeastern Australia (38° 16' 5" S, Longitude 144° 39' 6"E; Figure 1). Approximately 3.5 million people live in Melbourne, Geelong, and the surrounding townships that line the shores of Port Phillip Bay (Harris et al. 1996). These areas constitute Australia's second largest metropolitan area (Harris et al. 1996). PPB is largely marine with several freshwater inputs, the largest of which is the Yarra River near the city of Melbourne. Within PPB, there are a number of small estuaries. The largest estuaries are the Yarra estuary (salt wedge estuary) and the Maribyrnong river (partially mixed estuary). Other smaller estuaries include the Mordiollic river, Werribee river, and Patterson river. The shoreline habitats within PPB and the adjoining rivers vary considerably. While PPB is composed mostly of sandy beach, rocky riprap, hard rock shelves and boulders, and sandstone terraces, the various connecting rivers contain mostly sloping marshes, sandy beach, rocky riprap, concrete high tide walls, marsh banks, and some friable rock. Much of the shoreline of PPB is highly modified and urbanized. There are numerous wooden groins, weirs, jetties, concrete high tide walls, and rocky riprap. PPB has a long history of international trade and maritime traffic and is now recognized as the most invaded embayment in the Southern Hemisphere (Hewitt et al. 1999, 2004). Some of the common introduced fauna include the northern Pacific seastar (*Asterias amurensis*), Mediterranean fan worm (*Sabella spallanzanii*) and the Pacific spider crab (*Pyromaia tuberculata*; Hewitt et al 1999, 2004).

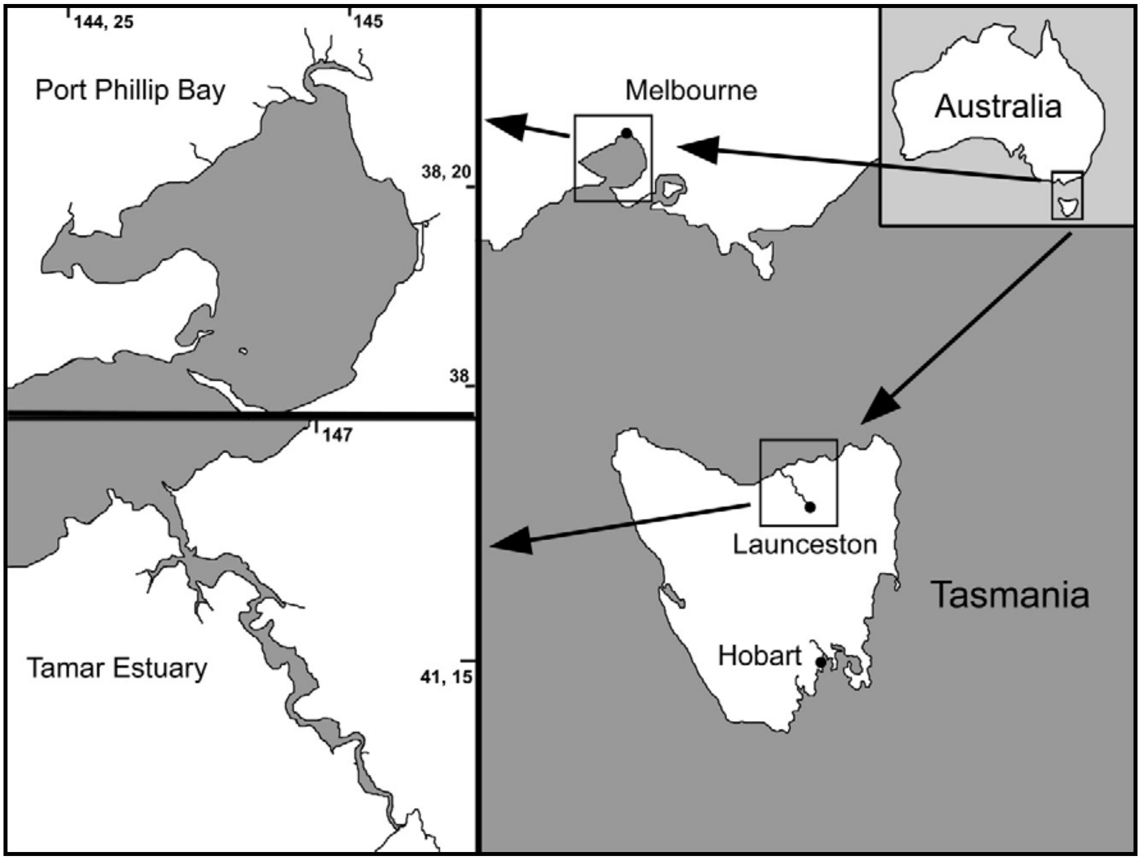


Figure 1. Locations of the two temperate embayments studied in Australia: Port Phillip Bay in southeastern Australia and the Tamar Estuary in northern Tasmania.

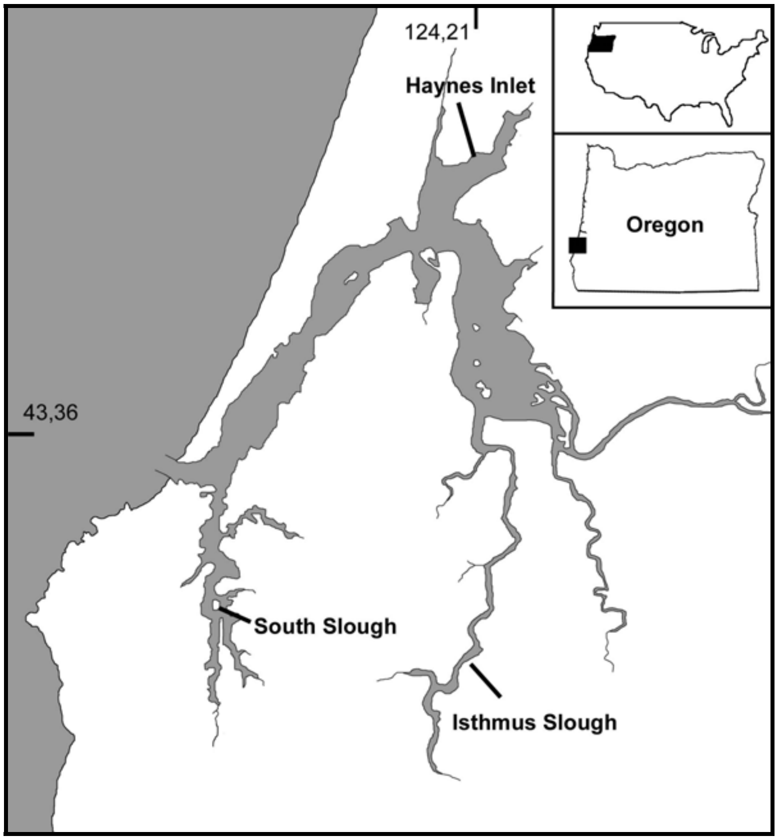


Figure 2. Temperate Coos Bay, Oregon, located on the Pacific Coast of the United States.

The Tamar Estuary (hereafter: Tamar) is a small estuary (98km²) located in north Tasmania (41° 4” 514'S, 146° 48” 399'E; Figure 1; Edgar et al. 1999). The Tamar is physically a drowned river estuary with major freshwater inputs from the North Esk and South Esk Rivers. The Tamar is tidally influenced for 63km and salinity can be highly variable annually (Smith 1995). Much of the shoreline habitat consists of sandy beach, marsh banks (*Spartina anglica*, *Sarcocornia* sp.), friable rock (mudstone, claystone, sandstone), hard rock (non-friable rock, riprap, concrete), and sloping marshes. The Tamar has received considerable ship traffic historically and remains an active international port; consequently, the Tamar has experienced a number of biological invasions. The most prominent invading species in the estuary, however, were introduced intentionally for aquaculture (*Crassostrea gigas*) and to alleviate erosion and siltation (*Spartina anglica*; Smith 1995). Japanese oysters (*C. gigas*) and rice grass (*S. anglica*) cover much of the intertidal, although erosion and siltation remain major issues. The Tamar valley watershed is a source of the significant amount of woody debris present in the estuary.

Coos Bay is a relatively small drowned-river estuary (50 km^2) located in southern Oregon, USA (43.354670º N, 124.338921ºW; Figure 2). It is largely marine with significant freshwater input from the Coos River, Millicoma River, and numerous creeks (Rumrill 2006). Coos Bay is heavily tidally influenced; salinity in the upper regions of the estuary can range from nearly fresh to full seawater during the same tidal cycle. In addition, areas as far back as 43 kilometers up river can experience significant salinity flux. Coos Bay is also heavily influenced by winter and spring precipitation, which can reduce salinity in many parts of the bay to oligohaline and mesohaline conditions for several weeks (Queen and Burt 1955, Burt and McAllister 1959). The shoreline is primarily composed of sandy beaches, sloping marshes, extensive marsh banks, rocky riprap, sandstone terraces and shelves. Abundant woody debris occurs along the shoreline from past and present logging operations. Coos Bay is also an international shipping port and hosts significant numbers of introduced species.

The Tamar, PPB, and Coos Bay are all temperate drowned river systems and exhibit similar mean water temperatures. Since the sampling sessions occurred during

Australian winter, the Australian data is compared to data collected in Coos Bay, Oregon during winter (see Chapter III). For all embayments, sampling occurred within about one month of the beginning of winter.

Intertidal Surveys

Shoreline surveys of all intertidal substrata located in select sites were conducted throughout the Tamar ($n = 70$ sites) between June 25 and July 5, 2006 and Port Phillip Bay ($n = 84$ sites) between July 13-29, 2006. To maximize effort, the study sites were haphazardly selected based upon accessibility by automobile, foot, or boat. Surveys began at the mouth of the estuary and ceased at the terminal ends of the estuary. However, some locations were not surveyed due to legal and logistical constraints. At each site, intertidal substrata were characterized as: 1) marsh bank (marshes with an abrupt edge/vertical face), 2) wood (including debris, pilings, docks, etc.), 3) friable rock (claystone, mudstone, sandstone), 4) hard rock (riprap, non-friable rock, concrete), 5) sloping marsh (marsh without a vertical bank), and/or 6) sandy beach. At sites that contained multiple substrata, each substratum type was noted and examined.

Within each site, the substrata types were examined for the presence of *Sphaeroma* individuals and burrows and the geographic coordinates were recorded using GPS. Sites were characterized as burrowed if at least one substratum hosted shallow cylindrical burrows between 1mm and 10mm in diameter. Since some estuarine fauna also create burrows in some of these substrata (i.e. grapsid crabs), the examination of burrow morphology was followed by a physical inspection of the interior of the burrows. Salinity was recorded by a hand-held refractometer in select sites.

Site characterization

Sites were characterized by the presence or absence of *Sphaeroma*, presence or absence of *Sphaeroma* burrows, and whether the substrata are suitable for burrowing by *Sphaeroma*. Suitable substrata include substrata previously observed to be burrowed into by *Sphaeroma* such as firm mud, clay, peat, wood, sandstone, claystone, mudstone, and Styrofoam. Sites with substrata unsuited for *Sphaeroma* burrows (hard rock riprap, sandy beaches, sloping marshes) were classified as unsuitable. Unsuitable substrata, however, were still examined for nestling *Sphaeroma* individuals. Sites were assigned a specific salinity class based upon field measurements and environmental data supplied by various sources (Poore and Kudenov 1978, Ellway et al. 1980, Thomson et al. 1981, Beckett et al 1982). Classes were designated as oligohaline (salinity 0.5-5), mesohaline (salinity >5-18), polyhaline (salinity >18-30), and euhaline (salinity >30).

Density measurements

To evaluate the density of *Sphaeroma* within burrowed marsh bank, wood, and friable rock, a series of representative intertidal sampling stations were selected in various locations throughout Coos Bay, the Tamar and PPB. Stations were selected in areas with established *Sphaeroma* populations. In the Tamar and Coos Bay, eight replicate stations were selected for each substrata. The lack of burrowed friable rock and marsh banks limited the replication level in PPB to two for these substrata. Eight replicate wood stations were established for PPB, however. Different methods were employed to sample each of the different substrata. At each marsh bank station, ten cores (6.2 diameter x 10cm depth) were randomly sampled along a 50m transect. At each wood station, discrete pieces of woody debris were randomly collected along a 50m transect. At each friable rock station, friable cobble was randomly collected as discrete pieces and friable rock terrace or shelf was randomly sampled along a 50m transect. Friable rock terrace/shelf was sampled using a PVC corer (6.2cm diameter) hammered to a depth of 6 cm. The depth of marsh bank and friable rock cores sampled were determined from field observations of the deepest burrows created by *Sphaeroma* in each respective substratum. Burrows were enumerated in the field and samples were returned to the lab for processing. Sampling occurred during winter 2006 (January 8-24 for Coos Bay, June 25 to July 5 for the Tamar, July 13-29 for PPB). The volume and surface area of wood and sandstone samples were calculated through a series of digital photographs and analyzed by Imagetool 3.0 image analysis software. All samples were physically sorted in the lab. *Sphaeroma* individuals and inquilines (fauna inhabiting the burrows) were placed in 70% ethanol and enumerated. To investigate any possible difference in reproductive output, the number of individuals under 5mm in length, which represent instars 1-4 (Schneider 1976) and a separate cohort, were also counted. These individuals will be called “young” for brevity.

Statistics

The relationships between *Sphaeroma*, burrow, and suitable substrata presence, within each embayment and between embayments were analyzed using single classification goodness of fit tests (Sokal and Rohlf 1981). The relationships between *Sphaeroma* and burrow presence and salinity class and substratum type were also evaluated. The *G* values were adjusted using Williams correction to account for higher than normal type I error associated with G-tests (Williams 1976). Randomization tests of goodness of fit (with 10,000 randomizations) were utilized when approximately 20% of the expected cell frequencies were less than 5 (Quinn and Keough 2002).

To determine if the mean densities of *Sphaeroma*, burrows, and inquilines differ between embayment and substratum, three-way partially nested mixed model ANOVA were used. The following factors were identified as fixed in this model: embayment, substratum, and the interaction between embayment and substratum. Station was considered a random effect and was nested within embayment and substratum. Assumptions of normality and homogenous variance were visually evaluated using scatterplots and box plots as recommended by Quinn and Keough (2002). All density data were then $\log\left(X + 10^{-6}\right)$ transformed to improve normality and variance homogeneity. This transformation was selected since the values analyzed were often decimals and an arbitrarily small number was needed so the transformation would not seriously affect the mean (as described in Underwood 1981, Quinn and Keough 2002). The transformation was unsuccessful in normalizing the data but variance homogeneity improved considerably for most variables. I recognize an unbalanced ANOVA is not as robust to deviations from normality and homogenous variance as a balanced ANOVA (Box 1953, Underwood 1981). To account for the increase in type I error associated with violations of normality and variance homogeneity, I adjusted the significance level to $p \leq 0.025$ for main effects. All *a posteriori* comparisons were tested using the conservative Scheffe test to account for the increased family-wise type I error of multiple comparisons (Zar 1996, Quinn and Keough 2002) and to account for the deviations from the homogenous variation and normality assumptions mentioned earlier. Inquiline density and young proportion data for PPB was absent, so the differences between mean inquiline density and proportion of young to total *Sphaeroma* were evaluated only between the Tamar and Coos Bay.

Results

Distribution

In all embayments, the distribution of *Sphaeroma* followed a similar pattern; *Sphaeroma* populations were mostly limited to brackish areas with salinity between 5-30 (Figures 3a-c). Occasionally, *Sphaeroma* individuals were found in euhaline conditions. *Sphaeroma* presence within suitable substrata was dependent upon salinity class in all embayments and most *Sphaeroma* were found at mesohaline and polyhaline salinities (Table 1; Figures 3a-c). Since *Sphaeroma* and burrows are dependent on salinity class, subsequent analyses were conducted on data only from the mesohaline and polyhaline sites.

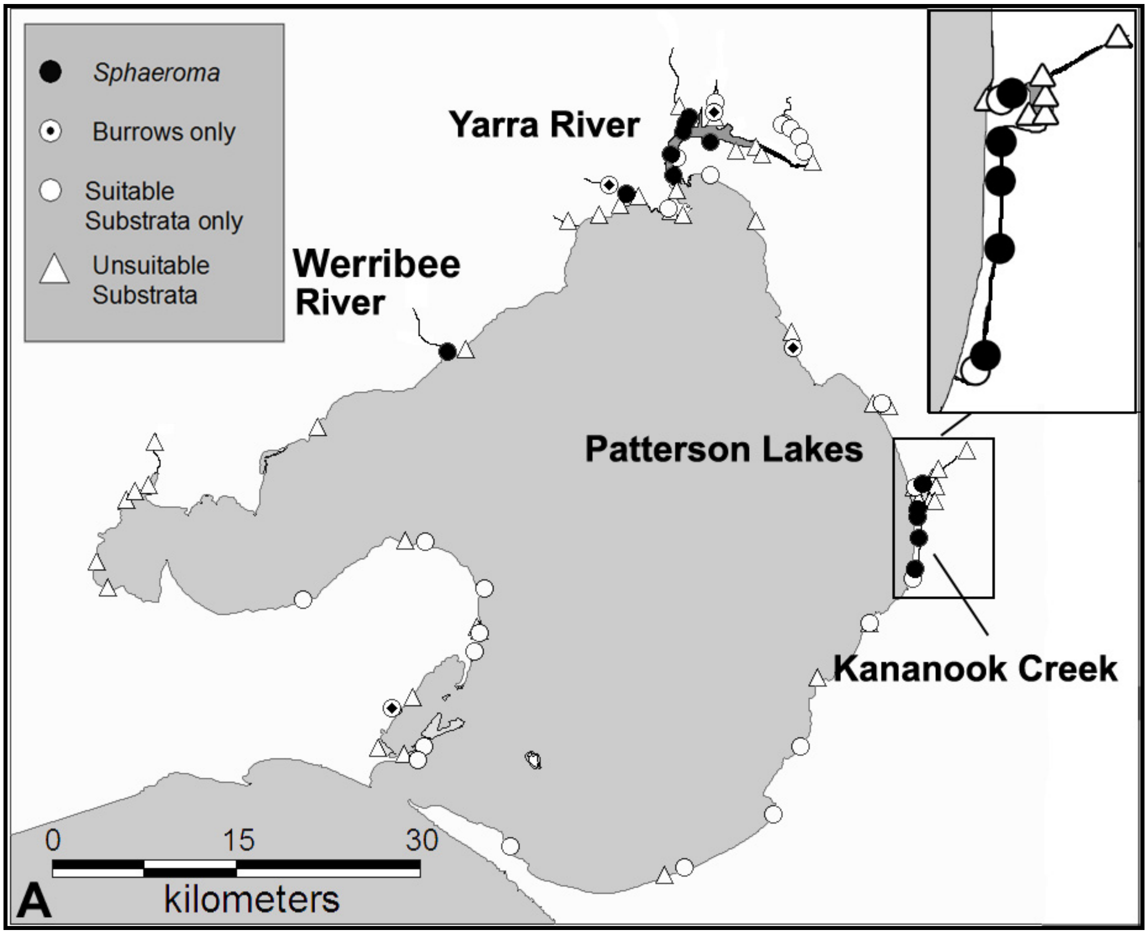
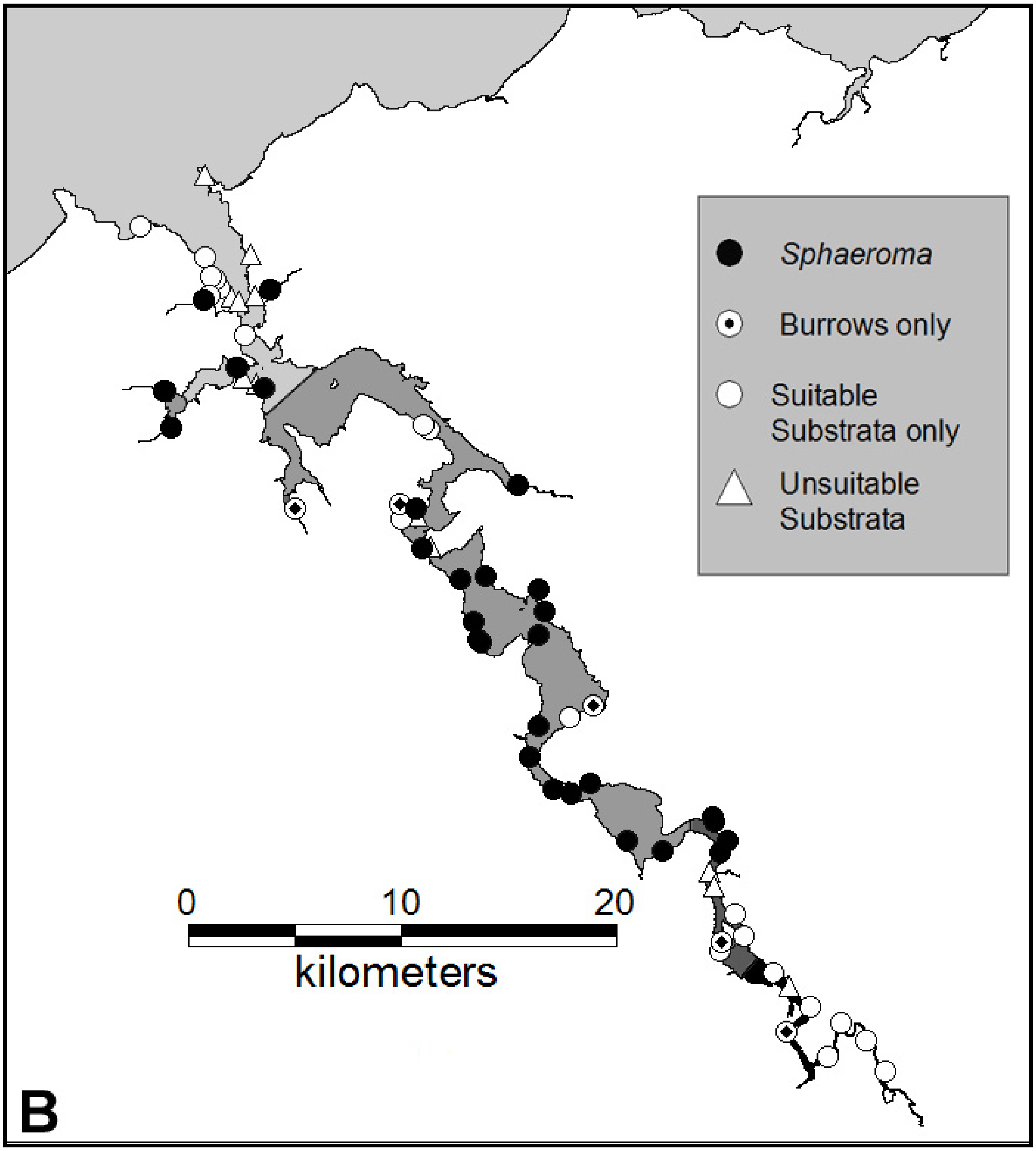


Figure 3. Surveyed points in **A.** PPB, **B.** Tamar, and **C.** Coos Bay. Closed circles (●) represent the presence of *Sphaeroma*; open circles with a dot (⊙) represent the presence of burrows only; open circles (○) represent suitable substrata lacking Sphaeroma and burrows; (Δ) open triangles represent a site without a suitable substratum. The shades represent the following salinity classes: oligohaline (0.5-5; black), mesohaline (>5-18; darkest gray), polyhaline (>18-30; dark gray), and euhaline (>30; light gray). Most *Sphaeroma* observations occur within polyhaline and mesohaline salinities. Note: some *Sphaeroma* observations occur in creeks adjacent to euhaline areas.


