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Invertebrate Community Composition Across Inundation Regimes and
Its Potential to Reduce Plant Stress

by

Inez Ilicia Lawson

A thesis submitted in partial fulfillment of the
requirements for the degree of

Master of Science
in
Environmental Science and Management

Thesis Committee:
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Portland State University
2017

Abstract

Appreciation of the ecological and economic values associated with healthy salt marshes has led to a recent rise in the number of marshes that are being targeted for restoration by dike removal. The success of restoration is often measured by the return of marsh plants, though this overlooks a key component of salt marshes, that of the invertebrate community within marsh sediments. To evaluate the short-term recovery of these invertebrates, sediment cores were collected across an elevational gradient in a recent dike removal marsh, one and two years post removal, and a nearby reference marsh. Abundance, richness and diversity as well as morphospecies community composition were compared across treatment groups (Reference, Removal) and elevation zone (High Marsh, Low Marsh). Morphospecies richness, abundance and diversity were significantly higher in Low Marsh samples than in High Marsh samples, though no statistically significant differences were found across treatments of the same elevation (e.g., Reference Low Marsh versus Removal Low Marsh). Pair-wise ANOSIM results found significant differences between community compositions across treatments, specifically Reference Low Marsh and Removal Low Marsh.

The marsh edge, the lowest point of vascular plant growth before transitioning to tide flats, is considered a high stress environment for emergent vegetation. Plant establishment and survival in this low elevation zone is limited by the tolerance to inundation duration and frequency and anoxic sediments. Bioturbation and burrowing by macroinvertebrates increases the surface area exposed to surface water for gas exchange,

increasing the depth of the redox potential discontinuity layer. Crabs that make stable, maintained burrows have been shown to increase oxygen penetration into sediment, improving plant productivity. Such crabs are not found in salt marshes of the Pacific Northwest of North America. However, other burrowing invertebrates may have a positive impact on plant health in these areas by reducing abiotic stress due to anoxic sediments, thereby allowing plants to establish and survive lower in the intertidal zone. To assess this potential relationship, study plots of *Distichlis spicata* were selected at equivalent elevations at the lowest point of plant establishment at the marsh edge. Focal plant rhizomes were severed from upland ramets and assigned an invertebrate abundance treatment based on a visual burrow count surrounding each plant (9 cm diameter). Focal plants were visited monthly from July to September 2016, plant health variables of chlorophyll content and chlorophyll fluorescence (photosynthetic efficiency), and sediment ORP readings were collected. Plant survivorship was significantly higher in plots with invertebrates, 96% of plants in ‘With Invertebrate’ plots and 50% of plants in ‘No Invertebrates’ plots survived the duration of the study. Plant health (chlorophyll content and chlorophyll fluorescence) generally increased with increased invertebrate presence though, not statistically significant. There may be potential for improved plant productivity and resilience to plants at the marsh edge due to invertebrate burrowing activity. This benefit could help mitigate projected losses in plant productivity due to sea level rise, though more research is needed to investigate the mechanism by which these invertebrates confer a health benefit to plants at the marsh edge.

Acknowledgements

I would first like to express my sincere gratitude to Dr. Catherine de Rivera for her continuous support, motivation, enthusiasm and patience throughout every stage of my graduate work. Thank you to my committee members, Dr. Amy Larson and Dr. Sarah Eppley, for their guidance and suggestions that greatly improved the quality of my research and thesis. I greatly appreciate everyone who assisted me in my research efforts, including the de Rivera laboratory members, past and present, Dr. Sarah Eppley and Dr. Martin Lafrenz and all their graduate and undergraduate students and fellows who collected data in the field and/or analyzed samples in the laboratory for the Bandon Marsh dike removal project. Thank you to Sharon Gordon, Shane Graham, Chancity Keller, and Rick Park for their assistance, perseverance and camaraderie during countless hours in the lab, learning to sort and identify salt marsh organisms. Thank you to Dr. Amy Larson and Michelle Marafino for imparting some of your vast invertebrate identification expertise with me. Finally, I would like to express my very profound gratitude to my family and friends for providing me with support and encouragement throughout my years of study and the process of researching and writing this thesis. This accomplishment would not have been possible without them. Thank you.

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Chapter 1: Introduction

Conducting research focused on understanding the fundamental ecology of salt marshes in ways that can improve restoration success is vital. Salt marshes provide an array of crucial ecological services and are of great economic importance (Costanza *et al.* 1997, Bertness *et al.* 2002). These coastal wetlands play pivotal roles in watersheds, serving as crucial habitats for wildlife by providing spawning grounds, nurseries, shelter and food for fishes, shellfish and many migratory birds (Minello *et al.* 2003, Burger *et al.* 1982). Moreover, salt marsh plants improve water quality by filtering and detoxifying runoff from urban and agricultural areas (Kennish 2001, Alberti *et al.* 2014). Coastal salt marsh plants also buffer coastlines against episodic storm impacts, wave damage, and climate change impacts (Knutson *et al.* 1981, Gedan *et al.* 2011).

Given the great many valuable services that salt marshes provide as well as the losses in area and productivity currently faced by these ecosystems as the result of coastal development, anthropogenic pollutants, and sea level rise, research on how to maintain high productivity and resilience in these areas is of ever increasing importance. Salt marshes are often described, and evaluated, based on services provided by the assemblages of plants that inhabit these areas. However, salt marsh ecosystem function involves close interactions between abiotic factors and biotic components as well as among the biotic components.

The primary driver of abiotic conditions and biotic communities is tidal inundation, both duration and frequency. Inundation not only influences sediment

conditions, but delivers sediments, nutrients and plant water supply to the marsh (Bromberg *et al.* 2009). Salt marshes are generally comprised of unvegetated tide flats, vegetated low marsh and highly vegetated high marsh. Across these habitats, inundation varies with elevation. The frequency and duration of inundation in each of these zones influences sediment chemistry and exposure to air and light (Fleeger *et al.* 2007). Low marsh areas, defined as vascular plant establishment between mean tide level (MTL) and mean higher high water (MHHW), are flooded twice daily. This frequent inundation makes the low marsh a high abiotic stress area for vascular plants. Submergence causes periodic decreases in light availability (Blom and Voosenek 1996, Janousek and Mayo 2013) and waterlogged soils that reduce oxygen diffusion to the sediments, leading to the accumulation of toxic reduced metals (Howard and Mendelssohn 2000). High marsh areas, generally considered being between mean higher high water (MHHW) and spring high water (MHHS), meaning inundation is infrequent, at least monthly during spring high tides and storm surge. This zone, due to less inundation, is a lower abiotic stress area to vascular plants. The terrestrial transition zone is inundated occasionally, primarily due to extreme storm surge or other high water events, and is characterized by more terrestrial plant species.

Factors such as initial elevation, marsh productivity, sediment delivery and accretion rate, and local rate of sea level rise affect salt marsh persistence (Thorne *et al.* 2015, Crosby *et al.* 2016). The rate of sea level rise determines the losses to each zone. Moderate sea level rise will likely yield losses to high marsh habitat due to plant

drowning, and gains of low marshes and tide flats, as sea level rise outpaces marsh accretion. Increases in low marsh area and tidal flats could potentially increase habitat for invertebrates, fishes, and migratory shore and wading birds (Thorne *et al.* 2015). Management methods, such as dike removal, may provide marsh species the ability to migrate inland as sea level rise increases, potentially reducing losses to high marsh area (Harley *et al.* 2006, Crosby *et al.* 2016).

My research examines the assembly of marine invertebrates after restoring tidal inundation to a previously diked area (Ch 2). Invertebrates such as annelid worms, nematodes, mollusks, insect larvae, and amphipods are found in high abundances in salt marshes (Heydemann 1981). These invertebrates are important components of estuary communities, influencing overall marsh productivity and food web health. Many species of invertebrates, like the tube-dwelling Polychaeta worms stabilize deposited sediments (MacKenzie *et al.* 2015). Species of *Amphipoda* consume plant materials (Levin *et al.* 2001), promote decomposition (Henriksen *et al.* 1983) and provide dissolved food resources for filter feeders (MacKenzie *et al.* 2015). Many of these invertebrates are often prey organisms for higher trophic level marsh animals. High tide predators such as fish and crustaceans, and low tide predators like wading and shore birds, depend on the abundance and diversity of invertebrates that occupy the sediments across a range of marsh elevations (MacKenzie *et al.* 2015, Warren *et al.* 2002).

The rate at which invertebrate communities can establish after dike removal influences the return of marsh functioning, due to the interconnected relationship of

invertebrate and plant communities in marshes. This recovery is important considering they are being degraded and face uncertain future impacts due to sea level rise as well as continued anthropogenic land use change and other stressors. The most recent Intergovernmental Panel on Climate Change (IPCC) report (2014) presented four different Representative Concentration Pathways (RCPs) for the 21st century based on levels of greenhouse gas (GHG) and air pollutant emissions, atmospheric concentrations, and land use. They include a stringent mitigation scenario (RCP2.6), two intermediate scenarios (RCP4.5 and RCP6.0) and one scenario with very high GHG emissions (RCP8.5). These RCP's predict the global mean sea level rise from 2081-2100 to likely be in the range of 0.26 to 0.55 m for RCP2.6 (strict mitigation scenario), and of 0.45 to 0.82 m for RCP8.5 (high GHG emissions). Although sea level rise will not be uniform across regions, it is expected that 70% of global coastlines are projected to experience sea level change within $\pm 20\%$ of the global mean (IPCC 2014). For the Pacific Northwest, sea level rise rates are likely to be in the range of 0.12 to 1.43 m, with local variation affected by ice sheet dynamics at a global scale, tectonic activity, freshwater and oceanic circulation patterns (National Research Council 2012). Even if the global mean temperature is stabilized, coastal systems will continue to be at risk from sea level rise for centuries. Although salt marshes on the Pacific coast will not be impacted immediately, considering only about 10 percent of the coastline could develop salt marshes, maintaining productivity and resilience in existing marshes is critical.

My final study focused on the potential for these marsh invertebrates to reduce stress on low marsh plants specifically at the marsh edge. There have been many studies linking plant-plant facilitations that alleviate abiotic stress and allow for expansion of plants into areas otherwise excluded (Bortolus *et al.* 2002, Normann and Pennings 1998, He and Cui 2015). The focus of these studies has primarily been the increase in plant distribution or abundance due to positive interactions (Normann and Pennings 1998, Bortolus *et al.* 2002) and not effects of reduced stress (Hacker and Bertness 1995).

Plant-animal facilitations have also been shown to lower the intertidal limits of marsh plants (Hacker and Bertness 1995, Bertness 1985, Daleo *et al.* 2008). Several studies, focused on marshes on the Atlantic coasts, cited increased plant production through stress amelioration due to *Uca* spp. and shore crabs such as *Chasmagnathus granulatus* burrowing activity, specifically increased soil aeration, oxygen redox potential and decomposition of belowground plant debris yielding increased plant productivity and range in the low marsh (Bertness 1985, Montague *et al.* 1982, Daleo *et al.* 2007).

Pacific Northwest salt marshes are relatively depauperate in decapod fauna, a major difference between Atlantic and Pacific Northwest salt marshes. Atlantic marshes are dominated by fiddler crabs (*Uca*) (Montague *et al.* 1982), along with other decapods such as the blue crab (*Callinectes sapidus*). *Uca* species maintain stable, often deep burrows, which they open when the tide has receded, that can deliver oxygen to plant

roots (Bertness and Miller 1984). However, only one decapod, *Hemigrapsus oregonensis*, is common to salt marshes in Oregon.

