Lisa J. Belleveau[1], U.S. Geological Survey, Western Ecological Research Center, 505 Azuar Dr, Vallejo, CA 94592; Evergreen State College and Nisqually River Foundation, Olympia, Washington 98505

John Y. Takekawa[2,3], U.S. Geological Survey, Western Ecological Research Center, 505 Azuar Dr, Vallejo, California 94592

Isa Woo, U.S. Geological Survey, Western Ecological Research Center, 505 Azuar Dr, Vallejo, California 94592

Kelley L. Turner[4], U.S. Geological Survey, Western Ecological Research Center, 505 Azuar Dr, Vallejo, California 94592

Jesse B. Barham[5], Nisqually National Wildlife Refuge, U.S. Fish and Wildlife Service, 100 Brown Farm Rd NE, Olympia, Washington 98516

Jean E. Takekawa[6], Nisqually National Wildlife Refuge, U.S. Fish and Wildlife Service, 100 Brown Farm Rd NE, Olympia, Washington 98516

Christopher S. Ellings, Department of Natural Resources, Nisqually Indian Tribe, 12501 Yelm Highway SE, Olympia, Washington 98513

and

Gerardo Chin-Leo, Oceanography and Marine Biology, The Evergreen State College, 2700 Evergreen Parkway NW, Olympia, Washington 98505

Vegetation Community Response to Tidal Marsh Restoration of a Large River Estuary

Abstract

Estuaries are biologically productive and diverse ecosystems that provide ecosystem services including protection of inland areas from flooding, filtering freshwater outflows, and providing habitats for fish and wildlife. Alteration of historic habitats, including diking for agriculture, has decreased the function of many estuarine systems, and recent conservation efforts have been directed at restoring these degraded areas to reestablish their natural resource function. The Nisqually Delta in southern Puget Sound is an estuary that has been highly modified by restricting tidal flow, and recent restoration of the delta contributed to one of the largest tidal salt marsh restorations in the Pacific Northwest. We correlated the response of nine major tidal marsh species to salinities at different elevation zones. Our results indicated that wetland species richness was not related to soil pore-water salinity ($R^2 = 0.03$), but were stratified into different elevation zones ($R^2 = 0.47$). Thus, restoration that fosters a wide range of elevations will provide the most diverse plant habitat, and potentially, the greatest resilience to environmental change.

Key words: tidal salt marsh, salinity, elevation, Nisqually River Delta

Introduction

Estuarine ecosystems are some of the most productive and sensitive landscapes on Earth (Adam 1990, USFWS 2005, Ellings 2011). They support numerous species of plants and animals, protect inland areas from flooding, filter sediments, nutrients, and pollution, and provide economic, recreational, and aesthetic ecosystem services (Kruckeberg 1991, Smith et al. 2000, Scavia et al. 2002, USFWS 2005). However, many of the habitats within coastal estuaries have been degraded and destroyed over the last 150 years. Human influences such as urbanization, damming of rivers, pollution, and agriculture have degraded the physical condition and resilience of estuaries, leaving them vulnerable to additional impacts (Adam 1990, Apostol and Sinclair 2006, Ellings 2011).

[1] Present address: Skokomish Indian Tribe; Habitat Biologist; 80 North Tribal St, Skokomish Nation, WA 98584

[2] Author to whom correspondence should be addressed. Email: john_takekawa@usgs.gov

[3] Emeritus. Present address: National Audubon Society, Science Division, 220 Montgomery Street, San Francisco, CA 94104

[4] Present address: Hamer Environmental, 1510 S 3rd St, Mt. Vernon, WA 98273

[5] Present address: City of Olympia Public Works Department, PO Box 1967, Olympia, WA 98507

[6] Retired

In the Pacific Northwest, over 80% of estuarine landscapes have been altered and degraded (Adam 1990, Simenstad and Cordell 2000, Dean et al. 2001, Apostol and Sinclair 2006, Weilhoefer et al. 2012). Recently, conservation efforts have focused on restoring estuaries to reestablish their ecosystem services and natural functions, such as recovery of habitats that support salmon (Simenstad and Cordell 2000). As one of the least developed major rivers in the Pacific Northwest, the Nisqually River and its delta were identified as an important restoration area, particularly for potential salt marsh restoration. In the past two decades, dike removal on the Nisqually River Delta (hereafter Nisqually Delta) has initiated the largest river delta restoration in the Pacific Northwest (Ellings 2011).