● *Sphaeroma*
⊙ Burrows only
○ Suitable Substrata only
△ Unsuitable Substrata
0
10
20
kilometers
B

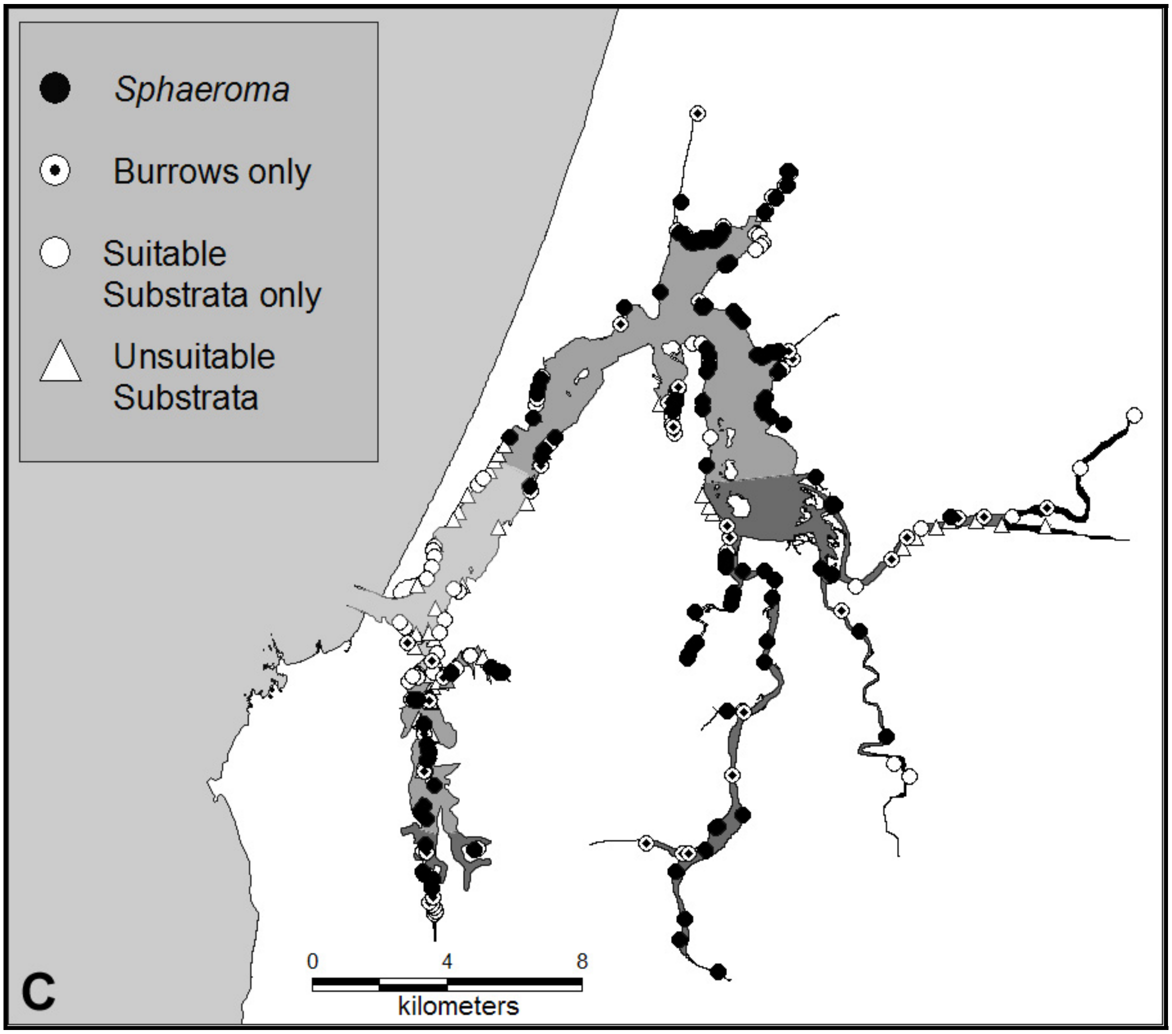

● *Sphaeroma*
Burrows only
Suitable Substrata only
Unsuitable Substrata
0
4
8
kilometers
C

Table 1. Prevalence of *Sphaeroma* individuals in sites with suitable substrata in different salinity classes in each embayment (Tamar Estuary and Port Phillip Bay, Australia, and Coos Bay, Oregon); Salinity classes are classified as oligohaline (0.5-5), mesohaline (>5-18), polyhaline (>18-30), and euhaline (>30); *obs/total* = observed sites with *Sphaeroma* / total examined sites; results of single classification goodness of fit tests with adjusted *G* statistics are displayed; * denotes the χ^2 statistic from a randomization test.

	Tamar Estuary		Port Phillip Bay		Coos Bay	
	obs/total	(%)	obs/total	(%)	obs/total	(%)
oligohaline	0/8	0	0/9	0	0/14	0
mesohaline	8/13	61.5	2/2	100	51/91	56
polyhaline	19/27	70.4	11/17	64.7	95/177	53.7
euhaline	3/9	33.3	0/13	0	1/25	4
***G*-adjusted**	10.5		15.9*		32.6	
P	**0.015**		**0.005**		**<<0.001**	

Prevalence

The presence of *Sphaeroma* individuals and burrows within suitable substrata in mesohaline and polyhaline salinities were not dependent on embayment (Table 2). The prevalence of *Sphaeroma* and burrows was comparable between the Tamar, Port Phillip Bay, and Coos Bay (Table 2). Suitable substrata were found throughout surveyed sites in all embayments and all salinity classes. Within the mesohaline and polyhaline areas, however, the presence of suitable substrata was not dependent upon embayment (Table 2). Within sites with burrowed substrata, *Sphaeroma* was found 75%, 73%, and 61% of the time in the Tamar, PPB, and Coos Bay, respectively. The presence of *Sphaeroma* in burrowed substrata was not dependent on embayment ($G_{adj} = 1.17, df = 2, P = 0.56$). In all embayments, the most commonly observed substrata suitable for *Sphaeroma* burrowing within mesohaline and polyhaline regions were marsh banks, wood, and friable rock, except PPB, which had a dearth of friable rock and few marsh banks.

Table 2. Prevalence of *Sphaeroma* individuals and burrows in sites with suitable substrata and prevalence of suitable substrata in mesohaline and polyhaline salinities within the Tamar Estuary (Tamar) and Port Phillip Bay (PPB), Australia, and Coos Bay, Oregon; results of single classification goodness of fit tests with adjusted *G* statistics are displayed; *obs/total* = observed sites with *Sphaeroma*, burrows, or suitable substrata / total examined sites.

	Sphaeroma		Burrows		Suitable Substrata	
	obs/total	(%)	obs/total	(%)	obs/total	(%)
Tamar	27/40	67.5	32/40	80	40/44	90.9
PPB	11/19	57.9	12/19	63.2	19/31	61.3
Coos Bay	145/268	54.1	228/268	85.1	268/313	85.6
***G*-adjusted**	1.07		1.16		2.4	
P	**0.59**		**0.66**		**0.30**	

Habitat use

In Coos Bay and the Tamar, *Sphaeroma* were found primarily within wood and friable rock (Table 3). *Sphaeroma* were also common within wood substrata in PPB. In contrast, marsh banks in Coos Bay were inhabited frequently by *Sphaeroma* but not in the Tamar or PPB. *Sphaeroma* were only found three times in the Tamar marsh banks and were not observed in PPB marsh banks. Burrows were found more frequently than *Sphaeroma* in the Tamar and PPB marsh banks but in very low densities compared to Coos Bay. In two locations in PPB, *Sphaeroma* were found nestling under rocky riprap but were not observed living under rocks in either the Tamar or Coos Bay. The presence of *Sphaeroma* was dependent on substratum type in the Tamar and Coos Bay but not in PPB (Table 3).

Table 3. Prevalence of *Sphaeroma* individuals within marsh bank, wood, and friable rock substrata in mesohaline and polyhaline salinities in the Tamar Estuary and Port Phillip Bay, Australia, and Coos Bay, Oregon; *obs/total* = observed sites with *Sphaeroma* / total examined sites; results of single classification goodness of fit tests with adjusted *G* statistics are displayed; * denotes the χ^2 statistic from a randomization test.

	Tamar Estuary		Port Phillip Bay		Coos Bay	
	obs/total	(%)	obs/total	(%)	obs/total	(%)
Marsh Bank	3/19	15.8	0/5	0	57/164	34.8
Wood	20/33	60.6	11/17	64.7	94/138	68.1
Friable Rock	8/11	72.7	0/2	0	42/68	61.8
***G*-adjusted**	7.6		3.76*		18.0	
P	**0.0223**		**0.1341**		**0.0001**	

Density

The mean density of *Sphaeroma*, burrows, and inquilines varied significantly between embayment, substratum type, and station (Table 4). The proportion of young in samples varied between embayment only. The degrees of freedom varied between tests due to missing values. The variation in the mean density of *Sphaeroma*, burrows, and inquilines between stations likely reflects normal variation expected from sampling different locations in these embayments. The significant interaction between embayment and substratum indicate that the effects of embayment are not the same across all substratum treatments. This interaction will be further evaluated below. The mean of *Sphaeroma*, burrows, and inquilines all varied significantly across embayment.

Table 4. Results of ANOVA tests for differences in mean A) *Sphaeroma*, B) Burrow, C) Inquiline densities and 4) the proportion of young to total isopods between embayment (Tamar Estuary and Port Phillip Bay, Australia, and Coos Bay, Oregon) and substratum type (marsh bank, wood, friable rock). All data were $\log\left(X + 10^{-6}\right)$ transformed. Embayment and substratum were considered fixed factors while station was considered a random factor. Degrees of freedom varied between tests due to missing values.

A. *Sphaeroma*

Source of Variation	**df**	**MS**	***F***	**P**
Embayment	2	142.57	38.71	< 0.001
Substratum	2	192.28	52.21	< 0.001
Embayment X Substratum	4	61.76	16.77	< 0.001
Station (Embayment, Substratum)	51	3.68	2.58	< 0.001
Residual	287	1.43		

B. Burrows

Source of Variation	**df**	**MS**	***F***	**P**
Embayment	2	6.02	20.56	< 0.001
Substratum	2	17.77	60.64	< 0.001
Embayment X Substratum	4	1.45	4.96	0.002
Station (Embayment, Substratum)	51	0.29	3.16	< 0.001
Residual	286	0.09		

C. Inquilines

Source of Variation	**df**	**MS**	***F***	**P**
Embayment	1	223.34	50.44	< 0.001
Substratum	2	109.08	24.63	< 0.001
Embayment X Substratum	4	20.99	4.74	< 0.001
Station (Embayment, Substratum)	42	4.43	1.96	0.001
Residual	239	2.25		

D. Proportion of young

Source of Variation	**df**	**MS**	***F***	**P**
Embayment	1	119.57	22.91	< 0.001
Substratum	1	21.72	4.16	0.051
Embayment X Substratum	1	1.31	0.25	0.620
Station (Embayment, Substratum)	28	6.23	1.19	0.266
Residual	79	5.22		

Pairwise contrasts revealed the mean density of *Sphaeroma* ($P < 0.001$), burrows ($P < 0.001$), and inquilines ($P < 0.001$) in Coos Bay were significantly greater than the Tamar and PPB. In addition, pairwise contrasts for substratum revealed *Sphaeroma* density in wood was significantly greater than both friable rock ($P = 0.004$) and marsh bank ($P < 0.001$); burrow and inquiline density were significantly greater in wood than marsh bank ($P < 0.001$ for both) and friable rock and marsh bank ($P < 0.001$ for both). There was a significantly greater proportion of young to total isopods in the wood and sandstone substrata samples from Coos Bay than the Tamar ($P < 0.001$; Figure 4).

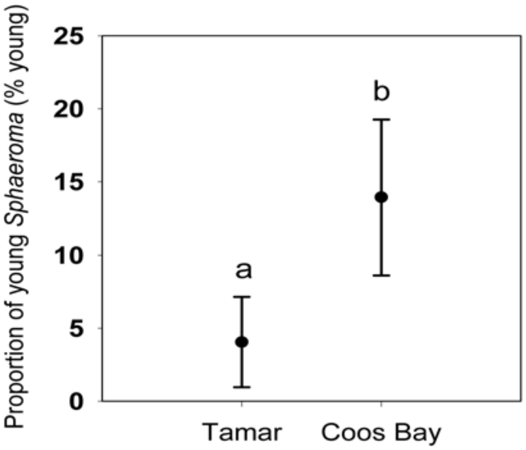


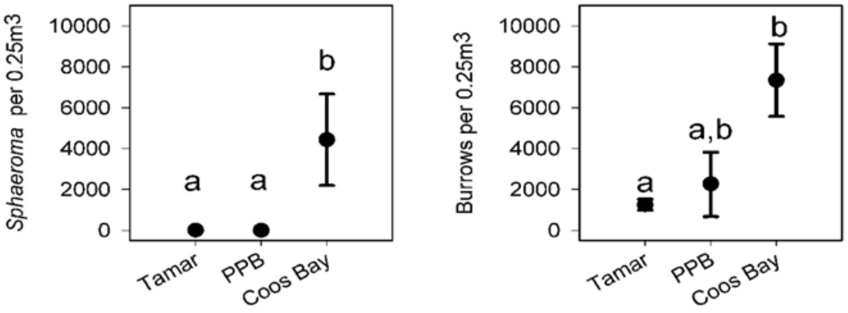
Figure 4. Mean percent of young (± 95% CI) within intertidal substrata samples in the Tamar Estuary (Tamar), Australia and Coos Bay, Oregon; different letters denote a significant difference between means; data is unavailable for Port Phillip Bay.

Marsh banks

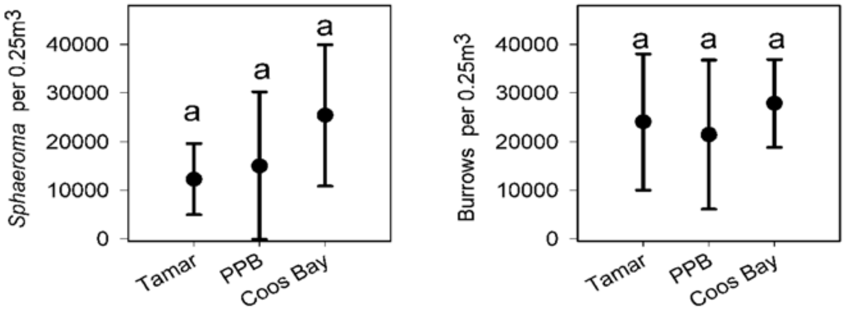
Within burrowed marsh banks, the mean densities of *Sphaeroma* in Coos Bay were significantly greater than the Tamar ($P < 0.001$) and PPB ($P < 0.001$; Figure 5a). Mean densities of *Sphaeroma* were 4,436 individuals/0.25m^3 in Coos Bay and 10 individuals/0.25m^3 in the Tamar. Maximum densities were 34,656 and 828 individuals/0.25m^3 in Coos Bay and the Tamar, respectively. Isopods were not found in the burrowed marsh banks of PPB, although only two stations could be sampled. Likewise, mean burrow densities were also significantly greater in Coos Bay than the Tamar ($P < 0.001$) and PPB ($P < 0.001$). The mean burrow densities were 7,346, 1,201, and 2,207 burrows/0.25m^3, in Coos Bay, Tamar, and PPB respectively.

In addition, the mean density of inquilines in marsh banks in Coos Bay was significantly greater than the Tamar ($P < 0.001$; Figure 6a). The marsh banks in the Tamar were depauperate of fauna compared to Coos Bay (3,974/0.25m^3); the mean was only 83 animals/0.25m^3.

A. Marsh bank



B. Wood



C. Friable rock

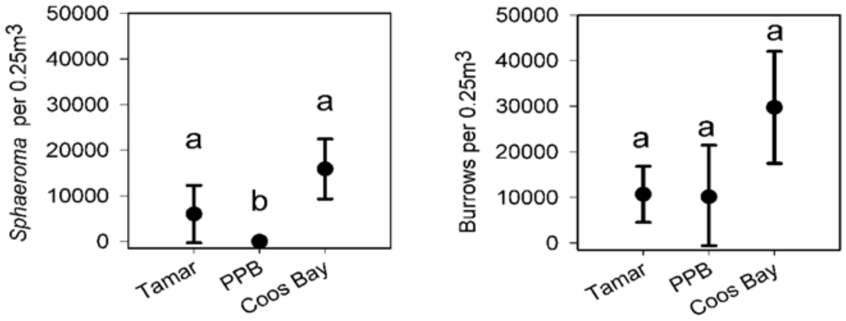


Figure 5. Mean *Sphaeroma* and burrow densities (± 95% CI) within three intertidal substrata in the Tamar Estuary (Tamar) and Port Phillip Bay (PPB), Australia and Coos Bay, Oregon; different letters denote a significant difference between means; results of Scheffe tests are presented below. **A.** Marsh bank substratum $n = 8$ for Tamar and Coos Bay; $n = 2$ for PPB; Coos Bay *Sphaeroma* mean was significantly greater than both Tamar and PPB ($P < 0.001$); Mean burrow density was different between Coos Bay and the Tamar ($P < 0.001$). **B.** Wood substratum $n = 8$ for all embayments; no significant difference detected between *Sphaeroma* or burrow means. **C.** Friable rock substratum $n = 8$ for Tamar and Coos Bay; $n = 2$ for PPB; Mean *Sphaeroma* in PPB were significantly lower than Coos Bay ($P < 0.001$) and the Tamar ($P = 0.025$); there was no difference detected between mean burrow densities.

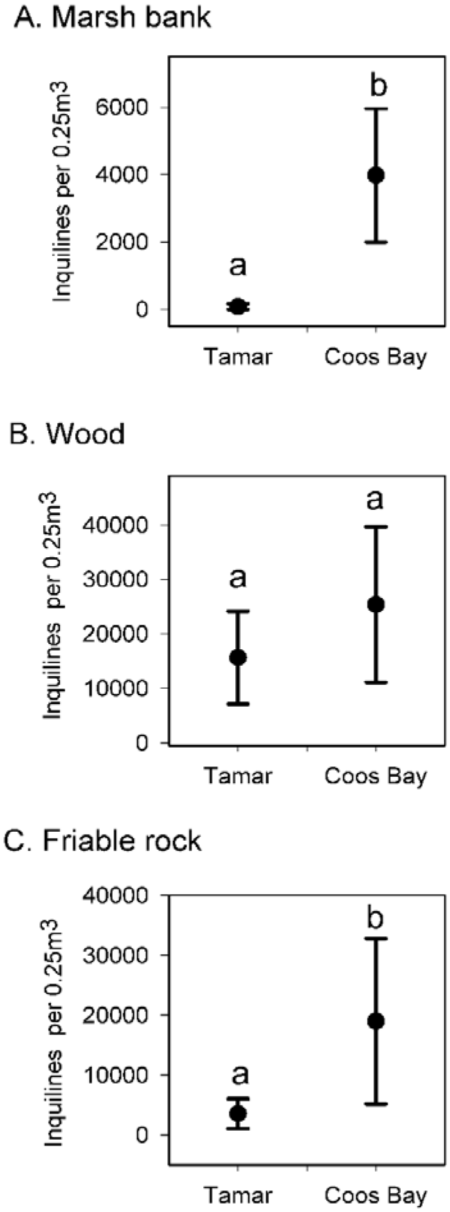


Figure 6. Mean inquiline densities (± 95% CI) within three intertidal substrata in the Tamar Estuary (Tamar), Australia and Coos Bay, Oregon; different letters denote a significant difference between means; data is unavailable for PPB; results of Scheffe tests are presented below. **A.** Marsh bank substratum $n = 8$ for Tamar and Coos Bay; Coos Bay mean was significantly greater than the Tamar ($P < 0.001$). **B.** Wood $n = 8$ for all embayments; no significant difference detected. **C.** Friable rock substratum $n = 8$ for the Tamar and Coos Bay; $n = 2$ for PPB; Coos Bay mean was significantly greater than the Tamar ($P < 0.001$).

Wood

The mean density of *Sphaeroma* in wood substratum was 12,302, 15,035, and 25,384 individuals/0.25m³ in the Tamar, PPB, and Coos Bay; however, there was no detectable statistical difference found (Figure 5b). Maximum *Sphaeroma* densities ranged from 49265 in the Tamar to 117,048 in PPB to 177,884 individuals/0.25m³ in Coos Bay. Mean burrow density did not vary significantly between Coos Bay (27,865/0.25m³) and the Tamar (24,276/0.25m³) but there was a difference in burrow density between Coos Bay and PPB (21,704/0.25m³; $P = 0.018$). There was also not a detectable difference between the density of inquilines in wood between Tamar (247/0.25m³) and Coos Bay (25,393/0.25m³; Figure 6b).

Friable rock

In friable rock, there was not a significant difference detected between the mean densities of *Sphaeroma* in Coos Bay (15,879/0.25m³) and the Tamar (6,245/0.25m³; $P = 0.546$; Figure 5c). This result is surprising given the large difference between means. A reevaluation of box plots revealed a large number of low value outliers in the Coos Bay data. To account for the effect of these outliers, these data were reevaluated using a non-parametric Mann-Whitney U test. The test found highly significant differences between the two embayments ($P < 0.001$). Although the pairwise comparison did not detect a significant difference, due to the nature of the data, I trust the validity of latter test. The pairwise comparisons did detect a difference between Coos Bay and PPB ($P < 0.001$)

and the Tamar and PPB ($P = 0.025$). Maximum densities were 32,428 in the Tamar, 0 in PPB, and 55,136 individuals/0.25m^3 in Coos Bay. In addition, mean burrow density in the Tamar (11,022/0.25m^3) and Coos Bay (29,710/0.25m^3; $P = 0.037$) were significantly different. Furthermore, anecdotal observations indicate burrow densities and the prevalence of burrows within the sites sampled were also different. Instead of having a relatively homogenous distribution of *Sphaeroma* burrows in friable rock shelves or terraces as observed in many areas of Coos Bay, the distributions of burrows in the Tamar and PPB were very disjunct. The mean density of inquilines in the Tamar was significantly lower than in Coos Bay (3,585/0.25m^3 vs. 18,960/0.25m^3, $P < 0.001$; Figure 6c).

Discussion

When introduced to a new environment, species can experience an ecological release from the factors normally maintaining their distribution and density. In the absence of these controlling factors, populations of introduced species can exhibit a distribution different from their native range and can attain densities considerably higher than populations within the native range (Carlton 1990, Behrens-Yamada 2001, Torchin et al. 2003).

Sphaeroma exhibited a similar intertidal distribution within the three embayments examined. Within each embayment, *Sphaeroma* was mostly limited to the mesohaline to polyhaline areas of the bay and to sites with suitable substrata. Prevalence was also similar. *Sphaeroma* individuals and burrows appear to be equally prevalent in suitable substrata within mesohaline and polyhaline areas of Coos Bay, the Tamar, and PPB. Since distribution and prevalence were similar, it seems likely that the factor(s) controlling the intertidal distribution and prevalence of *Sphaeroma* between these embayments were similar. In all embayments, *Sphaeroma* presence was related to the salinity class and presence of a suitable substratum. Although I did not evaluate the effects of all possible factors, the strong relationship between *Sphaeroma* presence and salinity class and the presence of suitable substrata suggests salinity (or a salinity correlate) and presence of marsh banks, wood, or friable rock are the most significant factors affecting the intertidal distribution and occurrence of *Sphaeroma*. The other strong correlate with salinity, temperature, is not likely a limiting factor since mean water temperatures in euhaline areas varied (~14º for Tamar, ~15º for PPB, ~13º Coos Bay) between embayments while *Sphaeroma* distribution remained the same. If temperature were a major factor shaping the distribution, than I would have expected to observe a different estuarine distribution within the warmer waters of the Tamar and PPB than in the cooler waters of Coos Bay.