This second study focuses on a single marsh along the Oregon coast. To evaluate whether invertebrate abundance in the low marsh has measurable benefits to marsh edge plant physiology, I focused on *Distichlis spicata* in the Salmon River estuary in Oregon. The burrowing, irrigation and feeding activity of small invertebrates are the main processes by which oxygen is transported past the diffusion layer (top several millimeters of substrate on the marsh surface) into the sediment (Rosenberg *et al.* 2001). It is unknown if this alone can affect sediment conditions for plants at the marsh edge.

Together these chapters aim to increase our understanding of the fundamental marsh components of invertebrates, how quickly and to what degree they establish after large-scale disturbance, in this case a dike removal restoration project after 100 years of tidal restriction. These organisms provide key functions critical for maintaining salt marsh ecosystem services. Additionally this research seeks to evaluate the potential positive relationship these organisms may provide to marsh plant health, especially those in the high stress lower marsh edge. Together these findings may further support the importance of including the consideration of the invertebrate community to restoration endpoints and monitoring.

Chapter 2: Salt Marsh Invertebrate Community Assembly after Dike Removal

Introduction

Nearly 50% of global salt marshes have been lost or severely degraded due to coastal development and land reclamation (Davy *et al.* 2011, Simenstad *et al.* 2011). Conversion of marsh to agricultural land or cattle grazing by diking was the largest human-induced change to Oregon's salt marshes (Boule and Bierly 1987), yielding 50-80% loss of pre-1850s acreage of salt marsh lands (Frenkel *et al.* 1981). Restriction of marshlands from tidal influence has been identified as a major factor linked to the decline of estuarine productivity in general (Myers *et al.* 1998, Bottom *et al.* 2004). The removal of tidal influence reduces soil organic matter inputs above the impoundment. Characteristic marsh plants, such as *Spartina alterniflora*, *Spartina patens*, common on the North American east coast (West Atlantic) marshes, *Deschampsia*, *Juncus spp.*, and *Distichlis spicata* are replaced with pasture grasses with very low salt tolerances (Roman *et al.* 1984).

In the Pacific Northwest, this salt marsh degradation is especially consequential because of the critical role of these habitats to socially and economically important fishes such as salmon (Cornu and Sadro 2002) and because of the small percentage of Pacific Northwest coast suitable for marsh formation, as compared to the Atlantic coast (Frey and Bason 1985). Within the last several decades, approximately 50 former Oregon coast salt marshes have been reconnected to tidal inundation (Hood 2014) primarily through

breaching of dikes or removal of tide gates (Chang *et al.* 2016, French 2006) in an effort to restore productivity and habitat for fishes.

The return of tidal inundation through dike breaching alone is thought to initiate natural establishment and succession of invertebrate communities (Cornu and Sadro 2002, Rosza 1995, Warren *et al.* 2001, Fell *et al.* 2000). Support for this has been reported by Fell *et al.* (2000), Burdick *et al.* (1997), and Rozsa (1995b) who found that characteristic salt marsh invertebrate communities similar to nearby reference communities established when tidal hydrology was restored. An important qualifier for restored tidal hydrologic connectivity to drive invertebrate community assembly is an adequate supply of propagules, primarily planktonic larvae, and sediment conditions suitable for subsequent survival (Warren *et al.* 2002).

The restoration of marsh plant communities has been well documented (Swamy *et al.* 2002) and is often examined as the primary restoration target endpoint. The general process for plant succession involves a rapid die off of terrestrial plants above the impoundment due to their low salinity stress tolerance (Warren *et al.* 2002). This die off event opens space for pioneer species, those species that are able to tolerate frequent salt water inundation, to establish. Eventually a gradient of plant species forms the salt marsh habitat, transitioning from salinity and water tolerant plant species dominating low marsh zones to plant species that are less tolerant of inundation and salt water but better competitors in high marsh areas (Bertness 1991). Though the general process for plant community succession in newly restored marshes is understood, the amount of time it

takes for this process to fully restore marsh communities to those typical of natural marshes is less well known (Fell *et al.* 1991). Differences between plant communities in removal and reference marshes have been detected several years (Darnell and Smith 2002, Morgan and Short 2002) and after many decades (Burd *et al.* 1994, Havens *et al.* 2002, Wolters *et al.* 2005b), suggesting that plant communities are slow to reassemble.

The assembly of invertebrates after dike breaching has been studied less frequently than plant assembly after disturbance (Swamy *et al.* 2002). Given the strong structuring influence of inundation regimes to the assembly of salt marsh plants (Heydemann 1981, van der Maarel and van der Maarel-Versluys 1996) though, the distribution of invertebrates in salt marsh sediment is likely to be controlled by species tolerance to the physiological stresses due to inundation frequency (Thakur *et al.* 2014). The infrequent inundation of high marsh zones allows for invertebrates with low salinity tolerances to establish (Pennings and Bertness 2001). These higher elevation sites are also characterized by higher abundances of burrow-dwelling amphipods, oligochaetes and shelled invertebrates, such as bivalves and gastropods, because they are more tolerant to desiccation and osmotic stress (Peterson 1991, Rouse 2000). In low marsh zones, areas with more frequent inundation, invertebrates must tolerate stress due to anoxic conditions and salinity (Hacker and Gaines 1997, Pennings and Bertness 2001). Organisms such as polychaetes and nematodes tend to be found in these zones (French *et al.* 2003).

This project focused specifically on the marine invertebrate community. It was conducted as part of a larger project to comprehensively evaluate the short-term recovery

of marsh component communities and sediment conditions, designed by a multidisciplinary team of Portland State University professors, Dr. Catherine de Rivera, Dr. Sarah Eppley and Dr. Martin Lafrenz. The goal of my project was to compare marine invertebrate abundance, diversity, and overall community composition of a dike removal marsh (Removal) to the community in a nearby reference marsh (Reference). This was evaluated specifically by examining the short-term trajectories (1 and 2 years after restored tidal influence) of community assembly across elevation zones (High Marsh and Low Marsh). We hypothesize that invertebrate community differences between Reference Marsh and Removal Marsh are a function of inundation frequency and stress tolerances. Given these relationships, we expect greater abundance and diversity of invertebrates in lower elevation zones as a function of lower abiotic stress to marine-derived invertebrates. When comparing Reference Marsh and Removal Marsh invertebrate community assembly, we expect Removal Marsh communities to have fewer species, with dominance by pioneer species.

Methods

Study site

Bandon Marsh National Wildlife Refuge (BMNWR) is located along the southern coast of Oregon, at the mouth of the Coquille River. BMNWR is comprised of two units; Bandon Marsh, which is located closer to the mouth of the river and served as a reference marsh for this study, and Ni-les'tun Marsh, located just upstream (Fig 2.1), the site of the impoundment and tide gates. Although this refuge is now managed as a natural area with

no habitat manipulation, historically it was one of the most altered estuaries on the Oregon coast. Extensive diking and drainage of marshes along the main channel of the Coquille River began in the mid-1800s, by 1870 most of the marshes were converted to farmland or cattle grazing, representing a loss of nearly 97% of marsh acreage (English and Skibinski 1973). About 25 km of drainage ditches were constructed by past landowners, damaging the natural tidal channel system, and over 2.5 km of dikes and three tide gates impeded hydrologic connectivity of the Ni-les'tun Unit with the estuary (USFWS and FHA 2009).

Summer 2011, the US Fish and Wildlife Service conducted the largest tidal marsh restoration project in Oregon, nearly doubling the area of salt marsh habitat within the Coquille estuary. Within the Ni-les'tun Marsh unit, several dike impoundments and tidal gates were removed and several kilometers of channels were excavated to approximate natural marsh channel systems. These activities restored tidal inundation after nearly 100 years of restriction. The primary short-term goals of this project were to improve productivity of the salt marshes for anadromous fish access and improve bird habitat (USFWS 2016). Long-term goals were to improve overall quality and quantity of tidal wetlands and estuarine conditions in the lower Coquille River by restoring unrestricted tidal influence (USFWS 2016).

Site Description

Plant species characteristics were collected by Dr. Eppley and honors undergraduate Robertson-Rojas along a semi-permanent transect in each marsh, also used

to collect sediment characteristics (Lafrenz) and invertebrate sampling (Lawson and de Rivera) used in my study. Dominant plant species were assessed by percent cover for each quadrat, and the number of quadrats each was dominant for each zone (e.g., Reference High Marsh). The number of quadrats of dominance for each plant species was divided by total number of quadrats for that zone, yielding a dominance frequency. Dominant plant species differed for Reference Marsh versus Removal Marsh for all zones (Eppley, unpublished data). Stark differences were observed in Low Marsh samples. Reference Low Marsh samples were dominated primarily by algae species, *Chaetomorpha linum* and *Fucus gardneri*; and to a lesser degree, *Distichlis spicata*, a common marsh grass (Table 2-1). Removal Low Marsh samples dominated by *Carex lyngbyei* (sedge), *Ulva* sp. (green algae), and herbaceous and rush species (Table 2-1). High Marsh dominant species were also different across treatments. High Marsh Reference plots were dominated by grass species such as *Deschampsia cespitosa* and *Distichlis spicata*, whereas Removal High Marsh plots were dominated by herb (*Argentina egedei*), sedge (*Carex obnupta*) and rush (*Juncus balticus*) species. Plant species richness was greater in Reference Marsh than Removal Marsh, for all zones, most substantially in the Transition and High Marsh zones (Table 2-2). Plant diversity, specifically Simpson's diversity, was higher in Reference Marsh than Removal Marsh for each zone comparison (Table 2-2).

Evaluating sediment characteristics one year after dike removal (Lafrenz, unpublished data), substantial differences were observed between Reference Marsh and

Removal Marsh for sediment oxygen redox potential (ORP). Organic matter was also slightly lower in Removal Marsh samples than Reference Marsh samples for most zones; the greatest difference was observed in Transition Zone, with average organic matter content nearly 50% greater in Reference Marsh compared to Removal Marsh. Salinity, pH, conductivity and field moisture were generally similar for Reference Marsh and Removal Marsh samples, with some variation in that trend for specific zones. For example, salinity in Transition Zone Reference which was lower than Transition Zone Removal (Lafrenz unpublished data, Table 2-3).

Table 2-1. Dominant plant species from quadrats placed along semi-permanent transects and frequency of dominance within each elevational zone (Eppley, unpublished data). Species dominant in a single quadrat were not reported.

Zone	Dominant Plants			
	Reference	Freq	Removal	Freq
Transition Zone	<i>Deschampsia cespitosa</i> (grass)	0.33	<i>Argentina egedei</i> (herb)	0.67
	<i>Heracleum maximum</i> (herb)	0.25	<i>Agrostis stolonifera</i> (grass)	0.33
	<i>Symphyotrichum chilense</i> (herb)	0.17		
High Marsh	<i>Deschampsia cespitosa</i> (grass)	0.64	<i>Argentina egedei</i> (herb)	0.25
	<i>Distichlis spicata</i> (grass)	0.28	<i>Carex obnupta</i> (sedge)	0.17
			<i>Juncus balticus</i> (rush)	0.17
			non-marine algae	0.17
Low Marsh	<i>Chaetomorpha linum</i> (green algae)	0.29	<i>Carex lyngbyei</i> (sedge)	0.22
			<i>Ulva</i> sp.	0.22
	<i>Distichlis spicata</i> (grass)	0.20	<i>Jaumea carnosa</i> (herbaceous)	0.11
	<i>Fucus gardneri</i> (brown algae)	0.20	<i>Juncus balticus</i> (rush)	0.11
	<i>Gracilaria pacifica</i> (red algae)	0.20	<i>Salicornia depressa</i> (herbaceous)	0.11
Tide Flats	<i>Gracilaria pacifica</i> (red algae)	0.67		
	<i>Chaetomorpha linum</i> (green algae)	0.33		

Table 2-2. One year post removal (2012) plant species richness was higher in the Reference Marsh than the Removal Marsh for each elevation zone comparison. Plant species diversity (Simpson's diversity) was greater in Reference Marsh than Removal Marsh for each elevation zone comparison (Eppley, unpublished data).