Vegetation is often used as a measurement of success when evaluating restoration projects (Mitsch and Wilson 1996, Kentula 2000, Thom et al. 2002). Depth and duration of inundation has direct influence on salt marsh vegetation composition and density (Adam 1990). Several studies (Bertness et al. 1992, Boumans et al. 2002, Hinkle and Mitsch 2005) have shown that vegetation communities can change dramatically along elevation and salinity gradients. Knowledge of the physical attributes that directly relate to salt marsh vegetation communities may be valuable for managers to predict the possible function of restored areas.

Studying key physical processes and the interactions they have with biological processes is essential for understanding these complex ecosystems (Williams and Faber 2001, Wolters et al. 2008). Previous studies of restored estuaries have suggested that salt marsh vegetation diversity increases with elevation, but that this also varies with salinity (Burg et al.1980, Weinmannn et al. 1984, Hutchinson 1988, Adam 1990, Bertness et al. 1992, Zedler et al. 1999, Simenstad and Cordell 2000, Tanner 2000, Roman et al. 2001, Zedler 2001, Boumans et al. 2002, Crain et al. 2004, Hinkle and Mitsch 2005, Weilhoefer et al. 2012). For example, Weilhoefer et al. (2012) found that the vegetation community changed dramatically across a salinity gradient in a study of fifty marshes along the Oregon Coast. High soil pore-water salinity and frequent inundation create inhospitable environments for plants leading to reduced productivity and survival (Hutchinson 1988, Adam 1990, Zedler et al. 1999, Zedler 2001). Pacific Northwest estuaries are still understudied (Weilhoefer et al. 2012), and species tolerance to submergence (i.e., elevation) and salinity have not been established for this area.

To understand the interactions between physical and biological processes in tidally influenced landscapes, we correlated the response of salt marsh vegetation to soil pore-water salinity and elevation at restored and reference sites on the Nisqually Delta (Figure 1). Our research question was to determine the submergence and salinity tolerance ranges of key tidal salt marsh plant species and to examine the differences in plant communities in reference and early restoration areas. Establishment of tolerance ranges may be valuable in identifying areas with the physical conditions capable of supporting salt marsh species and determining suitable estuarine locations for future salt marsh habitat restoration.

Methods

Study Area

Our research focused on the Nisqually Delta where dike removal led by the Nisqually National Wildlife Refuge and Nisqually Indian Tribe had re-established tidal flow and restored more than 360 hectares (ha) of former marshes to estuarine conditions (Ellings 2011). Vegetation surveys were conducted on two relatively undisturbed reference sites (Animal Slough, hereafter "Nisqually Reference" and a site that was between the Nisqually River and Red Salmon slough, hereafter "RSS Reference"), two vegetated restored parcels (Phase 1, hereafter "2002 Restored" and Phase 2, hereafter "2006 Restored"), and one early phase restoration parcel (2009 Restored), on the Nisqually Delta near Olympia, Washington (47.08°N 122.70°W; Figure 1). Two of the marshes (2006 Restored, Nisqually Reference) have significant freshwater inputs from the Nisqually River, two (2002 Restored, RSS Reference) have primarily salt water inputs