Density

In Coos Bay, *Sphaeroma* was present within marsh bank substrata at densities approximately 440 times the observed densities in the Tamar. Similarly, mean *Sphaeroma* densities were approximately 2.5 times greater in the friable rock substrata of

Coos Bay than the Tamar. Within wood substrata, the densities of *Sphaeroma* appear greater within Coos Bay but a statistical difference was not detected. So why does *Sphaeroma* appear at densities orders of magnitude greater in Coos Bay marsh bank and friable rock habitats than in the native Australian habitats sampled? To address this question we must evaluate the ecological factors that are likely limiting *Sphaeroma* densities in the areas where they are present. On a regional scale, there appear to be variations in the amount and quality of suitable substrata within the three embayments. However, on the scale of meters, space does not appear to be limiting the density of *Sphaeroma*. In all sites examined within the three embayments, there was considerable space (e.g., unburrowed suitable substrata) available for isopod colonization. The substrata also appear to be comparable in strength between embayments. In addition, all stations sampled in the three embayments were under similar hydrological conditions so abiotic factors cannot account for these differences. Therefore, I will consider some of the remaining biotic factors: predators, competitors, food limitation, parasites, and disease.

Predation does not seem to be a factor that could account for the large variation in density between native and introduced embayments. Anecdotal observations indicate *Sphaeroma* are mostly sedentary burrow dwellers so the effect of epibenthic predators is likely small. In addition, other smaller isopod predators such as nemerteans or polychaetes were never observed in the isopod burrows within the Tamar and PPB. Competition is also unlikely to be a factor significantly affecting densities since *Sphaeroma* does not appear to be space limited; at even the most heavily burrowed sites, there was still considerable substrata available for burrowing. Burrowing crabs and other sphaeromatid isopods may compete with *Sphaeroma* for burrow space, but densities of these animals do not appear to differ significantly between embayments (unpublished data). In addition, the mean densities of inquilines were lower within the Australian embayments than in Coos Bay so *Sphaeroma* has less possible competitors within burrows. Food limitation is also not likely to be a factor that could account for the low densities in the Tamar and PPB since all embayments are very productive temperature systems that receive significant nutrient inputs from terrestrial sources (Edgar et al. 1999, Hewitt et al. 1999). The proximity of PPB to a large metropolitan area results in large nutrient inputs, which can result in seasonal phytoplankton blooms (Hewitt et al. 1999). Similarly, the Tamar also hosts a relatively large population in relation to its size and receives significant amounts of nutrients from sewage discharge and from terrestrial sediments (Edgar et al. 1999). However, quantified comparative data on nutrient levels for the Tamar, PPB, and Coos Bay was not available and thus cannot be completely ruled out.

Parasites and/or disease are the remaining factors that could be responsible for low population densities of *Sphaeroma* in Tamar and PPB. Marine isopods have a number of parasites including forams, copepods, flukes, and more. (Svavarsson and Daviosdottir 1994, Rohde 2005). It is possible that the populations of *Sphaeroma* along the Pacific Coast lack these parasites. Biological invasions are often stochastic events. If the introduction of a small founding population of *Sphaeroma* had a low proportion of individuals infected by parasites then it is possible the parasite numbers (and infection rates) would remain low or become extinct. In addition, many parasites may require an intermediate host/vector to complete their life cycle. If this host is not present with the introduced species in the new system the parasite populations would go extinct. The absence of parasites has been suggested as a significant reason why some introduced species have flourished in introduced regions (see review by Torchin et al. 2002). For example, the invasive European green crab (*Carcinus maenas*) achieves high densities in its introduced range and has significantly less parasites (Torchin et al. 2001). Introduced populations of the northern Pacific sea star (*A. amurensis*) have nearly one half of the parasites present in native populations (Torchin et al. 2002). In addition, *Mytilus galloprovincialis*, an introduced mussel in South Africa, was found to be free of trematode parasites, yet trematodes infect almost half of all native co-existing *Perna perna* mussels (Calvo-Ugarteburu and McQuaid 1998). Introduced *Sphaeroma* populations may also be released from the normal diseases that afflict native populations. To evaluate the prevalence of parasites and disease in *Sphaeroma*, future studies should compare parasite abundance and prevalence of disease between native and introduced populations.

In addition to the significant differences in isopod density within marsh banks and friable rock, a significantly higher proportion of young to total isopods were found in the Coos Bay population than the Tamar and PPB populations. Assuming populations from all embayments reproduce in the same season, these results suggest that either the populations in Coos Bay are more fecund or young have higher survivorship than in the Tamar and PPB. Since density differences are likely impacted by the number of recruits, a lower recruitment of young may be a bottleneck limiting population densities. Perhaps parasites or diseases that target eggs or the reproductive structures of females could be responsible for this pattern.

Habitat use

Although the distribution and prevalence within embayments were similar, habitat use varied between populations living in Coos Bay and in the Australian marshes surveyed. In all embayments, *Sphaeroma* were mostly found within sites with wood and friable rock substrata. Interestingly, *Sphaeroma* and burrows in Coos Bay were found much more frequently within marsh banks than in either the Tamar or PPB. It is unclear why *Sphaeroma* is not present as frequently in marsh banks in the Tamar and PPB. The marsh banks in all embayments were approximately the same firmness (unpublished data). Since burrowing crabs may possibly affect isopod distributions via competition for space and predation, the density of crabs were noted during sampling. However, there is no statistical difference in the abundances of shore crabs found in all samples between the embayments (unpublished data). Furthermore, space competition does not seem to be a likely factor in these systems since space does not appear to be limited within any of the sites examined. Marsh banks may not be a preferred substratum. Isopod densities were so low in the Tamar and PPB because other substrata are utilized instead of marsh. In addition, marsh bank habitat within the heavily urbanized PPB was relatively rare. When marsh bank habitat was found it was often situated on top of cobblestone channels.

These marsh banks were short (often less than ½ meter) and situated at the high tide mark in the intertidal. Since *Sphaeroma* and burrow numbers appear to substantially decrease at the high tide mark (per. obs), these high intertidal marshes may actually be an unfavorable habitat. In contrast, Coos Bay and the Tamar, have many kilometers of very tall and firm marsh banks, which appear to be an ideal environment for *Sphaeroma*. Furthermore, in Coos Bay, *Sphaeroma* burrow into Styrofoam-based floating docks in high densities. In contrast, Styrofoam floats do not appear to be used in floating docks of the Australian embayments surveyed, thus *Sphaeroma* populations do not appear to be using this substratum as habitat.

The Tamar and Coos Bay had more suitable habitat sites than PPB. The lack of the available habitat may explain why *Sphaeroma* was found nestling under rocks in PPB but not in Coos Bay or the Tamar. These observations suggest that *Sphaeroma* adapts readily to the changing quality and availability of intertidal substrata.

Empty niche

Within Coos Bay, *Sphaeroma* appears to be creating a niche in marsh banks and friable rock that was not previously occupied (see Chapter III). *Sphaeroma* create numerous anastomizing burrows, which provide a novel habitat in the intertidal. *Sphaeroma* burrows provide a habitat for myriad organisms and alter some of the physical and environmental characteristics of burrowed substrata (Talley et al. 2001, Chapter III). The creation of numerous burrows in substrata not only affects the shear strength (Talley et al.

2001), but also likely changes humidity, temperature, and UV light exposure inquilines are exposed to. The burrows themselves may actually ameliorate environmental stresses and produce a more habitable microclimate, particularly during low tide when physical stresses are highest. Furthermore, inhabiting burrows also likely provides a refuge from many predators.

Inquilines were found in varying densities within the substrata in the Tamar and Coos Bay. In Coos Bay, burrows within marsh banks and friable rock host significantly more inquilines than in the Tamar. This pattern is likely a function of the higher burrow density in Coos Bay. Also, there were relatively few isopods and amphipods present in the Tamar samples. Since a majority of the inquilines inhabiting *Sphaeroma* burrows in Coos Bay were amphipods and isopods, the lack of these abundant inquilines in the Tamar could explain differences in inquiline abundance.

Within wood substrata, *Sphaeroma* is competing with the numerous marine wood-burrowing species (*Limnoria* spp. *Teredo navalis*, *Bankia setacea*) and has become the most prevalent wood borer in Coos Bay (per obs.). Although the mean densities of inquilines in wood appear higher in Coos Bay, I did not detect a significant difference between Coos Bay and the Tamar. The high densities and prevalence of *Sphaeroma* within wood substrata suggest *Sphaeroma* is primarily a wood boring species within their native range of Australia. The preference of *Sphaeroma* for wood substrata further supports the assertion that a likely vector responsible for their initial introduction to the Pacific Coast 100-150 years ago was through individuals inhabiting burrows bored into wooden ship hulls.

Conclusion

Sphaeroma may be impacting the estuarine communities in many embayments along the Pacific Coast of North America. The isopods achieve extremely high densities and riddle various substrata with burrows, which can reduce substrata integrity and lead to erosion. In the Tamar, PPB, and Coos Bay, *Sphaeroma* exhibited similar distributions and prevalence within intertidal substrata although population densities differed. In Coos Bay, *Sphaeroma* densities within marsh banks and friable rock were several orders of magnitude greater than in the native regions examined. The low densities observed in native regions are likely the reason *Sphaeroma* is not recognized as a bioeroding species in marsh banks and friable rock shoreline in Australia and New Zealand. *Sphaeroma* densities in the Tamar and PPB were significantly higher in wood substrata than friable rock and marsh bank substrata, which could explain why *Sphaeroma* is primarily recognized as a damaging wood boring species in Australia and New Zealand (Mills 1978, Cookson 1999, per. obs.). In Coos Bay, *Sphaeroma* facilitates the erosion of marsh bank and sandstone shoreline and damages wooden and Styrofoam maritime structures, but in the Tamar and PPB, they appear to only be damaging wooden structures. The autecological differences between native and introduced populations of *Sphaeroma* could be responsible for the profound impacts this species can have introduced habitats.

BRIDGE III

As demonstrated in previous chapters, *Sphaeroma* populations appear in varying densities within different intertidal substrata. While these densities may be affected by the relative availability of habitat, recruitment level, and the physical characteristics of those substrata, the role of substratum preference in *Sphaeroma* may also be an important factor. Chapter V examines the preference of *Sphaeroma* for select intertidal substrata (marsh bank, wood, sandstone, and Styrofoam) in Coos Bay. Preference of *Sphaeroma* is examined using a series of choice experiments. Burrowing rate is also measured to examine how quickly *Sphaeroma* colonize different substrata. Finally, this chapter determines the life stages of the colonizers and discusses the implications of these findings for the management of this invasive species.

CHAPTER V

SUBSTRATUM PREFERENCE OF AN INTRODUCED BURROWING ISOPOD (*SPHAEROMA QUOIANUM*) IN A TEMPERATE ESTUARY

Introduction

Habitat choice and preference can mediate the distributions and densities of many marine invertebrates. The intensity of the choice or degree of preference for a habitat is often a function of the external factors operating on these organisms (predation rate, environmental conditions, etc). Some habitat choices are compulsory due to their impact on survivorship. For example, the isopod *Limnoria tripunctata* burrows only within wood substrates and is completely dependent upon the consumption of wood for nutrition (Morris et al. 1980). The limpet *Lottia alveus* was driven extinct due to a slime mold plague that destroyed its obligatory eelgrass habitat, *Zostera marina* (Carlton et al. 1991). For other organisms, habitat use is more dynamic, and higher quality habitat may be desired but is not essential to survival. The estuarine isopod *Eogammarus confervicolus* exhibits a strong preference for habitat based on where it was raised but can survive in a variety of habitats without any clear reduction of fitness (Stanhope et al. 1985, Stanhope et al. 1992). Also, young-of-the-year Dungeness crabs (*Cancer magister*) prefer shell habitat over eelgrass but mortality does not differ substantially between these habitats (Fernandez et al. 1993).

The bioeroding isopod *Sphaeroma quoianum* (= *S. quoyanum*) has been recently introduced to Coos Bay, Oregon and has been observed boring into numerous shallow subtidal and intertidal substrata. The densities of these organisms can vary between substrata (Chapter III) suggesting isopods exhibit a preference.

Sphaeroma quoianum (hereafter: *Sphaeroma*) is a detrimental bioeroder in many estuaries along the Pacific Coast of North America. *Sphaeroma* was introduced to the Pacific Coast of North America during the late 19th century from its native region of Australia, Tasmania, and New Zealand (Carlton 1979). During this period of time, wooden ships from Australasia arrived in San Francisco Bay en masse to exploit the gold rush. Many of these ships were subsequently abandoned within San Francisco Bay, translocating the myriad biota living on the exterior (fouling species) and interior (boring species) of the ship hulls. Since the initial introduction of *Sphaeroma*, subsequent invasions have occurred within at least fourteen embayments along the Pacific Coast (Menzies 1962, Iverson 1974, Carlton 1979, Chapter II).

Sphaeroma are prodigious burrowers and inhabit a variety of substrata including mud, clay, or peat banks (hereafter: marsh banks), wood, sandstone, styrene plastic floats (Styrofoam) and more. *Sphaeroma* does not consume the material it excavates, but rather creates a burrow for protection and to facilitate filter feeding. During feeding, water is drawn in by the beating of the pleopods, which generates a current of water that moves suspended detritus and phytoplankton into the burrow (Rotramel 1975). The current passes over the dorsal surface of the isopod, hits the terminal end of the burrow, and flows through the dense setae on the front pereopods allowing food particles to be retained and consumed (Rotramel 1975).

By creating extensive anastomizing burrow networks, *Sphaeroma* can accelerate the rate of shoreline erosion and damage maritime structures (Barrows 1919, Chilton 1919, Higgins 1956, Mills 1978, Carlton 1979, Talley et al. 2001, per. obs.). In California, *Sphaeroma* burrowing has been implicated in extensive lateral erosion of saltmarshes and has been shown to significantly increase marsh bank sediment loss (Carlton 1979, Talley et al. 2001). *Sphaeroma* has also been noted as the chief agent of sandstone erosion in the sandstone shoreline of San Pablo Bay, California (Barrows 1919, Higgins 1956). In Hawke's Bay, New Zealand, *Sphaeroma* has extensively damaged sea walls made from friable rock causing them to crumble away (Chilton 1919). *Sphaeroma* can also damage wooden structures such as transmission poles (Mills 1978), docks (per. obs.), and other structures (Cookson 1999). Finally, *Sphaeroma* prodigiously burrows into Styrofoam floats used in floating docks, which appear to substantially reduce their integrity and longevity within the marine environment (Carlton 2001, per. obs.).

Life history and reproductive biology

Sphaeroma is gonochoric and undergoes direct development. Female isopods carry fertilized eggs within invaginations under a series of plates that together form a marsupium. The young develop within this protective marsupium until they crawl out as fully formed juveniles (Hill and Kofoid 1927, Schneider 1976). Once the small juveniles crawl out of the marsupium they often remain at the terminal end of the burrow under the protection of the mother (per. obs). By blocking the burrow opening with the pleotelson, an adult isopod may reduce predation risk for small juveniles and provide a more buffered microhabitat within burrow. This behavior, known as extended parental care, is common in many isopods and other peracarid species (Messana et al. 1994, Thiel 1999a-e, Thiel 2003) and likely increases the survivorship of small juveniles. It is unclear how long the juveniles remain within the burrow, but they are likely expelled when they reach sizes that interfere with adult isopod movement and feeding. This pattern has been observed in the congeneric *S. terebrans*, which exhibits a very similar behavior and will actively expel juveniles that have molted to a feeding stage (Thiel 1999e). Occasionally young *Sphaeroma* were observed creating their own burrows branching off of the main burrow, but most young isopods leave (or are expelled from) the maternal burrow to colonize a new substratum (per. obs).

In Coos Bay, Oregon (USA), *Sphaeroma* burrows occur in extremely high densities within marsh banks, wood, sandstone and Styrofoam floats (Chapter III). In some areas, high *Sphaeroma* densities appear to be accelerating the rate shoreline erosion and damaging wooden structures and Styrofoam floating docks. Within these different substrata, mean densities vary considerably, which may indicate preference for one substratum over others. This study seeks to determine the substratum preference, rate of burrowing, and elucidate some aspects of the biology of this bioeroder within temperate Coos Bay, Oregon. The following questions will be addressed:

1) How does substratum type influence the numbers of burrows and *Sphaeroma* present?, 2) Are *Sphaeroma* burrowing and colonization rates consistent across time and between substrata?, and 3) What life stage colonizes substrata? Answering these questions will reveal some of the factors that influence the colonization of substrata by a detrimental bioeroding species.

Methods

Study site

Coos Bay is a temperature drowned river system located in southern Oregon, USA (43.35º N, 124.34ºW; Figure 1). Numerous rivers and creeks feed into Coos Bay, producing substantial seasonal reductions in salinity. The shoreline is primarily composed of sandy beaches, marsh, rocky riprap, sandstone, and abundant woody debris from past and present logging operations. Experimental trials were conducted primarily within Haynes Inlet, located in the northeast corner of Coos Bay; additional replicates were placed in two other areas (Figure 1). Sandstone terraces are heavily bored by large populations of *Sphaeroma* in Haynes Inlet. It is a predominantly polyhaline region of the bay with salinities ranging from 25-32 and water temperatures from 16-21ºC during the summer.

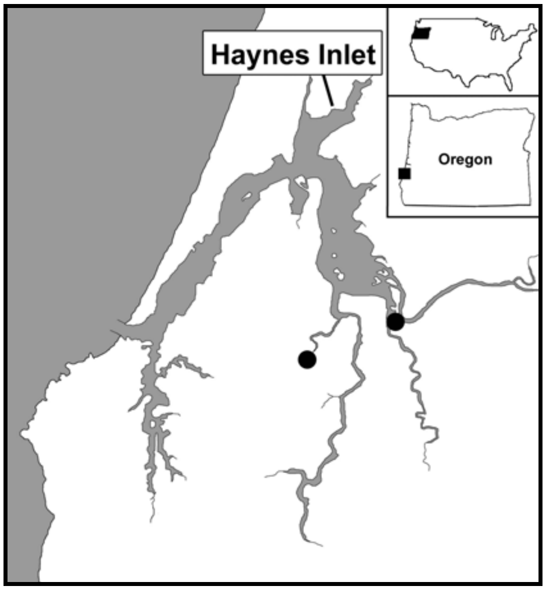


Figure 1. Map of Coos Bay, Oregon. Experiments were conducted primarily within Haynes Inlet (trials 1-3). Additional experimentation during trial one was conducted in two other locations as denoted by the closed circles (●).

Three experimental trials were conducted at different times. Trial one was conducted for nine weeks beginning on August 25, 2005. The second trial was conducted on April 19, 2006 and lasted two weeks. The third trial commenced on September 12, 2006 and lasted 12 days. All trials utilized the methodology described below.

Experimental design

Replicates of four types of substrata (marsh bank, wood, sandstone, and Styrofoam) were placed in the high intertidal near existing populations of *Sphaeroma*. Replication level varied between trial one and trials two and three. Eight replicates were used during trial one and five replicates were for trials two and three. For all trials, most replicates were separated by over 100m, although two replicates were separated by 20m. The dispersal range of this species is unknown but I assume the replicates were spaced far enough apart to ensure independence. In addition, the shoreline is complex and often separates the replicates, which likely prevents potential colonizers from reaching another replicate. The four substrata used in these experiments were obtained from identical intertidal locations. To ensure the substrata used in the experiment were suitable for burrowing, substrata were removed from larger sections already harboring *Sphaeroma* populations. However, only burrow-free pieces of substrata were used for the experiment. All substrata were defaunated prior to experimentation by freezing. To standardize volume and surface area (100cm^2), each substrata type was cut and shaped to fit within plastic containers (800ml). Encased substrata were then secured within cinder blocks with one exposed side. Each replicate of the four substratum blocks were placed in a row within 6cm of each other and were vertically oriented to simulate natural *Sphaeroma* habitat. To maximize the likelihood of *Sphaeroma* making contact, substrata blocks were placed facing the existing *Sphaeroma* burrows at a distance of 10cm from the nearest burrowed substratum.

Scoring

Each substratum block was examined during low tide and photographed. The numbers of burrows created in each substratum were enumerated in the field. Digital photographs of heavily burrowed substrata were later analyzed using ImageTool 3.0 to verify field burrow counts. Preference was determined by measuring a) the first substrata colonized and b) the number of isopods and burrows present in each substratum at the experiment end.

Statistics and analysis

Since this experimental is a choice experiment involving counts, normal parametric methods of analysis were not applicable. The data were analyzed using Chi-square goodness of fit tests as described in Sokal and Rohlf (1985) to test the null hypothesis that substratum type is independent of the numbers of burrows and *Sphaeroma* present at the experiment end. Replicates with an expected cell count below five were removed from the analysis since *G*-tests are not accurate with these data. When applicable, the William's correction was applied to the *G* statistic to account for increased type I error associated with *G*-tests using the Chi-square distribution (Williams 1976). The data were pooled when the heterogeneity *G* of replicated goodness of fit tests were non-significant. A non-significant result indicated the ratio of the treatments (blocks) were not different between replicates and could be treated as being from one experiment (Sokal and Rohlf 1985).

When an individual *G*-test yielded a significant result, standardized residuals were calculated to determine the sources of the deviation from independence (Wittham and Siegel-Causey 1981). Standardized residuals were then divided by the square root of variance to calculate the normal standard deviates (represented as: d_{ij}) to examine the preference within individual replicates. Thus, the amount of variance each cell contributes to the total deviation from independence could be calculated and compared to a *Z*-distribution ($d_{ij} \pm 1.96$ is significant at $P = 0.05$). For the purposes of this study, normal standard deviates $d_{ij} \geq 1.96$ were designated as "Preferred", $d_{ij} \leq -1.96$ were "Avoided", and if $1.96 > d_{ij} > -1.96$ then there was not a significant response at the $P = 0.05$ level ("No Response"). Each replicate was processed in this fashion.

The substratum with the highest numbers of burrows and isopods was noted for each of the replicates. These values were then analyzed separately to examine the relationship between the highest numbers of burrows/isopods present in a block and substratum type. This method removed the potential confounding effect of varying population density on the presence of burrows and isopods in the experimental substrata.

Due to logistical constraints and the erosion of marsh bank blocks, some replicates were retrieved or planted earlier than others. Data for these blocks were analyzed as if they were in the field for the same numbers of days. However, this was unlikely to impact the analysis since goodness of fit tests analyze the burrow frequencies relative to the treatment *within* each replicate. Since time does not appear to alter these ratios (see results), this difference was unlikely to affect the analysis.

Results

Marsh banks and wood were the first substrata burrowed into in nearly all observations from the three trials (Table 1). The first burrows were created in wood blocks in four replicates, marsh bank blocks in three replicates, both wood and marsh bank blocks were burrowed in two replicates, and in one replicate all substrata were burrowed into at the same time. The first burrows appeared after one day in trial three (Fall 2006) whereas burrows did not appear until two days later for trial one (Fall 2005) and at day ten in trial two (Spring 2006). The initial day of colonization for the remaining blocks was highly variable.

Table 1. Day the first burrow was observed in each substratum block within each replicate (labeled A-I). Replicates with the same letter were placed in the same location between trials. Not all replicates in the Fall 2005 trial were checked daily. The "<" indicates the first burrow observation occurred sometime before that respective day.

