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The Influence of Multiple Scales of Environmental Context on
the Distribution and Interaction of an Invasive Seagrass and
its Native Congener

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Abstract

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Predicting invasive species impacts is complicated by the variable context in which they occur. Furthermore, species invasion is an inherently multi-scale process, warranting examination at multiple spatial scales. In its introduced range, the invasive seagrass *Zostera japonica* often grows at higher elevations than its native congener, *Zostera marina*, but at some sites the congeners overlap. At overlapping sites, the two seagrasses often grow in a patch mosaic associated with intertidal microtopography. I examine the role of multiple scales of environmental context in the vertical zonation of *Z. japonica* and *Z. marina*, and the relationship of meter to decameter scale microtopography to the local distribution and biotic interactions of *Z. marina* and *Z. japonica*.

Nearshore intertidal topography, hydrodynamic exposure, and tidal range were examined as abiotic predictors of the deep extents of *Z. japonica* and *Z. marina*, the

shallow extent of *Z. marina* and the elevation overlap of the two species, both at within site and among site spatial scales. Bottom profile complexity was the most consistently important predictor studied, confirming the importance of the geomorphic template on the zonation of these species. *Z. japonica*'s deep extent was well-predicted by *Z. marina*'s shallow extent, but *Z. marina*'s shallow extent was best predicted by physical factors.

Using a terrestrial laser scanner, I mapped and monitored a one hectare study site for three years. The location and shape of microtopographic features were generally stable from year to year, but the magnitude of local relief was variable. *Z. marina* was more likely to occur in water-filled depressions than on well-drained mounds, but the presence of *Z. japonica*, was better predicted by low shoot densities of *Z. marina*. Transplant experiments revealed that *Z. marina* suppressed *Z. japonica* shoot densities, more so in pools than on mounds. Topographic context remained the most influential predictor of *Z. marina* responses, even when I transplanted *Z. marina* into higher densities of *Z. japonica*. I show that decameter to kilometer-scale environmental context influences the vertical zonation of *Z. marina* and *Z. japonica*, and that meter to decimeter-scale microtopographic relief influences their local spatial distribution. Furthermore, centimeter-scale topographic relief can modify competitive outcomes and promote decameter-scale coexistence of these two species.

TABLE OF CONTENTS

	Page
List of Figures	iii
List of Tables	v
Chapter 1: Introduction	1
1.1 Introduction and Rationale	1
1.2 Study Organisms	7
1.3 Study Sites	10
1.4 Approach	13
Chapter 2: Broad-Scale Environmental Predictors of Intertidal Zonation of <i>Z. japonica</i> and <i>Z. marina</i>	14
2.1 Introduction	15
2.2 Methods	18
2.3 Results	22
2.4 Discussion	32
Chapter 3: Local-Scale Environmental Variability Predicts Local Distribu- tion of <i>Z. marina</i> in a Mixed Intertidal Bed	38
3.1 Introduction	39
3.2 Methods	42
3.3 Results	46
3.4 Discussion	54
Chapter 4: Microtopography Mediates Competition between <i>Z. marina</i> and <i>Z. japonica</i>	61
4.1 Introduction	62

4.2	Methods	64
4.3	Results	69
4.4	Discussion	80
	Bibliography	86
	Appendix A: Model Selection Tables for Broad-scale Predictors of Zonation and Overlap	100

LIST OF FIGURES

Figure Number	Page
1.1	Location of study areas within the Salish Sea. 12
2.1	Location and magnitude of model residuals (circle diameter) of observed <i>Z. marina</i> shallow extent (a), <i>Z. japonica</i> deep extent (b), and vertical overlap of the <i>Z. marina</i> and <i>Z. japonica</i> (c) at the transect scale. 23
2.2	Frequency of seagrass-containing transects with respect to bottom slope showing the proportion of sites where only <i>Z. marina</i> was observed (dark blue), and where both <i>Z. marina</i> and <i>Z. japonica</i> were observed (light blue). 24
2.3	<i>Z. japonica</i> deep extent varies as a function of <i>Z. marina</i> shallow extent, and profile rugosity (shown as point diameter) at the site scale 28
2.4	Elevation range overlap of <i>Z. marina</i> and <i>Z. japonica</i> as a function of profile rugosity (a), and bottom slope (b). The influential sample removed from analysis is shown as a triangle. 29
2.5	The shallow extent of <i>Z. marina</i> along a transect as a function of bottom slope and exposure class. 31
2.6	Minimum elevation (5th percentile) of <i>Z. japonica</i> along a transect as a function of maximum elevation (95th percentile) of <i>Z. marina</i> along the transect. 33
3.1	Topographic change from 2009–2011. The top row shows DEMs for 2009–2012, and the bottom row shows change maps for 2009–2010 and 2010–2011. 47
3.2	BPI at 2 different scales for 2009–2011. The top row maps BPI calculated with a 5 meter annulus and the bottom row maps BPI calculated with a 10 meter annulus 49

3.3	Depth profiles of sediment porewater redox potentials in core samples taken from pools (light blue) and mounds (light red), along with best-fit model predictions for redox as a function of depth in pools (dark blue) and mounds (dashed red).	50
3.4	Example temperature profile during a low tide series, showing temperature 5 cm below the sediment surface in the left panel and sediment surface temperature in the right panel.	51
3.5	Daily temperature range (left) and maximum daily temperature (right) recorded by temperature loggers deployed on the sediment surface, and 5 cm below the surface in mounds and pools.	52
4.1	Temporal shoot density trajectories of reciprocal transplant experiments for a) <i>Z. marina</i> , b) <i>Z. japonica</i> , showing means \pm SE. Open symbols show transplants onto mounds, and filled show pools. Circles are monoculture and triangle are 2 species transplants, and diamonds show transplants into ambient <i>Z. marina</i>	72
4.2	Standing crop at the end of reciprocal transplant experiment. Means \pm SE shown for a) above ground biomass and b) rhizome biomass. Filled bars show pool transplants	73
4.3	<i>Z. marina</i> response to a range of <i>Z. japonica</i> densities on mounds (open bars) and pools (filled bars) as measured by a) Rhizome extension, b) Branching, c) Leaf length, and d) Leaf width. Means \pm SE are shown.	78

LIST OF TABLES

Table Number	Page	
2.1	Model-averaged linear regression coefficients and 95% confidence intervals for site-scale predictors of <i>Z. marina</i> shallow extent.	26
2.2	Model-averaged linear regression coefficients and 95% confidence intervals for site-scale predictors of <i>Z. marina</i> deep extent.	26
2.3	Model-averaged linear regression coefficients for site-scale predictors of <i>Z. japonica</i> deep extent.	27
2.4	Model-averaged linear regression coefficients for site-scale predictors of vertical range overlap of <i>Z. japonica</i> deep extent and <i>Z. marina</i> shallow extent.	29
2.5	Model-averaged coefficients and confidence intervals for <i>Z. marina</i> 's shallow extent. Shallow extent estimated by the 95th percentile of elevation with <i>Z. marina</i> along a transect.	30
2.6	Model-averaged coefficients and confidence intervals for <i>Z. japonica</i> 's shallow extent. Deep extent estimated by the 5th percentile of elevation with <i>Z. japonica</i> along a transect.	32
2.7	Model-averaged coefficients and confidence intervals for vertical overlap in the range of <i>Z. marina</i> and <i>Z. japonica</i> . Vertical overlap estimated by the difference of the 95th percentile of <i>Z. marina</i> elevation and the 5th percentile of elevation with <i>Z. japonica</i> along a transect.	33
3.1	Model averaged coefficients for daily maximum temperature	53
3.2	Model averaged coefficients for daily temperature range	53
4.1	Restricted Maximum Likelihood estimated of effects and standard errors from best fit models of <i>Z. marina</i> and <i>Z. japonica</i> shoot densities in 2010 and 2011.	71
4.2	Model selection details for transplant shoot densities of <i>Z. marina</i> and <i>Z. japonica</i> in 2010 and 2011. Best fit model according to AICc in bold. 74	74

4.3	Model selection details for shoot and rhizome biomass of <i>Z. marina</i> and <i>Z. japonica</i> at the end of the experiment. Best fit model according to AICc in bold.	76
4.4	REML estimates and standard errors of effects of topographic context and <i>Z. japonica</i> density on <i>Z. marina</i> morphology from the <i>Z. japonica</i> density manipulation experiment.	79
4.5	Model selection details for variable density experiment. Candidate models for <i>Z. marina</i> rhizome elongation, branching, Leaf Width, and Leaf Length listed in order of fit according to AICc.	80
A.1	Coefficients and model selection details for candidate models of <i>Z. marina</i> shallow extent with AICc weight greater than .001. Minus signs indicate variables in included in model.	101
A.2	Coefficients and model selection details for candidate models of <i>Z. marina</i> deep extent with AICc weight greater than .001. Minus signs indicate variables in included in model.	102
A.3	Coefficients and model selection details for candidate models of <i>Z. japonica</i> deep extent with AICc weight greater than .001. Minus signs indicate variables in included in model.	103
A.4	Coefficients and model selection details for candidate models of depth range overlap with AICc weight greater than .001. Minus signs indicate variables in included in model.	104
A.5	Coefficients and model selection details for candidate models of site-scale <i>Z. marina</i> shallow extent with AICc weight greater than .001. Minus signs indicate variables in included in model.	105
A.6	Coefficients and model selection details for candidate models of site-scale <i>Z. marina</i> deep extent with AICc weight greater than .001. Minus signs indicate variables in included in model.	106
A.7	Coefficients and model selection details for candidate models of site-scale <i>Z. japonica</i> deep extent with AICc weight greater than .001. Minus signs indicate variables in included in model.	107
A.8	Coefficients and model selection details for candidate models of site-scale depth-range overlap with AICc weight greater than .001. Minus signs indicate variables in included in model.	108

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Chapter 1

INTRODUCTION

1.1 Introduction and Rationale

Species invasions are occurring at alarming rates, and pose a major threat to biodiversity (Vitousek et al., 1996). Estuaries, which link terrestrial and marine systems, have been heavily impacted by invasions due to the copious anthropogenic supply of propagules from sources such as aquaculture and ballast water (Ruiz et al., 1997). Seagrass ecosystems, already declining in urbanizing estuaries (Short and Wyllie-Echeverria, 1996), face further threats from species invasions (Williams, 2007).

The Asian seagrass *Zostera japonica* (Ascherson & Graebner) may be one such threat. First collected in North America by N. Hotchkiss in 1957 in Willapa Bay, *Z. japonica* is thought to have been introduced near beginning of the 20th century. It now ranges from British Columbia to Humboldt Bay, California. *Z. japonica* has been shown to have diverse impacts, increasing infaunal diversity relative to bare sediment (Posey, 1988), but possibly competing with certain infauna, such as burrowing shrimp (Dumbauld and Wyllie-Echeverria, 2003; Berkenbusch et al., 2007), and clams (Tsai et al., 2010). It provides food for birds such as black brant (Baldwin and Lovvorn, 1994), but may diminish available food for consumers of infauna with which it competes. *Z. japonica* may compete with its native congener, *Zostera marina* L., where they co-occur (Bando, 2006), but these interactions appear to be highly context dependent (Hahn, 2003b). Furthermore, *Z. japonica* often inhabits higher intertidal elevations than *Z. marina*, but at some locations their elevational

ranges overlap (Shafer, 2007). Perhaps due to the complexity of *Z. japonica*'s effects, management of *Z. japonica* has been inconsistent throughout its introduced range (Mach et al., 2010). In Washington State, *Z. japonica* has both been proposed for listing as a noxious weed, and been statutorily protected. Effective and consistent management of this species will rely upon better understanding of its distribution, invasion patterns, and ecological impacts.

1.1.1 Zonation Along Elevational Gradients

The study of communities' responses to gradients has long been a part of ecology. Striking patterns of zonation present along rocky intertidal shorelines have fueled study for the better part of a century. Connell's famous demonstration of competitive exclusion (Connell, 1961), set forth what might now be considered a paradigm for rocky shores: environmental stress limits the shallow extents of species, while biotic interactions limit the deep extent (reviewed in Connell, 1972). Though perhaps not as spatially compact, gradients in salt marshes also result in species zonation, and have been the subject of much study. Again, the interaction of competition and environmental stress is often cited for the maintenance of zonation, with competitive dominants occupying the the least stressful environments, and stress tolerant species relegated to the harsher environments (reviewed in Bertness and Leonard, 1997). More attention seems to have been paid to facilitative interactions in salt marshes than in rocky shores (Bertness and Leonard, 1997).

The common theme among these habitats is that antagonistic biotic interactions are more important in constraining species distributions in less stressful areas (sensu Menge and Sutherland, 1987; Bertness and Callaway, 1994). To apply this paradigm to seagrass systems, we might first consider what important physical stresses charac-

terize their range. The most widely studied physical stress for seagrass ecosystems is light limitation, which is generally regarded to constrain the deep extent of seagrass distributions (Duarte, 1991). Less attention has been paid to the physical stresses that limit the shallow extent of seagrasses, but hydrodynamic energy, ice scour, and desiccation may all play a role (Koch, 2001). Light limitation is likely to be exacerbated by competition, but facilitative interactions could potentially ameliorate hydrodynamic forces or desiccation stress (Powell and Schaffner, 1991). Thus, I would predict that the deep extent of seagrasses is most likely to be influenced by interspecific competition (when another seagrass species is present), and the shallow extent is most likely to be influenced by environmental stress.

Z. japonica typically lives higher in the intertidal than the native *Z. marina* (Shafer, 2007), but the two species occur in mixed stands at some locations. Shafer (2007) described three zonation patterns of *Z. japonica* and *Z. marina*:

- Disjunct: Where *Z. japonica* lives at shallower elevations, and the two species are separated by unvegetated sediment
- Mixed: Where the elevation ranges of the two species overlap
- Mixed Mosaic: Where the elevation ranges of the species overlap, but the species are locally segregated in a patch mosaic.

Studies in Yaquina Bay, Oregon (Eldridge, 2008; Kaldy, 2006), South Slough, Oregon (Posey, 1988), and Shaw Island, Washington (Britton-Simmons et al., 2010), document the disjunct zonation of the two species. Studies in Willapa Bay, Washington (Bando, 2006), Padilla Bay, WA (Bulthuis, 1995; Shafer, 2007), and Boundary Bay, British Columbia (Harrison, 1982c), have documented mixed and mixed mosaic

zonations. While the reason for differing zonation patterns remains unclear, Shafer (2007) hypothesized that site morphology may play a role, and Britton-Simmons et al. (2010) hypothesized that variability in the vertical range of *Z. marina* drives the pattern. It is currently unclear what factors determine the zonation of these seagrasses in the Pacific Northwest. Elucidating factors that limit *Z. japonica*'s deep extent and *Z. marina*'s shallow extent will be critical to understanding this pattern.

Light limitation is generally responsible for setting the deep extent of seagrass beds (Duarte, 1991), but transplanted adult *Z. japonica* shoots survive at greater depths than they are found naturally occurring (Nomme and Harrison, 1991b; Hahn, 2003b). Nomme and Harrison (1991b) took this to be evidence of biotic interactions limiting *Z. japonica*'s lower extent, but Hahn found that even in plots of both species, *Z. japonica* shoots survived the two year duration of the study. Both aforementioned studies documented a reduction in flowering shoot density at deeper sites. Nomme and Harrison (1991b) found that deeper *Z. japonica* had a lower shoot density, but longer leaves than those growing shallower. In a study of a site displaying a disjunct zonation in the San Juan archipelago, WA, *Z. japonica* transplanted into unvegetated sediment between *Z. marina* and *Z. japonica* beds survived the length of the study, but performed more poorly than transplants into the *Z. japonica* zone (Britton-Simmons et al., 2010). Taken as a whole, these findings suggest that light limitation alone does not explain the deep limit of *Z. japonica*.

No studies of biotic interactions of *Z. marina* and *Z. japonica* have demonstrated competitive exclusion, although competitive interactions have been documented. When grown together, both species have shown reduced shoot density (Hahn, 2003b), and *Z. marina* has shown reduced shoot length. *Z. marina* grown with *Z. japonica* has displayed slower shoot growth in some experiments (Merrill, 1995), but not others

(Bando, 2006). *Z. japonica* tends to be quicker to colonized cleared areas (Bando, 2006), and better able to regrow after clipping (Hahn, 2003b). All of these investigations have focused on adult shoots which may not be the most sensitive life stage for these plants.

Studies of interspecific interactions among other seagrasses are uncommon. In a study of a Philippine seagrass meadow, only 2 of 7 species responded positively to removal of other species, and none responded positively to the removal of the dominant species (Duarte et al., 2000), suggesting that interspecific competition may not be important in structuring this community. The researchers were unable to test all combinations of removals in the experiment, however, so the nature of many of the interactions in that meadow remain unknown.

The shallow limits to seagrass distributions have been less well-studied than deep limits. Koch (2001) suggests a number of physical factors that may limit the shallow extent of seagrasses, including ice scour, hydrodynamic energy, and desiccation. Ice scour is an uncommon occurrence in *Z. japonica*'s introduced range. Desiccation is often thought to be a primary limiter of *Z. marina*'s shallow extent (Boese et al., 2005), particularly in a macrotidal environment such as the Puget Sound (Mumford, 2007). In the Wadden Sea, desiccation tolerance explains the zonation of *Z. marina* and *Z. noltii* (Leuschner et al., 1998). However, laboratory experiments showed that *Z. marina* leaves recover better from desiccation events than do *Z. japonica* leaves, suggesting that leaf-level desiccation stress does not explain the different shallow extents of these species (Shafer et al., 2007). Still, whole-plant response to desiccation may differ from leaf-scale response.

1.1.2 Scale and Topography

That local conditions may modify a community's response to a gradient is not a recent realization. Stephenson et al. (1949) acknowledged that the universality of intertidal zonation is manifest differently on different sides of the same island. More recently, ecology has adopted a more explicit focus on understanding scale's influence on the interpretation of ecological processes (Schneider, 2001). In the rocky intertidal, effective sea level predicts species ranges, but only in the context of larger scale temperature patterns (Harley and Helmuth, 2003), which are in turn affected by larger scale tidal timing (Helmuth et al., 2002). In salt marshes, elevational gradients are modified by local topographic setting (Zedler et al., 1999). Spatial structure in biological and environmental variables may not conform to hierarchical schemes of organization (Denny et al., 2004), making extrapolation of conceptual models between scales (eg Menge and Olson, 1990) challenging. Hewitt et al. (2007) suggest combining small-scale manipulative studies with broader-scale correlative studies to address the challenges of inference across scales.

Large scale topography may affect Puget Sound seagrass distribution in multiple ways, particularly if wave energy or desiccation stress are important. Tidal amplitude is greater in the distal portions of the Puget Sound compared to the mouth, changing the emersion time for a given elevation. Likewise, lower tides occur later in the day in the Sound's distal reaches, exposing emersed plants to more intense solar energy. South facing beaches will also receive greater insolation. The Puget Sound, being protected from oceanic swell represents a fetch-limited wave environment (Finlayson, 2006). Puget Sound beach morphology is not well-predicted by modeled estimates of wave energy (Finlayson, 2006), but may still influence hydrodynamic forces exerted on organisms inhabiting the shoreline. Beach morphology may also influence desiccation

stress in emersed seagrasses. More gently sloped beaches are likely to drain more slowly, particularly if vegetated (Powell and Schaffner, 1991), and thus decrease emersion time at give elevation relative to steeper beaches.

Microtopography may effect local distribution by trapping water during low tides and providing a refuge from low-tide desiccation stress. Such tidepools have been shown to harbor *Z. marina* (Harrison, 1982c; Shafer, 2007), but never has pattern been quantified or causal factors examined. One likely reason for this is the challenges in quantifying microtopographic relief in an intertidal soft sediment environment.

1.2 Study Organisms

Z. marina and *Z. japonica* are seagrasses, marine angiosperms in the family *Zosteraceae*. Within the family *Zosteraceae*, the genus *Zostera* comprises two subgenera, *Zostera* and *Zosterella*. *Z. marina* is member of the subgenus *Zostera* along with **Z. caespitosa*, *Z. caulescens*, and *Z. asiatica* (den Hartog and Kuo, 2006). Considerable attention has been paid to whether different varieties of *Z. marina* constitute unique species, or ecotypes. For example, conspicuous morphological differences have led some to refer to a wide-leafed variant of *Z. marina* as a separate species, *Z. latifolia*, though recent work by (Les et al., 2002) suggest that it is not distinct. I made no distinction among different forms of *Z. marina*. *Z. japonica* belongs to the subgenus *Zosterella*, along with *Z. noltii*, *Z. muelleri*, *Z. mucronata*, *Z. capricorni*, and *Z. novazelandica*, the last four of which may be a single species (Les et al., 2002). Tomlinson and Posluzny (2001) suggested that *Zosterella* be a distinct genus, named *Nanozostera*. Henceforth, I will consider *Zosterella* a subgenus of *Zostera*. Both morphological (den Hartog and Kuo, 2006) and molecular (Uchiyama, 1996) approaches confirm the close affinity among members of the subgenus *Zosterella*.

Both *Z. marina* and *Z. japonica* reproduce both clonally, via creeping rhizomes, and sexually. While both species inhabit sandy and muddy substrates, *Z. japonica* occurs primarily at intertidal elevations in its introduced range, where *Z. marina* occurs primarily at subtidal elevations, but often extends into the lower intertidal. *Z. japonica* tends to grow at higher densities than *Z. marina*, but has shorter, narrower leaves. *Z. japonica*'s native range extends from Vietnam north to Siberia, whereas *Z. marina* occurs throughout the northern hemisphere.