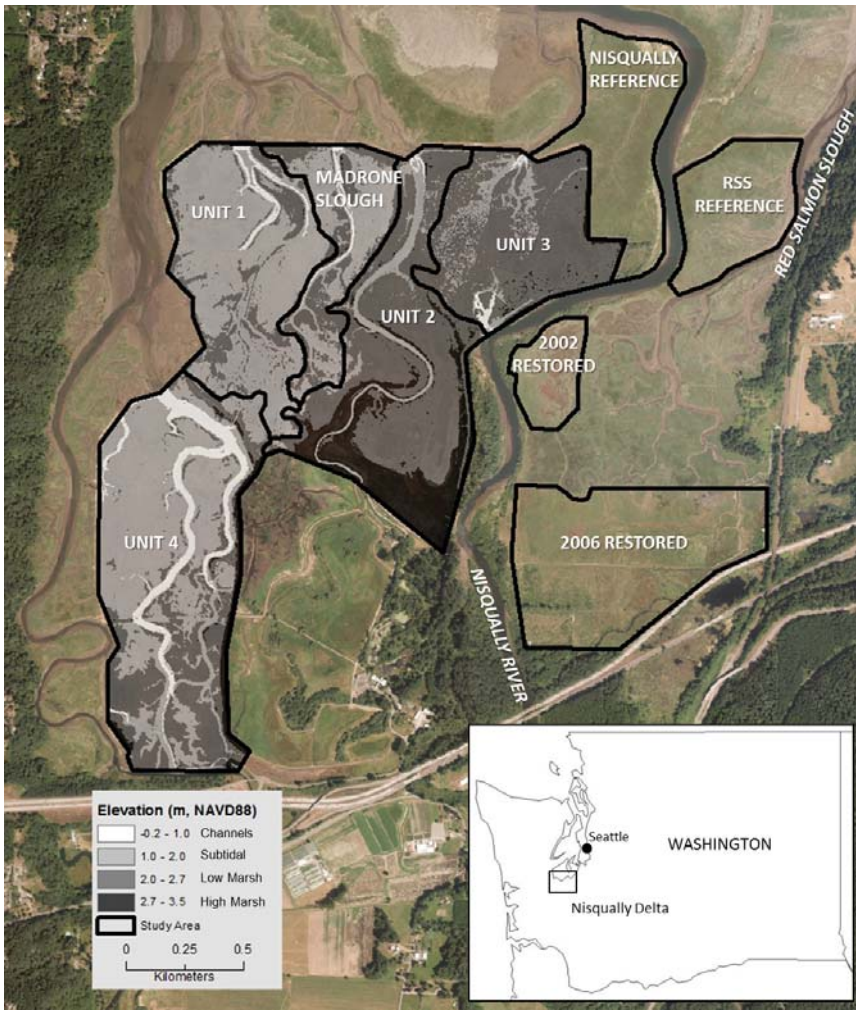

Figure 1: Location of the Nisqually Delta in south Puget Sound (inset) and units within the Nisqually Delta where this study was conducted. Unit 1, Unit 2, Unit 3, Unit 4, and Madrone constitute the 2009 Restored area (in gray). The map legend details elevations in the 2009 Restored area based on the 2011 LiDAR coverage (Watershed Sciences 2011).

from Red Salmon Slough and are influenced by freshwater to a lesser extent, and 2009 Restored is primarily influenced by estuarine tidewaters and to a smaller extent water from the Nisqually River.

Vegetation Surveys

We stratified samples into terciles along the second-order or higher slough edges to implement vegetation surveys. Ten 50-m transects were placed at the edge of each slough and run perpendicular to capture the environmental gradient. In August 2010, we surveyed 0.25-m^2 quadrats at 0, 20, and 40 m (n = 3) for soil pore-water salinity, elevation, percent cover, stem density, and maximum height for each species along each transect. In addition, we surveyed 21 quadrats (RSS Reference, n = 6; Nisqually Reference, n = 6; 2002 Restored, n = 3; 2006 Restored, n = 6) associated with terrestrial invertebrate sampling areas (Ellings 2011, Woo et al. 2011) for a total of 51 quadrats.

Soil Pore-Water Salinity and Elevation

At each site, we recorded pore-water salinity adjacent to each quadrat plot by squeezing pore-water from the substrate through a coffee filter onto a handheld NaCl Refractometer (Sper Scientific, Scottsdale, AZ). The refractometer was calibrated with DI water for each survey period, and data are presented in Practical Salinity Units (PSU; Fofonoff 1985).

At each site, we determined the elevation of the marsh platform (NAVD88 in meters) at the center of each quadrat and at 1-m intervals along each transect with a Leica Viva CS-15 Real-Time Kinematic (RTK) Global Positioning System (GPS) rover (Leica Geosystems, Norcross, GA; ± 3cm vertical accuracy). Two elevation zones (high and low marsh) were established by applying the tidal datum from the closest gage station to the Nisqually Delta, the Dupont Wharf tide gage station (Station ID: 9446828; (NOAA Tides and Currents [March 2011]). We used the relationship between a land vertical datum (NAVD88) and this station's tidal datum to convert to a local tidal datum Mean High Water (MHW = 2.7 NAVD88 m; Tanner 2000, Mofjeld et al. 2002). MHW was inundated twice daily by the average high tide. In this study, we used elevation synonymously with inundation; therefore, MHW (or 2.7 NAVD88 m) was used as the level at which low and high marshes were separated.