	N		Richness (average $\pm$ 1 SE)		Simpson's (average $\pm$ 1 SE)	
	Reference	Removal	Reference	Removal	Reference	Removal
Transition Zone	n=12	n=6	5.91 (0.45)	1.83 (0.16)	0.56 (0.05)	0.27 (0.09)
High marsh	n=15	n=12	5.53 (0.54)	2.58 (0.37)	0.57 (0.04)	0.37 (0.08)
Low marsh	n=24	n=20	3.37 (0.29)	2.25 (0.31)	0.43 (0.04)	0.27 (0.06)
Tide Flat	n=6	---	3.00 (0.25)	---	0.20 (0.06)	---

Table 2-3. Sediment characteristics measured one year after dike removal (in 2012). ORP and pH: Transition Reference (n=12), transition Removal (n=6), High Marsh Reference (n=15), High Marsh Removal (n=12), Low Marsh Reference (n=24), Low Marsh Removal (n=20), Tide Flats Reference (n=6). FM, OM, COND, SAL: Transition Reference (n=4), Transition Removal (n=2), High Marsh Reference (n=5), High Marsh Removal (n=5), Low Marsh Reference (n=8), Low Marsh Removal (n=6), Tide Flats Reference (n=2).

	Transition Zone average (± 1 SE)		High Marsh average (± 1 SE)		Low Marsh average (± 1 SE)		Tide Flats average (± 1 SE)
Name (unit of meas.)	Reference	Removal	Reference	Removal	Reference	Removal	Reference
Oxygen redox potential (SHE)	206.76 (30.20)	307.16 (6.13)	97.13 (45.57)	239.33 (28.84)	-99.87 (18.55)	-2.80 (14.39)	-116.00 (31.14)
pH	5.89 (0.19)	4.47 (0.08)	6.66 (0.22)	5.52 (0.34)	7.14 (0.12)	7.17 (0.11)	7.38 (0.12)
Field moisture (%)	55.25 (11.50)	54.00 (3.00)	65.00 (7.34)	49.20 (11.79)	42.25 (5.69)	50.66 (4.33)	32.00 (6.00)
Organic matter (%)	63.75 (8.62)	32.00 (4.00)	39.20 (7.37)	26.40 (10.92)	7.50 (2.42)	13.00 (4.86)	3.50 (0.50)
Conductivity (ms/m)	3.20 (1.39)	8.98 (3.68)	10.40 (3.50)	11.76 (3.58)	12.01 (0.68)	9.56 (0.97)	11.72 (2.47)
Salinity (PSU)	1.67 (0.75)	4.87 (2.08)	5.68 (2.02)	6.55 (2.18)	6.58 (0.39)	5.18 (0.55)	6.43 (1.44)

Field sampling

Survey and sampling protocols were implemented identically for each study marsh. Semi-permanent sampling transects were established at BMNWR in a dike removal marsh (Ni-les'tun Marsh) and nearby reference marsh location (Bandon Marsh) in August 2012 (Figure 2-1). Transects were established perpendicular to the shoreline,

from the channel at low tide to the upland zone, spanning a gradient of inundation from submerged, except at the lowest tides (~0.5 m above MLLW), to intertidal (flooded daily) to rarely flooded upland. Along these transects, every 0.10 m change in elevation was determined using a mobile survey station, marked and staked for later sampling.

Figure 2-1. Map of Bandon Marsh National Wildlife Refuge (BMNWR), on the mouth of the Coquille River, with transect locations for reference and dike removal sampling.

Invertebrate sample collection was conducted once per year along each established transect in August 2012 and September 2013, starting at lowest elevations during low tide and working toward higher elevations. Cylindrical push-core samples (2.5 cm diameter) were taken at random distances from a transect (0-20 m to either side) along the transects, at every 10 cm change in elevation (Figure 2-2). The cores sampled sediment and its invertebrates to 6 cm deep, and were separated into 0-3 cm and 3-6 cm depth samples immediately after collection. In addition to the 2.5 cm diameter cores, larger cores, 10 cm diameter by approximately 25 cm deep, were taken at the same 10 cm change in elevation as long as plant roots did not block this sampling (most were successful in Low Marsh; some were in High Marsh). For this analysis, only the 0-3 cm deep cores (2.5 cm diameter cores) were utilized as most invertebrate activity occurs between 0-4 cm (MacKenzie *et al.* 2015). Cores were labeled and stored for transport, preservation, and processing at Portland State University's Marine Ecology Laboratory.

Figure 2-2. Sampling transect illustrations depicting range in elevation (binned zones Transition Zone, High Marsh, Low Marsh, Tide Flats) for Reference (left) and Removal (right) transects. Black circles indicate invertebrate cores samples, not drawn to scale. Elevations were determined using mobile survey station, key tidal levels (HAT: Highest Astronomical Tide, MHHW: Mean Higher High Water, MHW: Mean High Water, MSL: Mean Sea Level) are marked on each transect as they were measured in the field (Lafrenz, unpublished data).

Sampling processing and specimen identification

Cores were preserved in 10% buffered formalin with Rose Bengal to aid detection of organisms from sediment and plant materials. Cores were transferred from 10% formalin solution (diluted with saltwater) to 70% ethanol after a week, to prevent the soft-bodied organisms from becoming brittle. Each preserved core sample was sieved in the laboratory through stacked sieves (1 mm, 500 μ m, 300 μ m sieves) by gently breaking

up sediment and root materials while rinsing with fresh water until completely separated. Material from each sieve was transferred into individual Qor-pak containers, filled with 70% ethanol and labeled for sorting.

Samples were sorted manually using a stereoscope (Zeiss Stemi 508 stereomicroscope), picking every invertebrate organism found within a sample (excluding Foraminifera because their tests were often broken, making accurate enumeration and identification unlikely). Organisms were placed in scintillation vials based on general morphological similarity using 30x magnification. These were later identified to lowest taxonomic unit possible (which was typically family), using compound microscopes when needed. Distinct morphospecies, organisms that differ in some morphological respect from all other groups, were identified using regionally appropriate taxonomic guides (Carlson and Kozloff 1996, Carlton 2007, Rudy and Rudy Oregon Estuarine Invertebrates). Morphospecies identifications were verified across marsh sites and sampling years to ensure consistency. Terrestrial insects (specifically adult *Diptera* and *Coleoptera*) were excluded from this analysis.

Data analysis

Samples were binned into tide flats, low, high, and terrestrial transition marsh categories based on elevation (Figure 2-2). Abundance was totaled across all sieve sizes as size distribution was similar across sampling sites, elevation and years. Morphospecies abundance, morphospecies richness, and Shannon diversity values were calculated for all elevation zones using the *vegan* package in R (Version 1.0.136, Oksanen 2015). Shannon diversity, being more sensitive to rare species, was selected for analysis, rather than

Simpson's diversity, which weighs more heavily on dominant species. Given the goal of evaluating the trajectory of marsh invertebrate community assembly within removal marsh, rare morphospecies (and taxa) may be an important aspect of potential functional diversity (Jain *et al.* 2014). Transition Zone and Tide Flat abundance, richness and diversity are displayed on graphs but not included in statistical analyses. Transition Zone was excluded due to low sample size for the Removal transects (Reference n=9, and Removal n=3). Tide Flat samples were excluded from comparisons because Removal Marsh had no comparable sites.

In order to explore invertebrate community composition across marsh treatment (Reference High Marsh, Reference Low Marsh, Removal High Marsh and Removal Low Marsh), non-metric multidimensional scaling (NMDS) was performed using fourth-root transformed taxa level (phyla, class, family levels) relative abundance (*vegan* package, Version 1.0.136, Oksanen 2015). Fourth root was selected for transformation to allow rare taxa to have influence (Maindonald and Braun 2007). NMDS ordination was an effective method to explore relationships among taxa composition across elevations and sites and map community similarity or dissimilarity. This method allows flexibility to select standardization, transformation, and similarity coefficients that are relevant to the goal and hypotheses for the study (Clarke 1993).

Shepard's diagram was generated, yielding a stress value used to determine how closely the Bray-Curtis distance represented the true distance of similarity of taxa composition between the samples. In general, the smaller the stress value, the better the

MDS map represents the true similarity of composition. A stress value <0.05 indicates an excellent representation of distance, <0.1 indicates good ordination, <0.2 indicates a usable representation, >0.2 will mostly likely return plots that could misinterpret relationships, and above 0.35 the sites are essentially randomized (Clarke 1993). However, even when stress is high, larger patterns are likely still accurate since longer distances tend to be more accurate than shorter distances (Kruskal and Wish 1978). NMDS is iterative and refines the configuration of the samples from a random point in the data until the lowest stress value can be reached (Clarke 1993). The ordination with the lowest stress was selected for further analysis.

An analysis of similarities (ANOSIM) was conducted to test the differences among invertebrate community assemblages in each marsh treatment and zone (Reference High Marsh, Reference Low Marsh, Removal High Marsh and Removal Low Marsh). ANOSIM measures the differences between average ranked values of Bray-Curtis measures of dissimilarity in abundance and the types of organisms between and within samples (Chapman and Underwood 1999), the null hypothesis is that similarities within groups are smaller or equal to the similarities between groups. If statistically significant differences were found, then pair-wise ANOSIM (Bonferroni correction $\alpha=0.008$) was conducted for marsh treatments by zone (Reference High Marsh, Reference Low Marsh, Removal High Marsh, Removal Low Marsh) to statistically compare levels of similarity between community composition. Similarity percentages (SIMPER) analysis (*vegan* package) was used to evaluate which taxa contributed to the differences observed

between marsh treatments and zones as determined by ANOSIM pairwise results. SIMPER measures dissimilarity by making pairwise comparisons of taxonomic abundance between marsh treatments and elevation zones, ranked in order of their percent contribution to the dissimilarity.

A Dufrene-Legendre indicator species analysis was conducted using the *labdsv* package (Version 1.0.136, Roberts 2016) to identify if any taxa were indicative of a specific marsh treatment and zone. Indicator value scores were calculated by the relative abundance (RA) and relative frequency (RF) of occurrence in each sample ($IV = RA * RF$) with the significant taxa ($p < 0.05$) reported.

Results

Abundance increased from High Marsh to Low Marsh for Reference Marsh 2012 (one year post removal), Reference Marsh 2013 (two years post removal) and Removal Marsh 2012 (one year post removal; Figure 2-3). Removal 2013 (2 years post removal) had a slight decrease in abundance with decrease in elevation (Figure 2-3). Highest abundance was found in Reference Tide Flats (184.14 ± 61.14) and lowest in Removal High Marsh (12.00 ± 2.23 ; Figure 2-4). Low Marsh samples had significantly higher abundance than High Marsh samples for both Reference Marsh and Removal Marsh (Dunn's test Z-score= 3.13, adjusted p-value=0.002; Figure 2-4). Morphospecies richness increased for all treatments and years with a decrease in elevation, though only a slight increase for Removal Marsh 2013 (Figure 2-5). Highest morphospecies richness was

found in Reference Tide Flats (8.14 ± 1.0) and lowest in the Terrestrial Transition Zone of the Removal Marsh (3.33 ± 1.2), Reference High Marsh (3.36 ± 0.48) and Removal High Marsh (3.27 ± 0.54). Morphospecies richness was significantly higher in Low Marsh samples than in High Marsh (Dunn's test Z-score=2.83, adjusted p-value=0.01; Figure 2-6). Shannon's diversity increased for all treatments and years with a decrease in elevation, though only a slight increase for Removal Marsh 2013 (Figure 2-7). Highest diversity was found in Reference Transition Zone (1.36 ± 0.10) and Reference Tide Flats (1.36 ± 0.09) and lowest in Removal Transition Zone (0.48 ± 0.26). Shannon's diversity was significantly higher in Low Marsh than High Marsh for both Reference Marsh and Removal Marsh (Dunn's test Z-score= 2.54, adjusted p-value=0.003; Figure 2-8).