The few studies of the interactions between *Z. marina* and *Z. japonica* suggest a complex, context-dependent relationship. *Z. japonica* is generally able to survive at deeper depths than it is observed inhabiting. In studies which distinguished biotic interactions from abiotic influences, competition has been evident, and the effects of *Z. marina* on *Z. japonica* appear more consistent than the reciprocal.

Harrison (1982a) grew *Z. marina* and *Z. japonica* separately in mesocosm under different simulated tidal regimes, and seasonal light regimes. Both species had higher leaf elongation rates in simulated subtidal conditions, than when exposed during a low tide. When continuously submerged, both species had similar leaf elongation rates in simulated spring light and temperature conditions, but *Z. marina* outgrew *Z. japonica* in warmer, brighter conditions with longer day length. When exposed during low tides, leaf growth was similar between the two species.

In a study in Roberts Bank, British Columbia Nomme and Harrison (1991a) examined morphological traits of *Z. marina* and *Z. japonica* at depths where each species occurred in monocultures, and at a depth where both species co-occurred. *Z. japonica* shoot density remained low throughout the growing season where it was observed growing with *Z. marina*, but increased exponentially, before decreasing late in the season where growing monospecifically *Z. marina* shoot density did not differ between

monospecific and mixed stands. Multivariate analysis of morphological traits of each species detected differences between elevation zones on some, but not all, dates of the study. This study did not distinguish between effects of tidal elevation per se and the biotic effect of co-occurring with a congener.

In a different study at Roberts Bank, Nomme and Harrison (1991b) found progressively reduced *Z. japonica* shoot density where *Z. japonica* was transplanted to deeper depths in monoculture. Both species grew longer leaves at deeper sites, but *Z. marina* shoot densities were unaffected by transplant elevation.

Manipulative studies of *Z. marina* and *Z. japonica* have consistently found *Z. japonica* to be competitively suppressed by *Z. marina* presence, although the mechanisms remain unclear. Hahn (2003a) transplanted sods from existing mixed-species and monospecific stands to tidal elevations in the *Z. japonica* zone, the *Z. marina* zone, and their overlapping zone. *Z. japonica* shoot densities were reduced by approximately 50% at all elevations where growing with *Z. marina*. Bando (2006) conducted a replacement transplant experiment, using individual shoots of *Z. marina* and *Z. japonica* at a set density. *Z. japonica* biomass per individual was reduced by 96% in mixed transplants versus monoculture.

Manipulative studies have also detected competitive effects of *Z. japonica* on *Z. marina*. (Merrill, 1995) found an increase in *Z. marina* shoot elongation in response to clipping *Z. japonica* shoots. In (Hahn, 2003b) *Z. marina* shoot densities were lower in mixed plots than in monocultures, but only in the deeper zones. (Merrill, 1995) found an increase in *Z. marina* shoot elongation in response to clipping *Z. japonica* shoots. Bando (2006) reported reduced *Z. marina* above-ground biomass per individual in response to *Z. japonica* transplantation, but the graphically presented data in the paper contradict this conclusion, showing greater *Z. marina* biomass per

individual in two-species plots.

Z. japonica has been quicker to recolonize experimentally disturbed sites whenever studies have addressed this (Hahn, 2003a; Bando, 2006). Such a finding is congruent with observations that *Z. japonica* devotes more to sexual reproduction than does *Z. marina*, and that *Z. japonica* is quick to recolonize disturbed areas (Park et al., 2011). *Z. marina* recolonization often proceeds at a slower pace, and may be more reliant on rhizome expansion than seed rain (Boese et al., 2009).

1.3 Study Sites

All investigations in this study were located within the Salish Sea, a fjord complex in the Northeast Pacific, encompassing the Greater Puget Sound, Strait of Juan de Fuca, and the Georgia Basin (Figure 1.1). My study area comprised the portions of the Salish Sea within Washington State, including the Puget Sound, Hood Canal, Strait of Juan de Fuca, and San Juan Islands. The Puget Sound and Hood Canal are sheltered, fetch-limited water bodies, but the Strait of Juan de Fuca and San Juan Islands are exposed to some oceanic swell (Finlayson, 2006). The study area experiences mixed, semidiurnal tides with a diurnal tide range varying from 1.9 m near Vancouver Island to 4.4 m in Olympia, WA (Finlayson, 2006).

I conducted experiments and microtopographic monitoring in Padilla Bay, a large, shallow bay located north of the Puget Sound in Washington. It is an “orphaned” estuary of the Skagit River (National Ocean Survey and State, 1980). Before European settlement, Padilla Bay was a part of the Skagit River distributary system. Diking and draining of agricultural lands on the Skagit delta have severed this intermittent connection to the river system. Extensive intertidal flats in the bay are populated with *Z. marina* and *Z. japonica* (Bulthuis, 1996), forming the largest seagrass meadow

in the greater Puget Sound (Berry et al., 2003). Centimeter to decimeter vertical scale microtopographic relief in the northern portion of the bay retains water during low tides, creating a mosaic of pools and mounds in the intertidal.

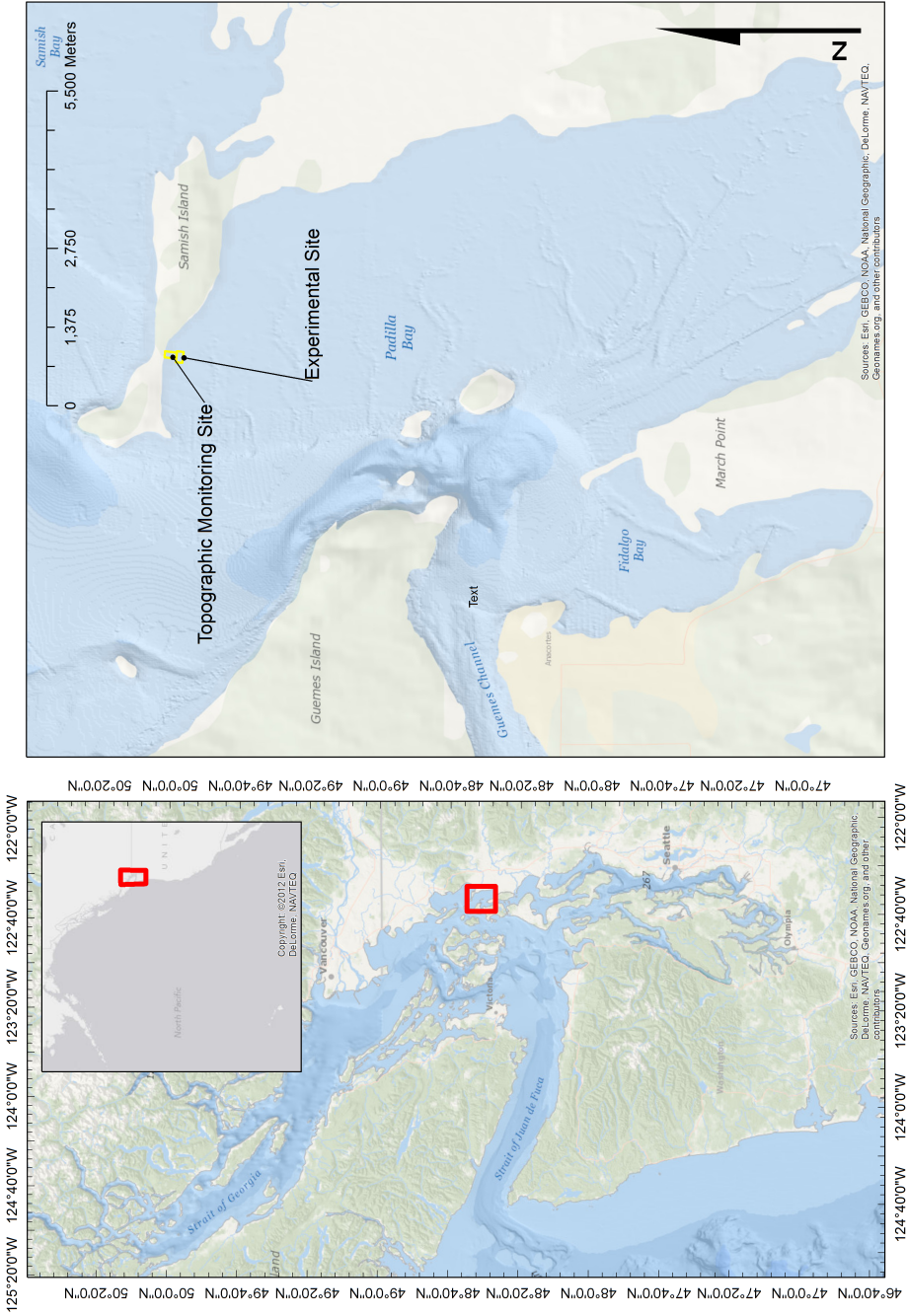


Figure 1.1: Location of study areas within the Salish Sea.

1.4 Approach

In Chapter 2, I examine the influence of physical environmental factors on the variation in vertical zonation of *Z. marina* and *Z. japonica* at horizontal spatial scales of $10^1 - 10^5$ meters. To do this, I have integrated data from a seagrass monitoring program and a shoreline mapping project and calculated new topographic predictors. In Chapter 3, I examine the influence of microtopographic relief on habitat potential for *Z. marina* and *Z. japonica* in a mixed intertidal flat. To measure microtopography I employed Light detection and ranging (LiDAR), a powerful tool for three dimensional habitat mapping (Vierling et al., 2008). LiDAR is a laser analogue to radar, and calculates the distance from the sensor to a reflective object by measuring laser time of flight. In Chapter 4, I examine the relative role of biotic and abiotic factors in maintaining an intertidal patch mosaic of *Z. marina* and *Z. japonica* using experimental field transplants.

Chapter 2

**BROAD-SCALE ENVIRONMENTAL PREDICTORS OF
INTERTIDAL ZONATION OF *Z. JAPONICA* AND *Z.
MARINA******Abstract***

Physical and biotic factors can influence the distribution of species at multiple scales, and are thus important when predicting invasive species impacts. I examined the influence of physical context and congener presence on variability the vertical zonation of an invasive seagrass, *Z. japonica* and its native congener *Z. marina*. Nearshore intertidal topography, hydrodynamic exposure, and tidal range were examined as abiotic predictors of the deep extents of *Z. japonica* and *Z. marina*, the shallow extent of *Z. marina* and the elevation overlap of the two species, both at within site and among site spatial scales. *Z. marina*'s extended to higher elevations at transects that were less rough, more gently-sloped, less wave exposed, and in the presence of *Z. japonica*. Site-scale rugosity was the best predictor of site scale shallow extent of *Z. marina*. *Z. japonica* deep extent was explained by *Z. marina* shallow extent at both spatial scales, and also by rugosity when examining site-averaged patterns. Overlap of the two species along a transect was poorly predicted by physical context, but site-averaged range overlap was greater where depth profiles were more linear. Bottom profile complexity was the most consistently important predictor studied, confirming the importance of the geomorphic template on the zonation of these species. Furthermore, these findings suggest a greater sensitivity of *Z. marina*

shallow extent to physical factors, and a greater sensitivity of *Z. japonica* deep extent to biotic factors.

2.1 Introduction

Broad-scale context plays an important role in all phases of invasion. Colonization, establishment, and impact of an invader may be influenced by broad-scale environmental filters (Theoharides and Dukes, 2007). Invasive spread is influenced by landscape connectivity, which is a product of both the geometry of potential habitat patches, the characteristics of these patches and their surrounding matrix, and the characteristics of the spreading invader (Tischendorf and Fahrig, 2000). Fine-scale heterogeneity may alter local environmental conditions to allow colonization, establishment, and impact by the invader, but the likelihood of these occurring depends on broader-scale conditions, and their influence on propagule supply. In other words, if the invader is absent from or rare in the regional species pool, it is unlikely to occur even at otherwise favorable sites.

Broad-scale physical setting can play an influential role in the spatial dynamics of seagrass beds. Hydrodynamic energy, in particular, has been a well-studied driver of seagrass patterns. Wave exposure can influence the shape and arrangement of seagrass patches (Fonseca and Bell, 1998; Frederiksen et al., 2004), their areal cover in shallow water (Krause-Jensen et al., 2000, 2003), the longevity of seagrass patches (Frederiksen et al., 2004), and govern the shallow extent of seagrass beds (Infantes et al., 2009; Stevens and Lacy, 2012). Seagrass cover may also be predicted by broad-scale patterns in sediment composition (Bradley and Stolt, 2006), shoreline shape, tidal range, and upland watershed characteristics (Li et al., 2007).

Physical factors limiting the deep extent of seagrass growth have been better

studied than those limiting the shallow extent. Light is the primary limiting resource for seagrasses at the deep edge of their range (Duarte, 1991), so physical factors influencing its availability are particularly well studied. Koch (2001) suggested wave energy, ice scour, and tidal exposure as primary limits to the shallow extents of seagrasses.

Wave exposure may increase local coexistence of *Z. marina* and *Z. japonica* via increased disturbance. Disturbance is widely recognized to be important for invasion success (Hobbs and Huenneke, 1992), by increasing resource availability (Davis et al., 2000). If wave disturbance selectively impacts the dominant competitor, coexistence should increase at scales larger than the disturbance patch size. If wave disturbance affects each species equally, but is not intense and frequent enough to completely exclude either or both species, *Z. japonica* cover should increase. *Z. japonica* is quick to colonize disturbed sediments (Park et al., 2011), and appears to do so more quickly than *Z. marina* (Bando, 2006), perhaps due to a greater investment in sexual reproduction (Harrison, 1979). *Z. japonica*'s superior colonization ability could promote its persistence in the presence of wave disturbance, even in environments where it might otherwise be competitively excluded. Similar patterns in response to disturbance have been described for the seagrasses *Halodule wrightii* and *Thalassia testudinum* (Bloom, 1987), and for the *Thalassia testudinum* and *Syringodium filiforme* (Williams, 1987). If wave disturbance is frequent and intense enough to exclude one or both species it may decrease the likelihood local coexistence.

Bottom slope may influence the intertidal distribution of seagrass species by either modifying wave energy, or tidal drainage. Wave energy is dissipated by friction with the seafloor, more so in shallower areas (Engineers, 1984). In broad shallow areas, wind waves are being generated and dissipated simultaneously (Young, 1997; Young

and Verhagen, 1996), making a quantitative understanding of wave dynamics more difficult in these locations (Koch, 2001). More gently sloping shorelines should be expected to drain more slowly than steeper shorelines during a low tide, and this drainage can be further slowed by the presence of vegetation (Powell and Schaffner, 1991). Whether by acting to decrease the influence of wave energy, or decrease the desiccation stress of low tide exposure, we might expect gentle slopes to ameliorate conditions that limit seagrass survival in shallow waters.

At gently sloping sites, local microtopography may influence the distribution of seagrasses by trapping water during a low tide and extending the shallow extent of a desiccation sensitive species (Wyer et al., 1977; Harrison, 1982c; Shafer, 2007). The local habitat heterogeneity that this microtopography provides can increase the likelihood of coexistence for multiple competitors (Melbourne et al., 2007; Tilman, 1994).

Greater tidal amplitudes restrict the depth range within which seagrasses can survive. As a result of their highly reduced cuticles (Larkum et al., 2006), seagrasses tend to be acutely susceptible to desiccation, and so tend to be limited to depths that are rarely exposed by a low tide (Boese et al., 2005). In water bodies such as the Puget Sound, which have large tidal ranges but are relatively protected from oceanic swell, desiccation is thought to be a common limit to the shallow extent of seagrass growth (Mumford, 2007).

Here I examine the role of physical context on the vertical zonation and co-occurrence of an invasive seagrass, *Zostera japonica*, and its native congener *Zostera marina*, in the greater Puget Sound, WA. The Puget Sound contains an exceptional diversity of shoreline settings and morphologies (Finlayson, 2006) as a result of its glacial origin and tortuous shorelines. As a result, it affords an excellent opportunity

to examine the influence of diverse physical settings on nearshore species. I examine how variability in the vertical zonation *Z. marina* and *Z. japonica* at scales of tens to hundreds of meters and kilometers to hundreds of kilometers can be explained by physical setting. Specifically I address the following questions: 1) Is the shallow extent of *Z. marina* in the greater Puget Sound explained by a) geographic and geomorphic variables associated with hydrodynamic energy, b) variables associated with desiccation stress (ie. tidal amplitude, slope, and rugosity), and c) presence of *Z. japonica*? 2) Is the deep extent of *Z. japonica* explained by a) geographic and geomorphic variables associated with hydrodynamic energy, b) the shallow extent of *Z. marina*? 3) Can the vertical overlap of *Z. marina* and *Z. japonica* be predicted by physical setting?

2.2 Methods

2.2.1 Data Sources

Seagrass Monitoring

This investigation utilized a seagrass monitoring dataset from the Washington Department of Natural Resources's (WADNR) Submerged Vegetation Monitoring Program (SVMP). This program monitors seagrass cover in the greater Puget Sound, including the Strait of Juan de Fuca and the San Juan Archipelago. Randomly selected sites are surveyed with shore-normal line transects, utilizing GPS-referenced underwater video and sonar. Sites consist of either a 1 km length of shoreline for linear shorelines, or a single embayment or delta. On average, 12–15 transects are surveyed at each site, and 60–108 sites are surveyed each year. With the exception of 9 core sites that are monitored every year, 20% of sites are replaced annually. A technician analyzes the video producing a presence/absence measurement for each second of data. The

compiled data include presence/absence data for *Z. marina* and *Z. japonica*, differentially corrected GPS coordinates, and a tide-corrected depth measurement relative to Mean Lower Low Water (MLLW).

ShoreZone Inventory

Additional environmental predictors were gathered from the Washington State Shorezone Inventory and the Puget Sound Nearshore Environmental Restoration Project (PSNERP) change analysis. Between 1994 and 2000, all Washington State's saltwater shorelines were videographically surveyed by helicopter. During the surveys, an on-board geomorphologist and marine ecologist provided real-time commentary for the subsequent video analysis. Shorelines were divided into geomorphic units. A team of biologists and geomorphologists analyzed the photography and video for each unit and combined their observations with geospatial analyses (eg. Fetch, Tidal Range) in a geospatial database. I utilized the Shorezone Inventory to record tidal range and hydrodynamic exposure class.

2.2.2 Data Processing

WADNR SVMP data were used to calculate both topographic predictors and seagrass zonation response measures. GPS data and sonar-derived depth data along each transect were integrated at each site to create a bathymetry map using ArcGIS (ESRI, Redlands, CA). Individual observations between 1 meter above and 1 meter below MLLW were used to construct a Triangulate-Irregular-Network (TIN), that was then gridded to a 2 meter resolution using Natural Neighbor interpolation. From this map, the mean slope was calculated along each surveyed transect. Also from the bathymetry map, I calculated the mean aspect. From the transect data, I calculated

the shallowest and deepest observation of *Z. marina* and *Z. japonica*, as well as the 5th, 50th, 90th, and 95th percentile depth at which each species was observed along each transect.

SVMP transect data were also used to calculate a bottom roughness index for each transect. I first projected x and y coordinates along each transect onto their first principle component in order to create a variable that represented length along transect. These projected coordinates were paired with their corresponding depth observation. From these data we calculated the roughness index as the sum of the distances between adjacent points along the transect divided by the total three-dimensional straight-line length of the transect (Connell and Jones, 1991). Rougher bottoms result in higher values of this fraction, and a perfectly smooth transect would result in a value of 1. All roughness analysis was performed in R (R Development Core Team, 2008), using the package `taRifx.geo` (Friedman, 2012).

Shorezone Inventory data were integrated with SVMP transect-derived data by spatially joining each transect point to the nearest Shorezone Inventory observation. I then summarized Shorezone inventory data along each transect as the mean value of the joined Shorezone data, or in the case of categorical variables, the most frequent category along each transect. The complete dataset included vegetation extents and environmental context variables for each transect in each site. These data were also summarized at the site scale. The mean of measurements from each transect, or the most frequent categorical observations across each transect at a site were integrated into a second data set with coarser spatial resolution.

2.2.3 Data Analysis

I examined the influence of environmental predictors on the zonation of each seagrass species at two different spatial scales. First, I examined the mean zonation response at a site as a function of the environmental predictors summarized across all transects. Then I examined the zonation of each transect as a function of the environmental predictor values along that transect. I fit linear models and linear mixed effects models in order to assess the value of broad scale topographic variables in predicting the shallow extent of *Z. marina*, the deep extent of *Z. japonica* and the vertical range overlap of the two species.

In order to reduce the influence of rare, extreme observations of each species depth, I estimated *Z. marina*'s shallow extent with the 95th elevation percentile of *Z. marina* observations along each transect (transect-scale models) or the mean of the 95th elevation percentiles across transects at a site (site-scale models). Likewise, I used the 5th elevation percentile of *Z. japonica* observations to estimate the deep extent of this species. All continuous independent variables were centered by subtracting the variable's mean value from each observation in order to improve interpretation of the modeled intercept (Gelman, 2008). All models were fit with a random effect for sampling site. Modeling was conducted using the base statistics package and the lme4 (Bates et al., 2012) package in R (R Development Core Team, 2008).

I modeled *Z. marina* shallow extent as a function of bottom slope, rugosity, tide range, exposure class, and *Z. japonica* presence. To account for the effect of bottom slope on wave energy, I included an interaction between slope and exposure class. To account for the influence of bottom slope on the effect of rugosity, I modeled an interaction between bottom slope and rugosity. Because *Z. japonica* was present on only 17% of transects at which *Z. marina* was observed, I did not include *Z. japonica*'s

deep extent as a predictor.

Z. japonica deep extent was modeled as a function of bottom slope, rugosity, tide range, exposure class, and *Z. marina* shallow extent. Because *Z. marina* was present at 94% of transects at which *Z. japonica* was observed, I did not include *Z. marina* presence as a predictor. I modeled vertical overlap of the two species as a function of bottom slope, rugosity, tide range, and exposure class.