Vegetation Analysis

We summarized salinity and elevation ranges for all plant species encountered (plant nomenclature follows Hitchcock and Cronquist 1973, updated nomenclature follows Flora of North America (Flora of North America Editorial Committee 1993). We then selected nine common species of Pacific Northwest salt marshes to summarize mean salinity and elevation occurrences for: Lyngby's sedge (*Carex lyngbyei*), seashore saltgrass (*Distichlis spicata*), entire-leaved gumweed (*Grindelia integrifolia*), salt marsh daisy (*Jaumea carnosa*), Baltic rush (*Juncus balticus* ssp. *ater*), silverweed (*Potentilla anserina*), pickleweed (*Sarcocornia perennis*), sand-spurry (*Spergularia* spp.), and sea arrow-grass (*Triglochin maritima*). We used a correlation analysis in R statistical software (version 2.12.0, The R Foundation for Statistical Computing) to explore the strength of the relationship among percent cover, height, and density of the vegetation with soil pore-water salinity and elevation. We assessed species richness in relation to soil pore-water salinity and elevation using regression analysis in JMP statistical software (version 11.0, SAS Institute Inc. 2013, Cary, NC).

Predicting Vegetative Cover

We measured pore-water salinity and RTK-GPS elevation data from survey transects in hydrologic study units that we identified along five sloughs (Unit 1, Unit 2, Unit 3, Unit 4, and Madrone Slough) within 2009 Restored (Figure 1). Although RTK-GPS data typically has much better accuracy than LiDAR (Foxgrover et al. 2011), LiDAR provided us with a more detailed digital elevation map (DEM) across the entire 2009 Restored area (Watershed Sciences 2011). We compared 1653 RTKGPS points within the 2009 Restored against existing LiDAR coverage of the Nisqually Delta and ≤ 5 cm elevation difference between the RTK GPS and LiDAR data (Woo et al. 2011). Thus we validated the accuracy of the LiDAR coverage with RTK GPS points prior to analyzing suitable areas for vegetation colonization within the 2009 Restored area.

Results

Vegetation Response to Pore-Water Salinity and Elevation

We observed a total of 27 marsh species during the surveys (Table 1). Nisqually Reference and 2006 Restored had pore-water salinity varying from 2 to 26 throughout the growing season (June–September 2010), while 2002 Restored and Nisqually Reference ranged from 15 to 45.

We calculated the mean, maximum, and minimum pore-water salinity and elevation for all species establishing their range of tolerance levels (Figure 2, Table 1). Of the 27 species surveyed, 12 were observed with a pore-water salinity range entirely below 30 (Figure 2, Table 1), indicating a salinity threshold above which their growth was compromised, or they were absent. Of the 27 species surveyed, 11 had an elevation range

TABLE 1. Soil pore-water salinity, elevation ranges, and marsh zone of plant species encountered in the Nisqually Delta. Species with a significant relationship of < 0.05 for salinity or elevation are indicated for percent cover (P), height (H), and density (D) for the nine most common species. Marsh zones of species occurrence are specified as low marsh (L; 2.0-2.7 NAVD88 m) and high marsh (H; > 2.7 NAVD88 m).

Species Code	Common Name	Scientific Name	Salinity Range (PSU)	Elevation Range (m, NAVD88)	Marsh Zone
CALY	Lyngby's sedge	*Carex lyngbyei*	2 – 30[PHD]	2.10 - 3.03	L/H
DISP	Salt grass	*Distichlis spicata*	4 – 45[PD]	2.08 - 3.11	L/H
GRIN	Entire-leaved gumweed	*Grindelia integrifolia*	20 – 45[PHD]	2.80 - 3.08 [PHD]	H
JACA	Salt-marsh daisy	*Jaumea carnosa*	4 – 45[PD]	2.57 - 3.08[PHD]	L/H
JUBA	Baltic rush	*Juncus balticus* ssp. *ater*	5 – 28[H]	2.51 - 3.09 [PHD]	L/H
POAN	Silverweed	*Potentilla anserina*	10 - 30	2.79 - 3.10 [PHD]	H
SAPE	Pickleweed	*Sarcocornia perennis*	5 – 45[PHD]	2.33 - 3.08	L/H
SPSP	Sand spurry	*Spergularia* spp.	11 - 32	2.08 - 2.95	L/H
TRMA	Sea arrow-grass	*Triglochin maritima*	10 - 45	2.19 - 3.05[PH]	L/H
AGGI	Redtop	*Agrostis gigantea*	12 - 23	2.75 - 3.07	H
ATPA	Spear saltbush	*Atriplex patula*	5 - 45	2.54 - 3.08	L/H
BOMA	Seacoast bulrush	*Bolboschoenus maritimus*	2 - 16	2.60 - 2.93	L/H
COCO	Brass buttons	*Cotula coronopifolia*	10 - 11	2.77 - 2.91	H
CUPA	Salt-marsh dodder	*Cuscuta pacifica*	28 - 45	2.57 - 3.01	L/H
DECE	Tufted hairgrass	*Deschampsia cespitosa*	10 - 30	2.78 - 2.99	H
ELPA	Dwarf spikerush	*Eleocharis parvula*	11 - 28	2.36 - 2.91	L/H
ELRE	Quackgrass	*Elymus repens*	13 - 18	2.78 - 3.29	H
LYMA	Sea milkwort	*Lysimachia maritima*	10 - 45	2.57 - 3.06	L/H
HOBR	Meadow barley	*Hordeum brachyantherum*	5 - 21	2.47 - 3.07	L/H
HOJU	Foxtail barley	*Hordeum jubatum*	16 - 30	2.81 - 2.91	H
LACA	Canadian lettuce	*Lactuca canadensis*	NA	2.90 - 3.07	H
LIOC	Western lilaeopsis	*Lilaeopsis occidentalis*	12 - 17	NA	NA
PLMA	Sea plantain	*Plantago maritima*	5 - 45	2.57 - 3.09	L/H
PUNU	Pacific alkali grass	*Puccinellia nutkaensis*	5 - 33	2.81 - 3.08	H
SPCA	Canadian sand spurry	*Spergularia canadensis*	15 - 45	2.47 - 3.08	L/H
STHU	Salt-marsh chickweed	*Stellaria humifusa*	22 - 45	2.90 - 2.98	H
SYSU	Douglas' aster	*Symphyotrichum subspicatum*	NA	2.88 - 3.10	H