Figure 2-3. Abundance (square root transformed) increased along elevational gradient from High Marsh to Low Marsh for Reference Marshes (Reference 2012-filled square, Reference 2013- filled triangle) and Removal Marshes (Removal 2012-hollow square, Removal 2013-hollow triangle) at one year post removal (2012) and two years post removal (2013). Linear regression for each treatment with associated R^2 at the end of each regression line (Reference 2012-dotted line, Reference 2013-solid line, Removal 2012-purple long dash line, Removal 2013-purple short dash line)

Figure 2-4. Abundance (average $\pm$ 1 SE) was significantly higher in Low Marsh than High Marsh for both Reference Marsh (green bars) and Removal Marsh (diagonal bars). Averages with different letters are significantly different (Dunn's test, $p=0.002$), Transition and Tide Flats excluded from statistical analysis. Reference Transition ($n=9$), Removal Transition ($n=3$), Reference High Marsh ($n=14$), Removal High Marsh ($n=11$), Reference Low Marsh ($n=31$), Removal Low Marsh ($n=28$), Reference Tide Flats ($n=7$).

Figure 2-5. Morphospecies richness increased with decrease in elevation from High Marsh to Low Marsh zone for Reference Marshes (Reference 2012-filled square, Reference 2013- filled triangle) and Removal Marshes (Removal 2012-hollow square, Removal 2013-hollow triangle) at one year post removal (2012) and two years post removal (2013). Linear regression for each treatment with associated R^2 at the end of each regression line (Reference 2012-dotted line, Reference 2013-solid line, Removal 2012-purple long dash line, Removal 2013-purple short dash line).

Figure 2-6. Morphospecies richness (average $\pm$ 1 SE) by treatment and elevation zone. Morphospecies richness significantly higher in Low Marsh than High Marsh, for Reference Marsh (green solid bars) and Removal Marsh (diagonal lines), means with different letters are significantly different (Dunn's test, $p=0.01$), Transition and Tide flats excluded from statistical analysis. Reference Transition ($n=9$), Removal Transition ($n=3$), Reference High Marsh ($n=14$), Removal High Marsh ($n=11$), Reference Low Marsh ($n=31$), Removal Low Marsh ($n=28$), Reference Tide Flats ($n=7$).

Figure 2-7. Shannon diversity increases slightly along elevational gradient from High Marsh to Low Marsh zone for Reference Marshes (Reference 2012-filled square, Reference 2013- filled triangle) and Removal Marshes (Removal 2012-hollow square, Removal 2013-hollow triangle) at one year post removal (2012) and two years post removal (2013). Linear regression for each treatment with associated R^2 at the end of each regression line (Reference 2012-dotted line, Reference 2013-solid line, Removal 2012-purple long dash line, Removal 2013-purple short dash line).

Figure 2-8. Shannon's (H) diversity index (average $\pm$ 1 SE) by treatment and elevation zone. Shannon's diversity was significantly higher in Low Marsh than High Marsh, for Reference Marsh and Removal Marsh, averages with different letters are significantly different (Dunn's test, $p=0.003$). Reference Transition ($n=9$), Removal Transition ($n=3$), Reference High Marsh ($n=14$), Removal High Marsh ($n=11$), Reference Low Marsh ($n=31$), Removal Low Marsh ($n=28$), Reference Tide Flats ($n=7$).

Invertebrate community assemblages grouped more strongly within elevation zone (High Marsh or Low Marsh) than treatment (Reference Marsh or Removal Marsh). High Marsh sites grouped within the negative NMDS2 axis and were dispersed across NMDS1 (Figure 2-9). NMDS plot was highly influenced by few taxa for High Marsh groupings, primarily *Collembola* (COLLE), *Chironomidae* (CHIRO), *Halacaridae* (HALA), *Gastropoda* (GAST), *Oligochaeta* (OLIG). Plots were influenced by several clustered taxa in the negative NMDS1 and positive NMDS2 quadrant for Low Marsh groupings (Figure 2-9).

When ordination was overlaid with one standard error ellipse, the distinctness of the four groupings (High Marsh versus Low Marsh for Removal Marsh versus Reference Marsh) becomes evident. High Marsh and Low Marsh samples grouped together, with wider variation in Removal sites than Reference sites. Reference Low Marsh and Removal Low Marsh ellipses had very little overlap but clustered closely. Reference High Marsh and Removal High Marsh ellipses had minimal overlap (Figure 2-10).

Figure 2-9. NMDS plot of invertebrate community composition sites by marsh zone. The four marsh treatments and elevation zones, Removal High Marsh (DR_HM; open circles), Removal Low Marsh (DR_LM; open triangles), Reference High Marsh (REF_HM; filled circles) and Reference Low Marsh (REF_LM; filled triangles), plotted with taxa. Stress value (0.1966) indicates a fairly high stress, at the high end of useable goodness-of fit.

Figure 2-10. NMDS plot of invertebrate community composition sites by marsh zone, Removal High Marsh (DR_HM; open circles), Removal Low Marsh (DR_LM; open triangles), Reference High Marsh (REF_HM; filled circles) and Reference Low Marsh (REF_LM; filled triangles) with ellipses of coordinating colors indicating one standard error of each group. Stress value (0.1966) indicates a fairly high stress, at the high end of useable goodness-of fit.

ANOSIM results for invertebrate community composition were significant (R value = 0.337, $p = 0.001$). Pair-wise comparisons were significant for all pairings except Reference High Marsh versus Removal High Marsh (Table 2-4). SIMPER analysis was used to evaluate Reference High Marsh versus Removal High Marsh and Reference Low

Marsh versus Removal Low Marsh, as these are the most relevant comparisons for this study. Six taxa were identified as being the most influential, driving 73.1% of the difference between Reference High Marsh and Removal High Marsh communities (Figure 2-11, Table 2-5). Six taxa were identified as being the most influential, driving 72.6 % of the difference between Reference Low Marsh and Removal Low Marsh communities (Figure 2-12, Table 2-5). For both comparisons, *Chironomidae* (CHIRO), *Nematoda* (NEMA), and *Sabellidae* (SABE) are key drivers.

Table 2-4. Pairwise ANOSIM analysis comparing invertebrate community compositions between the four treatment levels (Reference High Marsh, Reference Low Marsh, Removal High Marsh, and Removal Low Marsh). Significant pairings (p-value <0.008, Bonferroni correction) noted with asterisk.

Pairwise Test	R value (P-value)
Reference High Marsh vs Reference Low Marsh	0.439 (0.001*)
Reference High Marsh vs Removal High Marsh	0.151 (0.024)
Reference High Marsh vs Removal Low Marsh	0.240 (0.003*)
Reference Low Marsh vs Removal High Marsh	0.695 (0.001*)
Reference Low Marsh vs Removal Low Marsh	0.173 (0.001*)
Removal High Marsh vs Removal Low Marsh	0.308 (0.001*)

Table 2-5. Similarities percentages comparisons for Reference High Marsh and Removal High Marsh and Reference Low Marsh and Removal Low Marsh, showing the six taxa that contribute the greatest influence into the community differences. Values shown are the cumulative contribution of each taxa in descending order left to right.

Comparison	Influential taxa and cumulative contribution					
High Marsh Reference versus Removal	<i>Chironomidae</i> (CHIRO)	<i>Nematoda</i> (NEMA)	<i>Oligochaeta</i> (OLIG)	<i>Capitella</i> (CAPI)	<i>Halacaridae</i> (HALA)	<i>Sabellidae</i> (SABE)
	0.288	0.420	0.532	0.605	0.669	0.731
Low Marsh Reference versus Removal	<i>Nematoda</i> (NEMA)	<i>Sabellidae</i> (SABE)	<i>Chironomidae</i> (CHIRO)	<i>Ostracoda</i> (OSTR)	<i>Corophiidae</i> (CORO)	<i>Harpacticoid</i> Copepod (HACO)
	0.194	0.322	0.436	0.544	0.642	0.726

Figure 2-11. Relative abundance (average $\pm$ 1 SE), percent composition of each taxa relative to total taxa for each core, of the six most influential taxa driving 73.1% of the difference between Reference High Marsh (REF_HM, green bars) and Removal High Marsh (DR_HM, diagonal lined bars) determined using SIMPER.

Figure 2-12. Relative abundance (average $\pm$ 1 SE), percent composition of each taxa relative to total taxa for each core, of the six most influential taxa driving 72.6% of the difference between Reference Low Marsh (REF_LM, green) and Removal Low Marsh (DR_LM, diagonal lines) determined using SIMPER.

Indicator species analysis selected no statistically significant ($p < 0.05$) indicator species for Reference High Marsh. Reference Low Marsh had four statistically significant indicator species: *Corophiidae* (CORO), *Tubificidae* (TUBI), *Sphaeromatidae* (SPHA), and *Nematoda* (NEMA). Removal High Marsh had two indicator species: *Chironomidae* (CHIRO) and *Halacaridae* (HALA), and Removal Low Marsh had two indicator species: *Ostracoda* (OSTR) and *Sabellidae* (SABE; Table 2-6).

Table 2-6. Indicator species identified by treatment zone, indicator value, and significant p-value ($\alpha < 0.05$). Indicator value accounts for both relative abundance and relative frequency ($IV=RA*RF$) that a taxa occurs in samples for each treatment.

Treatment Zone	Taxa	Indicator Value (p-value)
Reference Low Marsh	<i>Corophiidae</i> (CORO) <i>Tubificidae</i> (TUBI) <i>Sphaeromatidae</i> (SPHA) <i>Nematoda</i> (NEMA)	0.60 (0.001) 0.48 (0.002) 0.36 (0.007) 0.55 (0.013)
Removal High Marsh	<i>Chironomidae</i> (CHIRO) <i>Halacaridae</i> (HALA)	0.55 (0.001) 0.26 (0.036)
Removal Low Marsh	<i>Ostracoda</i> (OSTR) <i>Sabellidae</i> (SABE)	0.59 (0.002) 0.25 (0.023)

Discussion

Invertebrate abundance, morphospecies richness, and Shannon's diversity were significantly higher in Low Marsh than High Marsh samples, regardless of marsh treatment (Reference Marsh and Removal Marsh). Using these indices alone, it would appear that two years after dike removal, the invertebrate community had approached the nearby reference community. However, these variables were compared across High Marsh and Low Marsh zones only, and did not compare Transition Zone and Tide Flats. Reference Tide Flats had the highest morphospecies richness (8.14 ± 1.0), abundance (184.14 ± 61.14) and Shannon's diversity (1.36 ± 0.09) of all elevation zones, and Removal Marsh had no similar zone for comparison. Reference Marsh Transition Zone also had the highest diversity (1.36 ± 0.10) while the Removal Transition Zone had the

lowest morphospecies richness (3.33 ± 1.2) and Shannon's diversity (0.48 ± 0.26). It is possible tide flats will develop in the Removal Marsh, given adequate time, though a literature search failed to yield research that addressed the time required for development after restoration. If we compared Reference Marsh abundance and morphospecies richness to Removal Marsh values as a whole, rather than by elevational zone, it is likely that abundance and morphospecies richness would be significantly higher in Reference Marsh than Removal Marsh.