Model fit was graphically assessed by examining residuals versus fit values, and plots of theoretical versus observed quantiles. To reduce the influence of extreme values on models, I removed outliers with residuals greater 2.5 times the residual standard deviation, and refit models. Outliers amounted to less than 2% of the data in all cases. All removed outliers were individually examined.

We used an information-theoretic approach to model selection and averaging to estimate the parameters of a best-fit model. Model averaging is a form of multi-model inference that accounts for uncertainty in model selection by averaging coefficient values across all candidate models, weighted by their relative likelihood, or Akaike weight (Anderson, 2008). For each response variable, our candidate set of models included models with each treatment separately, and models that included combinations of treatments additively and interactively. Model averaging was performed using the MuMIn (Barto, 2013) package in R (R Development Core Team, 2008).

2.3 Results

Z. marina occurred throughout much of the study site, including parts of the Strait of Juan de Fuca, although no sites from the Strait of Juan de Fuca were included in the study, because they did not employ straight line transect sampling (Figure 2.1). *Z. Marina* was observed at elevations of 2.98 ft above MLLW to 22.83 ft below MLLW.

Z. japonica observations were concentrated at gently sloped sites (Figure 2.2), with no *Z. japonica* observed at locations with bottom slopes steeper than 5 degrees from horizontal. Most *Z. marina* observations were at locations in this slope range, but *Z. marina* was observed at sites with slopes steeper than 15 degrees from horizontal. Model residuals showed no clear geographic patterns (Figure 2.1), nor any clear spatial autocorrelation.

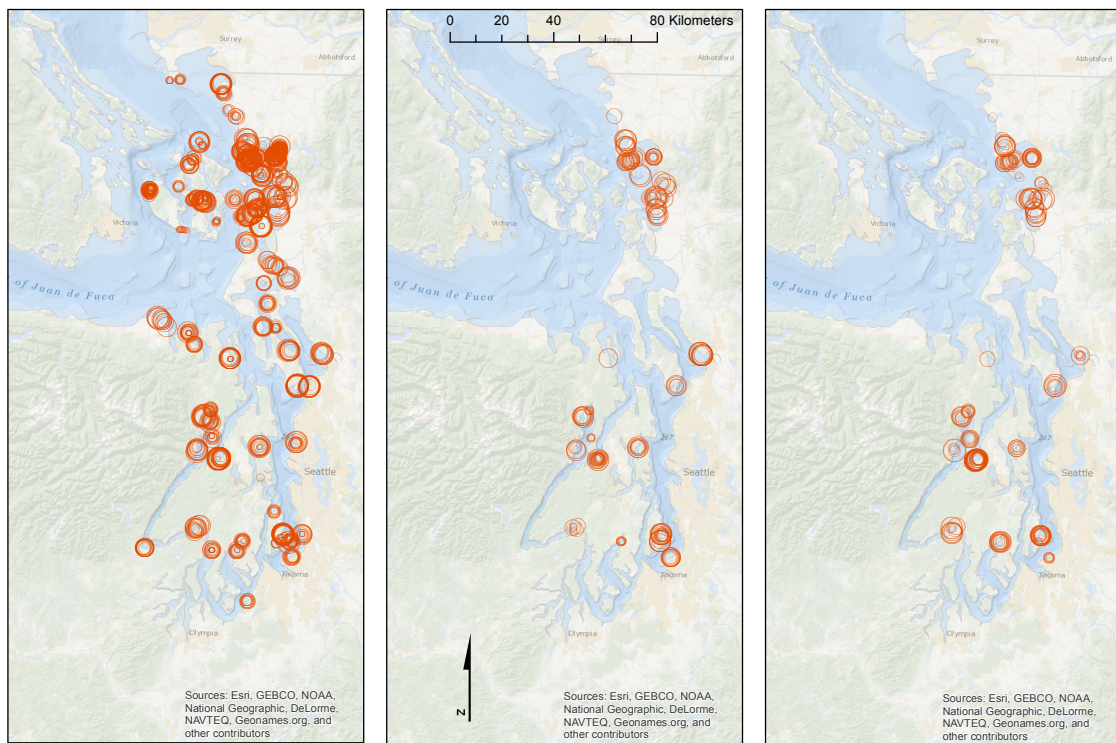


Figure 2.1: Location and magnitude of model residuals (circle diameter) of observed *Z. marina* shallow extent (a), *Z. japonica* deep extent (b), and vertical overlap of the *Z. marina* and *Z. japonica* (c) at the transect scale.

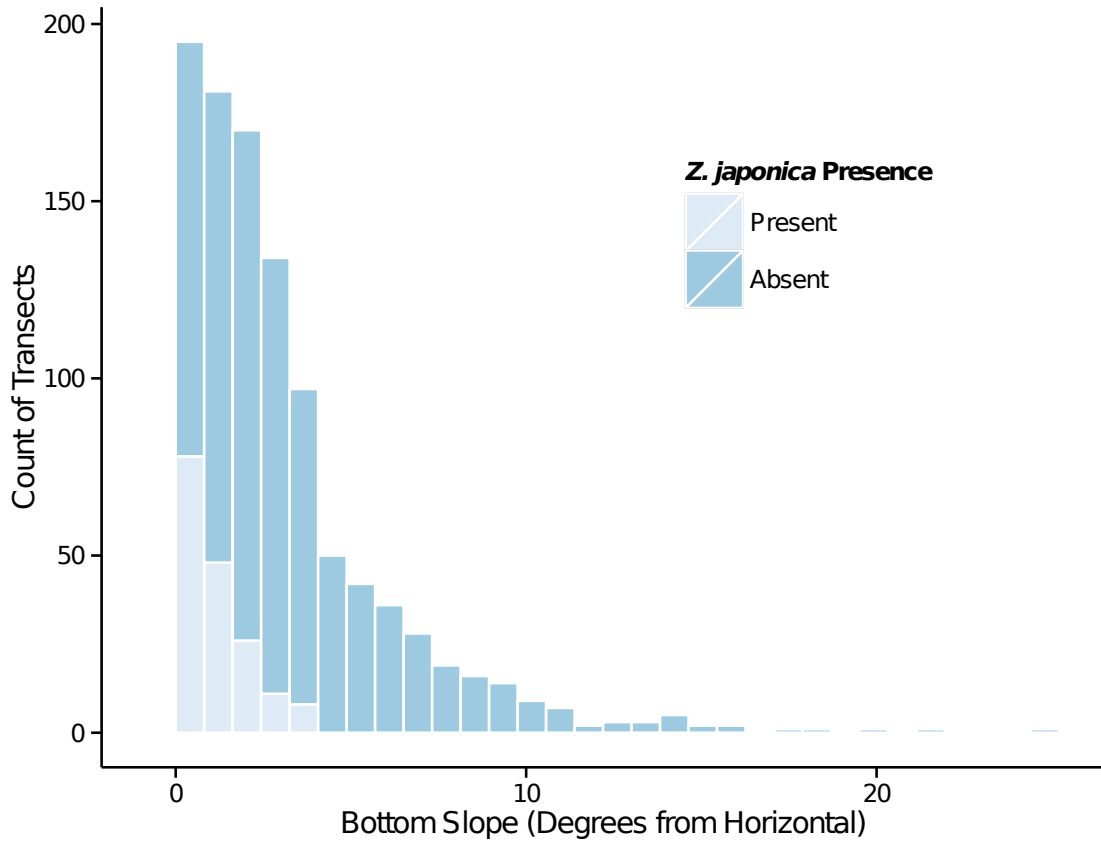


Figure 2.2: Frequency of seagrass-containing transects with respect to bottom slope showing the proportion of sites where only *Z. marina* was observed (dark blue), and where both *Z. marina* and *Z. japonica* were observed (light blue).

2.3.1 Site-Scale Patterns

Z. marina Zonation

The best fit model for the site-averaged shallow extent of *Z. marina* explained 33% of the variation observed as a function of rugosity, slope, exposure class, and *Z. japonica* presence. Model selection uncertainty was high, with four models at least one-third as likely as the best-fit model (Table A.5). Model diagnostics revealed 2 influential samples (Cook's Distance > 1). Examination of these samples revealed that they were two of only three sites in the 'very protected' exposure class, and their deletions had large impacts on this coefficient. Both samples were retained in the analysis.

The site-averaged shallow extent of *Z. marina* extended higher into the intertidal at sites with smoother depth profiles (Table 2.1). Rugosity was present in every model that was at least 10% as likely as the best fit model (Table A.5).

The average model predicted *Z. marina* extended higher into the intertidal at protected and very protected sites than at semi-protected. The very protected class only comprised 3 sites in comparison to 62 and 31 for the protected and semi-protected classes respectively.

The average model predicted that *Z. marina* extended higher into the intertidal at more gently sloping sites and in the presence of *Z. japonica*, although 95% confidence intervals for these coefficient encompassed zero. The slope effect varied among averaged models, being sensitive to the inclusion of *Z. japonica* presence (Figure 2.2), and the slope by exposure class interaction. While much of *Z. japonica*'s measured effect might be attributable to its covariance with slope, addition of *Z. japonica* presence to the model including slope, rugosity, and exposure class improved model fit.

The best fit model for *Z. marina*'s deep extent explained 20% of the variation

Table 2.1: Model-averaged linear regression coefficients and 95% confidence intervals for site-scale predictors of *Z. marina* shallow extent.

	Estimate	Std. Error	Adjusted SE	Lower CI	Upper CI
(Intercept)	-3.63	0.43	0.43	-4.48	-2.78
Cen.Rugosity	-2.4	1	1.01	-4.38	-0.42
Cen.Slope	-0.19	0.11	0.11	-0.41	0.03
Exposure.Class1	0.31	0.61	0.62	-0.9	1.51
Exposure.Class2	-0.45	0.24	0.24	-0.93	0.02
factor(MaxOfZjPres)1	0.94	0.51	0.51	-0.07	1.94
Cen.Slope:Exposure.Class1	0.05	0.18	0.18	-0.3	0.41
Cen.Slope:Exposure.Class2	-0.07	0.08	0.08	-0.22	0.08
Cen.Tide.Range	0.43	0.54	0.54	-0.63	1.49

observed as a function of tide range and exposure class. Model selection uncertainty was lower than for *Z. marina*'s shallow extent, but the second best fit model was 88% as likely as the best fit and differed only in the addition of a slope effect. The averaged model predicted *Z. marina* to extend to greater depths at sites with lower tide ranges and higher wave exposure (Table 2.2).

Table 2.2: Model-averaged linear regression coefficients and 95% confidence intervals for site-scale predictors of *Z. marina* deep extent.

	Estimate	Std. Error	Adjusted SE	Lower CI	Upper CI
(Intercept)	-8.28	0.85	0.86	-9.98	-6.59
Cen.Tide.Range	3.72	0.95	0.96	1.84	5.61
Exposure.Class1	-2.5	1.15	1.16	-4.78	-0.22
Exposure.Class2	-1.47	0.47	0.47	-2.4	-0.55
Cen.Slope	-0.17	0.14	0.14	-0.45	0.11
Cen.Rugosity	-0.45	1.84	1.86	-4.09	3.2
Cen.Slope:Exposure.Class1	0.22	0.35	0.36	-0.48	0.92
Cen.Slope:Exposure.Class2	0.05	0.15	0.15	-0.24	0.34

Z. japonica Zonation

The best-fit model for site-averaged deep extent of *Z. japonica* explained 40% of the observed variation as a function of *Z. marina*'s shallow extent and rugosity. The best fit model was approximately four times as likely as each of the next three models, which each incorporated one variable in addition to those included in the best fit model (Table A.7). The averaged model predicted *Z. japonica* to extend deeper at sites with smoother profiles, and where *Z. marina* did not extend far into the intertidal (Table 2.3).

Model diagnostics revealed one highly influential sample (Cook's Distance > 1). Examination of this sample revealed that the site had extreme variability in measured slope among transects, but *Z. japonica* was only present on the more gently sloped transects. Inclusion of this sample had profound effects on model coefficients, decreasing the rugosity coefficient by a factor of four and the *Z. marina* shallow extent coefficient by a factor of two. This sample was excluded from the analysis.

Table 2.3: Model-averaged linear regression coefficients for site-scale predictors of *Z. japonica* deep extent.

	Estimate	Std. Error	Adjusted SE	Lower CI	Upper CI
(Intercept)	-0.57	0.46	0.48	-1.52	0.37
Cen.Rugosity	8.55	3.06	3.22	2.23	14.87
Cen.Zm_95_Per	0.56	0.18	0.19	0.18	0.94
Cen.Slope	-0.1	0.18	0.19	-0.47	0.27
Cen.Tide.Range	-0.6	0.73	0.77	-2.1	0.9
Exposure.Class1	-0.14	0.28	0.29	-0.71	0.43
Cen.Slope:Exposure.Class1	-0.11	0.13	0.13	-0.38	0.15

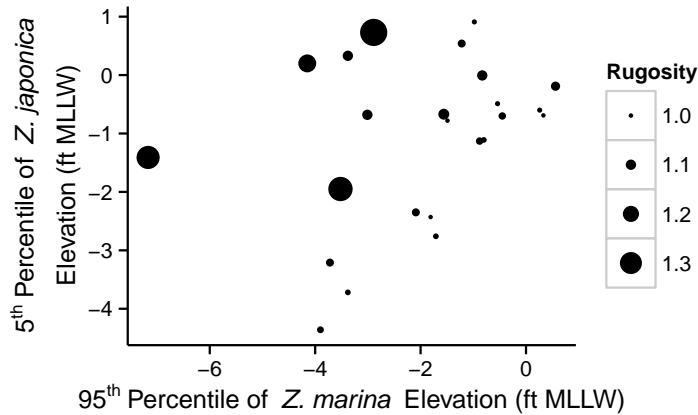


Figure 2.3: *Z. japonica* deep extent varies as a function of *Z. marina* shallow extent, and profile rugosity (shown as point diameter) at the site scale

Depth Range Overlap

The best-fit model for site-averaged vertical overlap of *Z. marina* and *Z. japonica* explained 55% of the observed variance as a function of rugosity. This model was four times as likely as the next best model that included only slope (Table A.8). The averaged model predicts that greater overlap between species at sites with more linear depth profiles (Table 2.4). Model diagnostics revealed the same influential observation that was present in the *Z. japonica* deep extent models. Inclusion of this variable reduced model fit and increased model selection uncertainty, but did not change the qualitative interpretation of the results (Figure 2.4). It was excluded from this analysis. A model with only slope as a predictor explained 23% of the observed variation in vertical range overlap (Figure 2.4), but high correlations between slope and rugosity (Pearson's $r = 0.7$) may explain the apparent influence of slope

Table 2.4: Model-averaged linear regression coefficients for site-scale predictors of vertical range overlap of *Z. japonica* deep extent and *Z. marina* shallow extent.

	Estimate	Std. Error	Adjusted SE	Lower CI	Upper CI
(Intercept)	-2.86	0.46	0.48	-3.81	-1.91
Cen.Rugosity	-12.6	2.64	2.79	-18.06	-7.14
Cen.Tide.Range	-0.28	0.64	0.68	-1.6	1.05
Cen.Slope	0.07	0.19	0.2	-0.32	0.46
Exposure.Class1	0.11	0.29	0.31	-0.49	0.71
Cen.Slope:Exposure.Class1	0.09	0.14	0.15	-0.2	0.37

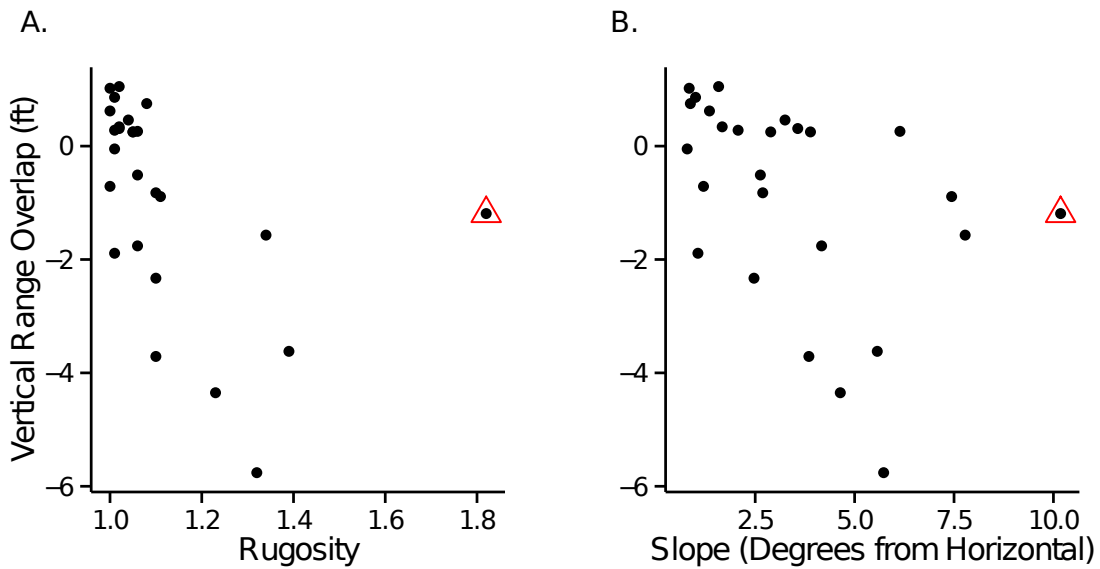


Figure 2.4: Elevation range overlap of *Z. marina* and *Z. japonica* as a function of profile rugosity (a), and bottom slope (b). The influential sample removed from analysis is shown as a triangle.

2.3.2 Transect-Scale Patterns

Z. marina Zonation

Z. marina was observed extending to higher elevations at transects with gentler slopes, less complex bottom profiles, lower wave exposure, and *Z. japonica* present (Table 2.5). Model selection uncertainty was considerable (Table A.1), but slope, rugosity, exposure class, and slope by rugosity interaction were included in all models with ΔAIC_c less than six. *Z. japonica* presence was also included in the two best fit models. Tide range and slope by the exposure class interaction were included in the best fit model, but confidence intervals for their coefficients included zero. The influence of rugosity and bottom slope were antagonistic, such that their combined influence on *Z. marina*'s shallow extent was less than the sum of their individual effects. This may have resulted from a positive correlation between these two variables (Pearson's $r = 0.49$).

Table 2.5: Model-averaged coefficients and confidence intervals for *Z. marina*'s shallow extent. Shallow extent estimated by the 95th percentile of elevation with *Z. marina* along a transect.

	Estimate	Std. Error	Lower CI	Upper CI
(Intercept)	-3.034	0.259	-3.542	-2.527
Cen.Rugosity	-0.842	0.185	-1.204	-0.48
Cen.Slope	-0.08	0.012	-0.104	-0.057
Exposure.Class.L	-1.116	0.426	-1.95	-0.281
Exposure.Class.Q	-0.214	0.249	-0.703	0.274
factor(ZjPres)Present	0.382	0.191	0.008	0.757
Cen.Rugosity:Cen.Slope	0.048	0.01	0.028	0.067
Cen.Tide.Range	0.307	0.415	-0.505	1.12
Cen.Slope:Exposure.Class.L	-0.036	0.031	-0.097	0.025
Cen.Slope:Exposure.Class.Q	0.013	0.019	-0.025	0.051

Bottom slope appeared to exert strong control on the upper limit of *Z. marina*

(Figure 2.5). Across the range of bottom slopes observed, the locations with the shallowest extents of *Z. marina*, correlated strongly with slope. At more protected sites, *Z. marina* was observed across a greater range of bottom slopes.

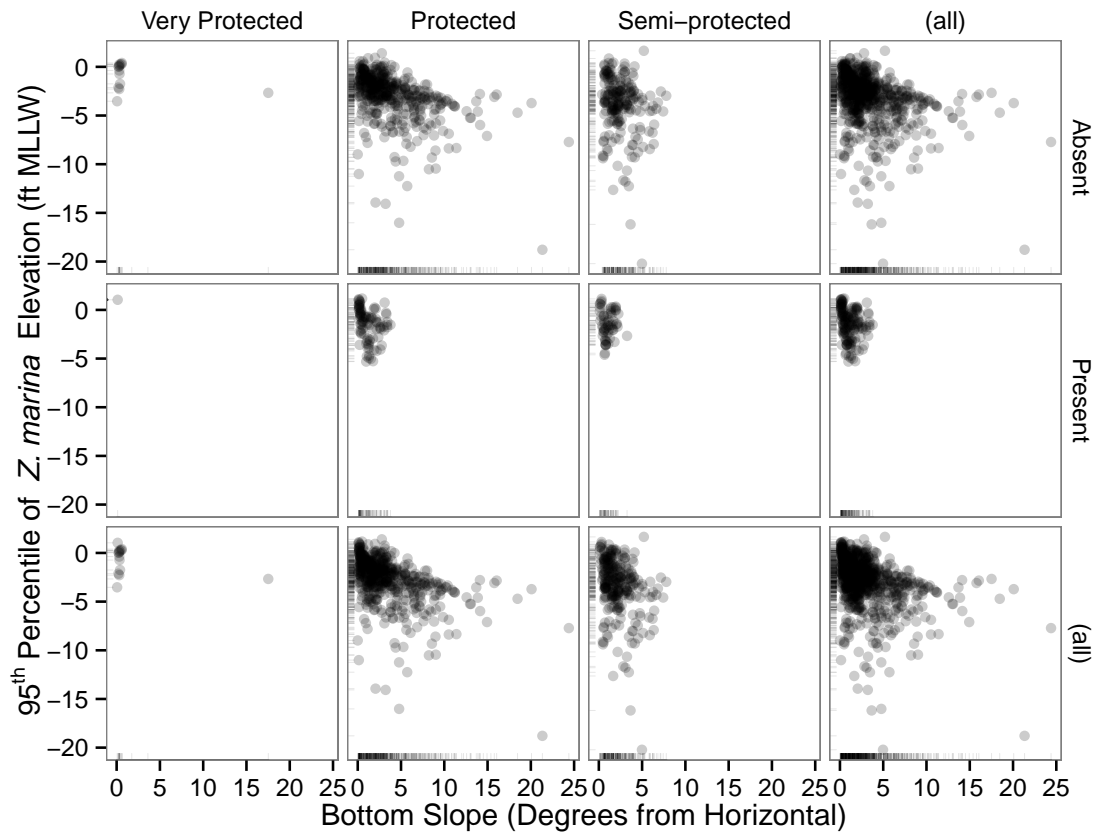


Figure 2.5: The shallow extent of *Z. marina* along a transect as a function of bottom slope and exposure class.