Day of first burrow observation

Fall 2005

	Replicate							
	A	B	C	D	E	F	G	H
Marsh Bank	<14	**<5**	<14	**2**	<13	<13	<12	<12
Wood	<14	**<5**	<14	<14	<13	<13	<12	<12
Sandstone	<14	<14	<14	<21	<13	-	<33	<12
Styrofoam	<14	<14	<14	<14	<13	<13	<12	<12

Spring 2006

	A	B	C	D	I
Marsh Bank	-	10	-	-	12
Wood	-	-	-	14	-
Sandstone	-	-	-	-	-
Styrofoam	-	-	-	-	-

Fall 2006

	A	B	C	D	I
Marsh Bank	1	2	2	1	3
Wood	1	1	1	1	1
Sandstone	5	3	6	1	3
Styrofoam	7	6	6	1	5

Rate of burrow creation

The cumulative number of burrows in each substratum increased at a relatively linear rate in the Fall 2005 and 2006 trials and was highly variable between replicates (Figure 2A). The burrowing rate varied according to substratum and time (Figure 2B). There were peaks in the burrowing rate in all substrata during week three in the Fall 2005 trial and a large spike in the burrows created in wood during day five in the Fall 2006 trial.

Over the nine weeks of exposure, the mean numbers and rate of burrows created per week during trial one was highest in marsh banks and wood and lowest in sandstone and Styrofoam (Table 2). In trial three, the mean burrowing rate during the twelve-day experiment was highest in wood and lowest in sandstone and Styrofoam, but there were fewer burrows created per week in marsh bank substratum compared to trial one. Very few burrows were constructed during trial three (five burrows over two weeks); therefore these data were not included in the subsequent analyses.

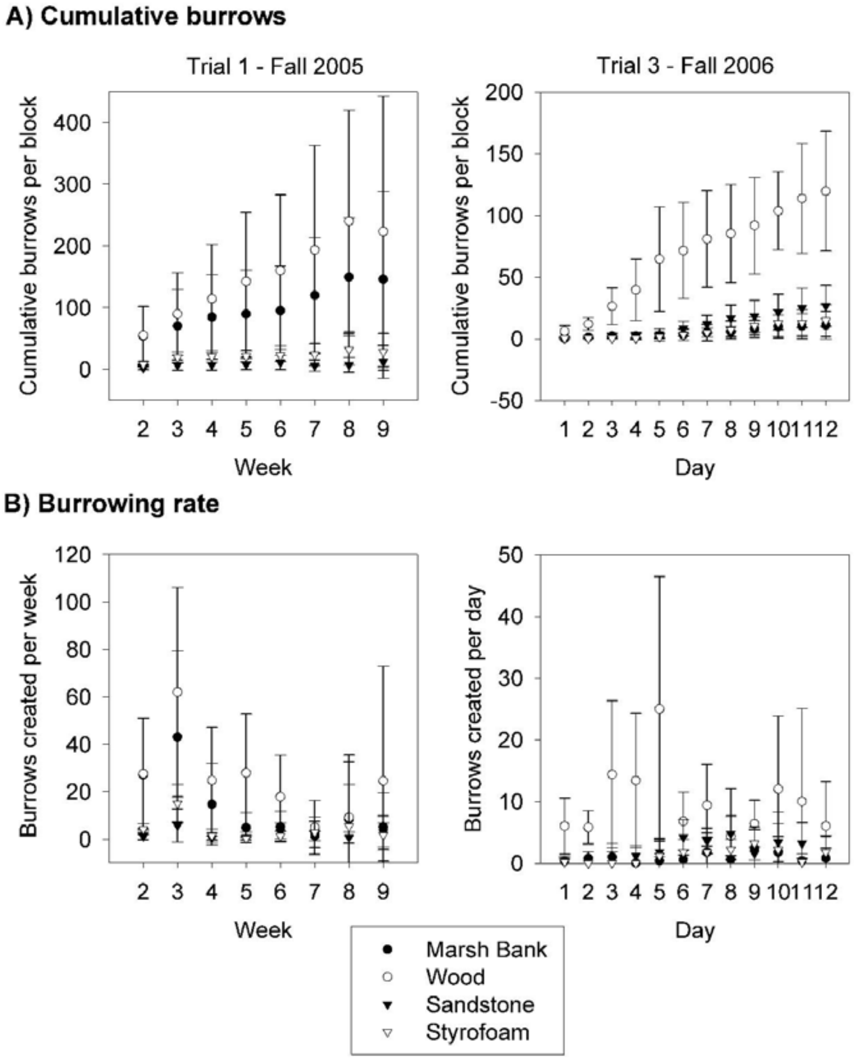


Figure 2. Cumulative burrows and burrowing rate in four different substrata. Mean **A.** number of cumulative burrows and **B.** burrows created during trial one (Fall 2005) and trial three (Fall 2006) in marsh bank, wood, sandstone, and Styrofoam (n=8 for Fall 2005, n=5 for Fall 2006). Error bars are 95% confidence intervals; Asterisk (*) indicates the weekly mean burrowing rate for the observation at week two was calculated as the mean of two weeks since data was not recorded on week one.

Table 2. The mean burrowing and colonization rate of *Sphaeroma* per week in all trials.

A. Burrowing rate (burrows created per week)

	Fall 2005	Spring 2006	Fall 2006
Marsh Bank	12.2	0.5	6.4
Wood	22.3	0.1	69.8
Sandstone	2.1	0.0	15.5
Styrofoam	3.7	0.0	8.5

B. *Sphaeroma* colonization rate (isopods per week)

	Fall 2005	Spring 2006	Fall 2006
Marsh Bank	3.7	0.4	1.5
Wood	18.9	0.1	36.1
Sandstone	1.1	0.0	11.3
Styrofoam	3.1	0.0	4.7

Relative numbers of burrows and isopods

The numbers of burrows and *Sphaeroma* present at the end of the experiment were highly variable between replicates (Table 3). Mean numbers of burrow and *Sphaeroma* appeared higher within wood substratum than all other substrata during both Fall 2005 and 2006 (Figures 2A and 3). Variations within wood blocks were greater during Fall 2005. Individual goodness of fit tests revealed that the presence of burrows and isopods is highly dependent on substratum type in nearly every replicate. These data were pooled and examined with a replicated goodness of fit test. The heterogeneity *G* was significant when Fall 2005 and 2006 trials were pooled together; this indicated the ratios of the treatment within each replicate were not equal and the data could not be pooled together to test the null hypothesis. These results illustrated the considerable variation between the ratios of burrows and isopods present in each substratum within the replicates. Despite this variation, wood substratum still appeared to be the most preferred substrata. When analyzed separately, replicated *G*-tests of the trials revealed that both trial one and three were highly variable, thus the replicates within each trial also could not be pooled (Table 3). This result suggests that the type of substratum preferred and the magnitude of that preference vary according to location. The exception was wood substratum; which was nearly always preferred over the other substrata.

Table 3. Results of replicated goodness of fit tests. The significance of the heterogeneity *G*-statistic (G_H) within trials and between trials indicates the ratios between the individual G tests are heterogeneous and thus cannot be pooled and analyzed as one replicate. Asterisks (*) indicate a test was not performed due to a violation of a goodness of fit assumption that no more than 20% of the expected cell counts are less than five. Boldface denotes statistical significance; non-boldface *p*-values represent non-significant results due to the significance of the G_H. Results of the individual goodness of fit tests indicate in nearly all replicates that the numbers of **A.** burrows and **B.** isopods at the end of the experiments are highly dependent on substratum type. Wood appears to be the preferred substratum while preference varies amongst the other substrata. Trial three (Spring 2006) was excluded from the analysis due to lack of data.

A. Burrows

Fall 2005

Replicate	Marsh Bank	Wood	Sandstone	Styrofoam	*G*-value	d.f.	*P*-value
A	196	222	8	37	368.5	3	**<0.001**
B	126	344	4	20	609.6	3	**<0.001**
C	145	227	37	22	275.4	3	**<0.001**
D	107	367	0	56	605.6	3	**<0.001**
E	7	30	0	2	56.5	3	**<0.001**
F	5	8	4	6	1.5	3	0.6837
G	7	73	24	22	72.8	3	**<0.001**
H	15	73	39	29	45.7	3	**<0.001**
					G_H 403.0	21	**<0.001**

Table 3. (continued)

Fall 2006

Replicate	Marsh Bank	Wood	Sandstone	Styrofoam	*G* -value	d.f.	*P* -value
A	5	82	9	10	129.6	3	**<0.001**
B	17	89	39	11	90.8	3	**<0.001**
C	4	104	16	8	176.0	3	**<0.001**
D	5	166	38	33	234.8	3	**<0.001**
I	24	157	31	11	212.6	3	**<0.001**
					G_H 53.8	12	**<0.001**

Fall 2005 and 2006 Pooled

					G_T 2879.3	39	<0.001
Pooled	625	1433	155	205	G_P 1650.1	3	<0.001
					G_H 1229.2	36	**<0.001**

B. *Sphaeroma*

Fall 2005

Replicate	Marsh Bank	Wood	Sandstone	Styrofoam	*G* -value	d.f.	*P* -value
A	30	123	1	35	179.4	3	**<0.001**
B	53	281	6	16	503.9	3	**<0.001**
C	58	223	10	52	285.9	3	**<0.001**
D	99	496	0	50	900.9	3	**<0.001**
E	0	13	0	0	*	*	*
F	4	57	15	11	70.1	3	**<0.001**
G	2	0	0	3	*	*	*
H	4	47	27	26	42.7	3	**<0.001**
					G_H 235.6	15	**<0.001**

Fall 2006

A	0	51	6	5	98.8	3	**<0.001**
B	5	49	40	3	80.6	3	**<0.001**
C	0	62	10	4	121.4	3	**<0.001**
D	2	57	19	20	68.5	3	**<0.001**
I	6	90	22	8	131.3	3	**<0.001**
					G_H 61.9	12	**<0.001**

Fall 2005 and 2006 Pooled

					G_T 2483.6	33	<0.001
Pooled	261	1536	156	230	G_P 2005.6	3	<0.001
					G_H 478.0	30	**<0.001**

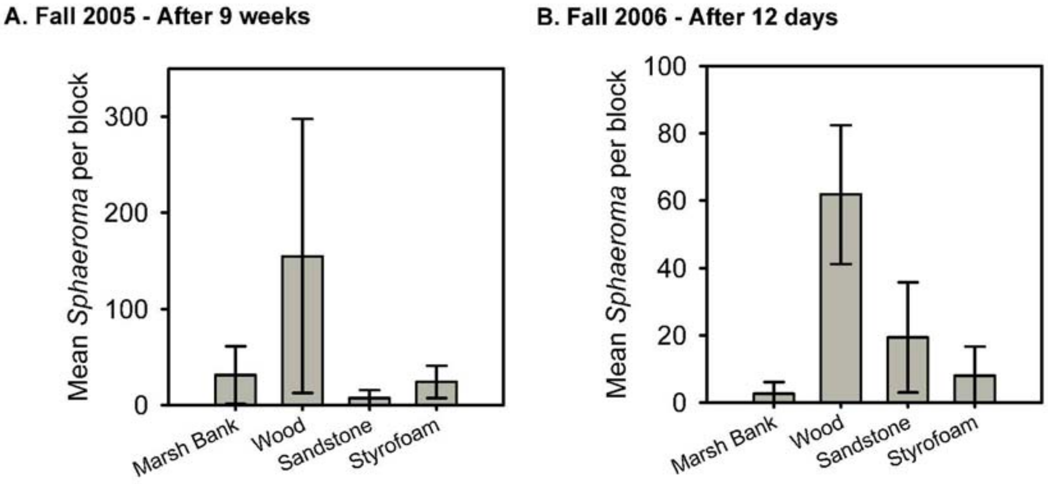


Figure 3. Mean number of isopods per block during **A.** Fall 2005 and **B.** Fall 2006. Error bars are 95% confidence intervals. The duration of the experiments varied from nine weeks for the Fall 205 trial and two days for the Fall 2006 trial.

Calculation of the normal standard deviates for the number of burrows present at the end of the experiment in thirteen replicates (eight in Fall 2005, five in Fall 2006) revealed that wood was the most preferred substratum (Table 4). Some replicates were not evaluated due to low expected cell counts (<5). Marsh bank was preferred in two replicates but was avoided in eight replicates. Sandstone was avoided in ten replicates and two replicates did not significantly contribute to the deviation from independence. Styrofoam substratum was avoided in twelve replicates and one replicate did not reveal any significant contribution to the deviation from independence. In all replicates, *Sphaeroma* greatly preferred to inhabit wood and avoided marsh bank blocks. Sandstone was preferred in one replicate, avoided in nine, and one was did not differ significantly. Styrofoam was avoided in nine replicates and there was not a significant response in two replicates.

Table 4. Compiled results of multiple goodness of fit tests with standardized residual analyses. The relationship between substratum type and **A)** *Sphaeroma* burrowing and **B)** *Sphaeroma* inhabitation were examined. Standardized residuals were analyzed to determine preference, avoidance, or if there was no response in *Sphaeroma* burrowing and presence in different substrata. The substrata within each replicate were classified as: 1) "Preferred" if their standardized residuals deviated significantly from independence ($d_{ij} \geq 1.96$), 2) "Avoided" if the standardized residuals deviated significantly from independence ($d_{ij} \leq -1.96$), or 3)"No Response" if the standardized residuals did not deviate significantly from independence ($1.96 > d_{ij} > -1.96$). Goodness of fit tests were not conducted when 20% of the expected cell counts were below five. See methods section for more detail on this analysis.

A. Burrows

Trial 1

	Preferred	Avoided	No Response
Marsh Bank	2	3	2
Wood	7	0	0
Sandstone	0	6	1
Styrofoam	0	7	0

Trial 3

	Preferred	Avoided	No Response
Marsh Bank	0	5	0
Wood	5	0	0
Sandstone	0	4	1
Styrofoam	0	5	0

Trials 1 and 3

	Preferred	Avoided	No Response
Marsh Bank	2	8	2
Wood	12	0	0
Sandstone	0	10	2
Styrofoam	0	12	0

Table 4. (continued)

B. *Sphaeroma*

Trial 1

	Preferred	Avoided	No Response
Marsh Bank	0	6	0
Wood	6	0	0
Sandstone	0	5	1
Styrofoam	0	5	1

Trial 3

	Preferred	Avoided	No Response
Marsh Bank	0	5	0
Wood	5	0	0
Sandstone	1	4	0
Styrofoam	0	4	1

Trials 1 and 3

	Preferred	Avoided	No Response
Marsh Bank	0	11	0
Wood	11	0	0
Sandstone	1	9	1
Styrofoam	0	9	2

Most heavily burrowed and colonized substratum

The most heavily burrowed substratum was wood in fourteen out of sixteen replicates, which differed significantly from expected ($G_{adj} = 9.82, P = 0.002 = 9.82$; Table 5). Marsh bank substratum were most heavily burrowed in two replicates but sandstone and Styrofoam blocks were never the most heavily burrowed. Isopods most heavily colonized wood substratum in thirteen replicates, marsh bank in two replicates, and Styrofoam in one replicate ($G_{adj} = 15.3, P < 0.001$).

Table 5. The most heavily burrowed substrata. Wood was most preferred out of all replicates analyzed; marsh bank was secondarily preferred. The substrata with the highest number of burrows and *Sphaeroma* within each respective replicate were analyzed using **G**-tests. Wood substrata contained the highest number of burrows in fourteen out of sixteen replicates and marsh bank was highest in two replicates. Boldface denotes statistical significance; G_{adj} represents the William's corrected *G*-statistics; Asterisks denote exclusion of that data from the test.

All Trials Ranked

	Preference Measure	
	Most Burrows	Most *Sphaeroma*
Marsh Bank	2	2
Wood	14	13
Sandstone	0*	0*
Styrofoam	0*	1
G_{adj}	9.8	15.3
d.f.	1	2
P-value	**0.002**	**<0.001**

Colonizer composition

Approximately 87% of all colonizers in trials one and three were young *Sphaeroma* (≤5mm). This pattern was consistent for most substrata (Table 6), except marsh banks where adults (>5mm) comprised ≈33% of the colonizers.

Table 6. The mean percentages of the colonizers by life history stage within each substratum. Young (≤5mm length) were the primary colonizers in all substrata.

	Adults (>5mm)	Young (≤5mm)
Marsh Bank	32.8	67.2
Wood	6.9	93.1
Sandstone	7.4	92.6
Styrofoam	9.1	90.9
All	13.5	86.5

Source of error for trial one

In trial one, the burrows within wood substrata began to coalesce in the last weeks of the experiment making discernment of individual burrows difficult in some replicates. This error is reflected in the occasional decrease in burrow counts from the previous week (Figure 2A, weeks 8-9 for example). In addition, the erosion of marsh bank blocks removed some of the burrows present in previous weeks. When erosion became significant (>10% of the surface area), replicates were removed. These errors may have decreased the power of this experiment, but likely did not impact the analysis since differences between wood and other substrata were so large. The same problems were not encountered within the shorter-term trials two and three, yet the variation remained high within all of the trials. Furthermore, I recognize that most Styrofoam floats are submerged subtidally. Thus, Styrofoam blocks placed in the intertidal may not simulate the exact habitat utilized by some *Sphaeroma* populations.

Discussion

Sphaeroma are habitat generalists capable of rapidly colonizing and burrowing into a variety of substrata. Results from this study, however, indicate they exhibit a strong preference for intertidal wood. In only nine weeks, *Sphaeroma* had riddled the experimental wood blocks with burrows. The preference for wood by *Sphaeroma* could be related to the physical characteristics of this substratum. Intertidal wood is often soft and spongy and can hold considerable amounts of water while maintaining its integrity. Other common intertidal substrata do not share the same characteristics as wood. Most sandstone is considerably harder than intertidal wood. Creating a burrow results in a greater expenditure of energy and more wear to the mandible used to chip chunks of substrata away. Burrowing into soft peaty marsh banks may be easy but that area is also dynamic and does not have the same strength as wood. Styrofoam is very firm and spongy but its hydrophobic nature means it absorbs and holds relatively little moisture, which suggests desiccation stress may be higher when the Styrofoam is in the intertidal zone. The following anecdotal observations support this idea. During a separate experiment, burrowed Styrofoam, marsh bank, and wood substrata were retrieved from the field and temporally stored in the sun. *Sphaeroma* within Styrofoam abandoned the shelter of their burrows en masse but *Sphaeroma* within burrowed marsh bank and wood retreated to the bottom of their burrows. This response may be due to the differing moisture capacity in these substrata.

Variation in the amount and rate of burrowing between replicates was very high. This variation between replicates may be related to the varying population densities in the substrata in front of the replicates. There were also variations in the response of *Sphaeroma* to marsh bank substrata between trials one and three. In trial one, marsh bank was burrowed into nearly as much as wood in some replicates while in trial three, marsh bank was avoided. The number of burrows within marsh bank blocks in trial one were 5-30 times greater than in trial three. These anomalous results cannot be attributed to location or methodology differences since both trials were conducted in the same location with the same methods and all substrata were collected from identical locations harboring existing *Sphaeroma* populations. It is possible there was some artifact from the freezing, cutting, and shaping of the marsh bank blocks, but processing was so minimal that this seems unlikely. The reason for this anomalous result remains unclear.

Interestingly, the observations of field densities do not align with the results of this experiment. Burrow densities in wood, sandstone, and Styrofoam substrata are highly variable and do not significantly differ from each other (Chapter III). Thus, other factors such as relative availability of substrata, propagule pressure, and gregarious behavior may be important determinants of *Sphaeroma* density.

Nearly 87% of the colonizers were young isopods, which suggests that juveniles disperse more than adults. This could be a function of their behavior or they may be actively evicted from a burrow by a larger isopod. This behavior is common in the congeneric isopod *S. terebrans* that eject young from the burrow, likely when they reach a size that interferes with feeding (Thiel 1999e). These results also indicate adults will occasionally leave existing burrows and colonize substrata, perhaps due to competition with other isopods.

Habitat use

The preference of *Sphaeroma* for wood substrata is congruent with natural history observations within its native region of Australia. In Australia, *Sphaeroma* is primarily recognized as a wood-boring organism; although occasionally it may be observed burrowing into friable rock and marsh banks and be found living under rocks or as a member of fouling communities (per. obs). The preference of *Sphaeroma* for wood may also be genetic in nature. Subpopulations of the estuarine amphipod *Eogammarus confervicolus* have genetically based preferences for the habitat in which the individuals were raised (Stanhope et al. 1992). Despite any genetic predilections towards wood substrata, the presence of large *Sphaeroma* populations in a diversity of intertidal and subtidal substrata illustrate the incredible ability of this organism to adapt to the changing quality, quantity, and type of intertidal habitat.

The numbers of *Sphaeroma* present in substratum blocks at the termination of the experiment was often considerably less than the numbers of burrows in those blocks. This indicates that *Sphaeroma* are creating burrows and then either dying or abandoning them. If the process of creating a burrow is energetically demanding, isopods may have reduced fitness and suffer higher mortality after creating burrows. Also, the burrows created by young colonizers are often very shallow and just barely enclose the isopod. Nemerteans may be able to prey upon young isopods within these shallow burrows, however, nemerteans were very rare within burrow samples taken in the experiment locations and in the surrounding intertidal areas (Chapter III, per. obs.). Another possibility is that colonizing isopods are for some unknown reason, finding their recently created burrow unsuitable, and are choosing to abandon it. The ratio of *Sphaeroma* to burrows was lowest in marsh bank substratum, which may be due to the physical characteristics of that substratum. Although burrows are relatively easy to create in marsh banks, they are not as stable as burrows within the other substrata and it is possible *Sphaeroma* choose to utilize these marsh bank burrows only temporarily.

Rate of burrowing

Sphaeroma colonization was rapid and considerably greater during trials one and three than trial two. These results suggest recruitment and thus the numbers of young are lower in April than the late summer-fall months. The rate of colonization varied greatly between and within replicates and across time. Within replicates, the rate of colonization is likely a function of the preference of *Sphaeroma* for certain substrata, while variation in the rate of burrowing between replicates is likely due to differences in *Sphaeroma* populations. The variation in burrowing rate over time may be an expression of variable reproductive timing and release of young. The peak in burrowing rate at week three in the Fall 2005 trial and in wood on day five in trial three is noteworthy since both peaks were measured on nearly the same day in September. This unusually high rate of colonization does not appear to be related to a specific abiotic condition and is most likely just normal seasonal variation.

Implications

Sphaeroma is a common invasive species within many estuaries along the Pacific coast of America. Prolific burrowing by *Sphaeroma* can lead to shoreline erosion and damage to maritime structures (Barrows 1919, Higgins 1956, Mills 1978, Carlton 1979, Talley et al. 2001). Results from this study indicate *Sphaeroma* can rapidly colonize intertidal substrata and in a matter of weeks completely riddle wood and other substrata. Burrowing rates can exceed 69 burrows per week within wood (of a surface area of 100cm^2) in areas with substantial *Sphaeroma* populations. The effects of burrowing are not limited to wood as, over time, *Sphaeroma* can also riddle marsh banks, sandstone terraces, and Styrofoam floating docks. Understanding the substratum preference of *Sphaeroma* and aspects of colonization may help determine methods to manage and control this invasion. For example, by outplanting a preferred substratum such as wood, and letting *Sphaeroma* colonize it, managers may be able to remove the newest cohort of *Sphaeroma* from an area. If this process were continued for several seasons, *Sphaeroma* populations may be lowered enough to reduce their impacts. Future research should examine the efficacy of different management strategies in reducing *Sphaeroma* populations.

CHAPTER VI

CONCLUDING SUMMARY

In as little as ten years, *Sphaeroma* has become a common member of the estuarine community in Coos Bay, Oregon. *Sphaeroma* are present in approximately one half of 373 intertidal sites and occurs primarily in waters with salinities between 5-30. While low salinity likely limits *Sphaeroma* populations at the terminal ends of the estuary and in the Coos River, the factor(s) limiting *Sphaeroma* from the lower estuary are unclear. Future experimentation should examine the role of decreased juvenile survivorship and the possible synergy between the effects of both low temperature and high salinity on survivorship.