Examining the invertebrate establishment from a community level, significant differences between community compositions were found in all pairwise ANOSIM comparisons except Reference High Marsh versus Removal High Marsh. Although statistically significant p-values were returned for these pairwise tests, the R value (ANOSIM R statistic) for many comparisons was low. The R statistic is based on difference of mean ranks between groups and within groups, with the expectation that if two groups (e.g., Reference High Marsh and Removal High Marsh) have different species compositions, the differences between groups should be greater than those within groups. The R statistic ranges from -1 to +1, 0 indicating completely random grouping, so the results of these pairwise comparisons, although significant, may not mean the communities are substantially different. For example, Reference Low Marsh versus Removal Low Marsh was significantly different (R value 0.173, $p=0.001$) but Reference High Marsh versus Removal High Marsh was not statistically different (R value=0.151, $p=0.024$). The greatest differences being Reference Low Marsh versus Removal High

Marsh (R-value 0.695) and secondarily Reference High Marsh versus Reference Low Marsh (0.439), which is expected given the obvious influence of elevation with regard to inundation observed in abundance, richness and less so for diversity (Figures 2-4, 2-6, 2-8).

Partial explanation for observed differences between Reference Marsh and Removal Marsh communities may be due to the limited sampling. Each elevation was sampled once per year (one and two years post removal) along the 10 cm elevation change gradient. These samples were binned into Low Marsh or High Marsh based on elevation, but there is no exact division between these groups. Examining Figure 2-3, morphospecies abundance plotted by elevation, 1.7 m (elevation relative to MLLW) is the approximate cutoff between Low Marsh and High Marsh however, we see variation of abundance by elevation in general.

The dominant plant species substantially differed between Reference Low Marsh and Removal Low Marsh. Reference Low Marsh dominant plant species were algae species while Removal Low Marsh samples had higher frequencies of herbaceous and grass species. This difference in plant species composition could be a factor accounting for observed differences in invertebrate community. *Chironomidae* larvae are generally associated with higher marsh elevations; however, they may have been abundant in the Removal Low Marsh samples because of the dominance of herbaceous and grass species there.

The similarities and differences between community compositions can further be evaluated by comparing the relative abundance of taxa found to be most influential to the observed differences, output from SIMPER (similarity percentages) analysis. Although pairwise ANOSIM determined there was no statistical difference between Reference High Marsh and Removal High Marsh community compositions, SIMPER included six taxa that account for observed differences. Of those six, four of them have distinct higher relative abundance in one group or the other. For example, *Sabellidae* are found in higher abundance in Reference High Marsh and rarely occurred in Removal High Marsh samples. However, the two taxa with the greatest contribution to the difference, *Chironomidae* larvae and *Nematoda*, are found in both Reference Marsh and Removal Marsh, with high variability within each. It is likely that dominance in relative abundance with high variability, accounts for the lack of statistical difference detected between community compositions. A criticism of SIMPER analysis is the potential to confound the between group difference and within group variation and may select highly variable factors (taxa, in this analysis) rather than truly characteristic species (Warton *et al.* 2012).

Good indicator species should be found in a single group and be present in most of the sites within that group. Indicator value takes into account fidelity (relative frequency) and exclusivity (relative abundance) within a group. Rare taxa, in low abundance, or highly variable taxa are not good indicators of a given grouping. In general, High Marsh samples had lower abundance and richness than Low Marsh samples, which influences the selection of indicator species. Reference High Marsh had

no indicator species, this is likely to be attributed to the similarity between Reference Marsh and Removal Marsh communities. The taxa comprising the majority of Reference High Marsh samples, such as *Chironomidae*, *Nematoda*, and *Oligochaeta* are also present in other groups, making the indicator values too low to be significant.

High Marsh communities for both Reference Marsh and Removal Marsh contained greater relative abundances of *Halacaridae* species (mites) and *Chironomidae* larvae than Low Marsh samples. These taxa were in higher abundance in Removal High Marsh samples than Reference High Marsh samples. This is consistent with Gray (2005) findings from Salmon River Estuary in Oregon, comparing benthic invertebrates in newly restored marsh to older restored and reference marshes, with *Chironomidae* larvae highly associated with decaying plant materials that occur in high marsh after initial inundation by salt water after a dike removal. High marsh Removal samples had fewer *Annelida* and *Nematoda* taxa. It is possible this is due to highly compacted sediment conditions, often indicative of recently converted agricultural and grazing land (Portnoy 1999), or due to the infrequent and irregular inundation of these areas, at extreme high tides and during storm surges, which reduced the delivery of propagules to these higher elevation areas in the marsh.

Oligochaetes were found in Reference Marsh and Removal Marsh, in High Marsh and Low Marsh. *Tubificids* generally dominated Low Marsh samples and *Enchytraeidae* more common in High Marsh samples for both Reference and Removal. This pattern is

consistent with Levin and Talley (2000) and Johnson (2007) who reported higher relative abundance of *Enchytraeidae* in vegetated sites in the high marsh.

These results agree with similar evaluations within Pacific Northwest marshes, that, in general, invertebrate communities establish fairly rapidly after breaching. In Snohomish River Estuary, Washington, Tanner *et al.* (2002) found restored marsh sites to have lower diversity of invertebrates (Shannon-Weiner index and taxa richness) than Reference sites, though relative abundances were quite similar. In Salmon River Estuary, Oregon, Gray *et al.* (2005) reported average greater density of invertebrates in Reference marsh samples and important differences between community structure between reference and restored marshes.

Generally higher abundance and diversity has been reported for low marsh and tide flats due to receiving higher rates of deposited food sources and frequent inundation with supply of larvae (specifically planktonic) from nearby intact marshes (Mackenzie *et al.* 2015, Tanner *et al.* 2002, Kneib 1984). Overall, marine invertebrate community composition has been shown to resemble nearby reference marsh community within 3-4 years (Moy and Levin 1991, Levin *et al.* 1996, Ray 2000, French 2004) though some deviations from this have been reported for marshes in Connecticut, which took several decades (11-21 years) to restore invertebrate community (Warren *et al.* 2002).

A potential consideration of these results is the high variability in abundances across taxa, morphospecies, and elevational zones observed in these samples, consistent with Fraschetti *et al.* (2005) and Johnson *et al.* (2007) who found abundance and

presence/absence patterns to be highly variable at the meter and even to centimeter scales. This variability, combined with relatively low samples, $n < 30$ for Reference Marsh and Removal Marsh and no replication within each 10 cm change in elevation may reduce confidence in any statistical analyses (Fraschetti *et al.* 2005). Additionally, the invertebrate community structure has been correlated to plant cover/complexity (MacKenzie 2005, de Szalay and Resh 2000), general sediment characteristics such as soil organic matter and salinity (MacKenzie 2005) as well as small-scale sediment conditions (Fleeger *et al.* 1995). Some of those general variables were presented in site descriptions here, though the values accounted for one year post removal only.

In order to have confidence in findings for community establishment, additionally samples and analyses would need to be conducted. However, these results suggest that some invertebrates return rapidly, and that the potential for community assembly that resembles reference invertebrate community within several years of dike removal is possible.

Chapter 3: Do burrowing invertebrates reduce stress to marsh edge plants?

Introduction

The marsh edge, the lowest point of vascular plant growth before transitioning to tide flats, is considered a high stress environment for emergent vegetation, though the stresses may be partly ameliorated by marine invertebrates. Plants at the marsh edge experience extended periods of inundation, leading to hypoxic sediment conditions (Crooks *et al.* 2002). Hypoxic sediments lead to reducing conditions (negative oxygen redox potential) creating greater demand for oxygen and hinders plants' ability to take up and transport nutrients (Dausse *et al.* 2008, Davy *et al.* 2011). Negative oxygen redox potential conditions also lead to accumulation of reduced substances such as sulphides, manganese and iron (Pezeshki 1997) that are toxic to plants.

The Stress Gradient Hypothesis (SGH) model, put forth by Menge & Sutherland (1987), has been applied to describe plant zonation in salt marshes (Alberti *et al.* 2014). The SGH model asserts that in areas of high stress, such as the low intertidal zone and especially the marsh edge, the importance of abiotic conditions are of relatively greater importance than biotic interactions like predation and competition. It is generally regarded that plant zonation in salt marshes is set by a species competitive advantage in the high marsh and stress tolerance in the low marsh (Bertness 1985). In 2003, Bruno *et al.* expanded the SGH model to include the influence of positive interactions, such as facilitation by stress amelioration, in high stress environments. Marsh edge plants may be

able to establish and persist in this zone because of stress amelioration, specifically from other plants or organisms increasing oxygen to hypoxic sediments.

Burrowing salt marsh invertebrates have been shown to aerate sediment through bioturbation, the excavation of sediment for burrow and mound construction, feeding, and other activity (Gribsholt *et al.* 2003, Gutierrez *et al.* 2006, Montague 1982). The presence of burrows with surface openings exposes hypoxic pore waters to oxygenated waters, increasing the effective surface area of sediment-water interface by up to 500% (Riedel *et al.* 1987, Davey 1994), which is critical in low elevation sediments with oxic layers less than 2 mm thick (Fenchel 1996).

Bioturbation and burrow presence by fiddler crabs (*Uca* spp.), found in high densities in Atlantic marshes, have been shown to increase plant productivity (Montague 1982) by ameliorating sediment stresses such as increasing oxygen penetration into sediment and oxygen redox potential (Bertness 1984). The substantial burrowing activity and associated sediment turnover by *Chasmagnathus granulatus*, a burrowing crab occurring in high densities ($> 60 \text{ m}^{-2}$), showed a strong positive effect on soil oxygen redox potential and soil oxygen availability, facilitating mycorrhizal associations with *Spartina densiflora* roots. This facilitation accounted for nearly 35% of vascular plant production (Daleo *et al.* 2007). These field studies have focused on decapod species that create and maintain stable burrows that extend many centimeters down from the sediment surface. In the case of *C. granulatus*, these burrows are always open to the surface, can be up to 100 mm diameter and nearly 1 m deep, making up a matrix of burrows that can

account for 25% of the top 0.5 m of sediment volume (Daleo *et al.* 2007). Fiddler crab burrows can exceed 500 individuals m⁻² and occur from depths of 3-25 cm into the sediment (Gribsholt *et al.* 2003).

The potential for invertebrates that do not create stable burrows to similarly ameliorate abiotic stress to plants in the lower intertidal has not been thoroughly studied. Unlike the crab species mentioned in studies above, invertebrates create smaller (1 mm - 20 mm diameter tubes), sometimes short-lived channels and transient burrows. However, these invertebrates often occur in high densities (several hundred individuals per m⁻²) throughout marsh sediments and have a variety of burrowing strategies (Zorn *et al.* 2006).

Laboratory studies have examined smaller (<500 µm) invertebrate activity using aquaria and a single species, to assess sediment condition and alteration of sediment profiles due to bioturbation activity. An omnivorous polychaete worm from the Nereid family was shown to increase the depth of oxygen saturation by 2.7 mm over a 24-hour period of study in hypoxic conditions, and even conducting burrow irrigation activity in anoxic conditions (Wenzhofer *et al.* 2004). In a separate study, polychaete worms, amphipod and bivalve activity increased the redox profile discontinuity (RPD) depth by 10 mm when compared with sediment profiles without organisms present (Weissberger *et al.* 2009). These suggest there may be potential for invertebrates to reduce stress in hypoxic marsh edge sediments that may yield benefits to plant health.

Given the predictions of increased sea level rise due to global climate change, lower intertidal zone plants will be exposed to longer durations of inundation, reducing gas diffusion, increasing reduced substance accumulation and reducing light availability (Janousek and Mayo 2013), threatening the long-term persistence of salt marshes (Crosby 2002). Research on potential positive plant-animal interactions in the low marsh that could allow plants to maintain productivity and resilience in the face of increased stress (longer daily inundation) is important. Stabilizing sediments to increase accretion is critical to marshes keeping pace with sea level rise. Maintaining above- and below-ground biomass of plants at the marsh edges is one way to stabilize low marsh sediments.