Z. japonica Zonation

Z. japonica's deep extent correlated positively with *Z. marina*'s shallow extent (Figure 2.6). In other words, where *Z. marina* extended higher into the intertidal, *Z. japonica* did not extend to as great a depth as where *Z. marina* remained at lower

elevations. Model selection uncertainty was high (Table A.3), but *Z. marina* shallow extent was included in every model with a ΔAIC_c less than 19. Slope, tidal range and exposure class were all included in the averaged model, but confidence intervals for all included 0 (Table 2.6).

Table 2.6: Model-averaged coefficients and confidence intervals for *Z. japonica*'s shallow extent. Deep extent estimated by the 5th percentile of elevation with *Z. japonica* along a transect.

	Estimate	Std. Error	Lower CI	Upper CI
(Intercept)	-1.261	0.54	-2.321	-0.202
Cen.Zm_95_Per	0.39	0.079	0.234	0.545
Exposure.Class.L	-0.566	0.676	-1.892	0.76
Exposure.Class.Q	-0.236	0.393	-1.007	0.535
Cen.Slope	-0.072	0.054	-0.177	0.034
Cen.Tide.Range	-0.412	0.545	-1.48	0.656
Rugosity	0.436	0.705	-0.947	1.818

Depth Range Overlap

None of the examined variables predicted the elevation range overlap of *Z. marina* and *Z. japonica* (Table 2.7). Despite considerable model selection uncertainty, the null model was the best-fit model examined (Table A.4). None of the estimated coefficients differed from 0 with 95% confidence.

2.4 Discussion

Z. marina's shallow extent responded to environmental context at both transect and site scales, and responded to *Z. japonica* presence at transect scales. *Z. japonica*'s deep extent was well explained by *Z. marina*'s intertidal extent at both transect and site scales, but the measured environmental variables were only influential at the site

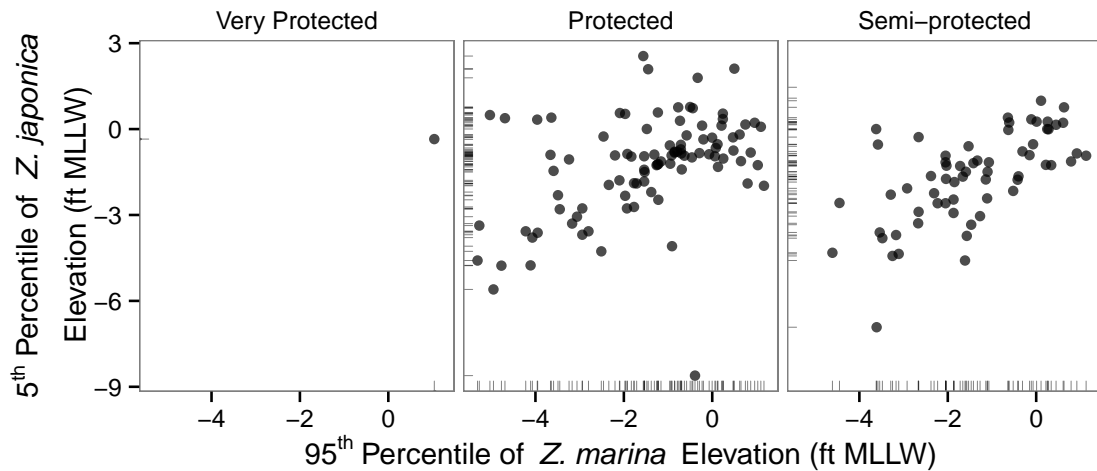


Figure 2.6: Minimum elevation (5th percentile) of *Z. japonica* along a transect as a function of maximum elevation (95th percentile) of *Z. marina* along the transect.

Table 2.7: Model-averaged coefficients and confidence intervals for vertical overlap in the range of *Z. marina* and *Z. japonica*. Vertical overlap estimated by the difference of the 95th percentile of *Z. marina* elevation and the 5th percentile of elevation with *Z. japonica* along a transect.

	Estimate	Std. Error	Lower CI	Upper CI
(Intercept)	-0.114	0.681	-1.449	1.221
Cen.Tide.Range	-0.472	0.559	-1.567	0.623
Cen.Slope	-0.034	0.07	-0.17	0.103
Exposure.Class.L	-0.335	1.03	-2.354	1.684
Exposure.Class.Q	0.671	0.6	-0.505	1.847
Rugosity	-0.065	1.07	-2.162	2.033

scale. I was unable to predict vertical overlap of *Z. marina* and *Z. japonica* at the transect scale, but profile rugosity predicted the extent of overlap at the site scale. While it is impossible to draw any causal links from this study, these results are congruent with the rule of thumb for rocky intertidal shorelines, that physical factors determine the shallow extents of species, and biotic interactions determine the deep extents.

Rugosity, the roughness of the transect profile, as measured by the ratio of its path length to its projected length was an important predictor of each seagrasses intertidal extent at both spatial scales, and of the degree of vertical overlap at site scales. The effect of rugosity was contrary to my expectations, with greater roughness decreasing range overlap and restricting *Z. marina* and *Z. japonica* to lower and higher elevations, respectively. This may be explained by the nature of the roughness index. It is an indicator of departures from linearity at any scale. Small undulations and large slope breaks can both increase the value of this index. Combining this index with a moving window analysis, or applying it to the residuals of a smoothing spline might afford more insights into the scale-specific effects of profile shape. Nonetheless, the ubiquity and explanatory power of this index in our analysis underscore the importance of the geomorphic template to the distribution of these species.

Hydrodynamic exposure may play an important role in determining *Z. marina*'s shallow extent in the Puget Sound. At the transect scale, *Z. marina* extended to higher elevations at more protected sites. As predicted, the effect of exposure was lessened at gently sloping sites. The trend of shallower extents at more protected sites was also suggested at the site scale, but the direction of the effect could only be established with 90% confidence, and no interaction with slope was apparent. The exposure class used in this study is a fetch-based variable calculated at a coarse spatial

scale ($10^2 - 10^3m$), and as such, cannot account for the complex interactions between bathymetry and wave propagation. Process based wave models at finer spatial scales have yielded mixed results in the Puget Sound, predicting *Z. marina* shallow extent in some examples (Stevens and Lacy, 2012), but not in others (Finlayson, 2006).

Surprisingly, tidal range offered little value in predicting *Z. marina*'s shallow extent at either scale. Desiccation stress is thought to limit *Z. marina*'s intertidal extent (Boese et al., 2005). The high tidal amplitudes in distal reaches of the Puget Sound, and the desiccation stress that accompany them, have been suggested as the explanation of *Z. marina*'s absence from the southern reaches of the Puget Sound (Mumford, 2007). Increased tidal range actually predicted increased shallow extents for *Z. marina* at both scales, albeit with very little confidence. While tidal amplitude and desiccation stress may limit the intertidal extent of *Z. marina*, this study suggest that other factors are more important at most sites in the Puget Sound.

The shallow extent of *Z. marina* and the deep extent of *Z. japonica* are positively correlated at site scales (Figure 2.3) and at transect scales (Figure 2.6). This pattern could result from competitive interactions between these species where they co-occur or from each species responding similarly to environmental conditions. *Z. japonica* doesn't appear to be restricting *Z. marina*'s shallow extent, because at the transect scale, *Z. marina* extended to higher elevations in the presence of *Z. japonica* than in it's absence. *Z. japonica* was only present at gently sloping transects, where *Z. marina* already reaches higher elevations, but *Z. japonica*'s effect improved model fit even when slope was accounted for. *Z. japonica* presence did not influence the site-averaged shallow extent of *Z. marina*.

The shallow extent of *Z. marina* was the only strong predictor of *Z. japonica*'s deep extent at transect scales, and was equally important site-scale predictor as ru-

gosity. These patterns are consistent with the notion that *Z. marina* competitively excludes *Z. japonica* from deeper areas, although that explanation does not account for the disjunct zonation pattern. Unmeasured biotic interactions could also explain the covariance between the two species's elevation ranges. Antagonistic interactions with bioturbators may limit *Z. japonica*'s distribution (Berkenbusch et al., 2007; Dumbauld and Wyllie-Echeverria, 2003), so it is conceivable that both species suffer competition with unobserved infauna, linking their intertidal extents.

Little work has focused on understanding the deep extent of intertidal seagrasses. Britton-Simmons et al. (2010) documented decreased survival and performance in lower intertidal transplants. They found little evidence for bioturbation, epiphyte load, or dispersal constraints in a study in the San Juan Islands of Washington State, and suggested that light limitation may restrict *Z. japonica* from lower depths. At site scales, *Z. japonica* extended to lower elevations at sites at sites with more linear depth profiles, and where *Z. marina* remained at lower elevations. At the transect scale, only *Z. marina*'s shallow extent explained *Z. japonica*'s deep extent.

Z. marina and *Z. japonica* inhabited overlapping elevations at 46% of sites and 52% of transects where *Z. japonica* was observed. Site-scale overlap was more likely at sites with smoother depth profiles.

Z. japonica was observed at 29% of the sites included in this study, and these represented a smaller range of slopes than occupied by *Z. marina*. A post-hoc examination of factors predicting *Z. japonica* presence confirmed that gentle slopes were the best predictor of *Z. japonica* presence examined. Many shorelines in the Puget Sound are characterized by a relatively steep cobble or gravel beach face that gives way to a more gently sloped low-tide terrace at lower elevations (Finlayson, 2006). If the elevation range suitable for *Z. japonica* colonization is composed of a steep cobble

or gravel slope, *Z. japonica* could be excluded from the site. Such a site would also exhibit a steeper average slope in the elevation range measured in this study.

The complexity of Puget Sound beaches presents a challenge to the methods employed in this study. A single beach slope is a coarse measure of the intertidal elevation profile at a site, just as a single index of roughness doesn't capture the diversity of shoreforms encountered. Automated identification of the location of slope breaks, or classification of beach profiles could improve both the explanatory power of this study and the interpretability of its results.

The question of whether *Z. japonica* actually facilitates *Z. marina* in the intertidal warrants further investigation. Seagrass colonization of disturbed areas in the Caribbean, can be facilitated by rhizophytic algae (Williams, 1990). This process was primarily driven by nutrient deposition by early colonizing algae, but sediment stabilization or accumulation, or water retention by an early colonizer could also facilitate seagrass survival. *Z. japonica* could retain water with its leaves during low tides (eg. Powell and Schaffner, 1991), or by accumulating sediment (eg. Bos et al., 2007) that acts to retain water, in turn facilitating *Z. marina* growth at higher tidal elevations (Local-Scale Environmental Variability Predicts Local Distribution of *Z. marina* in a Mixed Intertidal Bed (chapter 3)).

Chapter 3

**LOCAL-SCALE ENVIRONMENTAL VARIABILITY
PREDICTS LOCAL DISTRIBUTION OF *Z. MARINA* IN
A MIXED INTERTIDAL BED*****Abstract***

Local-scale environmental heterogeneity can provide microhabitats that influence the spatial distribution of plants and the coexistence of competing species. Such patterns are often manifest along strong environmental gradients. Microtopographic variability has been suggested to influence the distribution of seagrasses along elevation gradients, but difficulty measuring intertidal microtopography has hindered quantification of such patterns. Using a terrestrial laser scanner, I mapped and monitored a one hectare study site for three years in order to understand spatial patterns and temporal dynamics of sediment microtopography. The location and shape of microtopographic features were generally stable from year to year, but the magnitude of local relief was variable. A simple index of topographic context predicted the presence/absence of the native seagrass, *Zostera marina*. The presence/absence of the introduced seagrass, *Zostera japonica*, was better predicted by the shoot density of *Z. marina* than by topographic context. Compared to well-drained microsites, microtopographic depressions at the site, which retain water during low tides, exhibited lower diurnal temperature ranges and lower maximum temperatures on days with low tide exposure. Microtopographic relief at this site influences important seagrass habitat variables by retaining water and moderating temperature extremes, and appears to exert a strong influence

on the meter to decameter scale distribution of *Z. marina*.

3.1 Introduction

Spatial environmental heterogeneity can lead to spatial patterns in species distributions, allow for coexistence of species competing for the same limiting resource (Horn and Arthur, 1972), and influence biodiversity (Tamme et al., 2010). Environmental heterogeneity plays important roles in species invasion processes. Environmental heterogeneity is one explanation for the invasion paradox: that native species richness is inversely related to invasive species richness at local scales, but positively correlated at larger scales (Fridley et al., 2007). Increased native richness may make a site more resistant to invasion (Elton, 1958), by reducing resource availability (Davis et al., 2000) or empty niches (Shea and Chesson, 2002). At larger spatial scales, the environmental heterogeneity that promotes native species richness, can also promote invasive species richness (Fridley et al., 2007). Because habitat heterogeneity can allow for stable coexistence of species, environmental heterogeneity should both promote invasive species richness in an area, and simultaneously reduce invasive species impacts (Melbourne et al., 2007).

Environmental heterogeneity need not occur on broad spatial scales to have important ecological impacts. Based on classical niche theory, the Heterogeneity Diversity Hypothesis predicts greater diversity with increased environmental heterogeneity. However, heterogeneity at the scale of individual interactions and smaller may lead to both increases and decreases in biodiversity (Tamme et al., 2010). Small scale heterogeneity may extend species ranges by offering local refuge from inhospitable conditions, for example in alpine communities (Wundram et al., 2010), or salt marshes (Varty and Zedler, 2008).

Fine scale topographic heterogeneity can be particularly influential in intertidal communities. In the rocky intertidal, small crevices and tidepools can provide thermal refugia (Garrity, 1984). In soft sediments, microtopographic relief can trap water during low tides providing additional habitat for desiccation sensitive species (Wyer et al., 1977; Harrison, 1982c; Shafer, 2007), and affecting spatial patterns of herbivory (van der Heide et al., 2012). Intertidal microtopographic relief has been suggested to influence the local distribution of an invasive seagrass *Z. japonica*, and its native congener *Z. marina* (Harrison, 1982c; Shafer, 2007), but these observations have not been quantified or critically tested.

3.1.1 Terrestrial Laser Scanning

While microtopography is likely important to intertidal soft-sediment communities, is particularly difficult to measure. Soft, unconsolidated sediment hinders direct measurement both by limiting travel, and by making it difficult to measure elevations without disturbing or compacting sediments. Intertidal topography has been traditionally mapped with survey techniques such as level and stadia (Shafer et al., 2007, eg.), which are effective for constructing shoreline profiles. These techniques are too time-intensive to be practical for high-resolution mapping, and risk compacting and disturbing the sediment that is measured. Sediment Elevation Tables (Boumans and Day, 1993), and water levels (Bos et al., 2007) have been very successful at high precision (sub-centimeter) measurements of topography over small extents, and are particularly valuable for estimating rates of change in sediment elevations. These techniques are limited to spatial extents of only a few meters.

Unfortunately, remote measurements are also problematic. Typical aerial LiDAR data must be obtained during a low tide (Chust et al., 2008, eg.) which precludes the

use of much readily available LiDAR data. Even during a low tide exposure, standing water and saturated soils reduce the efficacy of the infrared lasers used in most aerial LiDAR applications. The shallow water depth at such locations inhibits sonar surveys, both by limiting the size of vessel that can carry out such surveys, and by reducing the swath width that can be mapped with a single pass.

Bathymetric LiDAR employs higher-energy green wavelengths that are less attenuated by water. These systems are capable of penetrating water depths of 25 m or more depending on water clarity (Brock et al., 2004), and have been successfully employed mapping *Zostera noltii* habitat (Valle et al., 2011), salt marsh habitat (Collin et al., 2010), and coral reef structure (Brock et al., 2004). There are relatively few bathymetric LiDAR systems in operation, often operated by government agencies (eg. EAARL, operated by NASA), which limits the availability of these data. Furthermore, despite their impressive capacity to map large extents of coastline, their ranging accuracy (15–50 cm, (Irish and Lillycrop, 1999; Quadros et al., 2008)), may be too coarse to map fine-scale intertidal topography and its temporal dynamics.

Terrestrial Laser Scanning (TLS), also known as ground-based LiDAR, may overcome some of the aforementioned challenges to topographic measurement in estuarine wetlands. These tripod-mounted instruments are capable of mapping surfaces with sub-centimeter precision (Vierling et al., 2008). Just as aerial LiDAR, TLS measures the time of flight of emitted laser pulses to create three dimensional point clouds of a surface (Figure 3). With this technique, sediment disturbance can be limited to the scanner location while remotely measuring undisturbed areas. TLS has mostly been applied to industrial and engineering studies (Fröhlich and Mettenleiter, 2004); terrestrial ecological applications include tree allometry (Clawges et al., 2007), measurement of leaf area index (Zheng et al., 2013), and characterize peatland morphol-

ogy (Anderson et al., 2010; Bennie et al., 2011). To date, there are few examples of TLS studies in intertidal areas, but it has been used to measure marsh morphology (Guarnieri et al., 2009), and tidal stream channels (Hetherington et al., 2007).

3.1.2 Objectives

Here I examine the role of local microtopographic relief and change in structuring environmental conditions and vegetation distribution in an intertidal seagrass mosaic composed of the invasive *Z. japonica* and its native congener *Z. marina*. Specifically I address the following questions: 1) Is TLS capable of effectively measuring a) spatial patterns of microtopographic relief at centimeter scales, and b) temporal change in microtopographic relief from year to year at centimeter scales? 2) Does intertidal microtopographic relief predict the habitat variables of temperature and reduction-oxidation potential? 3) Does microtopographic relief predict the intertidal distributions of *Z. marina* and *Z. japonica*?

3.2 Methods

3.2.1 LiDAR, GPS

To understand spatial and temporal patterns in intertidal microtopography, we mapped and monitored a 1.84 hectare intertidal study site with a ground-based LiDAR scanner (Leica Scanstation II). The site was scanned at least once in 2009, 2010, and 2011. All scans were geo-referenced using a survey grade Global Positioning System (Javad Maxor GGD-T), to facilitate the comparison of topography mapped on different dates. Raw LiDAR point clouds were pre-processed and geo-referenced using Cyclone software (version 7.3, Leica Geosystems), and exported to ArcGIS (version 10.0, ESRI) for further analysis.

Point clouds were gridded to raster Digital Elevation Models (DEMs) with a horizontal grain of 10 cm, using natural neighbor interpolation. From these DEMs, we mapped the slope and the Bathymetric Position Index (BPI) across the site. Bathymetric Position Index (BPI) is the difference the elevation at a point to the mean elevation in a user specified surrounding neighborhood (Lunblad, 2004). Positive values of BPI, thus indicate high points or ridges, negative values depressions, and very small values either flat or uniformly sloping surfaces. By varying the size of the annulus-shaped neighborhood, a researcher may inspect the influence of topographic position at multiple scales.

3.2.2 Redox

To assess the influence of microtopographic context on sediment reduction-oxidation potential (redox) and sulfide concentrations, we analyzed sediment cores collected at low tide. At randomly selected pools and mounds, we collected 20 cm deep cores as the oncoming tide flooded the site, such that cores collected from mounds included overlying water. Corers were constructed of 5 cm diameter ABS plastic tubing with 5 mm diameter holes drilled every centimeter along their length, and end caps. Prior to core collection, all of the 5 mm holes were covered and secured with electrical tape. Cores were pressed into the sediment, capped, and withdrawn. The bottom of each core was capped immediately upon withdrawal from the sediment. Cores were kept upright and immediately place on ice until placement in a laboratory freezer.

Redox potential was measured in a nitrogen-purged glove bag. In the glove bag, the 5 mm holes were uncovered one at a time, and redox potential measured with a redox micro-electrode (Lazar Research Laboratories, Inc.). Cores were then cut into 2 cm sections, and a sample of each section sealed into a nitrogen-purged 50

cc centrifuge tube, before removal from the glove bag. Sections were centrifuged for 15 minutes at 3900 RPM and the supernatant tested for sulfide concentration using a colorimetric technique (CHEMetrics). No more than trace levels of sulfide were detected in any of our samples.

We analyzed the influence of microtopographic relief on sediment redox potential with non-linear mixed effects models, fit with the fixed effects of topographic context (mound, pool) and sediment depth, and the random effect of sample site. We fit exponential decay models to the depth profile of redox potential for mounds and pools:

$$y = a + b \cdot e^{(c \cdot \text{depth})}$$

3.2.3 *Temperature*

In July 2009, waterproof temperature loggers (Hobo Pendant UA-001, Onset) were deployed on the sediment surface and 10 cm below the sediment surface at randomly selected locations throughout the study site. At each location two loggers were anchored to a 2 cm diameter PVC pipe such that one logger would rest on the sediment surface and the other was buried. Because we were interested in the temperature experienced by seagrasses rather than air temperature, we left the surface temperature logger exposed to sunlight rather than employing shades. We recorded the position of each logger with utilizing kinematic GPS, the percent cover of each species in $0.25m^2$ surrounding the logger, as well as the topographic context (pool or mound).