Sphaeroma also occur in prolific densities within the most common intertidal substrata. Mean isopod densities in marsh bank, wood, and sandstone were 4,257, 23,713, and 24,324 individuals per $0.25m^3$, respectively. Isopod densities varied significantly between marsh bank, wood, and sandstone substrata ($P < 0.001$) and month of the year ($P < 0.05$). Densities of inquilines (burrow cohabitants) also varied significantly with substratum type ($P < 0.001$) with more inquilines inhabiting wood and sandstone substrata over marsh bank substratum. The creation of the anastomizing burrow networks provides novel habitat in many intertidal areas and harbors significant numbers of inquilines. The primary taxa found within burrows were highly mobile epibenthic organisms such as isopods and amphipods. While many burrow dwellers are likely incidental inhabitants, other inquilines depend upon the characteristics of the burrows to live in different habitats or higher in the intertidal than their normal distribution. The extension of their intertidal distribution may be due to the creation of a more habitatable microclimate within the burrow, which could ameliorate the stresses incurred at low tide.

The ecology of *Sphaeroma* also differs between Coos Bay and the two Australian embayments surveyed: the Tamar estuary (Tasmania) and Port Phillip Bay (Victoria). Populations of *Sphaeroma* in their native regions (Tamar estuary and Port Phillip Bay) of are less prevalent within marsh banks than introduced populations in Coos Bay. In addition, mean densities of *Sphaeroma* are significantly lower within Tamar estuary and Port Phillip Bay marsh banks than Coos Bay marsh banks. Mean densities of *Sphaeroma* within friable rock and wood in Coos Bay are higher than both the Tamar estuary and Port Phillip Bay but statistical significance was not detected. The abundance of *Sphaeroma* within Coos Bay could result from an ecological release from the factors that normally control their abundance in native regions. Lack of parasites and disease are suggested as the possible means by which *Sphaeroma* attain prolific densities in Coos Bay, although other factors may also be involved. In addition, a greater proportion of young are present in Coos Bay populations than Tamar estuary populations, which could suggests *Sphaeroma* reproduction or recruitment are being inhibited. *Sphaeroma* are distributed in a similar pattern throughout all embayments; isopods are restricted to waters between approximately 5-30 salinity.

Sphaeroma are prodigious burrowers in a variety of intertidal substrata. Previous studies revealed how densities differ between substrata, which could reflect a preference of one substratum over others. When offered marsh bank, wood, sandstone, and Styrofoam substrata, *Sphaeroma* exhibit a clear preference for wood. The numbers of burrows created in wood were significantly higher than all other substrata in nearly every replicate experiment. The mean rate of burrowing was also considerably higher in wood, attaining just under 70 burrows created per week (per $100cm^2$) in one experimental trial. *Sphaeroma* are rapid colonizers, capable of colonizing intertidal substrata in as little 24 hours. Nearly 87% of the colonizing isopods in all experiments were young isopods (≤5mm), which suggests that young isopods are the primary dispersal stage of *Sphaeroma*.

APPENDIX A

NORTHERN RANGE SURVEYS

The Australasian burrowing isopod (*Sphaeroma quoianum*, H. Milne Edwards 1840) was introduced to the Pacific Coast of North America during the 19th century from its native region of Australia and New Zealand (Carlton 1979). *Sphaeroma* was first discovered in San Francisco bay in 1893 and was likely introduced during the Gold Rush era (1850-1890) via ship fouling or by boring into wooden ship hulls (Carlton 1979). Since the initial introduction of *Sphaeroma* to the Pacific coast, additional populations have been noted in at least fourteen embayments, ranging from San Quintin Bay, Baja California to Coos Bay, Oregon (Menzies 1962, Iverson 1974, Carlton 1979, Cohen and Carlton 1995). Although international traffic was likely the vector for some of these introductions, the role of intraregional traffic in spreading *Sphaeroma* species along the Pacific Coast should not be ignored (see Wasson et al 2001). In addition to ship fouling as a vector, *Sphaeroma* could also be introduced through the transport of timber (log rafts), marsh restoration, or by rafting on burrowed flotsam such as Styrofoam and wood.

Some embayments on the Pacific Coast of North America now harbor significant populations of *Sphaeroma* (Talley et al. 2001, Chapter III). The establishment of large populations *Sphaeroma* along the Pacific Coast and constant intraregional traffic may facilitate the introduction of *Sphaeroma* to other estuaries. To determine if populations of *Sphaeroma* have expanded north of Coos Bay, a series of short intertidal surveys were conducted in several Oregon and Washington Bays including: Chetco River, Rouge River, Coquille River, Umpqua River, Suislaw River, Alsea Bay, Yaquina Bay, Siletz Bay, Nestucca Bay, Netarts Bay, Tillamook Bay, Columbia River, Young’s Bay, Willapa Bay, and Gray’s Harbor (Figure 1). Multiple intertidal locations were searched within each embayment during a single low tide. To maximize effort surveys were concentrated within the most accessible brackish areas harboring marsh banks and woody debris. These surveys were by no means conclusive and additional effort should be devoted to monitoring for this introduced species. The presence of other introduced species were also noted.

During an intertidal survey of Yaquina Bay, Oregon, a single adult *Sphaeroma* specimen was discovered burrowed into a piece of decayed wood in Boone Slough on March 2, 2005 (latitude 44º57787’, longitude -123º988’). In a subsequent survey (August 29, 2005), numerous burrows were found in a marsh bank in the same location. Several adult and juvenile *Sphaeroma* were found within the burrows, suggesting the establishment of a reproducing population (Table 1). The introduced commensal isopod (*Iais californica,* Richardson 1904) was also found clinging to the ventral side of adult *Sphaeroma*. Given the prolific densities *Sphaeroma* achieve in some Pacific Coast estuaries (Schneider 1976, Talley et al. 2001, Chapter III) coupled with ever increasing intraregional ship traffic, *Sphaeroma* populations will likely continue to expand north and threaten additional estuarine habitat.

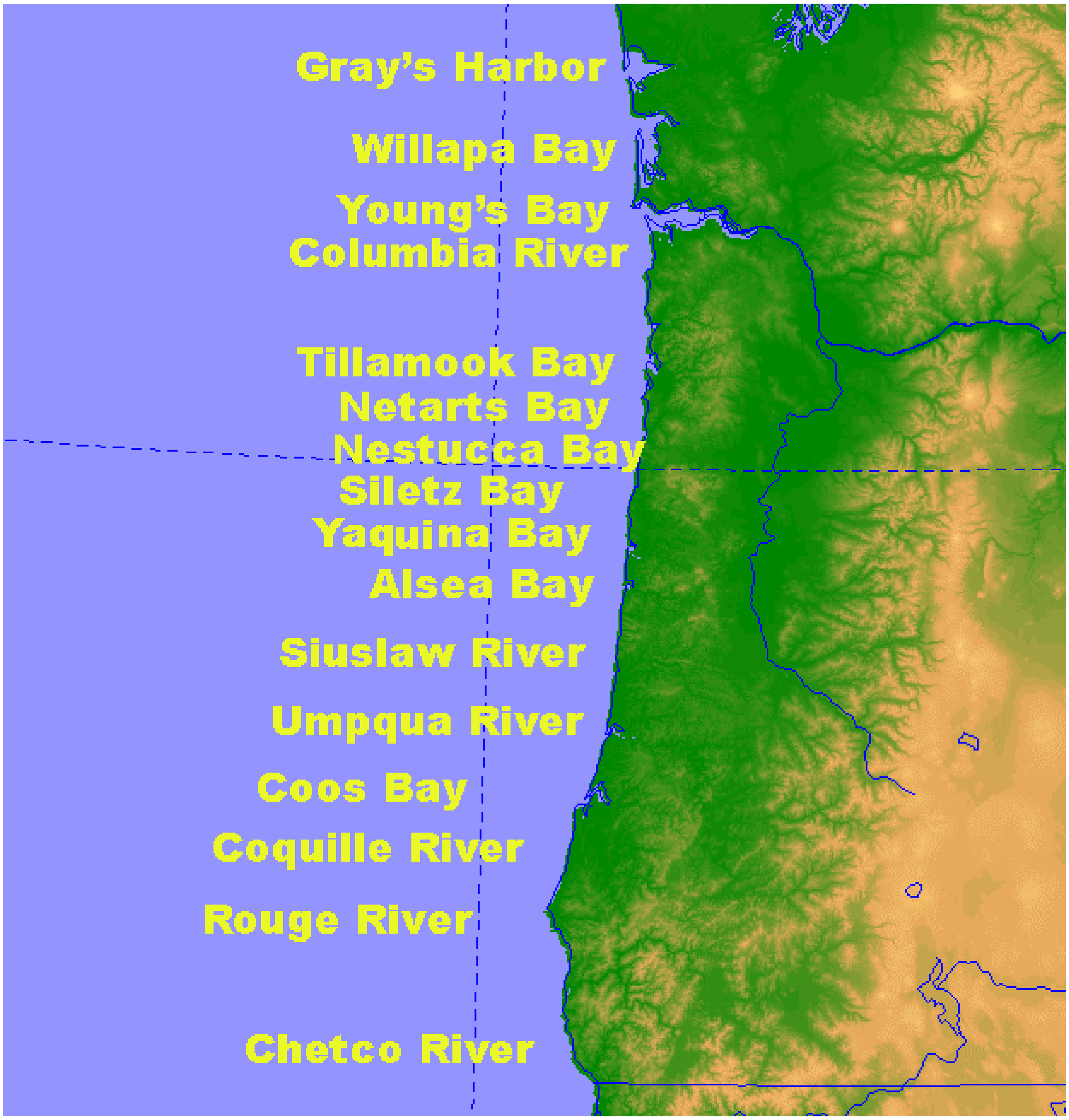


Figure 1. Locations of short intertidal surveys conducted in select Oregon and Washington embayments. *Sphaeroma* was found in marsh banks and wood within one site in Yaquina Bay, Oregon. Map modified from nationalatlas.gov.

Table 1. Raw data from distribution surveys of *Sphaeroma* (SQ) in select Pacific Coast embayments. Substrata include: M= peat, mud, or clay marsh bank, S= sandstone, C= claystone, W= wood, B= sandy beach, t= Styrofoam, F= fouling, L= sloping marsh, and R= hard rock riprap. Under the category *Burrowed?,* a “Y” denotes the presence of a burrowed substratum, “N” indicates no burrows were found, and “?” indicates burrows were found but could not confirm if they were created by *Sphaeroma*.. If *Sphaeroma* were found, a “Y” was noted under the category *SQ present?*.

Waypoint	Date	Embayment/Region	Location	Substrata	Burrowed?
A1	9/3/2005	Columbia	Pilings off of 30	W, R	N
A2	9/3/2005	Youngs Bay	off 202 near Dairy Queen	W, R	N
A3	9/3/2005	Youngs Bay	Tide Point Store	L, R, W	N
A4	9/3/2005	Youngs Bay	Turnoff	W, R	N
A5	9/3/2005	Youngs Bay	Near culvert	W, R	N
A6	9/3/2005	Columbia	Turnoff 101N Columbia	W, R	N
A7	9/3/2005	Columbia	Fort Columbia State Park	W, R	N
B1	9/5/2005	Willapa Bay	WNWR Boat Launch	M, R, t	N
B2	9/5/2005	Willapa Bay	Bridge off 101N	W, R	N
B3	9/5/2005	Willapa Bay	101N boat launch	M, R	N
B4	9/5/2005	Willapa Bay	Helen davis park, south bend launch	M, W	N
B5	9/5/2005	Willapa Bay	Turnoff	M, W	N
B6	9/5/2005	Willapa Bay	Willapa Harbor	t, F	N
B7	9/5/2005	Willapa Bay	Raymond Bridge	M, W	?
B8	9/5/2005	Willapa Bay	Near the junior scH. oregonensisol	M, W	N
C1	9/21/2005	Gold Beach		W	N
C2	9/21/2005	Gold Beach	Docks	t, F	N
D1	9/21/2005	Brookings	S. end of Port	R	N
D2	9/21/2005	Brookings	Docks	t, F	N
D3	9/21/2005	Brookings	Public Fishing Area	R	N
D4	9/21/2005	Brookings	Turnoff on north ** rd?	R	N
D5	9/21/2005	Brookings	Public Fishing Bar	Cobble, W	N
F1	9/6/2005	Suislaw	Park near FW outlet	W	N
F2	9/6/2005	Suislaw	Coffee Roasters, Old st	W	N
F3	9/6/2005	Suislaw	Docks	t	N
F4	9/6/2005	Suislaw	Turnoff	W, L	N
F5	9/6/2005	Suislaw	Weigh Station	W	N
F6	9/6/2005	Suislaw	off 126 near buisness	M, W	N
F7	9/6/2005	Suislaw	off 126	M, W	N
G1	9/4/2005	Gray's Harbor	backroads near airport	W, R	N
G2	9/4/2005	Gray's Harbor	Hoquim- under bridge	W, R	N
G3	9/4/2005	Gray's Harbor	Past bridge, Curtis boat ramp	W, M, R	N
G4	9/4/2005	Gray's Harbor	Near hwy 12 bridge	W, M, R	N
G5	9/4/2005	Gray's Harbor	off of 12 near mall	W, M	N
N1	9/1/2005	Nestucca	Public Boat Launch	W, M, R	N
N2	9/1/2005	Nestucca	Behind Thrift Store	W, R	N
N3	9/1/2005	Nestucca	Under Bridge	W, R	N
N4	9/1/2005	Nestucca	Bob Straub State park	R, L	N
NT1	9/1/2005	Netarts	Hatchery FW outlet	M, W, R	N
NT2	9/1/2005	Netarts	North of Hatchery	M, W, R	N
NT3	9/1/2005	Netarts	more North	M, W	N
NT4	9/1/2005	Netarts	Whiskey Creek Café	M, W	N
NT5	9/1/2005	Netarts	Turnoff near a culvert	W, R	N
NT6	9/1/2005	Netarts	Turnoff before Fork in road	W, M, R	N
R1	8/30/2005	Winchester	Marina	t, F	N
R2	8/30/2005	Winchester	Dock across RV Park	W, F	N
R3	8/30/2005	Winchester	Bridge near RV Park	W	N
R4	9/6/2005	Winchester	101 bridge under Les Schwab	M, W	N
R5	9/6/2005	Winchester	Weigh Station	W, R	N
R6	9/6/2005	Winchester	Turnoff Elk viewing area	M, W	N
S1	8/31/2005	Siletz	Turn out- No parking area	W	N
S2	8/31/2005	Siletz	Siletz Moorage	W, M, t	N
S3	8/31/2005	Siletz	Drift Creek	W, M, S	N
S4	8/31/2005	Siletz	Turn off of Siletz Wildlife Refuge	W, M, R	N
S5	8/31/2005	Siletz	Turn off East of S1	W, M, R	N
T1	9/2/2005	Tillamook	Bayocean - turnoff near dike	R, W	N
T10	9/2/2005	Tillamook	Garbaldi rip rap Boat basin	W, R	N
T11	9/2/2005	Tillamook	Boat Basin	t, F	N
T2	9/2/2005	Tillamook	turnoff near culvert	M, W	N
T3	9/2/2005	Tillamook	Oyster operation	M, W	N
T4	9/2/2005	Tillamook	Oyster Planting	W, L	N
T5	9/2/2005	Tillamook	Pilings	W, R	N
T6	9/2/2005	Tillamook	Rental house turnout	W, L	N
T7	9/2/2005	Tillamook	Pacific Oyster	W, R	N
T8	9/2/2005	Tillamook	Railroad turnout	W, R	N
T9	9/2/2005	Tillamook	Huge log down from T9	W, M, R	N
W1	8/30/2005	Alsea	Marina/Crabbing dock	t, F	N
W2	9/6/2005	Alsea	Bridge above slough	M, W	N
W3	9/6/2005	Alsea	Nelson Wayside	M, W	N
W4	9/6/2005	Alsea	Dock	t, W	N
W5	9/6/2005	Alsea	Turnoff old docks	M, W	N
Y1	8/31/2005	Yaquina	elbow near gas tank	W, M, R	N
Y2	8/31/2005	Yaquina	Sawyer's RV Park	W, R	N
Y3	8/31/2005	Yaquina	Bridge E of Sawyer's	W	N

Waypoint	SQ present?	Latitude	Longitude	Salinity	Temperature
A1	N	46.19007133	-123.8220437	6	NA
A2	N	46.1766975	-123.8525253	6	NA
A3	N	46.17669649	-123.8525207	6	NA
A4	N	46.1671894	-123.8167326	4	23
A5	N	46.16530901	-123.8386813	5	19.5
A6	N	46.24238907	-123.8865906	5	18.5
A7	N	46.25388318	-123.9241293	10	23
B1	N	46.41485771	-123.9357022	30	NA
B2	N	46.42940241	-123.9058616	NA	NA
B3	N	46.60837071	-123.9151295	21	NA
B4	N	46.6717757	-123.8157302	25	NA
B5	N	46.67817738	-123.7621632	NA	NA
B6	N	46.68348363	-123.7553503	18	NA
B7	N	46.68408595	-123.7359143	11	NA
B8	N	46.69086599	-123.7425474	17	NA
C1	N	42.42956794	-124.4020991	2	
C2	N	42.42155559	-124.4201343	8	
D1	N	42.05332048	-124.2693566	15	
D2	N	42.05037341	-124.2682289	21	
D3	N	42.0460926	-124.2691817	25	
D4	N	42.06564976	-124.2638253	16	
D5	N	42.06336712	-124.230308	0	
F1	N	43.96106587	-124.1013386	1	
F2	N	43.96579645	-124.1078121	20	
F3	N	43.96742094	-124.1016855	22	
F4	N	43.97461236	-124.0945883		
F5	N	43.97667398	-124.0771156	30	
F6	N	43.97780151	-124.0618584	19	
F7	N	43.98550079	-124.0438708	15	
G1	N	46.97148347	-123.9019675	29	NA
G2	N	46.97513119	-123.8760703	19	18.5
G3	N	46.97243784	-123.8039821	13	19
G4	N	46.97544484	-123.8114763	10	12
G5	N	46.97938677	-123.7813962	NA	NA
N1	N	45.19263717	-123.9552727	7	NA
N2	N	45.2043591	-123.9628926	2	NA
N3	N	45.20195366	-123.964205	3	NA
N4	N	45.19585406	-123.9640652	4	NA
NT1	N	45.39464205	-123.9366497	2	NA
NT2	N	45.39553287	-123.9371146	33	NA
NT3	N	45.39665773	-123.9368304	NA	NA
NT4	N	45.40146491	-123.9314213	31	NA
NT5	N	45.40702279	-123.9317289	33	NA
NT6	N	45.41475945	-123.9344398	33	NA
R1	N	43.68074343	-124.177113	25	NA
R2	N	43.67602777	-124.1845923	NA	NA
R3	N	43.67431518	-124.1784132	NA	NA
R4	N	43.6974245	-124.1149237	14	NA
R5	N	43.71549228	-124.0937165	19	NA
R6	N	43.69539876	-124.0437026	5	
S1	N	44.8955438	-123.9991612	15	NA
S2	N	44.90029634	-124.0071993	16	NA
S3	N	44.91225949	-124.0049806	3	NA
S4	N	44.89394101	-124.0143993	21	NA
S5	N	44.88718302	-123.9872969	16	NA
T1	N	45.50165305	-123.9365785	28	NA
T10	N	45.55421529	-123.9139419	30	NA
T11	N	45.55614959	-123.9137464	27	15
T2	N	45.49696941	-123.9309132	26	NA
T3	N	45.49059363	-123.9173232	0	11.5
T4	N	45.49052557	-123.9166711	NA	NA
T5	N	45.48817059	-123.9138533	24	NA
T6	N	45.47405538	-123.8969211	12	NA
T7	N	45.52342722	-123.8967736	17	NA
T8	N	45.55469256	-123.8998303	4	NA
T9	N	45.55540762	-123.8995369	2	NA
W1	N	44.43464616	-124.0585296	33	NA
W2	N	44.42247321	-124.0456959	20	NA
W3	N	44.41563408	-124.0337955	9	NA
W4	N	44.41416364	-124.0033585	19	NA
W5	N	44.41261534	-123.9922181	17	NA
Y1	N	44.62889107	-124.0231933	NA	NA
Y2	N	44.60107975	-124.00953	NA	NA
Y3	N	44.58946394	-124.0158082	NA	NA

APPENDIX B

NATURAL HISTORY NOTES ON *PSEUDOSPHAEROMA CAMPBELLENSE*

Pseudosphaeroma campbellense (=*P. campbellensis*) is a recent sphaeromatid invader in Coos Bay. It was discovered in 2003 in the Isthmus Slough and likely arrived through ship fouling (Carlton 2005). Populations have also been noted in San Francisco Bay. The isopod is native to New Zealand and possibly Australia. *Pseudosphaeroma* is present in Australia but there is some contention as to whether the species is native to Australia (Niel Bruce, per. comm.)

Pseudosphaeroma is found throughout Coos Bay including the South Slough, Isthmus Slough, Haynes Inlet, and Bridgeview marsh (Table 1). I conducted a snorkel survey at high tide (8ft) in September 2005 along the sandstone terraces in Haynes Inlet. During the survey, I found very large aggregations of *Pseudosphaeroma* clustered around the water-air interface. Thousands of isopods formed distinctive bands 4cm under to 2cm above the water level. Densities were approximately 200 *Pseudosphaeroma* per 100cm^2 and all isopods sampled were *Pseudosphaeroma*. Other sandstone terraces and rocks in area were also covered with a band of isopods.

When disturbed the isopods become very active and move quickly away either via swimming or walking. Large numbers of very small isopods were also found (51 out of 79 sampled) which could indicate recent reproduction. Coloration varies between greenish-black, gray, to bright green (similar to *Ulva* sp.). Coloration could reflect diet choice. The degree of tuberculation on the pleotelson also varies markedly. Older individuals have very distinct and large tubercles whereas very small isopods have very little or no tubercles present.

Pseudosphaeroma was also a common inquiline in *Sphaeroma* burrows (Chapter III). Mean densities of *Pseudosphaeroma* were higher within sandstone and wood substrata than marsh banks substratum (Figure 1).

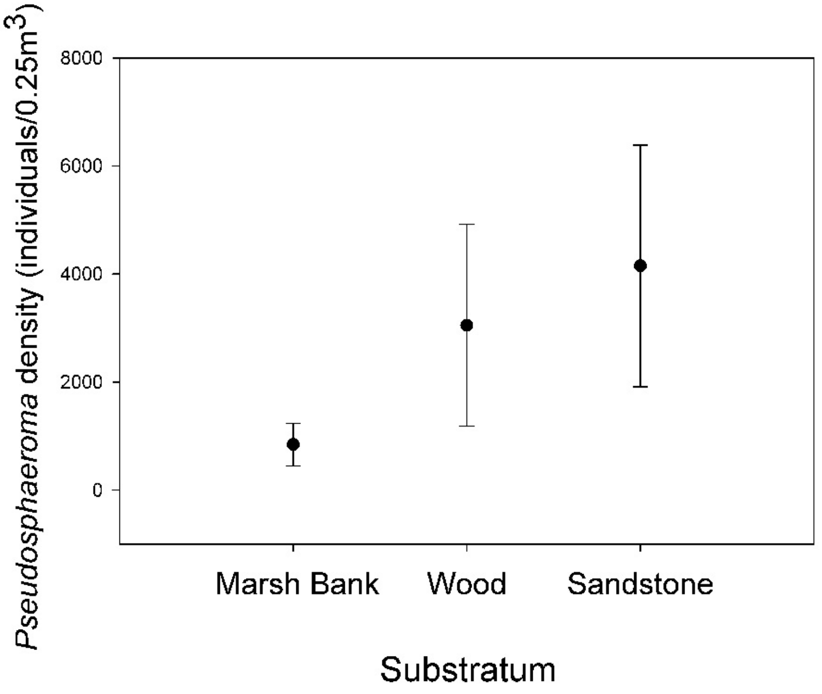


Figure 1. Mean number of *Pseudosphaeroma* (± 95% CI) per $0.25m^3$ in *Sphaeroma* burrows within three intertidal substrata.