limited to the high marsh (> 2.7 NAVD88 m; Figure 2b, Table 1). Only two vascular genera (*Spergularia* spp. and *Eleocharis parvula*) had average elevations below MHW (2.7 NAVD88 m; Figure 2b). No species were observed below 2 m, which indicated a lower elevation threshold below which salt marsh species did not occur. Thus, we defined low marsh as being from that lower elevation threshold to MHW (2.0–2.7 NAVD88 m) and high marsh as being from MHW to the upper elevation of marsh species surveyed by this study (2.7–3.5 NAVD88 m).

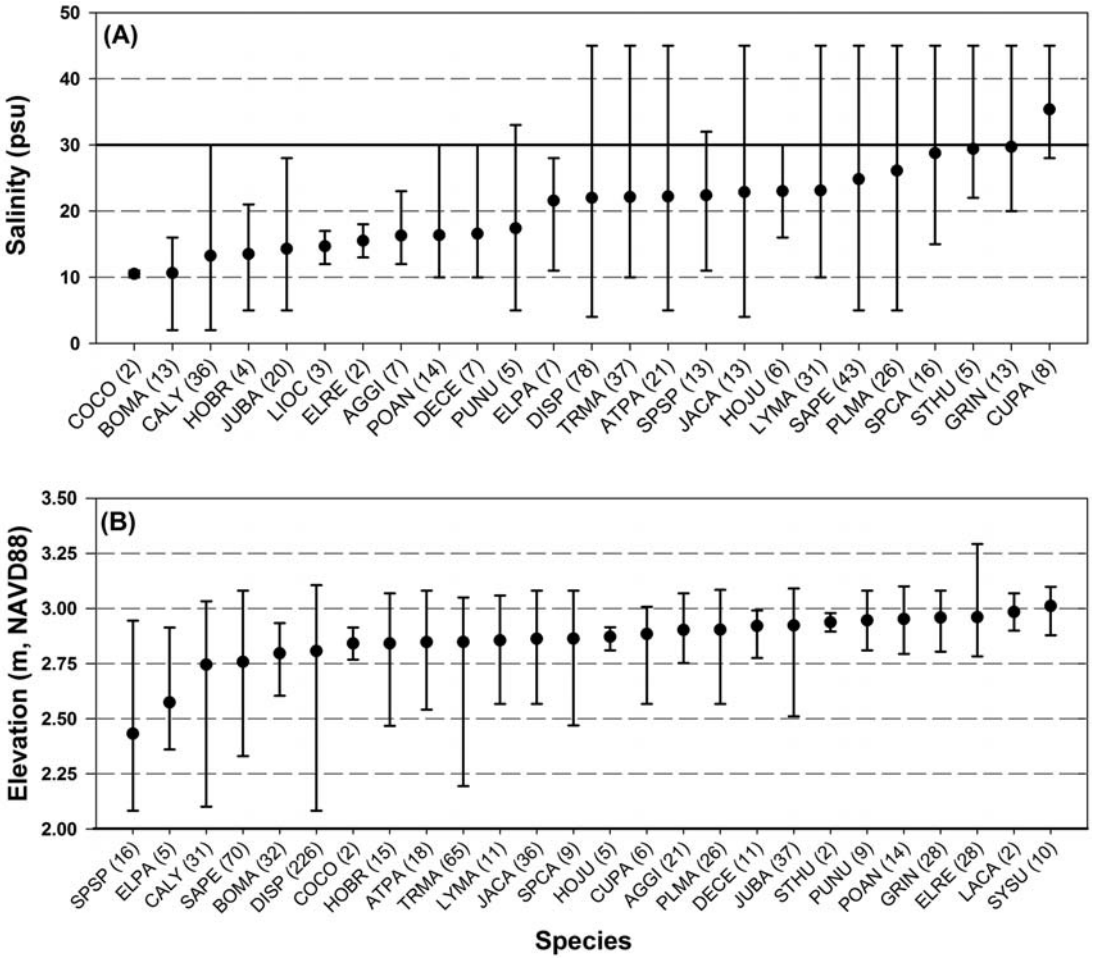

Figure 2: Summer soil pore-water salinity in Practical Salinity Units and elevation in meters (NAVD88) for the common plant species observed (means + max/min). The number of observations are indicated in parentheses. The four-letter species codes are defined in Table 1.

The average plant occurrence was between a relatively narrow elevation range of 53 cm (from 2.43 m to 2.96 m NAVD88) for the nine common wetland species (Figure 2). These species were further separated into two groups by salinity with *C. lyngbyei*, *Juncus balticus, and P. anserine* occupying a more brackish environment and *D. spicata, Spergularia* spp., *T. maritima, Jaumea carnosa, S. perennis, and G. integrifolia* occupying a more saline environment. Of the nine species examined in detail, only one species (*C. lyngbyei*) showed a negative relationship with soil pore-water salinity ($P < 0.001$; Table 1, Figure 2). Five of the nine species (*D. spicata*, *G. integrifolia*, *Jaumea carnosa*, *Juncus