Data loggers were retrieved and temperature data were analysed to assess the impact of topographic context on sediment surface and rhizosphere temperatures. Two data loggers were lost, presumably due to scour. Downloaded temperature measurements were managed in a relational database. Because we predicted that there would

be little difference in temperature between mounds and pools when fully submerged, we limited analyses to days on which the lowest tide was lower than mean lower low water (MLLW). From these days we modeled the daily maximum temperature, daily minimum temperature and the daily temperature range as a function of topographic setting (pool or mound) and sediment position (surface or rhizosphere). To do so, we utilized linear mixed models. In the full model, fixed effects included the separate, additive, and interactive effects of topographic setting and sediment position. To model the seasonal temperature trend, we also included parameters for the sine and cosine of time as the fraction of the year elapsed:

$$\beta_1 \sin(2\pi t) + \beta_2 \cos(1\pi t)$$

where t is equal the day of the year divided by 365). To estimate parameters of the best fit model, we utilized model selection and averaging (Anderson, 2008) using the second order Akaike's Information Criterion (AICc). We included a random effect for the site of each logger deployment.

3.2.4 *Vegetation Surveys*

In July 2011, we surveyed vegetation at the study site. Random survey locations were generated in a ArcGIS 10.0, and located in the field to the nearest 5 cm with kinematic GPS. At each survey site we counted all vegetative and generative shoots of *Z. marina* and *Z. japonica* in a 0.25 m \times 0.25 m quadrat and noted the presence of standing water. These data combined with LiDAR-generated DEMs and BPI maps to assess the influence of microtopographic context on the presence and density of *Z. marina* and *Z. japonica*. The count data were zero-inflated, so we modeled the num-

ber of vegetative and generative shoots using a non-parametric, distance based linear modeling technique, DistLM (Anderson, 2001b,c). Because we used only a single response variable, and euclidean distance measurement, the modeling and statistical test is equivalent to a linear model, but p-values are determined via permutations. When multiple predictors were tested, I present r^2 values and F-tests for each predictor with all other terms (not including interactions) in the model. For each species we tested the predictive value of the shoot density of the other species, elevation, change in elevation between 2010 and 2011, and BPI from 2009 and 2011.

3.3 Results

3.3.1 Pattern Description

The monitoring site elevations ranged from 0.22–0.78 m above MLLW (Figure 3.1). The overall slope of the site varied from 0.30% to 0.28% during the course of the study. The overall aspect of the site was southwest, at 210 degrees. According to our classification, the site was rather evenly divided between mounds and depressions. Depression cover varied from 48% in 2009 to 52% in 2010 and 2011, and mound cover varied from 48.5% in 2009 to 44% in 2010 and 2011. Mounds and depressions were generally elongate with their major axis oriented down the slope.

3.3.2 Topographic Change

At the site scale, elevation changes between 2009 and 2010 were negligible (Figure 3.1). The mean difference between 2009 and 2010 DEMs was a loss of just over 2mm of elevation, and a decrease in slope of 0.02%. At the scale of meters and decameters, however, elevation changes were more apparent. Elevation change between 2009 and 2010 was inversely correlated with BPI (Pearson's $r = -.52$), such that mounds were

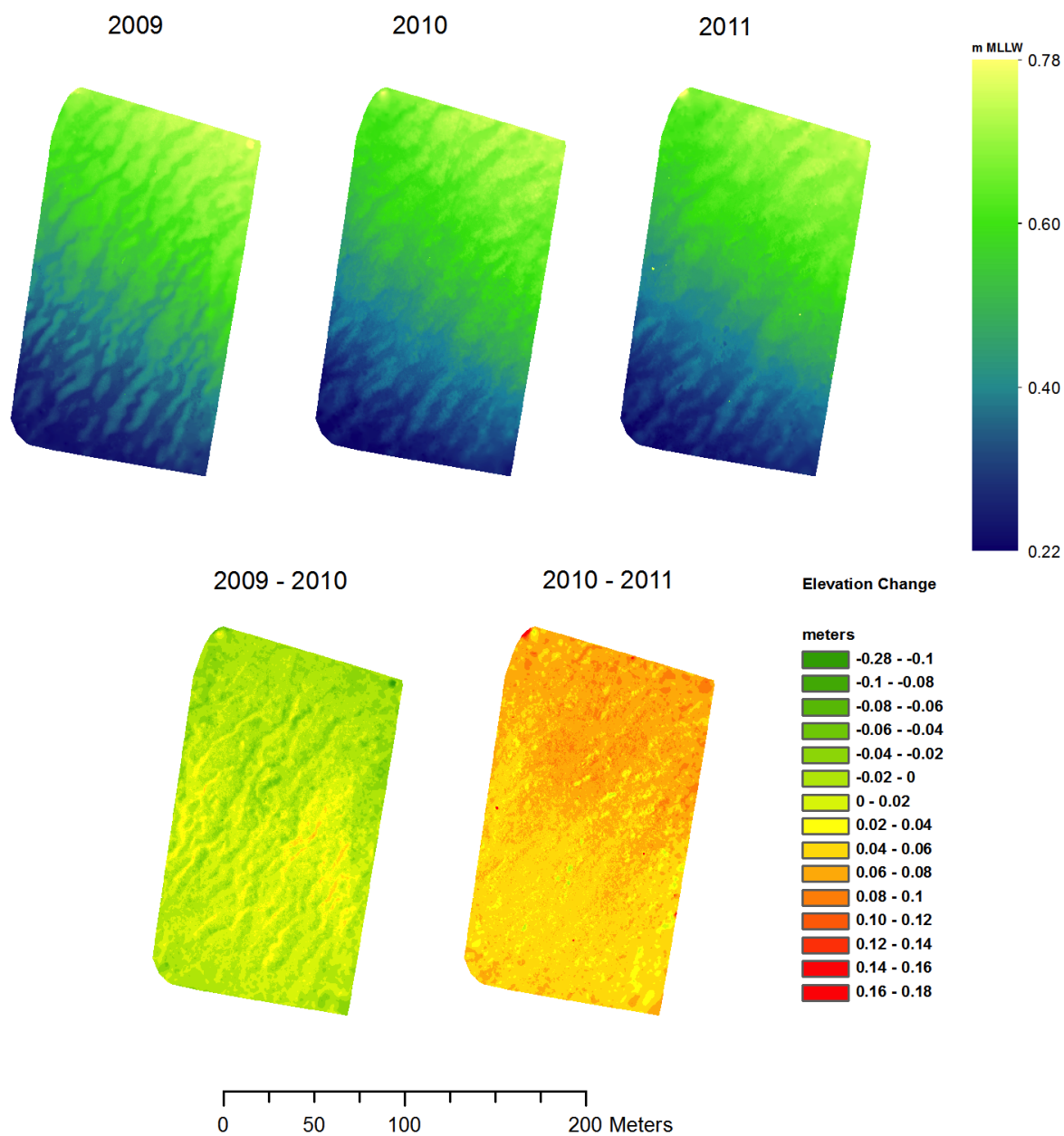


Figure 3.1: Topographic change from 2009–2011. The top row shows DEMs for 2009–2012, and the bottom row shows change maps for 2009–2010 and 2010–2011.

more likely to decrease in elevation and pools more likely to increase in elevation, leading to a less topographically variable site.

These changes were apparent when examining BPI in 2009 and 2010 (Figure 3.2). The topographic features are less distinct overall, although their shape and placement was very similar. BPI in 2010 was positively correlated with BPI in 2009 (Pearson's $r = 0.66$), but the slope of the best fit line of 2010 BPI as a function of 2009 BPI was 0.48 ± 0.02 , corroborating the decrease the magnitude of topographic relief between 2009 and 2010.

Between 2010 and 2011, we measured a net increase in elevation of 6 cm at the site scale. The increase was accompanied by an increase in mean slope of 0.01% rise. Localized patterns in elevation change were far less apparent. Elevation change was again negatively correlated with BPI, but less so (Pearson's $r = -.26$). BPI was more correlated between 2010 and 2011 (Pearson's $r = .76$) than between 2009 and 2010, and the slope of the best-fit line for 2011 BPI as a function of 2010 BPI was closer to one (0.76 ± 0.02).

3.3.3 Redox

We detected no significant differences between redox profiles at mound and pool sites. Mounds appeared to be more oxidized, particularly in the first 5 cm of sediment but there was considerable variability along the core depth, and between sample sites (Figure 3.3).

3.3.4 Temperature

The mean subsurface sediment temperature ($11.34^{\circ}\text{C} \pm 4.7$ SD) was slightly lower than the mean sediment surface temperature ($11.34^{\circ}\text{C} \pm 5.6$ SD). Both exhibited

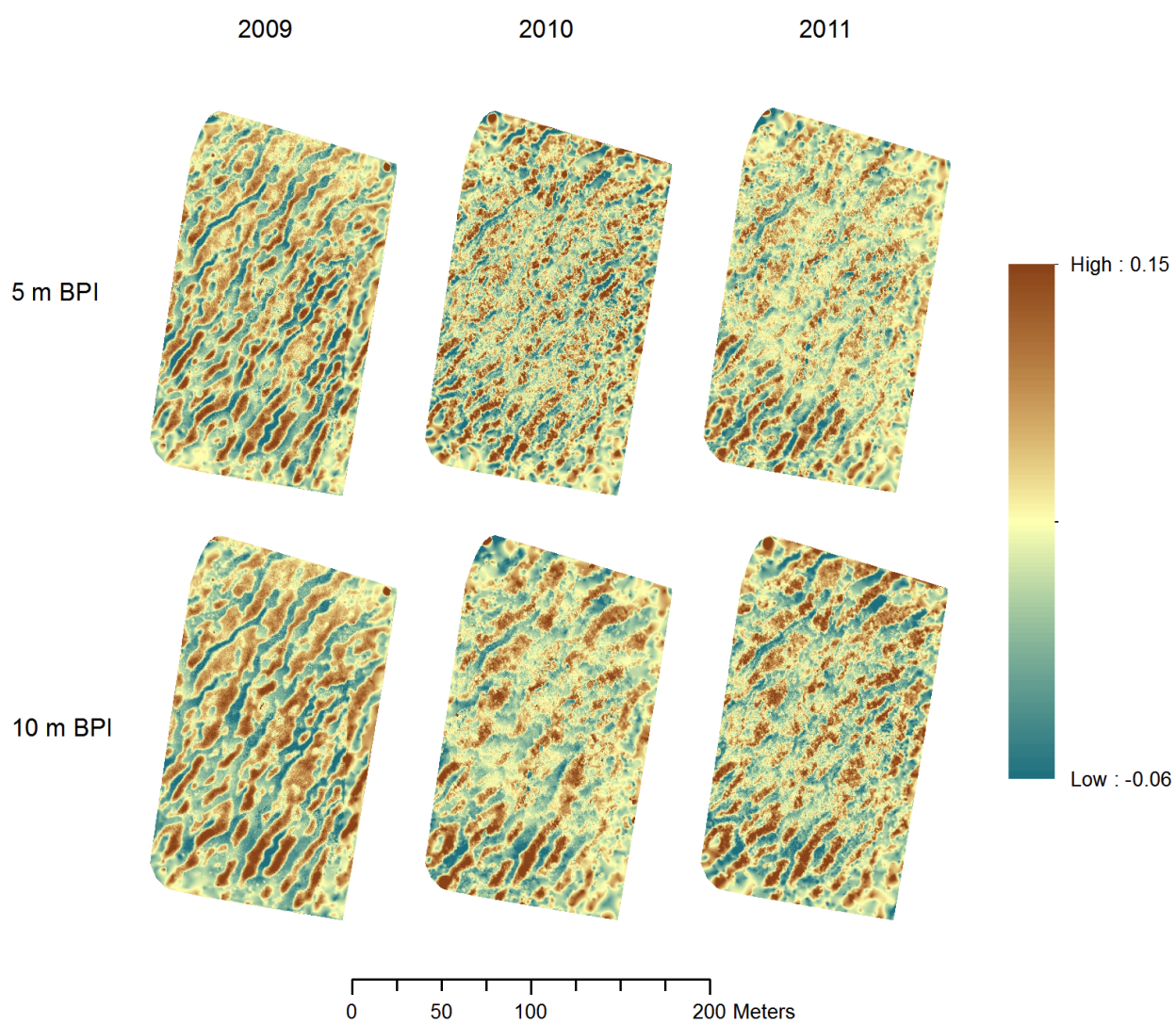


Figure 3.2: BPI at 2 different scales for 2009–2011. The top row maps BPI calculated with a 5 meter annulus and the bottom row maps BPI calculated with a 10 meter annulus

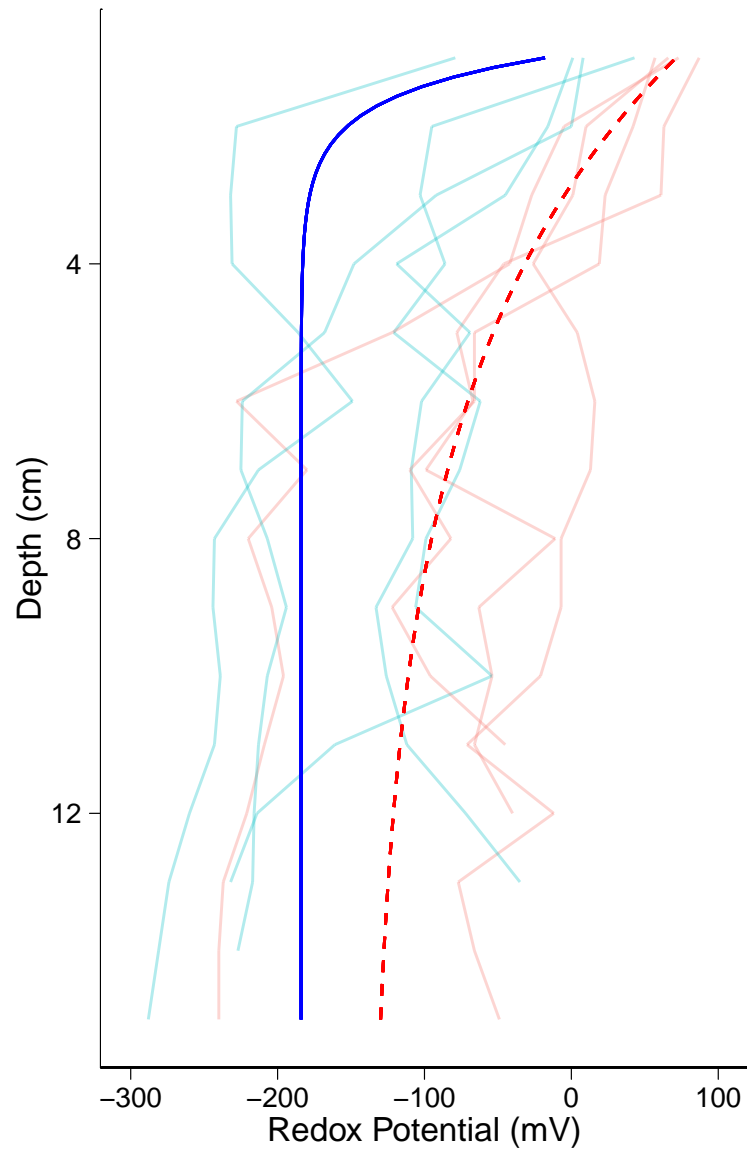


Figure 3.3: Depth profiles of sediment porewater redox potentials in core samples taken from pools (light blue) and mounds (light red), along with best-fit model predictions for redox as a function of depth in pools (dark blue) and mounds (dashed red).

considerable diurnal variation particularly on days with low tide exposure (Figure 3.4). On days when water levels were lower than MLLW, the best-fit models for both daily maximum temperature and daily temperature range included both additive and interactive effects of topographic setting and sediment strata. Maximum daily temperature and daily temperature range were greater on the surface than in the subsurface strata, and greatest on the surface of mounds (Figure 3.5).

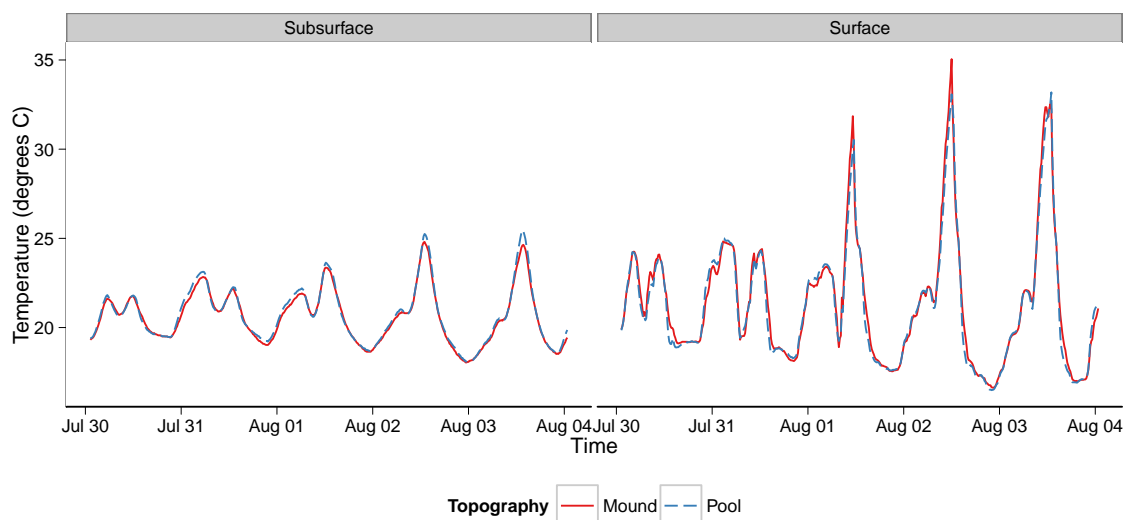


Figure 3.4: Example temperature profile during a low tide series, showing temperature 5 cm below the sediment surface in the left panel and sediment surface temperature in the right panel.

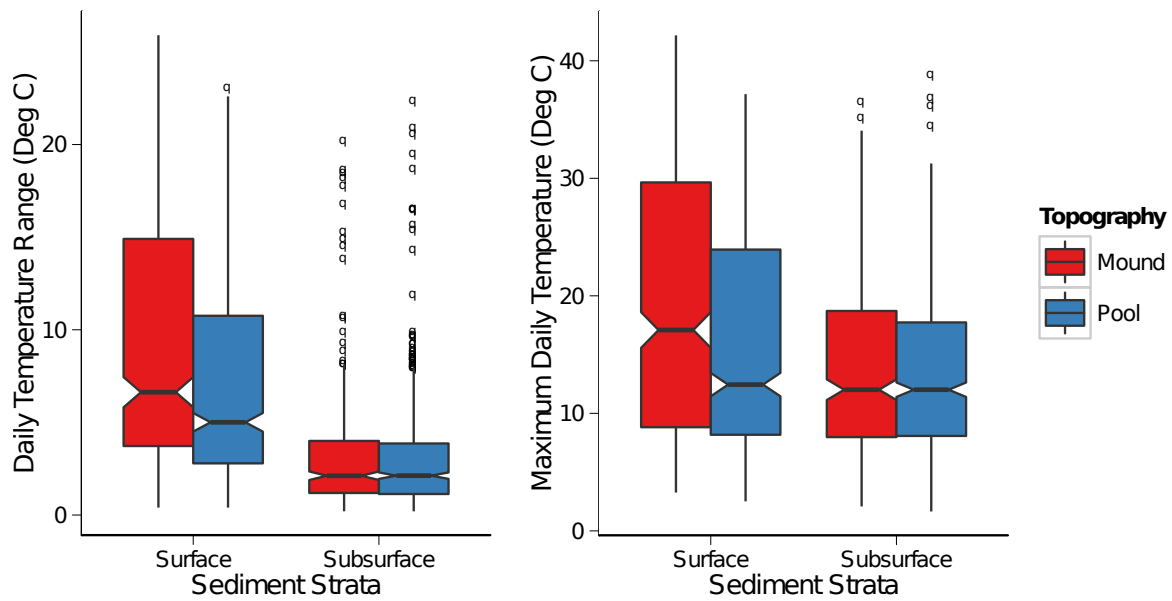


Figure 3.5: Daily temperature range (left) and maximum daily temperature (right) recorded by temperature loggers deployed on the sediment surface, and 5 cm below the surface in mounds and pools.

	Estimate	Std. Error	Adjusted SE	Lower CI	Upper CI
(Intercept)	18.18	0.31	0.31	17.57	18.79
PositionSubsurface	-3.06	0.45	0.47	-3.99	-2.13
TopographyPool	-0.80	0.39	0.39	-1.56	-0.05
cos(YrFrac * 2 * pi)	-10.75	0.19	0.19	-11.11	-10.38
PositionSubsurface:TopographyPool	0.96	0.52	0.56	-0.14	2.06
sin(YrFrac * 2 * pi)	0.16	0.19	0.19	-0.21	0.53

Table 3.1: Model averaged coefficients for daily maximum temperature

	Estimate	Std. Error	Adjusted SE	Lower CI	Upper CI
(Intercept)	18.18	0.31	0.31	17.57	18.79
PositionSubsurface	-3.06	0.45	0.47	-3.99	-2.13
TopographyPool	-0.80	0.39	0.39	-1.56	-0.05
cos(YrFrac * 2 * pi)	-10.75	0.19	0.19	-11.11	-10.38
PositionSubsurface:TopographyPool	0.96	0.52	0.56	-0.14	2.06
sin(YrFrac * 2 * pi)	0.16	0.19	0.19	-0.21	0.53

Table 3.2: Model averaged coefficients for daily temperature range

3.3.5 Vegetation

A model with only 2009 BPI explained 35% of the variation in *Z. marina* shoot density. *Z. marina* was less dense in areas with higher BPI in 2009 (DistLM, $n = 22$, 9999 permutations, $p = .003$, $r^2 = .35$) and 2011 (DistLM, 9999 permutations, $n = 39$, $p = .01$, $r^2 = .11$). A model with elevation, *Z. japonica* shoot density, and 2009 BPI explained 59% of the variation in *Z. marina* shoot density (DistLM, $n = 22$, 9999 permutations, $r^2 = .59$), predicting increased shoot density with lower BPI ($r^2 = .2$, $p = .03$) and lower *Z. japonica* shoot density ($r^2 = .13$, $p = .006$).