Table 1. Noted occurrences of *Pseudosphaeroma* during distribution surveys in Coos Bay. Substrata present at each site include: M= peat, mud, or clay marsh bank, S= sandstone, C= claystone, W= wood, B= sandy beach, t= Styrofoam, F= fouling, L= sloping marsh, and R= hard rock riprap.

Waypoint	Substratum type	Site Descriptor	Estuary Region	Latitude	Longitude
436	M		Kentuck Inlet	43.41662555	-124.1924722
334	M		Pony Slough	43.40834415	-124.2309221
310	M	North	Haynes Inlet	43.4523996	-124.2144593
7	M	Opening of fork	South Slough	43.30115872	-124.3224736
500	W, t	Boat Ramp	Isthmus	43.36333148	-124.206013
355	S, W, M	Tidal Gate	Haynes Inlet	43.46582179	-124.1896859
452	M, S, W		Kentuck Inlet	43.42025081	-124.1980521
311	M	North	Haynes Inlet	43.45263136	-124.2141101
304	S	North	Haynes Inlet	43.45150047	-124.2159247
284	S	North	Haynes Inlet	43.45087451	-124.2224099
275	S	North	Haynes Inlet	43.45036305	-124.2243389
277	S, W	North	Haynes Inlet	43.45043421	-124.2238489
294	S, W	North	Haynes Inlet	43.45148027	-124.2190537
427	M	Bridgeview Ln	Coos Bay	43.40442452	-124.1959514
429	S, W	Bridgeview Ln	Coos Bay	43.40538986	-124.1979753
417	M, W	East of Mc Bridge	Coos Bay	43.41612758	-124.218977
376	W, t	North	McCollough bridge	43.43365029	-124.2195937
17	M	Glascow	Coos Bay	43.43227498	-124.2091882
104	S	School house point	South	43.31755824	-124.3213851
111	S	Valino Island	South	43.31331189	-124.3214301
526	S, W, R, Wood chip bank	near Empire Docks	Coos Bay	43.39888601	-124.2743471
520	B, W	BLM Boat Ramp	Coos Bay	43.41228683	-124.280571

APPENDIX C

RAW DATA FROM DISTRIBUTIONAL SURVEYS IN COOS BAY

Presented below are raw data (Tables 1 and 2) from distributional surveys in Coos Bay (Chapter II).

Table 1. Raw data from distribution surveys of *Sphaeroma* (SQ) in Coos Bay. Substrata include: M= peat, mud, or clay marsh bank, S= sandstone, C= claystone, W= wood, B= sandy beach, t= Styrofoam, F= fouling, L= sloping marsh, and R= hard rock riprap. If burrowed substrata were found, the burrowed substratum was noted using the code described above under the category *Burrowed?*. If *Sphaeroma* were found, the substratum the isopod was found within was noted under the category *SQ present?*. X= *Sphaeroma* are unable to burrow or inhabit these areas.

Waypoint	Date	Substrata	Burrowed?	SQ Present?	Site Descriptor
1		S, W	S, W	S, W	Glasgow
2		M, W, R	M, W	M, W	**Bob Angel**
7	8/4/2005?	M	M	M	**Opening of fork**
8	1/22/2005	M	M		**next to broken Dike**
9	8/5/2005	M	M	M	**Broken Dike**
10	8/5/2005	M	M	M	**Broken Dike**
4	8/5/2005	W	W	W	**Broken Dike**
6	1/22/2005	M, W, S	M, W, S	W	Long Island North
5	1/22/2005	M	M	M	**Other dike**
11		M	M	M	Red Dike Rd
12		M	M	M	Red Dike Rd
13		M	M	M	Red Dike Rd
14		M	M	M	Ashley Rd
15		M	M	M	Englewood Market
16		M	M	M	Line X
17		M	M	M	Glasgow
18		M	M	M	Glasgow
19		M	M	M	Spruce Rd Outlet
20		M	M		Kadora st
21		S, M, W	S, M, W	S, M, W	Park off 101N
22		M	M		
23		M			
24		M	M	M	
25		S	S	S	
26		M	M	M	
27		M	M	M	
28		M	M		
29		M	M		
30		M	M	M	Wrecking Rd
31		M	M		
32		M	M		
33		M	M		
34		M	M		
35		M	M	M	Coos Bay Speedway
41		M, W, t	M, W, t	M, W	Lanway Ln, Boat Launch
43		M, W, C	M, W, C	M, W, C	turnoff of 42W, before Davis
44		M	M		bridge
47		M, W	M, W	M, W	Bridge
48		M	M		
49		M	M		
50		M, W	M, W	M, W	Fred Meyers Parking lot
51		M, W	M, W	M, W	Fred Meyers Parking lot
52		M	M	M	Bridge
54		M, W	M, W		Isthmus Slough Dock
55		M, W	M, W		bridge
56		M	M		
57		M, W	M, W	W	Gunnel Rd
60		M, W	M, W	W	turnout after old green house
61		M, W			turnout
62		M, W	M, W	M, W	Weird Place
64		M, W, S	M, W, S	W, S	Petite Ln
75		S	S	S	
76		S	S	S	
77		S	S	S	
79		S			Coliver Pt
80		S	S		Coliver Pt
81		S			Coliver Pt
82		S	S	S	Coliver Pt
83		S, W	S, W	S, W	Coliver Pt
86		L	x		Younker Pt
87		L	x		Younker Pt
88		M			Younker Pt
89		S	S	S	Younker Pt
90		S	S	S	Younker Pt
91		M	M		
92		L	x		Crown Point
93		L	x		Crown Point
94		L	x		Crown Point
95		L	x		Crown Point

101		L, B	x		School house point
104		S	S	S	School house point
106		S, W	W	W	School house point
107		W	W	W	School house point
108		L	x		School house point
109		S	S	S	School house point
110		L	x		School house point
111		S	S	S	Valino Island
112		S	S	S	Valino Island
113		S	S		Valino Island
115		S	S		Valino Island
116		L	x		Valino Island
117		L, B	x, x		Valino Island
118		M	M		Valino Island
119		M	M		Valino Island
121		L	x		
122		M, W	W	W	
123		W	W		
124		M, W	W	W	
131		W			BLM Boat Ramp
132		W	W	W	BLM Boat Ramp
133		W	W	W	bridge
134		M, S	M, S	M, S	Weigh station
135		M	M	?	across weigh station
141		M, W	M		
142		M, W			floating dock
143		S, M, W	S, M, W	S	
144		M, W			
145		M, W	M, W		Doris County Park
146		M, R, L	M		
147		L	X	X	
149		L	X	X	
150		L	X	X	
151		L	X	X	
152		L, S	S		
153		L	X	X	
154		L	X	X	
155		L	X	X	just after fork in river
159		M			
171	5/29/2005	M			Metcalf Marsh
186	5/29/2005	M			Metcalf Marsh
217	5/29/2005	M			Metcalf Marsh
256	5/29/2005	M			Metcalf Marsh
257	5/29/2005	M			Metcalf Marsh
272	5/29/2005	M			Metcalf Marsh
275	6/03/2005?	S	S	S	North
276	6/03/2005?	S, W	S, W	S, W	North
277	6/03/2005?	S, W	S, W	S	North
278	6/03/2005?	S	S	S	North
279	6/03/2005?	L	X	x	North
280	6/03/2005?	L	X	x	North
281	6/03/2005?	S, W	S, W	W	North
282	6/03/2005?	M			North
283	6/03/2005?	M			North
284	6/03/2005?	S	S	S	North
285	6/03/2005?	L	X	X	North
286	6/03/2005?	M			North
287	6/03/2005?	M	M	M	North
288	6/03/2005?	L, W	W	W	North
289	6/03/2005?	S, W	S, W	S, W	North
290	6/03/2005?	M			North
291	6/03/2005?	M			North
292	6/03/2005?	S, W	W		North
293	6/03/2005?	S, W	S, W	S, W	North
294	6/03/2005?	S, W	S, W	S, W	North
295	6/03/2005?	L	X	X	North
296	6/03/2005?	M			North
297	6/03/2005?	S	S		North
298	6/03/2005?	L	X	X	North
299	6/03/2005?	M			North
300	6/03/2005?	L, W	W	W	North
301	6/03/2005?	S	S	S	North
302	6/03/2005?	S	S		North
303	6/03/2005?	S, W	S, W		North

305	6/03/2005?	S	S		North
306	6/03/2005?	M	M		North
307	6/03/2005?	M	M		North
308	6/03/2005?	M	M		North
309	6/03/2005?	S	S	S	North
310	6/03/2005?	M	M	M	North
311	6/03/2005?	M	M		North
312	6/03/2005?	M, W	M, W	W	North
313	6/03/2005?	M	M		North
314	6/03/2005?	M, W	M, W	M, W	North
315	6/03/2005?	M			North
316	6/03/2005?	M			North
320		M	M		
321		M	M		
322		M	M	M	
323		M	M		
324		M	M		
325		M	M		
326		M	M		
327		M	M		
328		M	M		
329		M	M		
330		M	M		
331		M	M		
332		M	M		
333		M	M	M	
334		M	M		
335		M	M	?	Apartments
336		M	M	?	Apartments
337		M	M	?	Apartments
338		R	X		
339		M	M	M	
340		M	M	?	Taco Bell
341		M	M		
343		M	M		Cinema
345		M, R	M		Bridge behind high school
346		M			
347		M	M		
349		R	X	X	Marion St.
350		M			Terminal end of HI S
351		M	M		Old wood dike
352		M, W	M, W	M, W	Old wood dike
355		S, W, M	S, W, M	S, W	Tidal Gate
356		M			South
357		M, W	M, W	M, W	2nd tidal gate
358		M	M		South
359		M	M		South
360		M	M		Pull off
361		M, W	M, W	W	South
362		L	X		South
363		S			South
364		S			South
365		M			South
366		M			South
367		M			South
368		M			South
369		M, W			South
370		M, W	M	M	South
371		M, W	M		South
372		M, W	M, W	M, W	South
373		S	S	S	South
374		W	W	W	South
375		S, W	S, W	S, W	North
376		W, T	W, T	W	North
377		W, S	W	W	North
378		L, W	W		North
379		L, W			South
380		L	X		South
381		L, W			South
382		L, W	W	W	South
383		L, W	W		South
384		L, W	W	W	South
385		L, W	W	W	Empire Docks
386		R	X		Empire Docks

388		R	X		Empire Docks
389		L	X		Empire Docks
390		M, W	W		Empire Docks
391		R, M, W	W	W	Wastewater Plant
392		L, W	W	?	
393		R	X		Deliverance temple
394		L	X		Fossil Point and Utility Shed
395		L, S			Fossil Point
396		L, S			Fossil Point
397		R	X		Fisherman's Wharf
398		R	X		Fisherman's Wharf
399		L, W			Fisherman's Wharf
400		R, W, T	T		Fisherman's Wharf
401		M, W	M, W	M, W	Bay Front
402		R, D, W	W	W	Bay Front
403		R, S, D, W, F	S, W	?, ?, F	Bay Front
404		R, D, W	?, W	?	Bay Front
405		R, D, W	?, W	?	Bay Front
406		R, D, W	?, W	?	Bay Front
407		R	X		Bay Front
408		R	x		Bay Front
409		R	x		Bay Front
410		L, W	W	W	Bay Front
411		R, W			Bay Front
412		R, W	W	W	Bay Front
413		R, Dock, W	?, W	?, W	Bay Front
414		R, W	W		East of Mc Bridge
415		L, W	W		East of Mc Bridge
416		L, M, W	M, W	W	East of Mc Bridge
417		M, W	M, W	M, W	East of Mc Bridge
418		M	M	M	Weird Place
419		M, W	M, W	M, W	Weird Place
420		M, W	M, W	M, W	Weird Place
421		M, W	M, W	W	Weird Place
422		M, W	M, W	W	pull off
426		L	x		Bridgeview Ln
427		M	M	M	Bridgeview Ln
428		L, S, W	S, W	S, W	Bridgeview Ln
429		S, W	S, W	S, W	Bridgeview Ln
430		L, W	W	W	Bridgeview Ln
431		S, W	W	W	Bridgeview Ln
432		S			Bridgeview Ln
433		S, W	W	W	Bridgeview Ln
434		S, W	S, W	S, W	Bridgeview Ln
435		S, W	W	W	Bridgeview Ln
436		M	M		
437		M, W	M, W	W	
438		M, W	W		
439		M			
440		M, W	W		
441		M	M		
442		M	M	?	Tidal Gate
443		R, W	W	W	Tidal Gate
444		L	x		
445		M			
447		M ,W	M ,W	W	
448		M, W	M, W	W	
449		M			
450		M, W	M, W	W	
451		M	M	M	
452		M, S, W	M, S, W	M, S, W	
453		S, W	S, W	S, W	
454		S, W	S, W	S, W	
455		S, W	S, W	S, W	
456		S			
457	6/8/2005	R	x		shipyard
458	6/8/2005	L	x		shipyard
459	6/8/2005	T	I		broken dock
465	6/8/2005	L	x	x	
467	6/8/2005	S	S	S	
468	6/8/2005	S, W	S	S	
469	6/8/2005	W			
470	6/8/2005	L	x	x	Oyster Farm, dock
471	6/8/2005	S			

473	6/8/2005	L	x	x	
474	6/8/2005	L	x	x	
476	6/8/2005	L, W	W	W	
477	6/8/2005	L, W	w	W	
478	6/8/2005	L, W, R	W	W	
479	6/8/2005	M, W	M, W	M, W	End, Fish Ladder
481	6/8/2005	M			End
482	6/8/2005	M, W			
483	6/8/2005	M, W			
484	6/8/2005	M, W			
485	6/8/2005	M, W	M, W		
486	6/8/2005	M, W	M, W		
487	6/8/2005	M, W	M, W	M, W	
488	6/8/2005	M, W	M, W	M, W	
489	6/8/2005	M, W	M, W	M, W	
490	6/8/2005	M	M		
491	6/8/2005	M			
492	6/8/2005	M, W	M, W	M, W	
498	7/7/2005	F, W, S,	W, S	W, S	Carlton Class site
500	7/7/2005	W, T	W	W	Boat Ramp
553	2/22/2006	W			
552	2/22/2006	R	x	x	
551	2/22/2006	R	x	x	**Charleston Boat dock**
550	2/22/2006	M	M	M	
549	2/22/2006	M, W	M, W	, W	
548	2/22/2006	W	W		
547	2/22/2006	M, W	M, W	W	
545	2/22/2006	M	M		near the sampler
544	2/22/2006	W	W		
543	2/20/2006	M, W	M, W	M, W	**RSC place**
542	2/20/2006	M, W	M, W	M, W	
541	2/20/2006	M, W	M, W	M, W	
540	2/20/2006	S, W	S, W	S, W	**Animal shelter turnoff**
539	2/20/2006	M, W	M, W	M, W	**turnoff- marsh channel**
537	2/20/2006	M, W	M, W	M, W	**turnoff before speedway and after Hyland**
535	2/19/2006	B	x	x	**Near smoke stack**
534	2/19/2006	S, R			
533	2/19/2006	S, R			
532	2/19/2006	B	x	x	**across from waste treatment**
531	2/19/2006	B	x	x	
530	2/19/2006	B	x	x	
529	2/19/2006	B	x	x	
528	2/19/2006	B, W	W	W	**next to pier, across from Empire Docks**
527	2/19/2006	W, R			**near Empire Docks**
526	2/19/2006	S, W, R	S, W	S, W	**near Empire Docks**
525	2/19/2006	B, W	W	W	**near pier**
524	2/19/2006	B	x	x	
523	2/19/2006	B, W			
522	2/19/2006	B, W			
521	2/19/2006	R, B, W	x, x, I	x, x, W	**Near lumber processing plant**
520	2/19/2006	B, W	x, I	x, W	**BLM Boat Ramp**
518	2/19/2006	R	x	x	**Rocky point**
517	2/19/2006	B	x	x	across from smoke stack
516	2/19/2006	B	x	x	across from smoke stack
515	2/19/2006	B	x	x	
513	2/19/2006	S			**across from marina**
512	2/19/2006	S			**across from marina**
511	2/19/2006	B	x	x	**across from marina**
510	2/19/2006	B	x	x	**Marina opening**
509	2/19/2006	B	x	x	**Cove**
508	2/19/2006	B	x	x	
507	2/19/2006	B	x	x	
506	2/19/2006	B, W			
505	2/19/2006	B, W			
504	2/19/2006	B, W			
503	2/19/2006	B, W			
502	2/19/2006	B, R, W			**Cove**
501	2/19/2006	R	x	x	**OIMB dock**
554	2/24/2006	R, W			**Turnoff (pt58)**
555		B, W			**Coast Guard Beach**
556		S			**OIMB beach**
557		M	M		**Before Doris Park- next to house with weird garden**
559		S, W			**steep pulloff past Doris Park**
558		M, W			**Boat ramp past Doris**

Table 2. Geographical location of *Sphaeroma* in Coos Bay.

Waypoint	**Estuary location**	lat	long	Salinity Class
1	Coos Bay	43.42960828	-124.2061766	Polyhaline
2		43.36103006	-124.194103	mesohaline
7	**South Slough**	43.30115872	-124.3224736	polyhaline
8	**South Slough**	43.3006848	-124.3229887	polyhaline
9	**South Slough**	43.29969758	-124.323738	polyhaline
10	**South Slough**	43.29852018	-124.3230646	polyhaline
4	**South Slough**	43.29904413	-124.3231839	polyhaline
6	South Slough	43.30659	-124.318457	polyhaline
5	South Slough	43.297768	-124.321396	polyhaline
11	Coalbank	43.34029491	-124.2262907	mesohaline
12	Coalbank	43.34129127	-124.2258738	mesohaline
13	Coalbank	43.3435237	-124.2237887	mesohaline
14	Coalbank	43.3443971	-124.2229161	mesohaline
15	Coalbank	43.35263617	-124.2235354	mesohaline
16	Coalbank	43.35463978	-124.2103384	mesohaline
17	Coos Bay	43.43227498	-124.2091882	Polyhaline
18	Coos Bay	43.43085559	-124.2079106	Polyhaline
19		43.46119682	-124.228632	mesohaline
20		43.48473933	-124.2225235	oligohaline
21	North Slough	43.45056891	-124.2258182	Polyhaline
22	North Slough	43.45078918	-124.2259634	polyhaline
23	North Slough	43.45259808	-124.2270869	polyhaline
24	North Slough	43.45269992	-124.2281303	polyhaline
25	North Slough	43.45261551	-124.228194	polyhaline
26	North Slough	43.45292489	-124.2291432	polyhaline
27	North Slough	43.45296152	-124.2291622	polyhaline
28	North Slough	43.45307468	-124.229318	polyhaline
29	North Slough	43.45393206	-124.2299187	polyhaline
30	Shinglehouse Slough	43.32627215	-124.2114664	mesohaline
31	Shinglehouse Slough	43.32620485	-124.2061573	mesohaline
32	Davis	43.28833415	-124.2278673	mesohaline
33	Davis	43.28834471	-124.2278639	mesohaline
34	Davis	43.29123664	-124.2413815	oligohaline
35	Isthmus	43.26559237	-124.2291125	mesohaline
41	Isthmus	43.25709304	-124.2147876	mesohaline
43	Isthmus	43.28352252	-124.2303211	mesohaline
44	Isthmus	43.2885877	-124.2257976	mesohaline
47	Isthmus	43.29875529	-124.2059137	mesohaline
48	Isthmus	43.3093071	-124.2098073	mesohaline
49	Isthmus	43.3259119	-124.2056542	mesohaline
50	Coalbank	43.35636528	-124.2095841	mesohaline
51	Coalbank	43.35779188	-124.2094373	mesohaline
52	Isthmus	43.35635338	-124.1950923	mesohaline
54	Isthmus	43.3635298	-124.2059774	mesohaline
55	Catching	43.3621011	-124.174476	mesohaline
56	Catching	43.35281647	-124.1699999	mesohaline
57	Catching	43.34744769	-124.1632363	mesohaline
60	Catching	43.31948206	-124.1535225	mesohaline
61	Catching	43.30886101	-124.1450297	oligohaline
62	Cooston Channel	43.38092652	-124.1721128	mesohaline
64		43.40218856	-124.1912001	mesohaline
75	South	43.32926114	-124.3248275	polyhaline
76	South	43.32925603	-124.3257129	polyhaline
77	South	43.329338	-124.3260771	polyhaline
79	South	43.32916928	-124.3271806	polyhaline
80	South	43.32930288	-124.3262821	polyhaline
81	South	43.32887256	-124.3246247	polyhaline
82	South	43.32883626	-124.3252678	polyhaline
83	South	43.32882905	-124.3254826	polyhaline
86	South	43.3241942	-124.3241985	Polyhaline
87	South	43.32352398	-124.3231597	Polyhaline
88	South	43.32263131	-124.3223807	Polyhaline
89	South	43.3228515	-124.3223695	Polyhaline
90	South	43.32287623	-124.3222594	Polyhaline
91	South	43.32025613	-124.3222737	Polyhaline
92	South	43.33136726	-124.3199566	Polyhaline
93	South	43.33279453	-124.3191065	Polyhaline
94	South	43.33126836	-124.3203303	Polyhaline
95	South	43.3300042	-124.3203205	Polyhaline
96	South	43.329524	-124.3209093	Polyhaline
97	South	43.32917497	-124.3204697	Polyhaline
98	South	43.32910214	-124.3203409	Polyhaline
99	South	43.32857458	-124.3194722	Polyhaline