balticus*, and *S. perennis*) showed a positive relationship among one or more growth metrics and soil pore-water salinity ($P \leq 0.05$; Table 1). One species (*C. lyngbyei*) had a negative trend with elevation, but the relationship was not statistically significant ($P > 0.05$). Five of the nine species (*G. integrifolia*, *Jaumea carnosa*, *Juncus balticus*, *P. anserina*, and *T. maritima*) showed a positive relationship with elevation ($P \leq 0.05$; Table 1). Species richness was not correlated with increased soil pore-water salinity ($R^2 = 0.03$; $F_{1,41} = 1.2$, $P = 0.28$; Figure 3a), but species richness did show a strong positive correlation with elevation ($R^2 = 0.47$; $F_{1,49} = 37.3$; $P < 0.001$; Figure 3b).

We found a difference in salinity between sites that were primarily due to proximity to the Nisqually River as a freshwater source rather than an indication of restoration status. The mean salinity (15.8) at Nisqually Reference was lower than the mean salinity (20.3) of 2006 Restored. The mean salinity of RSS Reference (30.4) exceeded the mean salinity of 2002 Restored (26.2). We detected a mean elevation difference by site though some sites were similar. The mean elevation of 2006 Restored (2.83 NAVD88 m) was similar to the mean elevation of the RSS Reference (2.87 NAVD88 m), while the elevation of the 2002 Restored (2.51 NAVD88 m) was similar to the mean elevation of the Nisqually Reference (2.49 NAVD88 m). All sites' elevations were, on average, 0.50–0.88 m higher than the 2009 Restored area.