A model with only BPI explained only 11% of the variation in *Z. japonica* shoot densities, prediction lower densities where BPI was lower in 2011 (DistLM, 9999 permutations, $n = 39$, $p = .04$, $r^2 = .11$). A model with elevation, 2011 BPI, and *Z. marina* shoot density explained 50% of the variation in *Z. japonica* shoot density (DistLM, 9999 permutations, $n = 39$, $r^2 = .50$). *Z. japonica* grew more densely where *Z. marina* was less abundant ($p = .004$, $r^2 = .29$), and where BPI was greater ($p = .15$, $r^2 = .03$).

3.4 Discussion

3.4.1 Effectiveness of TLS

Despite the non-trivial logistical challenges of managing the equipment required for TLS surveys in soft sediment intertidal environments, we could relate species cover to centimeter scale topographic relief at the site. Quantification of temporal change in microtopography proved more difficult.

TLS data acquisition may be limited by characteristics of the landscape, and by characteristics of the instrument. Intertidal mudflats are characteristically wet, and periodically submerged. Although saturated sediments did not inhibit data acqui-

tion in this study, standing water did. Pools of standing water greatly reduced TLS return density, and introduced occasional reflection artifacts. This phenomenon has been described in TLS studies of river beds (Smith et al., 2012), and even capitalized upon to map the water surface in such studies (Milan et al., 2010). TLS has successfully mapped stream bottoms through as much as 20 cm of water (Smith et al., 2012), but these studies have been limited to small extents within a few meters of the scanner.

Water surface interference of sediment elevation measurements was even more apparent in an effort to compare TLS elevations with SET elevations elsewhere in Padilla Bay (data not presented). The SET sites did not dewater completely during low tides. The few centimeters of overlying water did not interfere with SET measurements, but prevented any TLS-based measurement of the sediment surface at this site.

Standing water in pools at the study site likely influenced the calculated Bathymetric Position Index. Pool elevations were most likely over estimated by 2–5 cm in most cases. This would lead to a positive bias in BPI in pools, and a negative bias in BPI on mounds at neighborhood scales large enough to incorporate both water surface and exposed sediment. Although pools at the study site retained water throughout the course of a low tide, I observed that the water level decreased in most pools during low tide exposures. This phenomenon would induce measurement inconsistencies between scans obtained after different durations of low tide exposure. Such inconsistencies were unlikely to have major impacts on inferences about the influence of microtopographic patterns on habitat attributes and vegetation distribution, but they add to the challenges of detecting temporal changes in microtopographic relief.

Refraction at the water surface would likely reduce the accuracy of measured pool bottom elevations, but the high density of seagrass leaves at the pool surface likely

occluded pool bottoms in most scans. Refraction effects can be corrected (Smith et al., 2012), but in this study site standing water would first have to be delineated. Point return density may be useful in classifying the LiDAR image into pools and mounds, but this first requires a correction for point spacing as a function of the distance to the scanner.

A common instrument-specific limitation of TLS is its stationary tripod mount. Due to the fixed vantage point, scanner height limits data acquisition. Because the vertical and horizontal angle between successive scan lines is fixed within a scan, data-point spacing increases as target range increases. This limited our useful scan radius to approximately 50 meters. Some researchers have extended the useful range of scans by elevation the scanner to considerable heights above the sediment surface (eg., Anderson et al., 2010).

Another challenge presented by the TLS vantage point is shadowing created by topography or erect vegetation. To overcome this challenge, the researcher may increase the point density of scans in order to penetrate more vegetation gaps, and scan from multiple vantage points. Although shadowing was nonexistent in our application due to the gentle nature of site topography and the lack of erect vegetation, it could pose a serious challenge in densely vegetated sites (Anderson et al., 2010).

Quantification of temporal change requires the spatial alignment of scans from different dates. This may be done by creating persistent, stable landmarks in the study area that can be referenced at different survey dates, or by georeferencing scans from different dates with GPS, as I did. The dynamic nature of an intertidal environment makes the former approach challenging, although permanent monuments can be created in tidelands (Boumans and Day, 1993).

GPS was our greatest source of positional error in my workflow. Between the

first and second year of TLS surveying, I was able to partially mitigate the GPS error with several changes to GPS data collection. In the first year of TLS surveys, a single GPS receiver was available to use, so scan target locations were obtained by static observations corrected by carrier-phase differential processing. In subsequent years the availability of a second receiver allowed for the installment of a base station at the study site during surveys. scan target locations were obtained by kinematic observations referenced to the nearby base station.

Despite the considerable improvement in GPS error afforded by kinematic observations, vertical RMS error of GPS locations was still on the order of centimeters. This level of precision was of a similar scale as observed changes in elevations from year to year, hindering most interpretation of the temporal dynamics of site microtopography and their influence on vegetation. Installation of multiple stable, permanent monuments at the study site would improve precision in future studies. Modified SET monuments offer a promising solution to this problem.

Perhaps the greatest challenge of many TLS-based studies is determining how to use the acquired data. A “shoot first and ask questions later” approach will likely cause frustration. TLS data are dense and detailed, and a researcher must first plan on how to extract useful summaries or measurements from the data. This can be both a conceptually and practically difficult problem.

3.4.2 Does microtopography predict habitat attributes?

Although redox potentials in pools appeared to decrease more quickly as a function of sediment depth, and reach lower extremes compared to mounds neither of these trends were statistically significant. Redox measurements were highly variable within and among core samples, and no measurable levels of hydrogen sulfide were found

in any samples. Due to these preliminary results, and the time consuming nature of redox analysis, I discontinued this portion of the study after the first field season. The consequently small sample size likely contributed to the lack of distinguishable differences between mounds and pools.

High variability of measured redox potential within cores may have resulted from actual natural variability at this scale, or measurement inconsistencies related to the redox electrode. Redox potentials is likely vary at sub-centimeter scales due to oxic microlayers around plant roots (Jensen et al., 2005), and likely due to the influence of infaunal burrows. It is unclear how potential differences in the oxidative environment between mounds and pools, manifest primarily during low tide exposures, would persist after tidal immersion.

Maximum temperatures and diel temperature ranges during days with low tide exposure were greater in pools than in mounds, and greater on the sediment surface than below the sediment surface. Shafer (2007) found no differences in mean minimum and mean maximum temperatures between pools and mounds at an adjacent study site, but did not distinguish between days with and days without low-tide exposure. Temperatures were far less variable during periods without low tide exposure, and there is little reason to expect temperature differences between these habitats during submersion. Extreme environmental conditions and events are often more influential stresses for organisms than mean conditions (Gutschick and BassiriRad, 2003; Gaines and Denny, 1993), so considering tidal-exposed variation separately from submerged variation is warranted.

3.4.3 Does microtopography predict seagrass distribution patterns?

Microtopographic context was an important predictor of both *Z. marina* and *Z. japonica* shoot densities, and shoot densities of each species were inversely correlated. As such, congener shoot density and microtopographic context explained much of the same variance in the models. BPI measurements from 2009 had greater explanatory power than 2011 BPI measurements for both species, but only 2011 measurements were significant for *Z. japonica*, likely a result of the smaller sample size in 2009 models. This was due to lower TLS return density in 2009, resulting in some 'no data' cells in BPI maps for that year. The greater explanatory power from the earlier year could be indicative of temporal carry-over effects, but may be due to the greater topographic amplitude in 2009.

Some of the uncertainty in model estimates can be attributed to BPI's performance as a predictor of mound and pool habitat. BPI is a useful but imperfect predictor of where water will be retained in an intertidal mosaic. A more mechanistic model of water flow off of the tideflat would likely offer better prediction of water retaining sites. Modeling techniques for very low gradient, low relief landscapes such as the study site are less well developed than for higher gradient terrestrial watersheds (Jones et al., 2008), and would likely require an understanding of subsurface water movement.

Z. marina's exclusion from sites with high BPI is congruent with observations by Shafer (2007), that *Z. marina* occupies depressions that retain water, and *Z. japonica* occupies mounds that drain during a low tide. The uncertainty in 2011 BPI coefficient estimates for *Z. japonica* density may be indicative of a broader microhabitat tolerance at these intertidal elevations. Furthermore, the best predictor of *Z. japonica* presence, was the shoot density of *Z. marina*. This is consistent with observations that *Z. japonica*'s deep extent is correlated with *Z. marina*'s shallow extent (chapter 2), and

could result from competitive exclusion of *Z. japonica* by *Z. marina* (eg.chapter 4).

Chapter 4

**MICROTOPOGRAPHY MEDIATES COMPETITION
BETWEEN *Z. MARINA* AND *Z. JAPONICA******Abstract***

Context dependence of invasion outcomes presents a challenge to the prediction of invasive species impacts, but few manipulative studies have addressed this in marine systems. In its introduced range, the invasive seagrass *Zostera japonica* often co-occurs with the native *Zostera marina* in a patch mosaic associated with intertidal microtopography (centimeter to decimeter relief over meter to decameter distances). At such sites, *Z. marina* inhabits depressions that retain water during low tides, and *Z. japonica* inhabits well-drained mounds. Transplant experiments revealed that *Z. marina* suppressed *Z. japonica* shoot densities, more so in pools than on mounds. *Z. marina* suppressed *Z. japonica* above and below ground biomass by 47% and 19% respectively, on mounds, but in pools suppressed above and below ground biomass by over 60%. *Z. marina* shoot densities and biomass were 40% and 95% lower, respectively, on mounds, regardless of *Z. japonica* presence. Topographic context remained the most influential predictor of *Z. marina* responses, even when we transplanted *Z. marina* into higher densities of *Z. japonica*. These results indicate that the native *Z. marina* is physiologically restricted from mounds and competitively excludes the introduced *Z. japonica* from pools. Such a pattern is consistent with physiological limitation of upper elevation extents, and biotic limitation of lower elevation extents commonly found in other intertidal systems. We show that centimeter-scale

topographic relief can modify competitive outcomes and promote decameter-scale coexistence.

4.1 Introduction

A primary goal of invasion biology is the prediction of invasion impacts (Parker et al., 1999). This task is complicated by the fact that invasion impacts often depend on the biotic and abiotic context in which they occur (Byers et al., 2002; Thomsen et al., 2011). Understanding the context dependence of invasion impacts is thus an important task for invasion biology (Byers et al., 2002). The local impact of a species introduction may be influenced by aspects of the biotic and abiotic context that vary at a regional (Cheng and Hovel, 2010; Wardle et al., 2008) or local scale (Gerhardt, 2007; Byers, 2002), but the context may also vary temporally as evidenced by the importance of disturbance history in invasion success (Hobbs and Huenneke, 1992; Altman and Whitlatch, 2007). Marine ecosystems exhibit patterns of variability across time and space (Denny et al., 2004) and have been a hotbed of experimental ecology. Surprisingly, a recent review of context dependence in marine invasions (Thomsen et al., 2011) found few marine studies have included manipulations of abiotic context in the examination of invasion impacts.

Topography has long been recognized for its effects on spatial patterns in ecological communities, whether influencing floristic composition along elevation gradients (Whittaker, 1956), zonation of intertidal communities (Stephenson et al., 1949), or species richness (Whittaker and Niering, 1975; Rahbek, 1995). Microtopographic context can also exert important influence, providing thermal refugia (Wundram et al., 2010), or suitable germination conditions (Harper et al., 1965). Such microtopographic context might be expected to be generally important in intertidal

invasions, where topographic features may have profound effects on influential environmental variables such as extremes of temperature (Helmuth and Hofmann, 2001; Jackson, 2010), humidity (Jackson, 2010), hydrodynamic energy (Jackson, 2010), insolation (Takada, 1999), soil salinity and oxygen availability (Varty and Zedler, 2008; Stribling et al., 2006).

Local topographic context appears to be influential in the invasion of *Zostera japonica* (Aschers. & Graebn.), an Asian seagrass that is invading estuaries on the west coast of North America. Amidst the backdrop of global seagrass declines, *Z. japonica* is likely the world's only invasive seagrass. In its introduced range, *Z. japonica* often inhabits higher intertidal elevations than its native congener, *Zostera marina* L., but at some locations their elevation ranges overlap (Shafer, 2007). Where elevation overlap occurs, the two species may occur in well-mixed stands, or in a more segregated patch mosaic. The mosaic tends to occur on tideflats with variable microtopography, where *Z. marina* inhabits depressions that retain water during a low tide, and *Z. japonica* inhabits mounds exposed by a low tide (Shafer, 2007), suggesting the importance of local microtopographic context. Studies in Willapa Bay, Washington (Bando, 2006), Padilla Bay, WA (Bulthuis, 1995; Shafer, 2007), and Boundary Bay, British Columbia (Harrison, 1982b), have documented this mixed mosaic zonation. *Z. japonica* may compete with its native congener, *Zostera marina* L., where they co-occur in well mixed stands (Bando, 2006), but no published studies to date have examined interactions between *Z. japonica* and *Z. marina* in the mixed mosaic zonation.

Temporal context may also play an important role in these patch mosaics. *Z. japonica* is quicker to colonize disturbed sites (Bando, 2006), perhaps by virtue of a higher relative investment in sexual reproduction (Harrison, 1979), and might

inhibit *Z. marina* recolonization (Bando, 2006). *Z. japonica* grows at higher densities in monoculture than when growing mixed with *Z. marina* (Nomme and Harrison, 1991b), and it is possible that dense, established patches of *Z. japonica* might exclude *Z. marina*, creating a seasonal or historical context dependence. Such a priority effect could lead to eventual dominance by *Z. japonica* at such sites in the presence of disturbance.

Washington State's recent listing of *Z. japonica* as a noxious weed has renewed calls for better understanding of *Z. japonica*'s impacts on native ecosystems. Here we examine the roles of intertidal microtopographic context and interspecific competition in structuring an intertidal patch mosaic of *Z. marina* and *Z. japonica*. Using field transplant experiments we investigate two primary questions. 1) How do microtopographic context and interspecific interactions influence the local distribution of *Z. marina* and *Z. japonica*? 2) How do *Z. japonica* density and microtopographic context influence resistance to *Z. marina* colonization? In addressing the first question, we tested the following competing hypotheses: Fundamental niche hypothesis: Each species is limited by sub-optimal abiotic conditions associated with microtopographic context, resulting in the observed patch mosaic. Realized niche hypotheses: One species is the dominant competitor, but is constrained by abiotic conditions associated with microtopographic context.

4.2 Methods

4.2.1 Reciprocal Transplants

To assess the relative importance of microtopographic context and interspecific interactions to the local distribution of *Z. marina* and *Z. japonica* in intertidal mosaics, we conducted additive reciprocal transplant experiments. Each species was transplanted

in monocultures, and with its congener, to intertidal pools and mounds. Monoculture transplants into pools served as controls for transplant effects on *Z. marina*, and monoculture transplants onto mounds served as controls for transplant effects on *Z. japonica*.

In June 2009, we delineated a 1.84 hectare monitoring site on the southern shore of Samish Island (Figure 1.1). In May 2010 we mapped a 100 m \times 50 m study region adjacent to the monitoring site, between 0 and 0.4 m above mean lower low water, with a Leica Scanstation II terrestrial laser scanner to produce a high-resolution 3-dimensional map of the mudflat topography. From this terrain map, pools and mounds were delineated in a geographic information system (ESRI, Redlands, CA), utilizing the Bathymetric Position Index (Lunblad, 2004).

Due to the size of pools and mounds, this study was designed as a split plot, with micro-topographic features as the whole-plot treatment, and species combinations as the split plot factors. This allowed us to ensure the independence of topographic treatments, while limiting the study site size. Five pools and five mounds were randomly selected from all delineated pools and mounds larger than 25 m^2 . These served as whole plot treatments, within which three subplots were cleared of existing vegetation. Into these subplots, three different planting treatments (*Z. marina* monoculture, *Z. japonica* monoculture, both species) were randomly assigned so that all planting treatments were present in each whole plot. In pools, we left a fourth subplot un-cleared, and transplanted *Z. japonica* into these ambient conditions. Subplots were arranged north, south, east or west of the whole plot center, such that the subplot centers were 1.5 m from the whole plot center.

Transplant techniques were based primarily on those recommended by Short et al. (2002). For all subplots except the ambient pool subplots, all plant material was

harvested from the center 0.09 m² of each subplot to be used for transplants, and all above ground biomass was removed from the remaining 1 m² at each subplot. We removed no biomass from ambient pool subplots. Shoots harvested from the 0.09 m² subplots were placed immediately in covered buckets full of cool seawater and transported to the laboratory within three hours. Using a modification of the Transplanting Eelgrass Remotely with Frame Systems method (Park and Lee, 2007), harvested shoots were affixed to .09 m² transplant frames, an outer square of rebar with a 3 × 3 grid of jute cord. Two shoots with 5 cm of rhizome and any daughter shoots emerging within that 5 cm were tied back to back with to each of the nine cord intersections. For mixed species frames, two shoots of each species were attached to each intersection. Because *Z. japonica* branches more frequently along the rhizome than does *Z. marina*, this arrangement led to a transplant shoot density of 190 ± 19 shoots/m² (mean ± standard deviation) for *Z. marina* and 329 ± 52 shoots/m² for *Z. japonica*. The loaded transplant frames were stored in coolers of seawater until installation at treatment sites the following day. We transplanted all plots on June 15th–17th, 2010. Transplant frames were placed into the center of subplots, and pressed into the sediment to ensure that rhizomes were not exposed above the sediment. At the ambient pool subplots, we took care to ensure that existing seagrass shoots were not pinned under the frames or jute grids.

We counted all vegetative and generative shoots in the transplant plots bi-weekly until August 2010, and 4 times from March 2011 through July 2011. Between July 31st and August 7th, 2011, all above-ground and below-ground seagrass biomass was harvested from each plot by digging the plot to a depth of 20 cm and sieving all materials through a 1 cm screen. Biomass samples were sorted by species, and above and below ground biomass sorted by cutting each ramet at the primordial node. Roots

were removed from rhizomes and discarded because many roots had been separated by the sieving process, and species discrimination of roots was not feasible. We measured the length and width of the longest leaf of each species, and dried all samples for 48 hours at 60°C before weighing.

4.2.2 Density Experiment

To test how *Z. japonica* density and microtopographic context influence resistance to *Z. marina* colonization, we transplanted individual shoots of *Z. marina* into pre-planted plots of varying *Z. japonica* density, in pools and on mounds. This study was designed as a split plot, with micro-topographic features as the whole-plot treatment, *Z. japonica* density as the split-plot treatments. Five pools and five mounds were randomly selected from all delineated pools and mounds larger than 25 m². These served as whole plot treatments, into which three different *Z. japonica* density subplots were transplanted. In May, 2011 at each whole plot location, a 2m x 2m plot was cleared of all above ground biomass. Into this, *Z. japonica* was transplanted into .3m x .3m plots at densities of 0, 100, and 200 shoots/m². After one month, *Z. japonica* transplants were counted, and shoots were added or removed to reach densities of 0, 500, and 1,000 shoots /m². *Z. marina* donor shoots were collected haphazardly throughout the study site, and standardized to consist of a single ramet with 5 cm of rhizome attached. Prior to transplantation, leaf length and width, and sheath length were measured and recorded, and the rhizome tagged with a cable tie behind the first fully developed root cluster. A single *Z. marina* shoot was anchored into each *Z. japonica* density subplot with a landscape staple. All *Z. marina* transplants were completed on June 16th and 17th, 2011.

Transplanted *Z. marina* shoots were recovered on August 9th and 10th, 2011, and

placed into labeled re-sealable plastic bags with a small amount of seawater. At the laboratory, we measured leaf width, leaf length, sheath length, the length of each rhizome internode for each ramet, and the location of every branch for each genet. The location of the cable tie was used to determine new rhizome segments for each shoot.

4.2.3 Data Analysis

Flowering shoot density and biomass data were zero-inflated, making them difficult to model with parametric models, so we analyzed these responses with Permutational Multivariate Analysis of Variance (Permanova) (Anderson, 2001a), using PRIMER 6.0. Repeated measures of *Z. japonica* flowering shoot density over time were modeled such that each date was a separate response variate in the multivariate split-plot analysis.

Treatment effects on shoot densities, leaf biomass, rhizome, rhizome elongation, leaf width, and length of longest leaf were explored with generalized linear mixed effects models using the lme4 and nlme packages in R (R Development Core Team, 2008). We modeled a random effect of whole plot for all response variables, and an additional random effect of split plot for the temporal trend of shoot densities. Model residuals were visually examined for normality (except for Poisson models), and for homogeneity across factors. Leaf biomass, rhizome biomass, and rhizome elongation were all log-transformed (Zar, 1999) to homogenize variance and approximate normal errors. To account for over-dispersion detected in models with Poisson errors, we included an observation level random effect (Elston et al., 2001) effectively changing the error distribution to Poisson lognormal. When heteroscedasticity was detected, we modeled separate variances for factor levels exhibiting different variances. Coefficients

were estimated from the global model.