I tested the hypothesis that plant health indicators of a common intertidal plant at the lower marsh edge would improve with greater abundance of invertebrates. Plant survivorship, chlorophyll content (nitrogen deficiency) and chlorophyll fluorescence (FV/FM; photosynthetic efficiency) were measured to assess plant health/plant stress. The marsh edge is considered high stress due to daily inundation and reducing sediment conditions, therefore provides an opportunity to evaluate the potential stress amelioration of burrowing invertebrates to marsh edge plants.

Methods

Study site

Salmon River estuary, located north of Lincoln City, Oregon, just south of Cascade Head Preserve, is approximately 800 hectares, half being emergent marshlands (Gray *et al.* 2002). Since 1978, the US Forest Service (USFS) has completed a series of

projects to remove dikes and tidal gates within the estuary, returning almost 70% of the historic wetlands to tidal inundation (Gray *et al.* 2002). Focal plots for this study were located on an island of low marsh, north of the main channel, at approximately river kilometer 1.6, in an area that had never been diked (Figure 3-1). Marsh edge zones contained Nereid polychaetes, various oligochaetes, bivalves, and shore crab, *Hemigrapsus oregonensis* (personal observations).

Figure 3-1. Study area location near Lincoln City, Oregon, within Salmon River estuary, with zoom of sampling locations along low marsh island along the main channel of Salmon River.

Distichlis spicata (marsh hay) was selected as the focal plant for this study. This widespread terrestrial plant in the grass (*Poaceae*) family is a significant species in salt marshes (Enberg and Wu 1995), providing food and cover for a variety of meiofauna and macroinvertebrates, as well as nesting areas for migratory birds (de Szalay and Resh 1997). In marsh ecosystems, it is a warm season growing perennial (Cronquist *et al.* 1977) that propagates primarily through monopodial rhizome growth (Goodrich and Neese 1986, Brewer and Bertness 1996).

Experimental treatments

Distichlis spicata plant plots (n=40) were selected at equivalent elevation at the lowest point of establishment in the low marsh, as defined by the end of vascular plant growth and the beginning of mud flats. Focal plant plots were staked and rhizomes were severed from higher elevation ramets using a shovel inserted to a depth of 10 cm just upland of each plant, to ensure plant health values recorded were due to low marsh conditions and not influenced by supporting upland plants.

Each plot was assigned an invertebrate abundance treatment ('No Burrows', 'Natural Low', 'Natural High', and 'Augmented') based on visible burrow counts within a 9 cm diameter of the focal plant main stem. We used counts of visible burrows as a proxy for abundance of invertebrates burrowing to avoid disrupting naturally occurring sediment conditions. 'Natural Low' treatment contained 2-10 visible burrows, and 'Natural High' treatment plots contained 11-20 visible burrows. 'Augmented' plots, a subset of 'Natural High' abundance plots, were assigned using a coin toss. Each

‘Augmented’ plot received 4 clams (*Tellinidae*-likely *Macoma spp*) and 2 polychaetes (*Nereidae*), collected nearby at similar elevation and identified to family in the field. Clams ranged between 2-5 cm length, and polychaetes in length between 5-8 cm length. Each ‘Augmented’ plot received organisms of similar size; each plot was given a clam of 5 cm length, 4 cm, 3 cm and 2 cm (± 0.5 mm). Clams were placed in sediment at a depth of 4 cm posterior up so siphons can be extended to surface, and under the bacterial mat on the sediment surface to reduce mortality.

ORP surface and burrow count

Plots were established in early July 2016, when *D. spicata* reached initial greening stage. This timing was later than anticipated, as *D. spicata* plants higher in the marsh greened out mid-May. Plots were visited monthly, from July to September, collecting surface oxygen redox potential (ORP), number of visible burrows, chlorophyll content and chlorophyll fluorescence measurements. Oxygen redox potential (ORP) was assessed immediately using two handheld meters (Extech Model ST20R ORP meter) placed at the sediment surface within 9 cm diameter of focal plant stem, avoiding visible burrow openings. Meters placed at the sediment surface recorded conditions at depth of 2 cm, due to the configuration of sensors. Each meter was left until measurement stabilized (up to 10 minutes). These two measurements were averaged to account for high variability of readings even short distances apart. Visible burrows were measured and counted within the same 9 cm diameter around each focal plant.

Plant health measures

The largest determinant of plant health is overall survivorship. This was recorded at each visit, binning all plots with invertebrates into 'With invertebrates' treatment and 'No burrow' plots into 'No invertebrate' treatment. Plants that were either missing from treatment plots or did not register a value using fluorometer or chlorophyll content meter were assumed to have died.

Chlorophyll fluorescence readings were collected using OS5p Modulated Fluorometer, specifically recording the ratio of variable fluorescence (maximum minus minimum fluorescence) to maximum fluorescence (FV/FM) 30 minutes prior to sunrise to ensure that plants had been sufficiently dark adapted (in the dark for an extended period of time before measurement). Due to the low elevation at the marsh edge, blades of *D. spicata* were silt covered. These were washed off before measuring fluorescence. Maximal fluorescence ratio is an indicator of photosynthetic efficiency of Photosystem II (Kitajima and Butler 1975) and is commonly used as a representation of most types of plant stress (Willits and Peet 2001). For the majority of species, optimal FV/FM levels for stress-free plants is in the range of 0.79 to 0.84, with plants at the lower end experiencing some stress (Maxwell and Johnson 2004).

Chlorophyll content (CCI) was also collected using a handheld chlorophyll meter (Apogee instruments CCM-200 plus) as a secondary indicator of plant condition and health, specifically nitrogen deficiency. This meter calculates a chlorophyll concentration index (CCI) by measuring leaf absorbance values. Because of the shape of the *D. spicata* leaves, each reading required multiple leaves (typically three) be used so that the reading

surface was covered. Leaves were often covered in silt, as is typical for low marsh plants, and were washed off before use.

Formula to calculate CCI:

$$\text{CCI} = \frac{\text{absorbance at 931 nm}}{\text{transmission at 653 nm}}$$

931 nm = chlorophyll absorbance range
653 nm = transmission at this spectrum accounts for leaf characteristics (tissue thickness)

ORP depth and invertebrate abundance

In September 2016, additional measurements for ORP at 10 cm depth were collected as described in ORP surface measurements. Invertebrate abundance was quantified by sieving, to 1 mm in the field, the surrounding sediment within 9 cm diameter and to a depth of 10 cm (approximately 636 cubic centimeters). Organisms were collected in scintillation vials and returned to the Marine Ecology Laboratory at Portland State University for preservation and identification.

Data analysis

Data were analyzed using the software program R (version 1.0.136). The two replicate ORP measurements for each plot, at surface (actual depth of 2 cm) were averaged within the plot and time period and reported with 1 standard error (mean $\pm$ 1SE). Fisher's exact test was used to examine plant survivorship across treatments, to determine whether the proportion of plants that died in plots without invertebrates differed statistically from the plants that died in plots with invertebrates. Additional plant health variables, the change in chlorophyll fluorescence and chlorophyll content index values from beginning to end, were analyzed for normality using Shapiro-Wilks

Normality test ($\alpha=0.05$), change in chlorophyll fluorescence ($W=0.74$, $\alpha=0.05$, $p=2.2e-6$) and change in chlorophyll content ($W=0.89$, $\alpha=0.05$, $p=3.3e-3$) data were not normally distributed even after log transformation. Levene's test, being more suitable for non-normal datasets, was used to test for equal variance ($\alpha=0.05$) the variance for change in chlorophyll fluorescence ($F=0.58$, $df=3$, $\alpha=0.05$, $pr=0.63$) and change in chlorophyll index ($F=1.17$, $df=3$, $\alpha=0.05$, $pr=0.34$) were not significantly different. Failing to meet the assumptions for one-way ANOVA (normality of data), a Kruskal-Wallis H test was used. This non-parametric method tests two or more independent samples of equal (or different) sample sizes that have nearly equal variances. A post hoc test (Dunn's test) was used to determine where any stochastic dominance occurred based on Kruskal-Wallis H findings of significance.

Results

Invertebrate counts

The average elevation of treatment plots ranged from 1.57 m ('Natural Low' min 1.5 m, max 1.6 m; 'Natural High' min 1.4 m, max 1.7 m; and "Augmented" min 1.5 m, max 1.6 m) to 1.64 meters ('No Burrow' min 1.5 m, max 1.7 m) (Table 3-1). Abundance at the final invertebrate count generally followed treatment bins from initial burrow counts. The fewest invertebrates were collected in the 'No Burrow' category (1 ± 0.42) and most invertebrates were collected from the 'Natural High' (4.3 ± 0.67) and 'Augmented' ($4.3 \pm 1.16^*$; Table 3-1).

Table 3-1. Environmental and plant health variables average (± 1 SE) for beginning (July 2016) and ending (September 2016) of the study.

Variable	Treatment			
	No burrows average (± 1 SE)	Natural low average (± 1 SE)	Natural high average (± 1 SE)	Augmented Average (± 1 SE)
Abundance	1.0 (0.42) (n=10)	1.9 (0.57) (n=10)	4.3 (0.67) (n=10)	4.3 (1.16)* (n=10)
Elevation	1.64 (0.02) (n=10)	1.57 (0.01) (n=10)	1.57 (0.03) (n=10)	1.57 (0.02) (n=10)

*Average abundance for augmented sites lower due to heavy mortality of clams in 3 plots.

ORP measurements

Surface ORP measurements were highly variable but showed more similarity among treatments at a time period than among time periods. At the start of the study, the lowest ORP was in the ‘Natural High’ plots ($-16.95 \text{ mV} \pm 10.82$) and highest at the ‘Augmented’ ($18.35 \text{ mV} \pm 12.26$). At the end of the study, the lowest was in the ‘Augmented’ plots ($-78.70 \text{ mV} \pm 10.84$) and highest in the ‘Natural High’ ($-31.15 \text{ mV} \pm 24.09$; Figure 3-2). Average ORP at 10 cm depth was lowest in ‘Natural High’ plots ($-124.70 \text{ mV} \pm 15.82$) and highest in ‘Natural Low’ plots ($-104.90 \text{ mV} \pm 16.24$; Figure 3-2).

Figure 3-2. Oxygen redox potential (ORP) across treatments for surface (2 cm deep) beginning (July) and end (September) and at 10 cm at the termination of the study (September). Generally ORP measurements were higher at the surface beginning, and increasing in reducing conditions at the end and at plant depth. (no_burrow-diagonal pattern; nat_low-white bar; nat_high-grid; augment-gray bar).

Plant health measures

In September, termination of the study, 6 plants had died, 5 from ‘No Burrow’ plots and 1 from ‘Natural High’ plots. A significant difference for plant survivorship was detected across treatments (‘With Invertebrates’ and ‘No Invertebrates’) (Fisher’s exact, $p=0.002$). In plots with ‘No Invertebrates’, 50% of plants survived the duration of the study while nearly 96% of plants survived ‘With Invertebrates’ in plots (Table 3-2).

Table 3-2. Contingency table (2x2) of categories used in Fisher's exact test, plots binned as either with invertebrates or no invertebrates, and plants either survived the duration of the study or died. A significant difference for plant survivorship was detected, higher survivorship of plants occurred in plots with invertebrates (Fisher's exact $p=0.002$).

	with inverts	no inverts	row total
survived	29	5	34
died	1	5	6
column total	30	10	40

Plots with plants that did not survive the duration of the study ($n=6$) were excluded from analysis of chlorophyll fluorescence (FV/FM) and chlorophyll content index (CCI). Chlorophyll fluorescence generally increased for treatments with invertebrates throughout the duration of the study, with greatest increase observed in the 'Augmented' treatment while 'No Burrow' treatment plants decreased (Figure 3-3). No significant difference was found between the mean change in chlorophyll fluorescence (FV/FM) (Kruskal-Wallis chi square= 4.46, $df=3$, $p=0.22$) (Figure 3-4) or chlorophyll content (CCI) (Kruskal-Wallis chi square= 1.96, $df=3$, $p=0.58$) of the remaining plants in the four treatments over the duration of the study (Figure 3-5). Chlorophyll content decreased in all treatments from the beginning to the end of the study, most rapidly in the 'No Burrow' treatment (Figure 3-6).