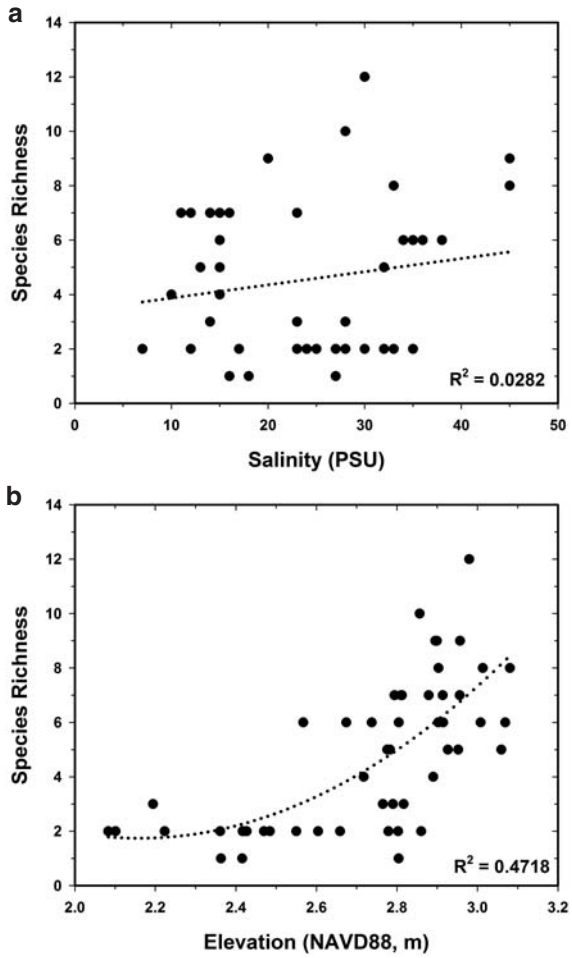

Figure 3: Relationship between species richness and (a) soil pore-water salinity or (b) elevation (m, NAVD88) in the Nisqually Delta. R^2 values are shown for the trend lines indicating the stronger relationship of species richness with elevation.

Pore-Water Salinity and Elevation of the Restoring Estuary

Vegetation surveys within 2009 Restored indicated low plant colonization and an upper pore water salinity threshold of 30 (Table 1, Figure 4). Eleven of the 15 surveyed locations within the restoration area were at or below this salinity threshold (Figure 4a). Most ($n = 10$) of the restored sampling locations were close to or below 2 NAVD88 m elevation, and only three transects had elevations above 2.7 NAVD88 m (Figure 4b). We did not find a gradient of significant differences in salinity or elevation from north to south or from the edge of Puget Sound inland in any of the study units (Figure 4).

Since submergence time (i.e., elevation) was a key factor in determining salt marsh vegetation growth, we used the LiDAR data to determine the extent of areas suitable for salt marsh plant colonization in the 2009 Restoration. Our analysis indicated that 49% of the 2009 Restored site was comprised of channels and subtidal habitats, 45% was suitable for low marsh, while 6% was suitable for high marsh plant communities (Figure 1).

Discussion

Several factors determine plant community distribution (Lortie et al. 2004) and colonization in tidal marsh restorations including landscape features such as proximity to bay edge (Zedler et al. 1999) or channels (Sanderson et al. 2000), nutrient availability (Valiela et al. 1985, Levine et al. 1998), and species competition (Bertness 1991, Bertness and Shumway 1993, Silliman and Zieman 2001, Pennings et al. 2005). However, while ecological interactions may constrain species to their realized niche (Crain et al. 2004, Redondo-Gomez et al. 2007, Engels and Jensen 2010), their physiological tolerance to estuarine conditions ultimately determines the fundamental niche of where plants can establish or grow.