Because degrees of freedom can be difficult to approximate for mixed effects models, we used an information-theoretic approach to evaluate treatment effects. For each response variable, our candidate set of models included models with each treatment separately, and models that included combinations of treatments additively and interactively. We selected best fit models using second order Akaike's Information Criterion (AICc), and examined Akaike weights and evidence ratios to compare the weight of evidence for each model compared to the best-fit model (Anderson, 2008). The Akaike weight for a model is the ratio of the likelihood of that model given the data, to the sum of the likelihoods of all of the models compared given the data. Akaike weights quantify the weight of evidence for a given model being the best of the models compared. An evidence ratio is the ratio of the Akaike weights for two different models, and quantifies the likelihood of one model relative to the other.

In the reciprocal transplant experiment, for each species, vegetative shoot densities were modeled with a Poisson error distribution. Each year of shoot density data was analyzed separately. In the variable density experiment, leaf length, leaf width and log-transformed rhizome extension were then modeled with normal errors, branching was modeled with Poisson errors. We first examined the influence of pre-transplant leaf length, width, and sheath length on the response variables and included any of these covariates improved the AICc rank of the full model.

4.3 Results

4.3.1 Reciprocal Transplants

All transplant plots survived through August of the first year of the experiment. By March 2011, two *Z. marina* subplots, all on mounds, were completely bare, showing

evidence of scour. In 2011 *Z. japonica* was notably absent from all but 1 ambient *Z. marina* transplant sites until July 28th when two of five ambient plots contained shoots of *Z. japonica*.

Z. marina Response

Z. marina shoot density and biomass were depressed in mound transplants, but little impacted by the presence of *Z. japonica*. In 2010 and 2011, best fit models for *Z. marina* shoot density included different temporal trends due to topographic setting, but not due to *Z. japonica* presence (Table 4.1). The best-fit models were strongly supported by the data, being seven times more likely than the second-ranked additive model in 2010 and over 40 times more likely than the second-ranked interaction model in 2011 (Table 4.2). *Z. marina* shoot density increased in pool transplants, but remained relatively constant on mounds in 2010 (Figure 4.1). By August 2010, shoot densities were 60% lower on mounds than in pools (Table 4.1). In 2011, *Z. marina* shoot densities on mounds were considerably lower than in 2010, and lower than in pools. *Z. japonica* presence appeared to limit *Z. marina* shoot densities in pools toward the end of the experiment, but this interactive effect was not part of the best fit model. No flowering shoots of *Z. marina* were observed.

Table 4.1: Restricted Maximum Likelihood estimated of effects and standard errors from best fit models of *Z. marina* and *Z. japonica* shoot densities in 2010 and 2011.

	Rhizome Extension (cm)1		Branching1		Leaf Width (mm)		Leaf Length(cm)	
	Estimate	(SE)	Estimate	(SE)	Estimate	(SE)	Estimate	(SE)
Intercept (Pool Monoculture)	18.935	(1.226)*	4.8	(1.226)*	5.293	(1.557)*	28.55	(17.406)*
Pre Transplant Leaf Width					0.216	(0.243)*	2.688	(2.707)*
Topographic Context								
Mound	0.32	(1.331)*	0.292	(1.537)*	-2.708	(0.519)*	-16.77	(6.225)*
<i>Z. japonica</i> Density								
500 shoots/m ²	0.639	(1.246)*	0.625	(-1.424)	-1.233	(-0.396)	-0.992	(-4.288)
1000 shoots/m ²	0.652	(1.212)*	0.625	(-1.366)	-1.066	(-0.367)	-1.134	(-3.946)
Mound 500 shoots/m ²	2.591	(1.361)*	1.905	(-1.982)	1.321	(-0.575)	-5.536	(-6.211)
Mound 1000 shoots/m ²	1.624	(1.322)*	1.829	(-1.83)	1.19	(-0.528)	-2.016	(-5.667)

Best fit models for *Z. marina* standing crop included only microtopographic context for above ground biomass (Table 4.1). At the end of the experiment, vegetative shoot standing crop was reduced by 90% and rhizome standing crop was reduced by 84% on mounds relative to pools (Figure 4.2). No *Z. marina* flowering shoots were observed in biomass samples.

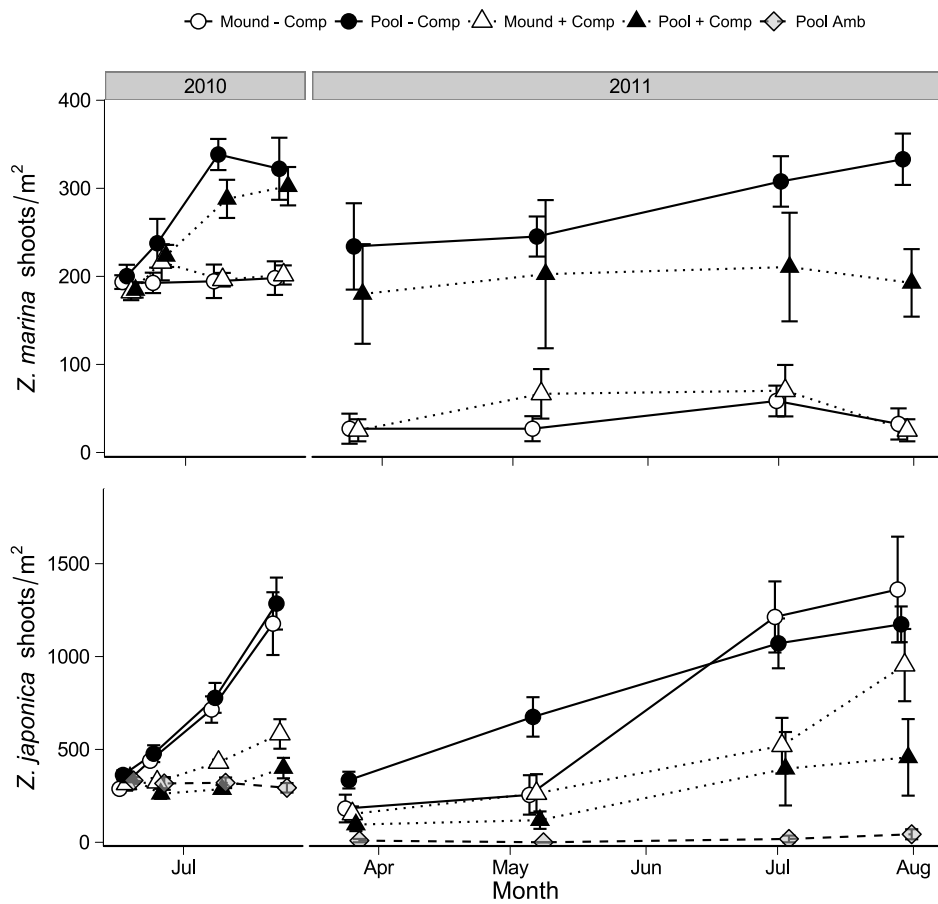


Figure 4.1: Temporal shoot density trajectories of reciprocal transplant experiments for a) *Z. marina*, b) *Z. japonica*, showing means \pm SE. Open symbols show transplants onto mounds, and filled show pools. Circles are monoculture and triangle are 2 species transplants, and diamonds show transplants into ambient *Z. marina*.

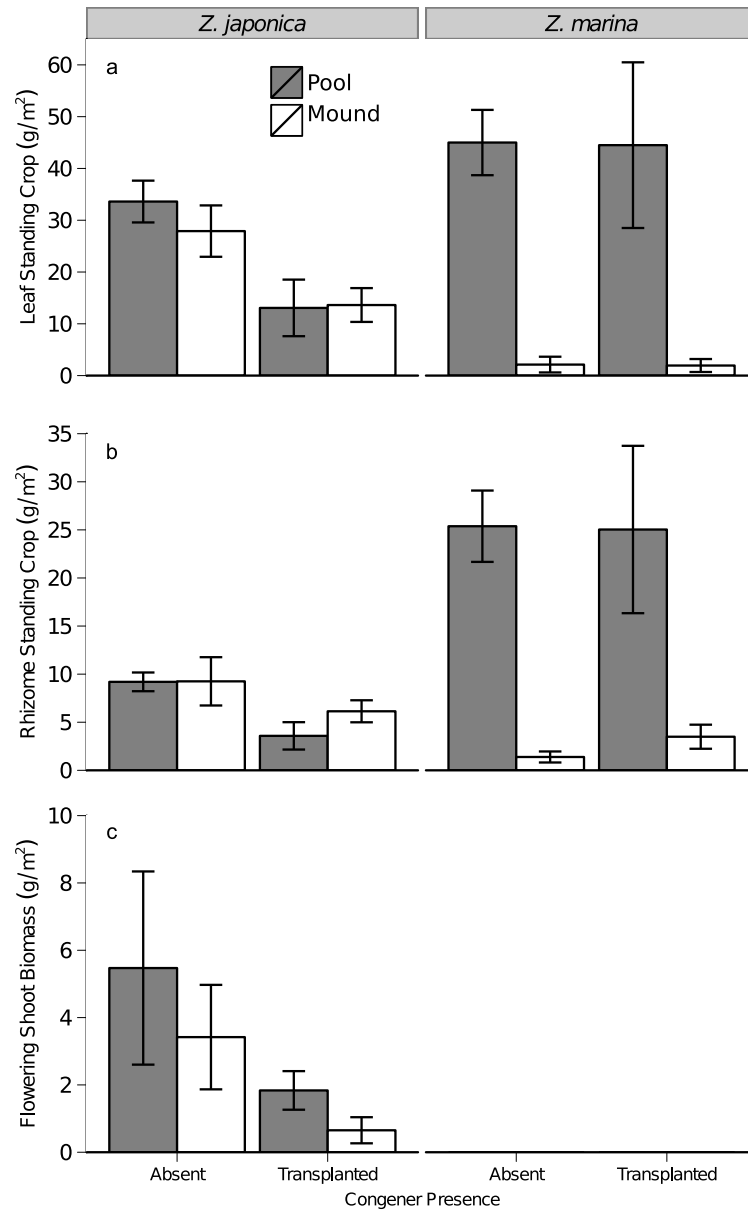


Figure 4.2: Standing crop at the end of reciprocal transplant experiment. Means \pm SE shown for a) above ground biomass and b) rhizome biomass. Filled bars show pool transplants

Table 4.2: Model selection details for transplant shoot densities of *Z. marina* and *Z. japonica* in 2010 and 2011. Best fit model according to AICc in bold.

Model	K	AICc	Δ AICc	Evidence Ratio	w_i	Log Likelihood
<i>Z. marina 2010</i>						
Topo	6	68.741	0	1	0.83	-27.762
Add	8	72.711	3.971	0.137	0.114	-27.281
Int	9	74.148	5.408	0.067	0.056	-26.711
Week	4	89.474	20.734	0	0	-40.456
Zj	6	93.167	24.426	0	0	-39.975
Null	3	109.48	40.739	0	0	-51.573
<i>Z. marina 2011</i>						
Topo	7	222.657	0	1	0.854	-103.517
Add	9	226.705	4.048	0.132	0.113	-103.009
Int	10	229.33	6.673	0.036	0.03	-102.998
Week	5	235.111	12.454	0.002	0.002	-112.133
Null	4	236.507	13.85	0.001	0.001	-113.976
Zj	7	238.99	16.332	0	0	-111.683
<i>Z. japonica 2010</i>						
Int	13	160.693	0	1	0.995	-64.411
Zm	9	171.55	10.857	0.004	0.004	-75.411
Add	11	175.918	15.225	0	0	-74.896
Week	7	256.486	95.793	0	0	-120.42
Topo	9	260.532	99.839	0	0	-119.903
Null	6	278.394	117.7	0	0	-132.588
<i>Z. japonica 2011</i>						
Int	15	360.089	0	1	0.986	-161.11
Add	13	369.714	9.625	0.008	0.008	-168.968
Zm	11	370.181	10.091	0.006	0.006	-172.06
Week	9	393.483	33.394	0	0	-186.398
Topo	11	394.472	34.383	0	0	-184.205
Null	8	405.629	45.54	0	0	-193.756

Z. japonica Response

Z. japonica vegetative and flowering shoot density and vegetative shoot biomass were reduced in the presence of *Z. marina*, but this effect sometimes depended on topographic context. In 2010 and 2011, best fit models for *Z. japonica* shoot density included interactive effects of *Z. marina* presence and topographic setting (Table 4.1). *Z. japonica* shoot density increased more slowly when transplanted with *Z. marina* during 2010 (Figure 4.1), and this effect was greater in pools than on mounds. By summer of 2011, monoculture plots had the highest *Z. japonica* shoot density, but two-species plots on mounds, where little *Z. marina* remained at this point, were approaching the shoot density of monoculture plots. In pools, two-species and ambient plots exhibited the lowest densities of *Z. japonica*. *Z. japonica* produced fewer flowering shoots in the presence of *Z. marina* (Permanova pseudo-F (2,12) = 4.4, p = .016, nperms = 999).

Best fit models for *Z. japonica* above and below ground standing crop included only the effect of *Z. marina* presence. At the end of the experiment *Z. marina* presence reduced *Z. japonica* above ground biomass by 47%, and reduced below ground biomass by 19% on mounds, but reduced both above and below-ground biomass by over 60% in pools (Figure 4.2). No difference in flowering shoot standing crop was detected at the end of the experiment.

4.3.2 Density Experiment

Topographic context consistently depressed all measured *Z. marina* responses, and the effects of *Z. japonica* density were smaller when detectable. Best fit models for all response variables included microtopographic context as a predictor. *Z. marina* branched less frequently, produced shorter rhizomes, and grew shorter, narrower leaves

Table 4.3: Model selection details for shoot and rhizome biomass of *Z. marina* and *Z. japonica* at the end of the experiment. Best fit model according to AICc in bold.

Model	K	AICc	Δ AICc	Evidence Ratio	w_i	Log Likelihood
<i>Z. marina Leaf Biomass</i>						
Topo	4	38.3	0	1	0.82	-13.82
Add	5	41.66	3.36	0.19	0.15	-13.69
Int	6	45.6	7.3	0.03	0.02	-13.57
Null	3	58.62	20.31	0	0	-25.56
Zj	4	61.52	23.22	0	0	-25.43
<i>Z. marina Rhizome Biomass</i>						
Topo	4	34.21	0	1	0.85	-11.77
Add	5	37.71	3.5	0.17	0.15	-11.71
Int	6	45.6	11.39	0	0	-13.57
Null	3	51.06	16.85	0	0	-21.78
Zj	4	54.11	19.9	0	0	-21.72
<i>Z. japonica Leaf Biomass</i>						
Zm	4	36.95	0	1	0.82	-13.14
Add	5	40.57	3.62	0.16	0.13	-13.14
Int	6	43.79	6.84	0.03	0.03	-12.66
Null	3	45.46	8.51	0.01	0.01	-18.98
Topo	4	48.62	11.67	0	0	-18.98
<i>Z. japonica Rhizome Biomass</i>						
Zm	4	29.07	0	1	0.61	-9.2
Null	3	31.78	2.71	0.26	0.16	-12.14
Add	5	32.09	3.02	0.22	0.14	-8.9
Int	6	33.86	4.79	0.09	0.06	-7.7
Topo	4	34.43	5.36	0.07	0.04	-11.88

on mounds than it did in pools (Figure 4.3). Rhizome elongation was modeled best by the full interaction model, although there was considerable model selection uncertainty, and the topography-only model was 84% as likely as the best fit given the data. Shoots transplanted onto mounds suffered a 68% reduction in rhizome growth, but this effect was partially ameliorated in both *Z. japonica* transplant treatments (Table 4.4). In pools, however, both densities of *Z. japonica* decreased *Z. marina* rhizome growth by about 35% (Table 4.4). Best fit models for leaf length and leaf width also included pre-transplant leaf width (Table 4.4). The data offered some support for the additive effect of *Z. japonica* and microtopography on *Z. marina* leaf length, with that model 28% as likely as the best-fit model (Table 4.5).

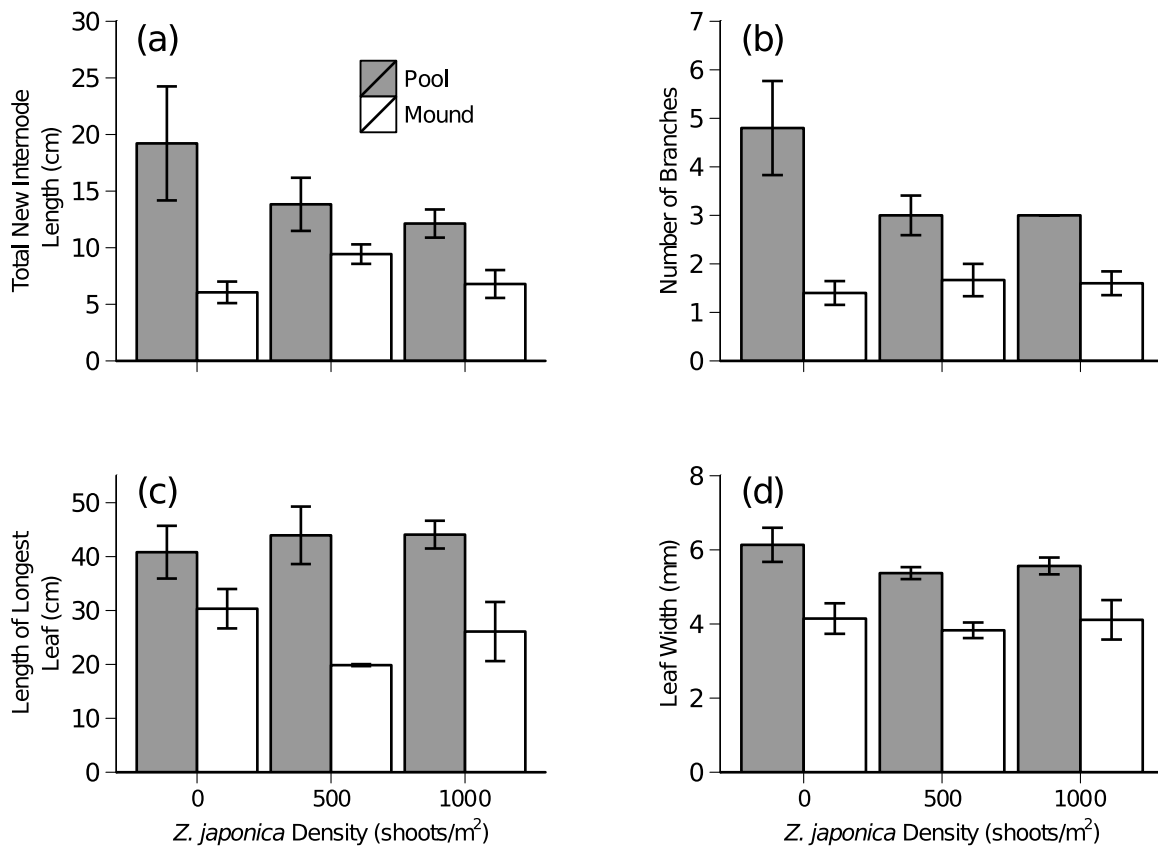


Figure 4.3: *Z. marina* response to a range of *Z. japonica* densities on mounds (open bars) and pools (filled bars) as measured by a) Rhizome extension, b) Branching, c) Leaf length, and d) Leaf width. Means \pm SE are shown.

Table 4.4: REML estimates and standard errors of effects of topographic context and *Z. japonica* density on *Z. marina* morphology from the *Z. japonica* density manipulation experiment.

	Estimate	(SE)	Estimate	(SE)	Estimate	(SE)	Estimate	(SE)
Intercept (Pool Monoculture)	5.349	(3.432)*	1.569	(0.204)*	5.293	(1.557)*	28.55	(17.406)*
Pre Transplant Leaf Width					0.216	(0.243)*	2.688	(2.707)*
Topographic Context								
Mound	-1.268	(4.855)*	-1.232	(0.430)*	-2.708	(0.519)*	-16.77	(6.225)
<i>Z. japonica</i> Density								
500 shoots/m ²	-0.839	(0.089)*	-0.47	(0.354)	-1.233	(0.396)	-1.134	(3.946)*
1000 shoots/m ²	-0.822	(0.084)*	-0.47	(0.312)	-1.066	(0.367)	-0.992	(4.288)
Mound 500 shoots/m ²	1.070	(0.214)*	0.644	(0.684)	1.321	(0.575)	-5.536	(6.211)
Mound 1000 shoots/m ²	0.597	(0.219)*	0.604	(0.604)	1.19	(0.528)	-2.016	(5.667)

Table 4.5: Model selection details for variable density experiment. Candidate models for *Z. marina* rhizome elongation, branching, Leaf Width, and Leaf Length listed in order of fit according to AICc.