Figure 3-3. Chlorophyll fluorescence (FV/FM) increased in the ‘Augmented’ treatment, and decreased most rapidly in the ‘No Burrow’ treatment. (no_burrow-diagonal pattern; nat_low-white bar; nat_high-grid; augment-gray bar)

Figure 3-4. 'Augmented' plots showed slight decrease in plant stress (increased FV/FM) while plants in all other treatments showed an increase in plant stress (reduced FV/FM) Means were not significantly different (Kruskal-Wallis, $p=0.22$). (no_burrow-diagonal pattern; nat_low-white bar; nat_high-grid; augment-gray bar).

Figure 3-5. Chlorophyll content decreased in all treatments from the beginning to the end of the study, most rapidly in the 'No Burrow' treatment. (no_burrow-diagonal pattern; nat_low-white bar; nat_high-grid; augment-gray bar).

Figure 3-6. Change in chlorophyll content (CCI) from July to September for *D. spicata* plants generally decreased chlorophyll content over time, with the lowest readings observed from plants in the ‘No Burrow’ and ‘Natural Low’ treatments, the readings were highly variable with the exception of plants from the no invertebrate treatment. No significant difference between change in chlorophyll content across treatments (Kruskal-Wallis, $p=0.58$). (no_burrow-diagonal pattern; nat_low-white bar; nat_high-grid; augment-gray bar).

Discussion

We found that *D. spicata* plants were significantly less apt to die (96% more likely to survive in low marsh environments) if they were in plots with invertebrates than none. While the stress measurements of the surviving plants suggested plants were also less stressed if they were surrounded by more invertebrates, these trends were not statistically significant. Given the high stress associated with the marsh edge, we expected to see the greatest positive impact to plants in this zone. Increased survivorship

suggests the presence of invertebrates is conferring a benefit to these plants, likely due to the presence of burrows always enhancing the total flux of oxygen diffusion from increased surface area contact with oxygenated water (Zorn *et al.* 2006), though benefits of invertebrate presence may be due to factors such as nutrient enrichment or disturbance from predation rather than individual burrowing activity. Activity from invertebrates and their predators may disrupt lower layers of sediments, pushing to the surface nutrient such as nitrogen and phosphorus (Katz 1980). Toxic reduced metals and sulfides that accumulate in reducing environments may be released due to burrow and bioturbation activity, providing a benefit to plants and impacting overall sediment (Katz 1980).

It is possible additional inquiry and manipulative studies could further elucidate if there is a biologically meaningful relationship between invertebrate abundance and plant stress. Comparing the chlorophyll fluorescence and chlorophyll content data, we see that there is likely some plot specific influences. Starting values of chlorophyll fluorescence for all plots were fairly similar. However, chlorophyll content starting values for 'No Burrow' plots suggests that some of those plots were nitrogen limited when compared to the higher starting measurements for other treatments. These plot differences could have influenced survivorship. In order to control for marsh areas that are just not as good as others, it will be important to distribute 'Augmented' plots across all other treatments, including plots with 'No Burrows' to determine if some characteristic of the site itself is more stressful to the plant and is avoided by invertebrates.

Rhizomes were severed at the onset of the study, an action that may have temporarily compromised the health of the plants given that the initial chlorophyll fluorescence measurements suggests the plants were at least slightly stressed (range of initial chlorophyll fluorescence values 0.719-0.767). For further research, it may be beneficial to have replicates that have not been severed from upland ramets, and also potentially including replicates for plants that are transplanted in as distinct individuals.

In 30% of the 'Augmented' plots, several marked clam shells were found, indicating predation had occurred on the clams added to augment the density of burrowing invertebrates at some point during the study. Given this mortality, it is possible that the reduced plant stress measured in plants from this treatment was partly due to increased predator activity and not necessarily the presence of the invertebrates themselves or that stress could have been further reduced if the burrowing invertebrates were able to remain through to the end of the experiment. The most likely predator we saw was *H. oregonensis* as they were detected throughout the study area, though few were collected in sediment for final invertebrate abundance counts. These crabs are primarily herbivores and feed on green algae, but will opportunistically consume smaller clams (Jensen *et al.* 2002).

From the perspective of the invertebrate community and limitations to altering oxygen penetration and redox potential, trophic mode of feeding influences the burrowing strategies and shape, as well as amount of irrigation that occurs within the burrow (Kristensen and Kostka 2004). Burrow design, whether it has a mucous lining and

whether that lining is permeable to oxygen, sorting of sediment grain, and shape, is highly specialized often to the species level (Zorn *et al.* 2006). Of the species present in this study site, the burrow activity of *H. oregonensis* has been shown to increase oxygen penetration into the substrate between 0.8-2 mm; with an average burrow diameter of 20-30 mm, while *Corophium* spp, found in high densities (several hundred individuals m⁻²), the maximum oxygen penetration was about .5 mm (Zorn *et al.* 2006). These values suggest that any oxygenation of sediment is at a small scale and not likely to have been captured by ORP measurements taken at 2 cm and 10 cm depths.

It might be of value to include other dominant low marsh species, such as *Salicornia* spp., given that *D. spicata* is a hearty plant with large amounts of aerenchyma tissues throughout rhizomes and stems to assist in nutrient transport and oxygenation of roots even in reducing conditions (Cronquist *et al.* 1977). Being highly rhizomatous, it also has the ability to share resources. High marsh ramets can expand into suitable habitat and support ramets lower in the marsh that are experiencing greater stresses (Brewer and Bertness 1996). Being highly adapted to stresses, it is possible that invertebrate activity in sediment surrounding this *D. spicata* may be less important than for a newly establishing plant or species that is slightly less tolerant. It is equally possible that being highly adapted to anoxic sediments, that the plants themselves are oxygenating sediments surrounding roots, increasing usage of these sediments by burrowing invertebrates.

Studies involving positive relationships, facilitations, to extend a species distribution beyond the extent of their physiological range is not widely explored in the

scientific literature (He and Cui, 2015), however knowledge on these relationships could provide managers with valuable strategies for maintaining long term plant productivity in the context of uncertain conditions, such as climate change. The premise of this study could be further developed to provide greater knowledge about the interaction between invertebrates and plants at the marsh edge, a critical area of plant growth for reducing erosive forces and increasing marsh accretion.

Chapter 4: Conclusion

These studies focused on invertebrate community assembly after large-scale and long-term disturbance, a dike removal that returned tidal inundation to former marsh that had been restricted for almost 100 years. They further focused on a positive relationship, facilitation, to marsh edge plants, those vascular plants that are often considered to be in areas of high abiotic stress due to duration of inundation, given their low elevation relative to tidal range.

Scientific literature generally concludes that salt marsh invertebrate community will establish fairly rapidly (<10 years) after a return to natural tidal inundation, provided there is an adequate supply of propagules from nearby marshes as well as suitable conditions for subsequent survival and establishment (Cornu and Sadro 2002, Rosza 1995, Warren *et al.* 2001, Fell *et al.* 2000, Warren *et al.* 2002). In the case of Bandon Marsh, dike removal abundance and richness values resemble reference communities within 2 years of restored inundation, while community level analysis suggests that there are still taxa differences across elevations, especially in the low marsh zone. This is striking as low marsh invertebrate communities are generally reported to be functionally equivalent to reference within 2-3 years, considering these areas have greater influx of larvae when compared to the infrequent high marsh inundation (Levin *et al.* 1996). The placement of the dike structures lower in the marsh than is generally reported may have influenced this slow recovery, with herbaceous and grass species dominating removal low marsh plots rather than algae.

The coarse identification of most taxa in this analysis does not allow for a comparison of functional group or feeding guild, to evaluate which functions may be impaired by the incomplete assembly in removal marshes after two years. This is a fundamental question that would allow for more informative assessment of the degree of recovery and what functions are restored. Whether invertebrates that stabilize sediments, consume plant materials, or promote decomposition and other nutrient cycling return soon after removal or require greater time to establish is critical to understanding how rapidly marsh productivity can be restored.

From taxa level analysis, we can say that the removal marsh can provide valuable habitat soon after removal. Many of the invertebrates found in high relative abundance in the restored marsh, primarily *Chironomidae* larvae and *Corophiidae* are prey resources for birds and fish (Tanner *et al.* 2002, Gray 2005). The degree to which this newly restored marsh is utilized by fish species depends upon species prey preference. Newly restored marshes function as suitable habitat, though, may be influenced by individual species requirements. Chinook salmon (a target species for the Bandon Marsh restoration project) and staghorn sculpin in West Coast marshes are known to consume high proportions of *Amphipoda*, *Polychaeta* and *Chironomidae* larvae (Cooksey 2006).

Burrowing invertebrate presence influences plant survival at the marsh edge, and may potentially provide other health benefits, though the results of this study suggest the mode by which the benefit is conferred may differ from the one evaluated here. Many salt marsh plants, including *D. spicata* and especially those that most often occur in lower

elevations, have aerenchyma tissues that transport oxygen through roots, stems, and leaves (Armstrong *et al.* 1994). This system allows a plant to transport the needed oxygen to the roots for maintaining aerobic respiration and to oxidize reducing compounds in the rhizosphere (Pezeshki 2001), so it is possible that mobile invertebrates such as polychaetes, prefer areas surrounding plants to exploit oxidized rhizosphere or protection from wave action. In this case, there would still be facilitation, though reversed from expectations established in Chapter 3. Similarly, structure from plants can reduce predation to burrowing invertebrates (Wiggington *et al.* 2014), also facilitating them. Overall, our findings support the premise that burrowing invertebrate communities are associated with increased plant health, which together can improve the odds of low marsh plant survival and subsequent productivity.

Evaluating these studies in the context of sea level rise, there is potential for increased plant health and potentially increasing plant establishment in the low marsh. Removal Low Marsh samples morphospecies richness and abundance were similar to Reference Low Marsh samples, suggesting that many species return rapidly (< 2 years) after a major disturbance. However, functional diversity is uncertain, since the exact species composition of these rapidly returning organisms was not identified at this time. Assembly of invertebrates appears to be dependent upon supply from nearby intact marshes that tend to establishment in areas with lower stress, as indicated by the reduced abundance and richness measured in High Marsh and Transition Zones. As mean sea levels rise, it is generally assumed that plant productivity will decrease, potentially

reducing plant cover in the low marsh (Crosby *et al.* 2016, Thorne *et al.* 2015, Janousek and Mayo 2013). This may negatively influence establishment of invertebrates through increasing stress due to reduced food sources, habitat structure, less protection from wave/tidal energy, and greater temperature fluctuations (Posey *et al.* 1997, Levin *et al.* 2001, Gutierrez *et al.* 2011.).

Distichlis spicata is an important marsh building plant. The dense sod-building, rhizomatous growth form reduces erosion from low marsh areas and may also aid in marsh accretion, both of which are necessary for marsh plants to keep pace with sea level rise. Meta-analysis of salt marsh vegetation in the US and Europe by Shepard *et al.* (2011) determined that intact marsh plants enhanced accretion by dampening wave action from above ground structures and the binding ability of the roots, especially sod building species. If burrowing invertebrate communities are able to increase survival and productivity to important sod forming low marsh species, there is potential for these areas to keep pace with sea level rise.

Evaluation of the health and potential resilience of salt marshes should include all functional components of the marsh system, as these together will affect the ability of marshes to respond to changing conditions. Salt marsh systems are dynamic with close interactions and feedbacks between abiotic factors and associated biotic components influencing productivity.