101	South	43.32008447	-124.3195189	Polyhaline
104	South	43.31755824	-124.3213851	Polyhaline
106	South	43.3161925	-124.3209512	Polyhaline
107	South	43.31546838	-124.3204027	Polyhaline
108	South	43.31554952	-124.320588	Polyhaline
109	South	43.31569503	-124.3207874	Polyhaline
110	South	43.31581699	-124.3209615	Polyhaline
111	South	43.31331189	-124.3214301	Polyhaline
112	South	43.313231	-124.3215327	Polyhaline
113	South	43.31305507	-124.3216179	Polyhaline
115	South	43.31349059	-124.3210999	Polyhaline
116	South	43.31180558	-124.3225105	Polyhaline
117	South	43.31073923	-124.3228772	Polyhaline
118	South	43.31031318	-124.3221051	Polyhaline
119	South	43.31037629	-124.3225163	Polyhaline
121	South	43.31320133	-124.3225952	Polyhaline
122	Catching	43.36422809	-124.1773756	mesohaline
123	Coos Bay	43.42877126	-124.2507331	polyhaline
124	Jordan's Cove	43.43326044	-124.2493197	polyhaline
131	Coos Bay	43.41479184	-124.2792678	polyhaline
132	Coos Bay	43.4142497	-124.2795075	polyhaline
133	North Slough	43.43751518	-124.2361856	polyhaline
134	Coos River/Catching Slough	43.36223588	-124.1734466	mesohaline
135	Coos River/Catching Slough	43.36227939	-124.173432	mesohaline
141	Coos River	43.37216232	-124.146132	mesohaline
142	Coos River	43.37473087	-124.1407715	mesohaline
143	Coos River	43.37775707	-124.1302361	mesohaline
144	Coos River	43.37771592	-124.1074768	mesohaline
145	Coos River	43.38016184	-124.0949959	oligohaline
146	Coos River	43.36640546	-124.1515798	mesohaline
147	Coos River	43.3696454	-124.1472789	mesohaline
149	Coos River	43.37222049	-124.1426963	mesohaline
150	Coos River	43.37517033	-124.1351966	mesohaline
151	Coos River	43.37671168	-124.1304529	mesohaline
152	Coos River	43.37742649	-124.1271118	mesohaline
153	Coos River	43.37682174	-124.1208767	mesohaline
154	Coos River	43.37582957	-124.1112704	mesohaline
155	Coos River	43.37523588	-124.0954577	oligohaline
159	Coos River/Catching Slough	43.3591645	-124.1649495	mesohaline
171	South Slough	43.33627545	-124.3246464	euhaline
186	South Slough	43.33584705	-124.3251769	euhaline
217	South Slough	43.33504625	-124.3244975	euhaline
256	South Slough	43.33406531	-124.3278721	euhaline
257	South Slough	43.33419289	-124.3278223	euhaline
272	South Slough	43.33551144	-124.3266139	euhaline
275	Haynes Inlet	43.45036305	-124.2243389	Polyhaline
276	Haynes Inlet	43.45044301	-124.2241108	Polyhaline
277	Haynes Inlet	43.45043421	-124.2238489	Polyhaline
278	Haynes Inlet	43.45052188	-124.223713	Polyhaline
279	Haynes Inlet	43.45062993	-124.2235749	Polyhaline
280	Haynes Inlet	43.45072405	-124.2230505	Polyhaline
281	Haynes Inlet	43.45059439	-124.2229132	Polyhaline
282	Haynes Inlet	43.45073093	-124.2227694	Polyhaline
283	Haynes Inlet	43.450815	-124.2225079	Polyhaline
284	Haynes Inlet	43.45087451	-124.2224099	Polyhaline
285	Haynes Inlet	43.45089857	-124.2223541	Polyhaline
286	Haynes Inlet	43.45096294	-124.2221774	Polyhaline
287	Haynes Inlet	43.45111859	-124.2220736	Polyhaline
288	Haynes Inlet	43.45115949	-124.2219876	Polyhaline
289	Haynes Inlet	43.45147063	-124.2209009	Polyhaline
290	Haynes Inlet	43.45182845	-124.2204038	Polyhaline
291	Haynes Inlet	43.45160893	-124.2197813	Polyhaline
292	Haynes Inlet	43.45168965	-124.2194745	Polyhaline
293	Haynes Inlet	43.45153961	-124.2192567	Polyhaline
294	Haynes Inlet	43.45148027	-124.2190537	Polyhaline
295	Haynes Inlet	43.45160399	-124.2189578	Polyhaline
296	Haynes Inlet	43.45155763	-124.2187029	Polyhaline
297	Haynes Inlet	43.45163483	-124.218328	Polyhaline
298	Haynes Inlet	43.45160348	-124.2180574	Polyhaline
299	Haynes Inlet	43.45135605	-124.2178819	Polyhaline
300	Haynes Inlet	43.45129394	-124.2176957	Polyhaline
301	Haynes Inlet	43.45102455	-124.2173302	Polyhaline
302	Haynes Inlet	43.4509709	-124.2169215	Polyhaline
303	Haynes Inlet	43.45115706	-124.2164521	Polyhaline

305	Haynes Inlet	43.4515257	-124.2155657	Polyhaline
306	Haynes Inlet	43.45167657	-124.2153647	Polyhaline
307	Haynes Inlet	43.45178009	-124.2150973	Polyhaline
308	Haynes Inlet	43.45201906	-124.2147956	Polyhaline
309	Haynes Inlet	43.45220505	-124.2146925	Polyhaline
310	Haynes Inlet	43.4523996	-124.2144593	Polyhaline
311	Haynes Inlet	43.45263136	-124.2141101	Polyhaline
312	Haynes Inlet	43.45281299	-124.2139574	Polyhaline
313	Haynes Inlet	43.45358991	-124.2134204	Polyhaline
314	Haynes Inlet	43.45387347	-124.2132167	Polyhaline
315	Haynes Inlet	43.4544592	-124.2131182	Polyhaline
316	Haynes Inlet	43.45474712	-124.2130613	Polyhaline
320	Pony Slough	43.4084765	-124.2304072	Polyhaline
321	Pony Slough	43.40822646	-124.2303525	Polyhaline
322	Pony Slough	43.40864564	-124.230363	Polyhaline
323	Pony Slough	43.4086863	-124.2308756	Polyhaline
324	Pony Slough	43.40897949	-124.2307904	Polyhaline
325	Pony Slough	43.40953538	-124.2303978	Polyhaline
326	Pony Slough	43.41014458	-124.2304105	Polyhaline
327	Pony Slough	43.41070483	-124.230392	Polyhaline
328	Pony Slough	43.4109075	-124.2302025	Polyhaline
329	Pony Slough	43.41147923	-124.2299688	Polyhaline
330	Pony Slough	43.41188785	-124.2298625	Polyhaline
331	Pony Slough	43.4119026	-124.2295788	Polyhaline
332	Pony Slough	43.41229563	-124.2294519	Polyhaline
333	Pony Slough	43.40842713	-124.2307835	Polyhaline
334	Pony Slough	43.40834415	-124.2309221	Polyhaline
335	Pony Slough	43.40798649	-124.2310929	mesohaline
336	Pony Slough	43.40785305	-124.2311773	mesohaline
337	Pony Slough	43.40765566	-124.2311829	mesohaline
338	Pony Slough	43.40749699	-124.2311932	oligohaline
339	Pony Slough	43.40599948	-124.2313264	mesohaline
340	Pony Slough	43.40608288	-124.2316606	mesohaline
341	Pony Slough	43.40435654	-124.2320369	mesohaline
343	Pony Slough	43.40244463	-124.2320385	oligohaline
345	Pony Slough	43.39998043	-124.2310551	oligohaline
346	Pony Slough	43.40146344	-124.2315994	mesohaline
347	Pony Slough	43.40792673	-124.2331991	polyhaline
349	Pony Slough	43.40776856	-124.2360662	Polyhaline
350	Haynes Inlet	43.46922677	-124.1887119	Mesohaline
351	Haynes Inlet	43.46938494	-124.1891869	Mesohaline
352	Haynes Inlet	43.46944436	-124.1895093	Mesohaline
355	Haynes Inlet	43.46582179	-124.1896859	Mesohaline
356	Haynes Inlet	43.46554452	-124.1904136	Mesohaline
357	Haynes Inlet	43.46235009	-124.1939857	Mesohaline
358	Haynes Inlet	43.46254153	-124.1945019	Mesohaline
359	Haynes Inlet	43.46273415	-124.1953531	Mesohaline
360	Haynes Inlet	43.45878585	-124.1977419	Polyhaline
361	Haynes Inlet	43.45847555	-124.1982708	Polyhaline
362	Haynes Inlet	43.45815009	-124.1983198	Polyhaline
363	Haynes Inlet	43.45298868	-124.2010601	Polyhaline
364	Haynes Inlet	43.45268995	-124.2011184	Polyhaline
365	Haynes Inlet	43.45251887	-124.2000091	Polyhaline
366	Haynes Inlet	43.45040672	-124.1987132	Polyhaline
367	Haynes Inlet	43.44959686	-124.1993082	Polyhaline
368	Haynes Inlet	43.44875112	-124.2012932	Polyhaline
369	Haynes Inlet	43.4450107	-124.2112981	Polyhaline
370	Haynes Inlet	43.44523064	-124.2106108	Polyhaline
371	Haynes Inlet	43.44492763	-124.2115323	Polyhaline
372	Haynes Inlet	43.44476754	-124.2117939	Polyhaline
373	Haynes Inlet	43.44460099	-124.2123172	Polyhaline
374	Haynes Inlet	43.44461457	-124.2124915	Polyhaline
375	McColough bridge	43.43339791	-124.2202542	Polyhaline
376	McColough bridge	43.43365029	-124.2195937	Polyhaline
377	McColough bridge	43.43337477	-124.2212008	Polyhaline
378	McColough bridge	43.43493087	-124.2217674	Polyhaline
379	McColough bridge	43.42393021	-124.2244475	Polyhaline
380	McColough bridge	43.42410372	-124.2230869	Polyhaline
381	McColough bridge	43.42363215	-124.2211273	Polyhaline
382	McColough bridge	43.42240999	-124.2192274	Polyhaline
383	McColough bridge	43.42070234	-124.2183433	Polyhaline
384	McColough bridge	43.4208543	-124.2183655	Polyhaline
385	Cape Arago	43.39366366	-124.2798242	Polyhaline
386	Cape Arago	43.39505187	-124.2788486	Polyhaline

388	Cape Arago	43.39336225	-124.2802263	Polyhaline
389	Cape Arago	43.39247243	-124.2803437	Polyhaline
390	Cape Arago	43.39121732	-124.2797655	polyhaline
391	Cape Arago	43.38581007	-124.2837328	polyhaline
392	Cape Arago	43.38456418	-124.2835784	polyhaline
393	Cape Arago	43.38143597	-124.284646	euhaline
394	Cape Arago	43.35958226	-124.3082628	euhaline
395	Cape Arago	43.35798198	-124.3095283	euhaline
396	Cape Arago	43.35857743	-124.3113894	euhaline
397	Cape Arago	43.33944893	-124.3185864	euhaline
398	Cape Arago	43.33984924	-124.3179239	euhaline
399	Cape Arago	43.34158815	-124.3175238	euhaline
400	Cape Arago	43.33953819	-124.3195477	euhaline
401	Coos Bay	43.36458357	-124.2120864	Mesohaline
402	Coos Bay	43.36572544	-124.2121893	Mesohaline
403	Coos Bay	43.36720317	-124.2121643	Mesohaline
404	Coos Bay	43.36860068	-124.2118362	Mesohaline
405	Coos Bay	43.3723251	-124.2107759	Mesohaline
406	Coos Bay	43.37541785	-124.2117369	Mesohaline
407	Coos Bay	43.37868746	-124.216863	Mesohaline
408	Coos Bay	43.38032353	-124.218229	Mesohaline
409	Coos Bay	43.38354235	-124.2204972	Mesohaline
410	Coos Bay	43.39133718	-124.2189993	Polyhaline
411	Coos Bay	43.39884795	-124.2178969	Polyhaline
412	Coos Bay	43.40622562	-124.2207906	Polyhaline
413	Coos Bay	43.40827709	-124.2207963	Polyhaline
414	Coos Bay	43.41942385	-124.2182622	Polyhaline
415	Coos Bay	43.41810102	-124.2183583	Polyhaline
416	Coos Bay	43.41777806	-124.218456	Polyhaline
417	Coos Bay	43.41612758	-124.218977	Polyhaline
418	Cooston Channel	43.38106683	-124.172607	Mesohaline
419	Cooston Channel	43.38077003	-124.1730072	Mesohaline
420	Cooston Channel	43.38044473	-124.173394	Mesohaline
421	Cooston Channel	43.38107773	-124.1738948	Mesohaline
422	Cooston Channel	43.38833747	-124.1791231	Mesohaline
426	Coos Bay	43.40540084	-124.1964758	Polyhaline
427	Coos Bay	43.40442452	-124.1959514	Polyhaline
428	Coos Bay	43.40548022	-124.1975718	Polyhaline
429	Coos Bay	43.40538986	-124.1979753	Polyhaline
430	Coos Bay	43.40599897	-124.1986194	Polyhaline
431	Coos Bay	43.40669367	-124.1990978	Polyhaline
432	Coos Bay	43.40726464	-124.1989493	Polyhaline
433	Coos Bay	43.40789085	-124.1986813	Polyhaline
434	Coos Bay	43.40894538	-124.198066	Polyhaline
435	Coos Bay	43.40957176	-124.1978272	Polyhaline
436	Kentuck Inlet	43.41662555	-124.1924722	Polyhaline
437	Kentuck Inlet	43.41627644	-124.1927761	Polyhaline
438	Kentuck Inlet	43.41598609	-124.1933418	Polyhaline
439	Kentuck Inlet	43.41714271	-124.191999	Polyhaline
440	Kentuck Inlet	43.41955913	-124.1877815	Mesohaline
441	Kentuck Inlet	43.41700039	-124.1912937	Polyhaline
442	Kentuck Inlet	43.42185477	-124.1893744	Mesohaline
443	Kentuck Inlet	43.42160692	-124.1926948	Polyhaline
444	Kentuck Inlet	43.42142494	-124.194289	Polyhaline
445	Kentuck Inlet	43.4215303	-124.1946475	Polyhaline
447	Kentuck Inlet	43.4214723	-124.1956775	Polyhaline
448	Kentuck Inlet	43.42137465	-124.1961274	Polyhaline
449	Kentuck Inlet	43.42126695	-124.1963508	Polyhaline
450	Kentuck Inlet	43.42082991	-124.1969253	Polyhaline
451	Kentuck Inlet	43.42076722	-124.1971377	Polyhaline
452	Kentuck Inlet	43.42025081	-124.1980521	Polyhaline
453	Kentuck Inlet	43.42019331	-124.1995283	Polyhaline
454	Kentuck Inlet	43.42071877	-124.2004672	Polyhaline
455	Kentuck Inlet	43.42083821	-124.200676	Polyhaline
456	Kentuck Inlet	43.42004486	-124.1990224	Polyhaline
457	John Ney	43.33579525	-124.3198981	Euhaline
458	John Ney	43.33399574	-124.3170178	Euhaline
459	John Ney	43.33520374	-124.3153353	Euhaline
465	John Ney	43.33435826	-124.3137756	Euhaline
467	John Ney	43.33613849	-124.3124896	Euhaline
468	John Ney	43.33640898	-124.3125203	Euhaline
469	John Ney	43.33758932	-124.3107451	Euhaline
470	John Ney	43.3401033	-124.3089657	Polyhaline
471	John Ney	43.34091282	-124.3057644	Polyhaline

473	John Ney	43.34170424	-124.3025087	Polyhaline
474	John Ney	43.34048317	-124.3006765	Polyhaline
476	John Ney	43.33788285	-124.2979508	Polyhaline
477	John Ney	43.33689814	-124.2957662	Polyhaline
478	John Ney	43.33639381	-124.2939791	Polyhaline
479	John Ney	43.33651559	-124.2950763	Polyhaline
481	South Slough	43.27229999	-124.3186144	oligohaline
482	South Slough	43.27296627	-124.3182251	oligohaline
483	South Slough	43.27422288	-124.3187973	oligohaline
484	South Slough	43.2747952	-124.3194564	Mesohaline
485	South Slough	43.27544832	-124.3203038	Mesohaline
486	South Slough	43.27698765	-124.3192225	Mesohaline
487	South Slough	43.27918916	-124.3197506	Mesohaline
488	South Slough	43.2815029	-124.3192637	Mesohaline
489	South Slough	43.28370256	-124.3228333	Mesohaline
490	South Slough	43.2886188	-124.3215593	Mesohaline
491	South Slough	43.28908106	-124.3229993	Mesohaline
492	South Slough	43.29077538	-124.3217683	Mesohaline
498	Isthmus	43.363327	-124.198221	Mesohaline
500	Isthmus	43.36333148	-124.206013	Mesohaline
553		43.33657536	-124.3191386	Polyhaline
552		43.34341231	-124.3254215	Euhaline
551	South Slough	43.34681888	-124.3252181	Euhaline
550	South Slough	43.28351104	-124.3227979	Mesohaline
549	South Slough	43.28296747	-124.3221487	Mesohaline
548	South Slough	43.28257897	-124.3207865	Mesohaline
547	South Slough	43.28933269	-124.3039482	Mesohaline
545	South Slough	43.28965941	-124.3027501	Mesohaline
544	South Slough	43.34430892	-124.3285829	Mesohaline
543	Isthmus	43.34468426	-124.196919	Mesohaline
542	Isthmus	43.33936812	-124.1979264	Mesohaline
541	Isthmus	43.29528644	-124.2157472	Mesohaline
540	Isthmus	43.29554661	-124.2149476	Mesohaline
539	Isthmus	43.28927955	-124.2197392	Mesohaline
537	Isthmus	43.27092041	-124.2273714	Mesohaline
535		43.37483279	-124.2995028	Euhaline
534		43.38519978	-124.2977266	Euhaline
533		43.38692126	-124.295463	Euhaline
532		43.38901263	-124.2935168	Polyhaline
531		43.39179181	-124.2914989	Polyhaline
530		43.3934718	-124.2899871	Polyhaline
529		43.39595041	-124.2874311	Polyhaline
528	Coos Bay	43.39796651	-124.2856954	Polyhaline
527	Coos Bay	43.39732655	-124.2762414	Polyhaline
526	Coos Bay	43.39888601	-124.2743471	Polyhaline
525	Coos Bay	43.40383627	-124.2825151	Polyhaline
524		43.40507772	-124.2820561	Polyhaline
523		43.40750881	-124.281539	Polyhaline
522		43.40927328	-124.2812012	Polyhaline
521	Coos Bay	43.41033485	-124.2812694	Polyhaline
520	Coos Bay	43.41228683	-124.280571	Polyhaline
518	Coos Bay	43.38254674	-124.3012978	Euhaline
517	Coos Bay	43.37824951	-124.3043116	Euhaline
516	Coos Bay	43.37596519	-124.3064787	Euhaline
515	Mouth	43.35345249	-124.3181277	Euhaline
513	Mouth	43.35044866	-124.3149153	Euhaline
512	Mouth	43.34719791	-124.3167447	Euhaline
511	Mouth	43.34547233	-124.3185032	Euhaline
510	Charleston Harbor	43.34713521	-124.3206729	Euhaline
509	North Spit	43.35966524	-124.3245754	Euhaline
508	North Spit	43.35966691	-124.3245498	Euhaline
507	North Spit	43.37072533	-124.318122	Euhaline
506	North Spit	43.36982545	-124.3186124	Euhaline
505	North Spit	43.36889078	-124.3190202	Euhaline
504	North Spit	43.36726243	-124.3186458	Euhaline
503	North Spit	43.36427864	-124.3196314	Euhaline
502	North Spit	43.36145653	-124.3216135	Euhaline
501	Charleston Harbor	43.34588899	-124.3285032	Euhaline
554	Catching Slough	43.31237974	-124.1505107	oligohaline
555	Mouth	43.348442	-124.329407	Euhaline
556	Mouth	43.349645	-124.3312308	Euhaline
557	Coos River	43.377719	-124.11792	oligohaline
559	Coos River	43.390736	-124.082698	oligohaline
558	Coos River	43.404607	-124.062988	oligohaline

APPENDIX D

RAW DATA FROM DENSITY MEASUREMENTS IN COOS BAY

Presented below are the sampling locations (Figure 1) and raw data from the density measurements (Table 1) taken in August, January, and April of 2005-2006 (Chapter III).

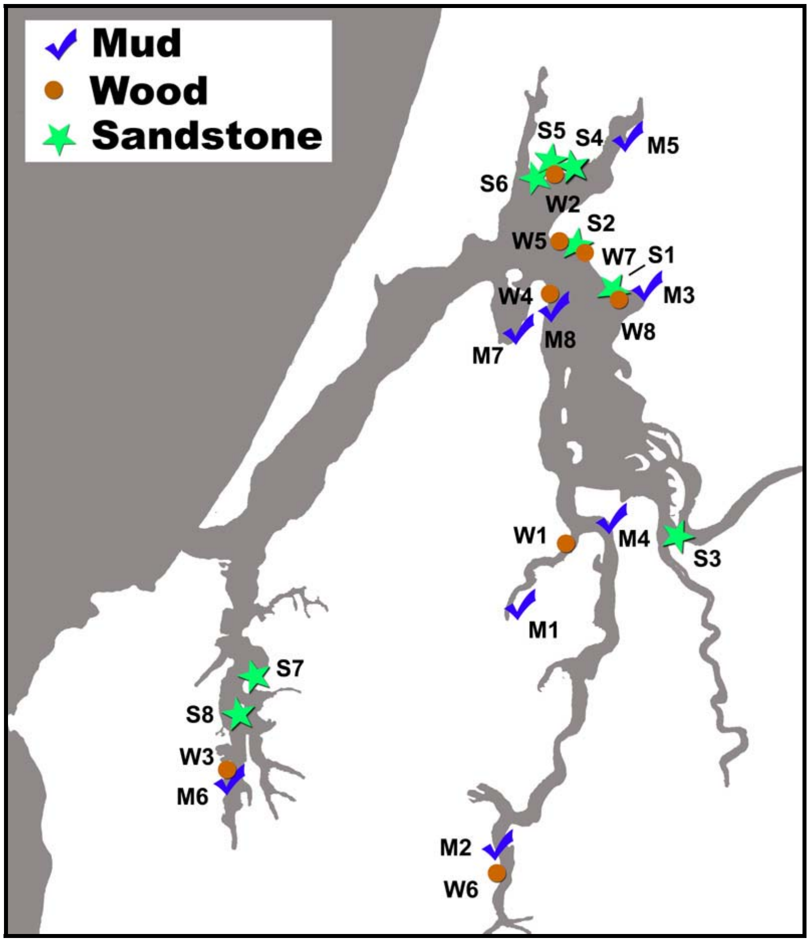


Figure 1. Sampling stations for density measurements (Chapter III). The substrata sampled at each station are noted by check marks (marsh banks), circles (wood), and stars (sandstone). Stations are designated as marsh bank (M1-M8), wood (W1-W8), or sandstone (S1-S8).

Table 1. Raw data from *Sphaeroma* density measurements in Coos Bay (Chapter III). Values represent mean density measurements (mean individuals per 0.25m^3). Stations are designated as marsh bank (M1-M8), wood (W1-W8), or sandstone (S1-S8). PC= *Pseudosphaeroma*.