Model	K	AICc	Δ AICc	Evidence Ratio	w_i	Log Likelihood
<i>Rhizome Elongation</i>						
Int	8	62.59	0	1	0.463	-21.349
Topo	4	62.936	0.346	0.841	0.389	-26.98
Add	6	65.166	2.576	0.276	0.128	-25.506
Null	3	69.329	6.739	0.034	0.016	-31.379
Zj Treat	5	72	9.41	0.009	0.004	-30.25
<i>Branching</i>						
Topo	3	16.871	0	1	0.866	-4.936
Add	5	20.96	4.089	0.129	0.112	-4.117
Null	2	25.263	8.392	0.015	0.013	-10.392
Int	7	26.494	9.623	0.008	0.007	-3.447
Treat	4	29.147	12.276	0.002	0.002	-9.704
<i>Leaf Width</i>						
Topo	5	57.601	0	1	0.76	-21.925
Topo + Treatment	7	60.127	2.527	0.283	0.215	-19.064
Topo X Treatment	9	65.339	7.738	0.021	0.016	-16.17
Null	4	66.565	8.964	0.011	0.009	-28.106
Treatment	6	71.365	13.765	0.001	0.001	-26.883
<i>Leaf Length</i>						
Topo	5	156.812	0	1	0.925	-71.531
Topo + Treatment	7	163.273	6.461	0.04	0.037	-70.636
Null	4	163.287	6.475	0.039	0.036	-76.467
Treatment	6	169.385	12.573	0.002	0.002	-75.892
Topo X Treatment	9	173.065	16.253	0	0	-70.032

4.4 Discussion

We have demonstrated that spatial patterns in intertidal beds of a native seagrass and its introduced congener can arise from topographically mediated competitive interactions. In intertidal pools, *Z. marina* severely reduced the growth of *Z. japonica*, and in some cases completely excluded it. On mounds, however, *Z. marina* performed poorly regardless of *Z. japonica* presence, apparently limited by abiotic stress. *Z. japonica*

grew equally well in either microhabitat in the absence of *Z. marina*. By virtue of this wider environmental tolerance, *Z. japonica* was able to persist on mounds that were devoid of *Z. marina*. It appears that the patch mosaic is a manifestation of *Z. japonica*'s realized niche, as constrained by competition with *Z. marina*. This resembles the commonly observed pattern in the rocky intertidal, where deep extents of zonation are set by biotic interactions, and shallow extents by abiotic stress (Connell, 1972).

Together with the work of Bando (2006) and Harrison (1979), which showed that *Z. japonica* devotes more resources to seed production and more quickly colonizes disturbed areas, these results suggest the presence of a competition-colonization tradeoff between *Z. japonica* and *Z. marina*. Theory predicts that competition-colonization tradeoffs can allow coexistence of multiple species competing for a single limiting resource even in the absence of habitat heterogeneity (Skellam, 1951; Horn and Arthur, 1972). This could be an important mechanism promoting coexistence of *Z. marina* and *Z. japonica* at sites with more homogenous microtopography. Theory also predicts that the species with better dispersal but worse competitive abilities will occupy the lower quality habitat, even if that habitat is equally unsuitable to each species (Skellam, 1951). While that mechanism could explain the patterns we investigated, *Z. marina* is clearly less tolerant of mounds than *Z. japonica*, favoring the realized niche explanation.

Complete competitive exclusion of *Z. japonica* by *Z. marina* was only observed in plots where *Z. japonica* was transplanted into ambient densities of un-cleared *Z. marina*. Where we transplanted both species into cleared plots, transplant stress or edge effects may have prevented competitive exclusion. If *Z. marina* competes with *Z. japonica* primarily through shading, the transplant plots may have exhibited an edge

effect of increased light penetration compared with the larger contiguous patches of *Z. marina* in the ambient transplant plots. Alternatively, transplantation stress may have limited *Z. marina*'s competitive effect on its non-native congener in experimental transplants.

Topographic context was the primary controlling factor of *Z. marina* morphology and growth in the variable density transplant experiment. *Z. marina* performance was consistently reduced on mounds, in any density of *Z. japonica*. *Z. japonica*'s influence was observed in the rhizome growth of *Z. marina*, but this effect depended on topographic context, was only half the size of the topography effect. In pools, *Z. marina* rhizome growth was depressed in presence of *Z. japonica*, but on mounds it was slightly enhanced. In neither case were there substantial differences between the effect of 500 or 1000 shoot/m² densities. The data provided some support for *Z. japonica* effects on branching and leaf length, but this was at best inconclusive. While *Z. japonica* shoot densities in this experiment did not reach the highest reported densities in its introduced range, they did exceed the 75th percentile for naturally *Z. japonica* shoot densities measured in the absence of *Z. marina* at the study site. Very high densities of *Z. japonica* may compete with *Z. marina*, but we saw little evidence of increasing *Z. japonica* shoot density influencing the relationship between these two species, suggesting that priority effects associated with *Z. japonica* colonization are not often important in these patch mosaics. Nevertheless, further study seems warranted given the potential importance of priority effects.

We did not determine the mechanisms of competition between *Z. marina* and *Z. japonica* or of abiotic limitation of *Z. marina*. Light is often the limiting resource at the deep extent of seagrasses (Duarte, 1991), and has been suggested to limit of *Z. japonica* production (Kaldy and Lee, 2007). Regardless of whether light limits *Z.*

japonica in monoculture at these depths, shading by the larger *Z. marina* could limit *Z. japonica* performance. At low tide in shallow pools, leaves of *Z. marina* float mostly horizontally at the water surface, and we observed near complete canopy closure by *Z. marina*. Little is known about the importance of air-exposed photosynthesis to *Z. japonica*'s carbon budget, but the study of another intertidal seagrass, *Zostera noltii* has yielded varied results. Some studies suggest reduced photosynthesis during areal exposure (Perez-Llorens and Niell, 1993), but others have found enhanced photosynthesis under such conditions (Leuschner and Rees, 1993; Silva et al., 2005), particularly if leaves remained hydrated. If *Z. japonica* responds similarly to aerial exposure, low tides could be important to its carbon balance.

Aerial exposure (Phillips, 1984), and more specifically desiccation (Boese et al., 2005), have been suggested as mechanisms limiting *Z. marina*'s shallow extent, however laboratory studies of sub-leaf-scale desiccation have shown *Z. japonica* leaf segments to be less resilient to desiccation than *Z. marina* leaf segments (Shafer et al., 2007). While whole plants in situ may desiccate differently than leaf segments in a laboratory, this has not been tested. Boese et al. (2003) developed a desiccation index for *Z. marina* based on patterns of leaf necrosis on low-tide exposed plants. Mound-transplanted leaves of *Z. marina* in our study showed similar patterns of necrosis reported by Boese et al., but neither their study nor ours distinguished between actual desiccation damage, and other emergence-related injury. Similar leaf injury was neither evident on *Z. japonica*, nor on pool-transplanted *Z. marina*.

Other studies of competition between *Z. marina* and *Z. japonica* have either focused on sites with well-mixed stands of the two species or ignored topographic context. These studies have reported competitive effects on both species, but none have reported competitive exclusion. The common observation of well-mixed stands of the

two species (Shafer, 2007) indicates that competitive exclusion may not be the norm outside of sites with the two-phase microtopographic morphology. Further investigation of intertidal pool habitats in which *Z. marina* excludes *Z. japonica* may yield deeper understanding of the mechanisms of competition between these two species. Particularly because the proximity of these pools to dense stands of *Z. japonica* suggests that propagule supply does not limit *Z. japonica* colonization.

The cause of the microtopographic variability observed in our study is unclear, but seagrass growth promotes similar patterns at some locations. Seagrasses are known for ecosystem engineering of hydrodynamics and sediment dynamics. Seagrasses can reduce current velocity (Gambi et al., 1990), increase sedimentation (Gacia et al., 1999) and increase local elevation (Ganthy et al., 2011; Bos et al., 2007). *Z. noltii*'s influence on hydrodynamics and sediment stability can lead to self-organizing banded vegetation patterns at some locations (van der Heide et al., 2010). At other sites, herbivory interacts with *Z. noltii*'s sediment stabilization to create hummock and hollow intertidal patterns similar to those observed in our study (van der Heide et al., 2012). Both of the aforementioned patterns in *Z. noltii* beds consist of unvegetated depressions and vegetated mounds at sites with a single seagrass species, in contrast to the two-species mosaic that we have studied. Nevertheless, it is likely that *Z. marina* and *Z. japonica* influence the microtopographic dynamics at our study site.

Given the impact of centimeter to decimeter scale local topography on competitive outcomes in this study, any effect that the seagrasses have on local topography could lead to feedbacks in this landscape. Our study suggests that *Z. japonica* poses little immediate threat to *Z. marina* at mixed mosaic intertidal sites. As such, immediate active control of *Z. japonica* at such sites seems unnecessary and potentially undesirable. *Z. marina* appears to be a superior competitor in the microsites that

it can inhabit, and is not inhibited by relatively high densities of *Z. japonica*. If *Z. japonica* is speeding the accretion of sediments and shrinking pool habitat, it could eventually displace *Z. marina* at such sites. However, if *Z. japonica* is effectively stabilizing mounds, its removal could lead immediately to increased disturbance, which has been shown to benefit *Z. japonica* (Bando, 2006). To fully understand the implications of management actions at mixed-mosaic intertidal sites will require improved understanding of vegetation sediment feedbacks.

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Appendix A

**MODEL SELECTION TABLES FOR BROAD-SCALE
PREDICTORS OF ZONATION AND OVERLAP**

Table A.1: Coefficients and model selection details for candidate models of *Z. marina* shallow extent with AICc weight greater than .001. Minus signs indicate variables included in model.

(Intercept)	Rugosity	Slope	Tide Rg.	Exp	Zj	Rug.:Slope	Slope:	Exp	df	LL	AICc	$\Delta AICc$	Wt.
-3.06	-0.84	-0.08	-	+	+	0.05	-	-	9	-1506.72	3031.65	0	0.39
-3.06	-0.84	-0.08	0.29	+	+	0.05	-	-	10	-1506.47	3033.2	1.55	0.18
-3	-0.86	-0.08	-	+	-	0.05	-	-	8	-1508.75	3033.67	2.02	0.14
-3.03	-0.82	-0.07	-	+	+	0.05	+	-	11	-1505.99	3034.3	2.65	0.1
-3	-0.85	-0.08	0.35	+	-	0.05	-	-	9	-1508.4	3035.02	3.37	0.07
-3.03	-0.81	-0.07	0.29	+	+	0.05	+	-	12	-1505.74	3035.86	4.21	0.05
-2.97	-0.84	-0.08	-	+	-	0.05	+	-	10	-1507.95	3036.17	4.52	0.04
-2.97	-0.83	-0.08	0.35	+	-	0.05	+	-	11	-1507.6	3037.52	5.87	0.02

Table A.2: Coefficients and model selection details for candidate models of *Z. marina* deep extent with AICc weight greater than .001. Minus signs indicate variables included in model.

(Intercept)	Rugosity	Slope	Tide Rg.	Exp.	Slope:Exp.	df	LL	AIC _c	ΔAIC_c	Wt.
-2.8	-	-0.11	-	+	-	6	-1808.72	3629.54	0	0.24
-2.76	-	-0.1	-	+	+	8	-1807.08	3630.33	0.79	0.16
-2.8	-	-0.11	0.44	+	-	7	-1808.19	3630.52	0.98	0.15
-2.81	-0.15	-0.11	-	+	-	7	-1808.34	3630.81	1.27	0.13
-2.77	-	-0.1	0.45	+	+	9	-1806.52	3631.25	1.71	0.1
-2.77	-0.14	-0.1	-	+	+	9	-1806.75	3631.71	2.17	0.08
-2.81	-0.14	-0.11	0.41	+	-	8	-1807.86	3631.89	2.35	0.08
-2.78	-0.13	-0.1	0.43	+	+	10	-1806.23	3632.72	3.18	0.05

Table A.3: Coefficients and model selection details for candidate models of *Z. japonica* deep extent with AICc weight greater than .001. Minus signs indicate variables included in model.

(Intercept)	Slope	Tide	Rg	Zm shallow	Exp.	Rugosity	df	LL	AICc	$\Delta AICc$	Wt.
-1.1	-	-	0.4	+	-	-	6	-223.33	459.22	0	0.14
-1.14	-	-	0.4	-	-	-	4	-225.55	459.37	0.15	0.13
-1.1	-0.07	-	0.38	+	-	-	7	-222.44	459.64	0.42	0.12
-1.13	-0.06	-	0.39	-	-	-	5	-224.84	460.09	0.87	0.09
-1.17	-	-0.46	0.39	-	-	-	5	-225.18	460.76	1.54	0.07
-1.5	-	-	0.4	+	0.38	-	7	-223.18	461.11	1.89	0.06
-1.12	-	-0.27	0.39	+	-	-	7	-223.2	461.15	1.93	0.05
-1.17	-0.07	-0.55	0.37	-	-	-	6	-224.32	461.2	1.98	0.05
-1.52	-	-	0.4	-	0.36	-	5	-225.42	461.24	2.02	0.05
-1.67	-0.08	-	0.38	+	0.54	-	8	-222.15	461.28	2.06	0.05
-1.13	-0.08	-0.37	0.37	+	-	-	8	-222.21	461.4	2.18	0.05
-1.66	-0.07	-	0.39	-	0.5	-	6	-224.6	461.76	2.54	0.04
-1.53	-	-0.44	0.39	-	0.34	-	6	-225.07	462.69	3.48	0.03
-1.67	-0.08	-0.54	0.37	-	0.49	-	7	-224.09	462.93	3.71	0.02
-1.68	-0.08	-0.35	0.37	+	0.52	-	9	-221.94	463.1	3.88	0.02
-1.5	-	-0.26	0.39	+	0.37	-	8	-223.06	463.1	3.88	0.02

Table A.4: Coefficients and model selection details for candidate models of depth range overlap with AICc weight greater than .001. Minus signs indicate variables included in model.

(Intercept)	Cen.Slope	Cen.Tide.Range	Exposure.Class	Rugosity	df	logLik	AICc	delta	weight
-0.33	-	-	-	-	3	-255.58	517.32	0	0.23
-0.18	-	-	+	-	5	-254.08	518.55	1.23	0.13
-0.35	-	-0.45	-	-	4	-255.3	518.86	1.54	0.11
-0.61	-	-	-	0.27	4	-255.53	519.33	2.01	0.09
-0.33	0	-	-	-	4	-255.58	519.42	2.1	0.08
-0.22	-	-0.66	+	-	6	-253.47	519.49	2.17	0.08
-0.42	-	-	+	0.23	6	-254.04	520.64	3.32	0.04
-0.18	0.01	-	+	-	6	-254.06	520.68	3.36	0.04
-0.59	-	-0.44	-	0.22	5	-255.27	520.93	3.61	0.04
-0.35	0	-0.46	-	-	5	-255.3	520.99	3.67	0.04
-0.61	0	-	-	0.26	5	-255.53	521.46	4.14	0.03
-0.38	-	-0.65	+	0.15	7	-253.45	521.65	4.33	0.03
-0.22	0	-0.66	+	-	7	-253.47	521.68	4.36	0.03
-0.41	0.01	-	+	0.22	7	-254.03	522.81	5.49	0.02
-0.59	0	-0.45	-	0.23	6	-255.26	523.08	5.76	0.01
-0.37	0	-0.65	+	0.15	8	-253.45	523.87	6.55	0.01

Table A.5: Coefficients and model selection details for candidate models of site-scale *Z. marina* shallow extent with AICc weight greater than .001. Minus signs indicate variables included in model.

(Intercept)	Rugosity	Slope	Tide.Rg.	Exp.	Zj	Slope:Exp.	df	LL	AICc	ΔAIC_c	Wt.
-3.68	-2.23	-0.14	-	+	+	-	7	-191.3	397.91	0	0.22
-3.53	-2.37	-0.17	-	+	-	-	6	-193.11	399.2	1.28	0.12
-3.68	-3.19	-	-	+	+	-	6	-193.33	399.63	1.72	0.09
-3.74	-2.28	-0.21	-	+	+	+	9	-189.75	399.67	1.75	0.09
-3.65	-2.06	-0.14	0.28	+	+	-	8	-191.12	399.96	2.05	0.08
-3.59	-2.42	-0.23	-	+	-	+	8	-191.22	400.15	2.24	0.07
-3.49	-2.13	-0.17	0.4	+	-	-	7	-192.77	400.86	2.95	0.05
-3.56	-2.08	-0.26	0.56	+	-	+	9	-190.53	401.22	3.31	0.04
-3.7	-2.01	-0.23	0.45	+	+	+	10	-189.3	401.28	3.37	0.04
-3.7	-	-0.22	-	+	+	-	6	-194.34	401.67	3.75	0.03
-3.67	-3.12	-	0.14	+	+	-	7	-193.28	401.88	3.97	0.03
-3.63	-	-0.22	0.6	+	+	-	7	-193.52	402.36	4.45	0.02
-3.47	-3.71	-	-	+	-	-	5	-196.31	403.32	5.4	0.01
-3.71	-	-0.33	0.77	+	+	+	9	-191.65	403.48	5.57	0.01
-3.47	-	-0.26	0.73	+	-	-	6	-195.26	403.49	5.58	0.01
-3.53	-	-0.27	-	+	-	-	5	-196.45	403.59	5.68	0.01
-3.56	-	-0.36	0.9	+	-	+	8	-192.97	403.66	5.74	0.01
-3.78	-	-0.32	-	+	+	+	8	-193	403.72	5.81	0.01
-3.61	-	-0.35	-	+	-	+	7	-194.8	404.91	7	0.01
-3.45	-3.58	-	0.26	+	-	-	6	-196.18	405.34	7.42	0.01

Table A.6: Coefficients and model selection details for candidate models of site-scale *Z. marina* deep extent with AICc weight greater than .001. Minus signs indicate variables included in model.

(Intercept)	Rugosity	Slope	Tide Rg.	Exp.	Slope:Exp.	df	LL	AICc	$\Delta AICc$	Wt.
-8.15	-	-	3.84	+	-	5	-254.97	520.64	0	0.35
-8.24	-	-0.15	3.73	+	-	6	-253.95	520.89	0.25	0.31
-8.19	-1.03	-	3.65	+	-	6	-254.74	522.46	1.82	0.14
-8.23	0.31	-0.16	3.78	+	-	7	-253.94	523.2	2.56	0.1
-8.4	-	-0.29	3.79	+	+	8	-253.73	525.17	4.53	0.04
-9.7	-	-	2.92	-	-	3	-260.01	526.29	5.65	0.02
-9.71	-	-0.15	2.78	-	-	4	-259.12	526.7	6.07	0.02
-8.4	0.43	-0.32	3.86	+	+	9	-253.7	527.57	6.93	0.01
-9.72	-0.93	-	2.73	-	-	4	-259.84	528.13	7.49	0.01
-9.71	0.43	-0.16	2.85	-	-	5	-259.1	528.89	8.25	0.01

Table A.7: Coefficients and model selection details for candidate models of site-scale *Z. japonica* deep extent with AICc weight greater than .001. Minus signs indicate variables in included in model.

(Intercept)	Rugosity	Slope	Tide Rg.	Zm	Exp.	Slope:Exp.	df	LL	AICc	$\Delta AICc$	Wt.
-0.49	8.48	-	-	0.59	-	-	4	-37.1	84.2	0	0.44
-0.52	9.88	-0.11	-	0.58	-	-	5	-36.81	86.77	2.57	0.12
-0.51	7.71	-	-0.37	0.55	-	-	5	-36.89	86.93	2.74	0.11
-0.49	8.63	-	-	0.58	+	-	5	-36.93	87.02	2.82	0.11
-0.54	10.36	-0.14	-	0.57	+	-	6	-36.52	89.7	5.5	0.03
-0.54	9.11	-0.12	-0.38	0.53	-	-	6	-36.58	89.83	5.63	0.03
-0.51	7.93	-	-0.32	0.55	+	-	6	-36.77	90.21	6.02	0.02
-0.97	-	-	-1.26	-	-	-	3	-41.56	90.26	6.06	0.02
-1.26	-	-	-1.1	0.22	-	-	4	-40.44	90.87	6.68	0.02
-1.48	-	-	-	0.27	-	-	3	-42.05	91.23	7.04	0.01
-1.16	-	-	-	-	-	-	2	-43.53	91.6	7.4	0.01
-0.68	1.88	-	-1.14	-	-	-	4	-41.25	92.5	8.3	0.01
-0.55	11.1	-0.19	-	0.55	+	+	7	-35.96	92.51	8.31	0.01
-1.16	-	0.18	-	0.37	-	-	4	-41.26	92.53	8.33	0.01
-0.68	2.94	-	-	-	-	-	3	-42.83	92.8	8.61	0.01
-0.99	-	-	-1.24	-	+	-	4	-41.54	93.09	8.89	0.01
-1.01	-	-0.01	-1.27	-	-	-	4	-41.55	93.11	8.91	0.01

Table A.8: Coefficients and model selection details for candidate models of site-scale depth-range overlap with AICc weight greater than .001. Minus signs indicate variables included in model.

(Intercept)	Rugosity	Slope	Tide Rg.	Exp.	Slope:Exp.	df	LL	AICc	$\Delta AICc$	Wt.
-2.86	-12.32	-	-	-	-	3	-40.18	87.51	0	0.5
-2.86	-12.57	-	-0.27	-	-	4	-40.08	90.16	2.66	0.13
-2.84	-13.21	0.07	-	-	-	4	-40.11	90.21	2.7	0.13
-2.86	-12.46	-	-	+	-	4	-40.12	90.23	2.73	0.13
-2.86	-12.8	-	-0.32	+	-	5	-39.98	93.11	5.61	0.03
-2.84	-13.5	0.07	-0.27	-	-	5	-40	93.15	5.65	0.03
-2.84	-13.58	0.08	-	+	-	5	-40.01	93.17	5.66	0.03
-2.83	-14.22	0.12	-	+	+	6	-39.76	96.19	8.68	0.01
-2.84	-14.04	0.09	-0.34	+	-	6	-39.85	96.36	8.85	0.01

VITA

Michael Hannam was born in Newport News, Virginia, on 31 August, 1977, the son of James and Maureen Hannam. After graduation from Thomas Jefferson High School for Science and Technology, he attended the University of Notre Dame, where he studied biology and earned a Bachelor of Sciences degree in May 1999. Following this, Michael served in the United States Army for four years and worked as a land manager and scientific technician for the Washington Department of Natural Resources. In 2006, Michael began his studies at the University of Washington.