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Appendix A: Summary tables by sampling year and invertebrate occurrence.

Figure A-1. Morphospecies richness (mean $\pm$ 1 SE) by treatment, elevation zone, and sampling year. Generally, higher richness was found in Removal than Reference sites in High Marsh elevations. In Low Marsh sites, richness remained consistent for Removal and increased substantially for Reference samples between 2012 and 2013.

Figure A-2 Abundance (mean $\pm$ 1 SE) by treatment, elevation zone, and sampling year for morphospecies diversity. Low marsh sites regardless of treatment had greater average abundance, except for Removal 2013. Average abundance was highest in Reference Low Marsh (260.88) and lowest in Reference High Marsh 2013 (6.00).

Figure A-3 Shannon's (H) diversity index (mean $\pm$ 1 SE) by treatment, elevation zone, and sampling year for morphospecies diversity. Shannon's H diversity values were fairly similar across treatment, elevation zone and year, highest in Reference Low Marsh 2013 (1.4) and lowest in Removal High Marsh 2012 (0.60)

Figure A-4 Relative abundance ($\pm$ SE) of the seven most influential taxa driving 76.7% of the difference between Reference High Marsh (REF_HM, dark green) and Reference Low Marsh (REF_LM, light green). Cumulative contribution of each taxa: *Nematoda* (NEMA) 0.151, *Sabellidae* (SABLE) 0.300, *Chironomidae* (CHIRO) 0.424, *Oligochaeta* (OLIG) 0.536, *Capitella* (CAPI) 0.630, *Enchytraeidae* (ENCH) 0.698, *Corophiidae* (CORO) 0.767.

Figure A-5 Relative abundance ($\pm$ SE) of the six most influential taxa driving 75.6% of the difference between Removal High Marsh (DR_HM) and Removal Low Marsh (DR_LM). Cumulative contribution of taxa: *Chironomidae* (CHIRO) 0.292, *Nematoda* (NEMA) 0.439, *Ostracoda* (OSTR), *Sabellidae* (SABE) 0.623, *Halacaridae* (HALA) 0.690, *Harpacticoid* copepod (HACO) 0.756.

Table A-2 Morphospecies abundance, sum of counts by treatment, elevation zone and collection year 2012, 1 year after dike removal.

		REF HM 12	DR HM 12	REF LM 12	DR LM 12
BIVALVIA	BIVA			1	15
Bivalvia Sp 1	BIVA1			1	2
Bivalvia Sp 2	BIVA2				8
Bivalvia Sp 3	BIVA3				2
Bivalvia Sp 4	BIVA4				1
Bivalvia Sp 5	BIVA5				1
Bivalvia Sp 6	BIVA6				1
GASTROPODA	GAST				12
Assiminea Sp 1	ASSI				11
Gastropoda Sp 2	GAST2				1
Gastropoda Sp 3	GAST3				
ARACHNIDA	ARAC	17	17	1	1
Halacaridae Sp 1	HALA1	17	14	1	
Halacaridae Sp 2	HALA2		1		
Halacaridae Sp 4	HALA4		2		
Halacaridae Sp 5	HALA5				1
HEXAPODA	HEXA	1	1		4
Collembola Sp 1	COLLE1	1			
Collembola Sp 2	COLLE2				
Collembola Sp 3	COLLE3		1		2
Collembola Sp 4	COLLE4				2
INSECTA	INSE	6	57	5	24
Chironomidae Sp 1	CHIRO	6	57	5	24
MALACOSTRACA	MALA	11	8	426	285
Amphipoda Sp 8	AMPH8			2	
<i>Americorophium salmonis</i>	AMSA	1		2	31
Corophiidae Sp 1	CORO1			324	106
Corophiidae Sp 2	CORO2			62	
Corophiidae Sp 3	CORO3			1	
Gammaridae Sp 1	GAMMA 1	4		1	
Gammaridae Sp 2	GAMMA 2			4	
Gammaridae Sp 3	GAMMA 3			1	
<i>Gnorimosphaeroma noblei</i>	GNNO	4		7	

<i>Gnorimosphaeroma oregonensis</i>	GNOR	1		18	6
Hyalidae Sp 1	HYAL1		3	1	
Hyalidae Sp 2	HYAL2		5		1
Leuconidae Sp 1	LEUC			1	113
<i>Nippoleucon hinumensis</i>	NIHI	1		2	28
MAXILLOPODA	MAXI			244	304
Copepoda Sp 1	COPE1				3
Copepoda Sp 2	COPE2				1
Harpacticoida Copepod Sp 1	HACO1				
Harpacticoida Copepod Sp 2	HACO2			45	5
Harpacticoida Copepod Sp 4	HACO4			163	45
Harpacticoida Copepod Sp 5	HACO5			1	114
Harpacticoida Copepod Sp 6	HACO6			2	3
Harpacticoida Copepod Sp 7	HACO7				1
Huntemannia jadensis	HUJA			33	132
NEMATODA	NEMA	59	8	778	890
Nematoda	NEMA	59	8	778	890
OLIGOCHAETA	OLIG	41	18	274	99
Enchytraeida Sp 1	ENCH1	20			2
Enchytraeida Sp 2	ENCH2			11	4
Enchytraeida Sp 3	ENCH3			1	1
Oligochaeta Sp 1	OLIG1		2	2	11
Oligochaeta Sp 2	OLIG2	3		8	
Oligochaeta Sp 3	OLIG3	4			12
Oligochaeta Sp 4	OLIG4	14		22	
Oligochaeta Sp 5	OLIG5			71	3
Oligochaeta Sp 6	OLIG6		2	1	
Oligochaeta Sp 8	OLIG8				2
Tubificidae Sp 1	TUBI1			7	38
Tubificidae Sp 2	TUBI2		14	151	26
OSTRACODA	OSTR	8		68	549
Ostracoda Sp 1	OSTR1	8		11	450
Ostracoda Sp 2	OSTR2			57	99
POLYCHAETA	POLY	66	3	343	1189
<i>Ampharete finmarchica</i>	AMFI			1	32
<i>Amphicteis floridus</i>	AMFL			7	19
Capitella Sp 1	CAPI1	8	2	64	59
Capitella Sp 2	CAPI2	24		18	12
Capitella Sp 3	CAPI3			9	17
Capitella Sp 4	CAPI4				

<i>Chone minuta</i>	CHMI	34		239	978
<i>Eteone californica</i>	ETCA				2
Eteone Sp 1	ETEO1				7
Eteone Sp 2	ETEO2				3
Eteone Sp 3	ETEO3				1
<i>Glyphanostomum pallescens</i>	GLPA			2	2
Magelona Sp 1	MAGE1		1	1	1
Magelona Sp 2	MAGE2				
<i>Neanthes limnicola</i>	NELI			2	1
Nereididae Sp 1	NERE				
<i>Pygospio elegans</i>	PYEL				39
<i>Streblospio benedicti</i>	STBE				7
Streblospio Sp 1	STRE				9
PLATYHELMINTHES	PLAT		3		
Turbellaria Sp 1	TURB		3		

Table A-3 Morphospecies abundance, sum of counts by treatment, elevation zone and collection year 2013, 2 years after dike removal.

		REF HM 13	DR HM 13	REF LM 13	DM LM 13
BIVALVIA	BIVA				2
Bivalvia Sp 1	BIVA1				1
Bivalvia Sp 2	BIVA2				1
Bivalvia Sp 3	BIVA3				
Bivalvia Sp 4	BIVA4				
Bivalvia Sp 5	BIVA5				
Bivalvia Sp 6	BIVA6				
GASTROPODA	GAST				1
Assiminea Sp 1	ASSI				
Gastropoda Sp 2	GAST2				
Gastropoda Sp 3	GAST3				1
ARACHNIDA	ARAC	2	4	1	5
Halacaridae Sp 1	HALA1	2	1	1	5
Halacaridae Sp 2	HALA2		1		
Halacaridae Sp 4	HALA4				
Halacaridae Sp 5	HALA5		2		
HEXAPODA	HEXA		1		1
Collembola Sp 1	COLLE1				
Collembola Sp 2	COLLE2				1
Collembola Sp 3	COLLE3		1		
Collembola Sp 4	COLLE4				
INSECTA	INSE	7	17	12	15
Chironomidae Sp 1	CHIRO	7	17	12	15
MALACOSTRACA	MALA		3	180	
Amphipoda Sp 8	AMPH8				
<i>Americorophium salmonis</i>	AMSA			142	
Corophiidae Sp 1	CORO1			16	
Corophiidae Sp 2	CORO2				
Corophiidae Sp 3	CORO3				
Gammaridae Sp 1	GAMMA1				
Gammaridae Sp 2	GAMMA2				
Gammaridae Sp 3	GAMMA3			2	
<i>Gnorimosphaeroma noblei</i>	GNNO			12	
<i>Gnorimosphaeroma oregonensis</i>	GNOR			5	
Hyalidae Sp 1	HYAL1		3		

Hyalidae Sp 2	HYAL2				
Leuconidae Sp 1	LEUC			3	
<i>Nippoleucon hinumensis</i>	NIHI				
MAXILLOPODA	MAXI		7	88	29
Copepoda Sp 1	COPE1				
Copepoda Sp 2	COPE2				
Harpacticoida Copepod Sp 1	HACO1		1		1
Harpacticoida Copepod Sp 2	HACO2				3
Harpacticoida Copepod Sp 4	HACO4			12	
Harpacticoida Copepod Sp 5	HACO5			25	4
Harpacticoida Copepod Sp 6	HACO6			5	
Harpacticoida Copepod Sp 7	HACO7			6	
<i>Huntemannia jadensis</i>	HUJA		6	40	21
NEMATODA	NEMA	6	2	583	34
Nematoda	NEMA	6	2	583	34
OLIGOCHAETA	OLIG	10	3	414	1
Enchytraeida Sp 1	ENCH1			1	
Enchytraeida Sp 2	ENCH2			167	1
Enchytraeida Sp 3	ENCH3				
Oligochaeta Sp 1	OLIG1	9	3	72	
Oligochaeta Sp 2	OLIG2				
Oligochaeta Sp 3	OLIG3				
Oligochaeta Sp 4	OLIG4				
Oligochaeta Sp 5	OLIG5				
Oligochaeta Sp 6	OLIG6				
Oligochaeta Sp 8	OLIG8				
Tubificidae Sp 1	TUBI1	1		131	
Tubificidae Sp 2	TUBI2			43	
OSTRACODA	OSTR	1	1	25	24
Ostracoda Sp 1	OSTR1	1	1	11	18
Ostracoda Sp 2	OSTR2			14	6
POLYCHAETA	POLY	4	1	784	22
<i>Ampharete finmarchica</i>	AMFI			1	
<i>Amphicteis floridus</i>	AMFL			1	
Capitella Sp 1	CAPI1	1		29	3
Capitella Sp 2	CAPI2			16	2
Capitella Sp 3	CAPI3				
Capitella Sp 4	CAPI4				4
<i>Chone minuta</i>	CHMI	3	1	728	13
<i>Eteone californica</i>	ETCA				
Eteone Sp 1	ETEO1			1	
Eteone Sp 2	ETEO2			3	

Eteone Sp 3	ETEO3				
<i>Glyphanostomum pallescens</i>	GLPA				
Magelona Sp 1	MAGE1				
Magelona Sp 2	MAGE2			1	
<i>Neanthes limnicola</i>	NELI				
Nereididae Sp 1	NERE			1	
<i>Pygospio elegans</i>	PYEL				
<i>Streblospio benedicti</i>	STBE			3	
Streblospio Sp 1	STRE				
PLATYHELMINTHES	PLAT				
Turbellaria Sp 1	TURB				