Month	Location	Station Code	Sphaeroma	Burrows	Inquilines	PC
August	Red Dike Road	M1	1130.1	4294.4	9568.1	0.0
August	Coos Speedway	M2	1657.5	3850.7	1506.8	0.0
August	Near Bridgeview ln	M3	7835.3	4520.4	5273.8	301.4
August	Contractor's Place	M4	7006.6	5198.4	3314.9	0.0
August	Haynes Inlet Tide Gate	M5	5725.8	6027.2	1205.4	0.0
August	Broken Dike	M6	4843.3	5381.4	3874.6	0.0
August	Pony Slough Marsh	M7	5273.8	6705.2	4746.4	226.0
August	Ferry Road Park	M8	9417.5	7910.7	3917.7	979.4
January	Red Dike Road	M1	2260.2	4972.4	5047.8	0.0
January	Coos Speedway	M2	1808.2	5951.8	1205.4	0.0
January	Near Bridgeview ln	M3	7986.0	7006.6	8664.1	4445.0
January	Contractor's Place	M4	8890.1	10698.2	2184.8	0.0
January	Haynes Inlet Tide Gate	M5	3993.0	5273.8	4219.0	226.0
January	Broken Dike	M6	2335.5	7081.9	2335.5	979.4
January	Pony Slough Marsh	M7	3314.9	7609.3	2938.2	0.0
January	Ferry Road Park	M8	4897.1	10170.8	5198.4	3993.0
April	Red Dike Road	M1	1356.1	6780.6	14992.6	0.0
April	Coos Speedway	M2	828.7	5499.8	3541.0	0.0
April	Near Bridgeview ln	M3	5198.4	7910.7	9191.4	2712.2
April	Contractor's Place	M4	5650.5	7006.6	1054.8	0.0
April	Haynes Inlet Tide Gate	M5	2034.2	5951.8	1883.5	0.0
April	Broken Dike	M6	3239.6	5876.5	5424.5	3616.3
April	Pony Slough Marsh	M7	2712.2	7986.0	13787.2	75.3
April	Ferry Road Park	M8	4219.0	7910.7	3541.0	2184.8
August	Line X	W1	25349.8	15378.3	11618.2	0.0
August	Haynes Inlet Wood	W2	80313.7	49279.3	55232.4	24518.8
August	Near Broken Dike	W3	53996.1	14147.5	62282.3	0.0
August	Ferry Road Park	W4	31063.7	13121.2	18859.7	486.5
August	McColough Bridge	W5	23588.4	8920.9	36584.6	3613.1
August	Coos Speedway	W6	81165.1	24029.4	13242.1	0.0
August	Glasgow	W7	8638.2	11639.5	7097.7	347.2
August	Near Bridgeview ln	W8	9098.1	12382.3	17065.5	3371.6
January	Line X	W1	16378.8	17857.5	12113.4	0.0
January	Haynes Inlet Wood	W2	45243.4	32569.6	14765.4	7151.3
January	Near Broken Dike	W3	28978.0	37062.6	45835.6	0.0
January	Ferry Road Park	W4	10701.4	26349.6	8560.1	1951.3

January	McColough Bridge	W5	27321.9	29977.9	23969.7	875.6
January	Coos Speedway	W6	3811.6	15386.3	11158.3	0.0
January	Glasgow	W7	16027.0	17554.1	33440.6	768.8
January	Bridgeview	W8	54606.0	46166.3	53300.9	9216.9
April	Line X	W1	4132.1	13524.4	6959.7	0.0
April	Haynes Inlet Wood	W2	7164.3	24528.8	46287.4	590.3
April	Near Broken Dike	W3	12108.5	12531.0	9943.7	8819.9
April	Ferry Road Park	W4	3157.7	7708.5	9969.8	2522.4
April	McColough Bridge	W5	4783.0	9941.8	10519.0	0.0
April	Coos Speedway	W6	4469.9	15346.4	25975.8	0.0
April	Glasgow	W7	3998.4	19467.6	20018.4	5484.6
April	Near Bridgeview ln	W8	9242.3	8544.9	8772.2	0.0
August	Bridgeview	S1	66594.9	30102.9	9624.2	591.3
August	Glasgow	S2	52350.0	52391.6	47892.9	0.0
August	Weigh Station	S3	63749.6	21113.6	31447.8	0.0
August	Haynes Inlet 304	S4	50010.1	23260.4	24064.9	0.0
August	Haynes Inlet 294	S5	38799.7	18180.9	19502.2	1612.7
August	Haynes Inlet 277	S6	89355.2	29456.5	27457.7	12889.6
August	Schoolhouse Pt	S7	9445.5	10028.6	10614.5	1268.6
August	Valino Island	S8	2792.6	11271.5	4555.1	158.8
January	Near Bridgeview ln	S1	25651.8	44580.8	7465.6	0.0
January	Glasgow	S2	22895.3	47237.3	52026.4	480.3
January	Weigh Station	S3	7486.3	33087.1	3999.9	207.5
January	Haynes Inlet 304	S4	8231.2	9577.3	10930.9	1108.4
January	Haynes Inlet 294	S5	22384.9	29694.3	10278.8	5482.0
January	Haynes Inlet 277	S6	21695.9	42123.2	35135.6	29791.6
January	Schoolhouse Pt	S7	9917.7	12842.2	20548.4	2114.6
January	Valino Island	S8	8769.8	18536.1	11296.0	0.0
April	Near Bridgeview ln	S1	15573.1	74047.6	97156.3	0.0
April	Glasgow	S2	11213.9	41855.8	58138.0	0.0
April	Weigh Station	S3	4796.8	13581.2	3883.1	0.0
April	Haynes Inlet 304	S4	11260.6	12791.2	4415.3	364.4
April	Haynes Inlet 294	S5	18273.4	19415.5	18045.0	7537.8
April	Haynes Inlet 277	S6	13361.8	25693.6	38187.1	35991.1
April	Schoolhouse Pt	S7	8698.8	9303.0	2997.9	0.0
April	Valino Island	S8	456.8	7470.0	2275.7	0.0

APPENDIX E

IDENTIFYING CHARACTERISTICS OF *SPHAEROMA QUOIANUM*

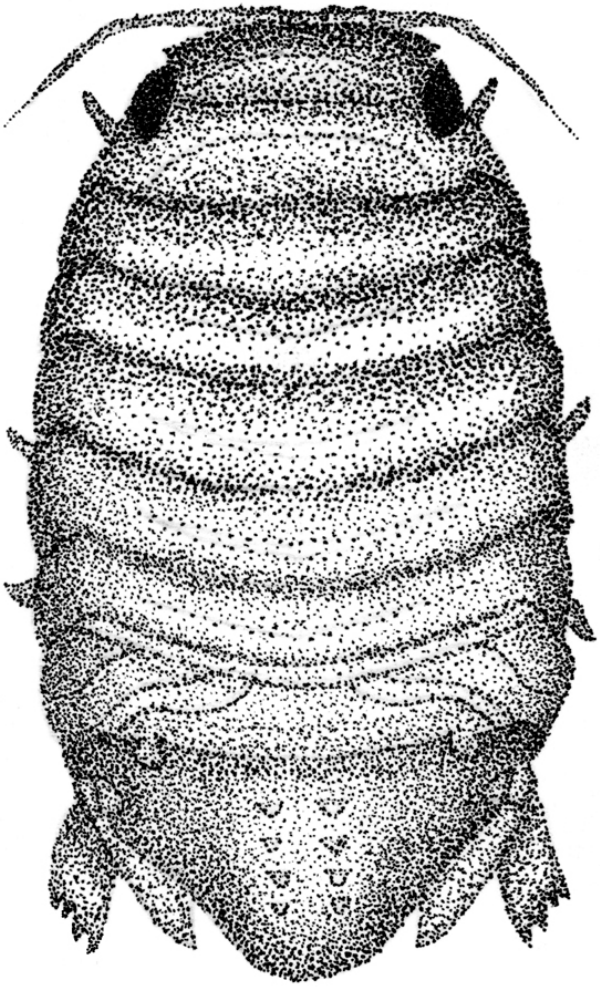


Figure 1. The Australasian burrowing isopod, *Sphaeroma quoianum*. *Sphaeroma* is a rotund sphaeromatid isopod ranging from dark gray/green to sandy in color. It may be distinguished from other common estuarine sphaeromatid isopods by the presence of a double longitudinal row of 4-5 tubercles on the pleotelson, long dense setae on pereopod one, the arrangement of the pleonites, and serrated outer uropods.

BIBLIOGRAPHY

Aikins S, Kikuchi E (2001) Studies on habitat selection by amphipods using artificial substrates within an estuarine environment. Hydrobiologia 457: 77-86

Arneson RJ (1975) Seasonal variations in tidal dynamics, water quality, and sediments in the Coos Bay estuary. PhD Thesis. Civil Engineering, Corvallis, Oregon

Baker WH (1926) Species of the isopod family Sphaeromidae from the eastern, southern, and western coasts of Australia. Trans Proc R Soc South Aust 50: 247-279

Baptista AM (1989) Salinity in Coos Bay, Oregon. Review of historical data (1930-1989). Army Corps of Engineers, ESE-89-001, Portland, Oregon

Barrows AL (1919) The Occurrence of a rock-boring isopod along the shore of San Francisco Bay, California. Univ Calif Publ Zool 19: 299-316

Bartsch P (1916) Marine borers. Naval Station, Pearl Harbor, Hawaii

Beckett R, Easton AK, Hart BT, McKelvie ID (1982) Water movement and salinity in the Yarra and Maribyrnong estuaries. Aust J Mar Freshw Res 33: 401-415

Behrens-Yamada S (2001) Global invader: the European green crab. Oregon Sea Grant, Corvallis, Oregon

Box GE (1953) Non-normality and tests on variances. Biometrika 40: 318-335

Boyd MJ, Mulligan TJ, Shaughnessy FJ (2002) Non-indigenous marine species of Humboldt Bay, California. Humboldt State University, Arcata, California

Brooks RA, Bell SS (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

Burt W, McAlister WB (1959) Recent studies in the hydrography of Oregon estuaries. Department of Oceanography, Oregon State College, Volume 7, Number 1, Corvallis, Oregon

Calvo-Ugarteburu G, McQuaid CD (1998) Parasitism and introduced species: Epidemiology of trematodes in the intertidal mussels *Perna perna* and *Mytilus galloprovincialis*. J Exp Mar Biol Ecol 220: 47-65

Carlton JT (1979) History, biogeography, and ecology of the introduced marine and estuarine invertebrates of the Pacific Coast of North America. PhD. Ecology, Davis, California

Carlton JT (1989) Man's role in changing the face of the ocean: biological invasions and implications for conservation of near-shore environments. Conserv Biol 3: 265-273

Carlton JT (1996) Marine Bioinvasions: The alteration of marine ecosystems by nonindigenous species. Oceanography 9: 36-43

Carlton JT (2001) Introduced species in U.S coastal waters: environmental impacts and management priorities. Pew Oceans Commission, Arlington, Virginia

Carlton JT (2005) Introduced and cryptgenic marine, brackish, and maritime organisms of Coos Bay, Oregon. Unpublished report. Williams College, Massachusetts

Carlton JT, Iverson EW (1981) Biogeography and natural history of *Sphaeroma walkerii* Stebbing (Crustacea: Isopoda) and its introduction into San Diego Bay, California. J Nat Hist 15: 31-48

Carlton JT, Thompson JK, Schemel LE, Nichols FH (1990) Remarkable invasion of San Francisco Bay (California, USA) by the Asian clam *Potamocorbula amurensis* . I. Introduction and dispersal. Mar Ecol Prog Ser 66: 81-94

Carlton JT, Vermeij GJ, Lindberg DR, Carlton DA, Dudley EC (1991) The first historical extinction of a marine invertebrate in an ocean basin: The demise of the eelgrass limpet *Lottia alveus*. Biol Bull 180: 72-80

Castilla JC, Guinez R, Caro AU, Ortiz V (2004) Invasion of a rocky intertidal shore by the tunicate *Pyura praeputialis* in the Bay of Antofagasta, Chile. Proceedings of the National Academy of Sciences 101: 8517-8524

Chilton C (1912) Miscellaneous notes on some New Zealand crustacea. Transactions of the New Zealand Institute 44: 128-135

Chilton C (1919) Destructive boring crustacea in New Zealand. N Z J Sci Tech 2: 1-15

Cohen AN, Carlton JT (1995) Nonindigenous aquatic species in a United States estuary: a case study of the biological invasion of San Francisco Bay and Delta. Biological study. University of California, Berkley, final report no. NOAA-NA36RG0467, FWS -14-48-0009-93-9 61, Berkley, California

Cohen AN, Carlton JT (1998) Accelerating invasion rate in a highly invaded estuary. Science 279: 555-558

Cohen BF, McArthur MA, Parry GD (2001) Exotic marine pests in the Port of Melbourne, Victoria. Marine and Freshwater Resources Institute, Report No. 25, Queenscliff, Victoria

Cookson LJ (1999) Twenty year marine trial of single and double preservative treated timber specimens in Australia. Material und Organismen 33: 65-79

Crooks JA (1998) Habitat alteration and community-level effects of an exotic mussel, *Musculista senhousia*. Mar Ecol Prog Ser 162: 137-152

Crooks JA (2002) Characterizing ecosystem-level consequences of biological invasions: the role of ecosystem engineers. Oikos 97: 153-166

Edgar GJ, Barrett NS, Graddon DJ (1999) A classification of Tasmanian estuaries and assessment of their conservation significance using ecological and physical attributes, population and land use. Tasmanian Aquaculture and Fisheries Institute, University of Tasmania, Series Number 2, Hobart, Tasmania

Eldredge LG, DeFelice, RC (2002) Checklist of the marine invertebrates of the Hawaiian Islands. Hawaii Biological Survey, Bishop Museum, Honolulu, Hawaii

Ellaway M, Beckett R, Hart BT (1980) Behaviour of iron and manganese in the Yarra estuary. Aust J Mar Freshw Res 31: 597-609

Elton C (1958) The ecology of invasions by animals and plants. Methuen, London, UK

Fernandez M, Iribarne O, Armstrong D (1993) Habitat selection by young-of-the-year Dungeness crab *Cancer magister* and predation risk in intertidal habitats. Mar Ecol Prog Ser 92: 171-177

Glude J (1955) The effect of temperature and predators on the abundance of the soft-shell clam, *Mya arenaria*, in New England. Trans Am Fish Soc 84: 13-26

Grosholz ED (2002) Ecological and evolutionary consequences of coastal invasions. Trends Ecol Evol 17: 22-27

Grosholz ED, Ruiz GM (2003) Biological invasions drive size increases in marine and estuarine invertebrates. Ecol Lett 6: 700-705

Hahn DR (2003) Alteration of microbial community composition and changes in decomposition associated with an invasive intertidal macrophyte. Biol Invasions 5: 45-51

Hale HM (1927) The crustaceans of South Australia. Handbooks of the flora and fauna of South Australia. British Science Guild (South Australian Branch), Adelaide, South Australia

Harris G, Batley G, Fox D, Hall D, Jernakoff P, Molloy R, Murray A, Newell B, Parslow J, Skyring G, Walker S (1996a) Port Phillip Bay environmental study - Final Report. CSIRO, Canberra, Australia

Harrison K, Holdich DM (1984) Hemibranchiate sphaeromatids (Crustracea: Isopoda) from Queensland, Australia, with a world-wide review of the genera discussed. Zool J Linn Soc 81: 275-387

Hass CG, Knott B (1998) Sphaeromatid isopods from the Swan River, Western Australia: diversity, distribution, and geographic sources. Crustaceana 71: 36-46

Hewitt CL (1993) Marine biological invasions: the distributional ecology and interactions between native and introduced encrusting organisms, PhD thesis, University of Oregon, Eugene, Oregon

Hewitt CL, Campbell ML, Thresher RE, Martin RB, Boyd S, Cohen BF, Currie DR, Gomon MF, Keough MJ, Lewis JA, Lockett MM, Mays N, McArthur MA, O'Hara TD (2004) Introduced and cryptogenic species in Port Phillip Bay, Victoria, Australia. Mar Bio 144: 183-202

Hewitt CL, Campbell ML, Thresher RE, Martin RB (1999) Marine biological invasions of Port Phillip Bay, Victoria. Centre for Research on Introduced Marine Pests, 20, CSIRO Marine Research, Hobart, Tasmania

Higgins CG (1956) Rock-boring isopod. Bull Geo Soc Amer 67: 1770

Hill CL, Kofoid CA (1927) Marine borers and their relation to marine construction on the Pacific Coast. Final Report of the San Francisco Bay Marine Piling Committee, San Francisco

Holdich DM, Harrison K (1983) Sphaeromatid isopods (Crustacea) from brackish waters in Queensland, Australia. Zool Scr 12: 127-140

Hurley DE, Jansen KP (1977) The marine fauna of New Zealand: Family Sphaeromadtidae (Crustacea: Isopoda: Flabellifera). Mem N Z Ocean Inst 63: 1-95

Iverson EW (1974) Range extensions for some California marine isopod crustaceans. Bull. South. Calif. Acad. Sci. 73: 164-169

Jansen KP (1970) Effect of temperature and salinity on survival and reproduction in Baltic populations of *Sphaeroma hookeri* Leach, 1814 and *S. rugicauda* Leach, 1814. Ophelia 7: 177-184

Jansen KP (1971) Ecological studies on intertidal New Zealand Sphaeromatidae (Isopoda: Flabellifera). Mar Bio 11: 262-285

Johnson ME, Snook HJ (1927) Seashore animals of the Pacific Coast. Dover Publications, New York

Jones CG, Lawton JH, Shachak M (1994) Organisms as ecosystem engineers. Oikos 69: 373-386

Jones CG, Lawton JH, Shachak M (1997) Positive and negative effects of organisms as physical ecosystem engineers. Ecology 78: 1946-1957

Kelley BJ, Burbanck WD (1972) Osmoregulation in juvenile and adult *Cyathura polita* (Stimpson) subjected to salinity changes and ionizing gamma irradiation (Isopoda, Anthuridea). Chesapeake Science 13: 201-205

Kouwenberg J, Pinkster S (1985) Population dynamics of three brackish water isopod species (Crustacea) in the lagoon system of Bages-Sigean (France). 2: Life cycles, sexual activity and fecundity. Vie Milieu 35: 79-92

Kussakin OF, Malyutina MV (1993) Sphaeromatidae (Crustacea : Isopoda : Flabellifera) from the South China Sea. Invertebr Taxon 7: 1167-1203

Levin L, Blair N, DeMaster D, Plaia G, Fornes W, Martin C, Thomas C (1997) Rapid subduction of organic matter by maldanid polychaetes on the North Carolina slope. J Mar Res 55: 595-611

Lodge DM, Kershner MW, Aloi JE, Covich AP (1994) Effects of an omnivorous crayfish (*Orconectes rusticus*) on a freshwater littoral food web. Ecology 75: 1265-1281

Meadows P, Meadows A (1991) The environmental impact of burrowing animals and burrows Symposia of the Zoological Society of London. Oxford University Press, Oxford

Menzies RJ (1962) The marine isopod fauna of Bahia De San Quintin, Baja California, Mexico. Pacific Naturalist 3: 337-348

Messana G, Bartolucci V, Mwaluma J, Osore M (1994) Preliminary observations on parental care in *Sphaeroma terebrans* Bate 1866 (Isopoda Sphaeromatidae), a mangrove wood borer from Kenya. Ethol Ecol Evol 3: 125-129

Miller RC (1926) Ecological relations of marine wood-boring organisms in San Francisco Bay. Ecology 7: 247-254

Mills PE (1978) *Sphaeroma quoyana* on treated poles in New Zealand. International Biodeterioration Bulletin 14: 35-36

Morton B (1987) Recent marine introductions into Hong Kong. Bull Mar Sci 41:503-513

Morton J, Miller M (1968) The New Zealand sea shore. Collins, London - Auckland

Murata Y, Wada K (2002) Population and reproductive biology of an intertidal sandstone-boring isopod, *Sphaeroma wadai* Nunomura, 1994. J Nat Hist 36: 25-35

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.

Paradice WEJ (1926) Some recent Natural History Observations. A Note on the Occurences of burrowing crustacean, *Sphaeroma quoyana* at Cockatoo Island, Sydney. Aust Zool 4: 319

Poore GCB, Kudenov JD (1978) Benthos of the Port of Melbourne: The Yarra River and Hobsons Bay, Victoria. Aust J Mar Freshw Res 29: 141-155

Posey MH (1988) Community changes associated with the spread of an introduced seagrass, *Zostera japonica*. Ecology 69: 974-983

Queen J, Burt WV (1955) Hydrography of Coos Bay. School of Science, Oregon State College, Data Report No. 1, Corvallis, Oregon

Quinn GP, Keough MJ (2002) Experimental design and data analysis for biologists. Cambridge University Press, Cambridge, U.K.

Ricketts EF, Calvin J, Hedgpeth JW (1968) Between Pacific Tides. Stanford University Press, Stanford, California

Riegel JA (1959) Some aspects of osmoregulation in two species of Sphaeromid isopod crustacea. Bio Bull 116: 272-284

Roegner GC, Shanks AL (2001) Import of Coastally-Derived Chlorophyll a to South Slough, Oregon. Estuaries 24: 244-256

Rohde K (2005) Marine parasitology. CSIRO ; CABI, Collingwood, Victoria

Rotramel G (1975) Filter-feeding by the marine boring isopod, *Sphaeroma quoyanum* H. Milne Edwards, 1840 (Isopoda, Sphaeromatidae). Crustaceana 28: 7-10

Ruiz GM, Fofonoff P, Hines AH, Grosholz ED (1999) Non-indigenous species as stressors in estuarine and marine communities: Assessing invasion impacts and interactions. Limnol Oceanogr 44: 950-972

Rumrill S (2006) Site profile of the South Slough Estuary, Oregon: a National Estuarine Research Reserve. National Oceanic and Atmospheric Administration. National Ocean Service. Estuarine Reserves Division, Charleston, Oregon

Schneider MR (1976) Population Dynamics of the Symbiotic Marine Isopods, *Sphaeroma quoyana* and *Iais californica*. Masters Thesis. Biology, San Francisco State University, San Francisco

Smith BJ (1995) Tamar Intertidal Invertebrates an Atlas of the Common Species. Queen Victoria Museum and Art Gallery, Launceston, Tasmania

Sokal R, Rohlf FJ (1981) Biometry. W.H. Freeman and Company, New York

Stanhope MJ, Connelly MM, Hartwick B (1992) Evolution of a crustacean chemical communication channel: Behavioral and ecological genetic evidence for a habitat-modified, race-specific pheromone. J Chem Ecol 18: 1871-1887

Stanhope MJ, Levings CD (1985) Growth and production of *Eogammarus confervicolus* (Amphipoda: Anisogammaridae) at a log storage site and in areas of undisturbed habitat within the Squamish Estuary, British Columbia. Can J Fish Aquat Sci 42: 1733-1740

Svavarsson J, Daviosdottir B (1994) Foraminiferan (Protozoa) epizoites on Arctic isopods (Crustacea) as indicators of isopod behaviour? Mar Bio 118: 239-246

Talley TS, Crooks JA, Levin LA (2001) Habitat utilization and alteration by the invasive burrowing isopod, *Sphaeroma quoyanum*, in California salt marshes. Mar Bio 138: 561-573

Thiel M (1998) Extended parental care in marine amphipods. I. Juvenile survival without parents. J Exp Mar Biol Ecol 227: 187-201

Thiel M (1999a) Duration of extended parental care in marine amphipods. J Crustac Biol 19: 60-71

Thiel M (1999b) Duration of extended parental care in marine amphipods. J Crustac Biol 19: 60-71

Thiel M (1999c) Extended parental care in marine amphipods II. Maternal protection of juveniles from predation. J Exp Mar Biol Ecol 234: 235-253

Thiel M (1999d) Host-use and population demographics of the ascidian-dwelling amphipod *Leucothoe spinicarpa*: indication for extended parental care and advanced social behaviour. J Nat Hist 33: 193-206

Thiel M (1999e) Reproductive biology of a wood-boring isopod, *Sphaeroma terebrans,* with extended parental care. Mar Bio 135: 321-333

Thiel M (2003) Reproductive biology of *Limnoria chilensis*: another boring peracarid species with extended parental care. J Nat Hist 37: 1713-1726

Torchin ME, Lafferty KD, Dobson AP, McKenzie VJ, Kuris AM (2003) Introduced species and their missing parasites. Nature 421: 628-630

Torchin ME, Lafferty KD, Kuris AM (2001) Release from parasites as natural enemies: increased performance of a globally introduced marine crab. Biol Invasions 3: 333-345

Torchin ME, Lafferty KD, Kuris AM (2002) Parasites and marine invasions. Parasitology 124: S137-S151

Underwood AJ (1981) Techniques of analysis of variance in experimental marine biology and ecology. Oceanogr. Mar. Biol. Annu. Rev. 19: 513-605

Vitousek PM, D'Antonio CM, Loope LL, Rejmanek M, Westbrooks R (1997) Introduced species: a significant component of human-caused global change. N Z J Ecol 21: 1-16

Wasson K, Zabin CJ, Bedinger L, Diaz MC, Pearse JS (2001) Biological invasions of estuaries without international shipping: the importance of intraregional transport. Biol Conserv 102: 143-153

Whittam T, Siegel-Causey D (1981) Species incidence functions and Alaskan seabird colonies. J Biogeogr 8: 421-425

Williams D (1976) Improved likelihood ratio tests for complete contingency tables. Biometrika 63: 33-37

Wilson E (1961) The nature and the taxon cycle in the Melanesian ant fauna. Am Nat 95: 169-193

Zar JH (1996) Biostatistical analysis. Prentice Hall Upper Saddle River, New Jersey