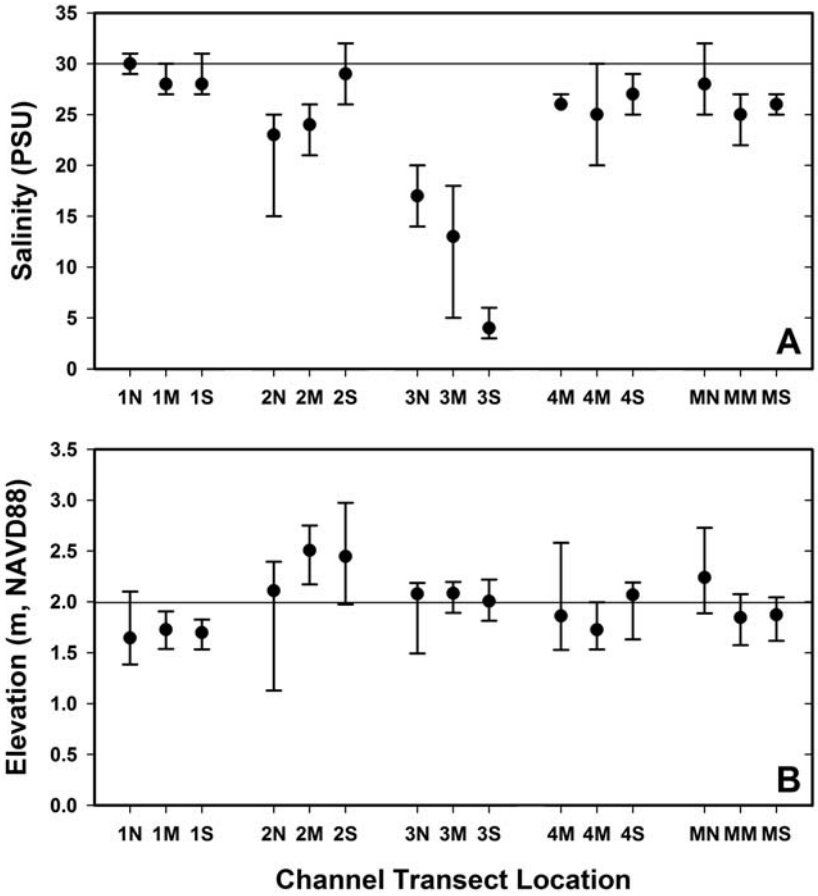

Figure 4: Soil pore-water salinity and elevation ranges from channel transect surveys of the 2009 Restored area. Points represent mean values, while error bars represent the minimum and maximum values. Numbers on the horizontal axis indicate the study unit (1= Unit 1, 2 = Unit 2, 3 = Unit 3, 4 = Unit 4, M = Madrone Slough), while the letters indicate the area divided into terciles (North, Middle, or South) extending inland from Puget Sound. Bold lines indicate the salinity (30) and elevation (2 m) thresholds in this study.

Of the key physical conditions, soil salinity and elevation have been identified as two of the main drivers for tidal marsh plant species (Mahall and Park 1976a, 1976b; Woo and Takekawa 2012; Snedden and Steyer 2013; Janousek and Folger 2014). Our results confirmed that soil pore-water salinity and elevation were key factors correlated with salt marsh vegetation on the Nisqually Delta (Figure 2, Table 1).

Individual plant species occurred along a salinity gradient ranging from freshwater to marine (Figure 2), but overall species richness did not vary appreciably with salinity (Figure 3). *C. lyngbyei* occurred at low marsh elevations and was negatively influenced by increasing pore-water salinity, suggesting that it may be dominant in areas with a significant freshwater influence. Indeed, we observe this species often along the river banks. In contrast, species richness increased markedly with greater elevation (Figure 2, Figure 3), and only two species had average elevations below 2.7 m NAVD88. *D. spicata, S. perennis, Spergularia* spp. and *T. maritima* were present in areas of higher pore-water salinity but were observed at low marsh elevations, suggesting that those low marsh species are likely to be dominant in early phases of restoration. Rasser et al. (2013) found that species grouped into two plant assemblages

of low and high marsh communities at microtidal (< 2 m) sites on the coastal marshes of Texas. Our results were similar in that we found two main plant assemblages, based on low and high marsh potential, although tides in our region were macrotidal (> 4 m).

Our analysis indicated that approximately half of the 2009 Restored area had suitable elevations for tidal marsh vegetation colonization and plants are currently occurring in the low marsh zone (< 2.7 NAVD88 m, Figure 4b). There may also be a notable lag time (sometimes years) for vegetation colonization following estuarine restoration (Thom et al. 2002) since other factors besides elevation can influence plant colonization and establishment (Zedler et al. 1999, Sanderson et al. 2000, Engels and Jensen 2010). Once established, salt marsh plants can trap and stabilize sediment, resulting in faster sediment accretion rates and increased elevation of the marsh plain (Adam 1990, Pojar and MacKinnon 1994, Simenstad and Cordell 2000).

Understanding salinity tolerances and suitable elevations of local tidal marsh communities can inform restoration design. Although tidal marsh plants are adapted to varying levels of inundation and salinity, it is at a physiological cost. Many plant species are found across a narrow elevation range on the Pacific coast, such as the 53-cm elevation range (this study) and at San Quintin Bay, Mexico (Zedler et al. 1999), and that small differences in elevation (~4 cm) may shift the competitive dominance of species distributions (Scholten and Rozema 1990). Furthermore, vegetation within such narrow elevation zones suggests high vulnerability to projected sea level rise for the Washington coast by 2100 (63 cm mid scenario, 142 cm high scenario; NRC 2012) and supports the need for high resolution elevation studies on local management parcels for climate change models and adaptation scenarios (Takekawa et al. 2013, Thorne et al. 2014). Climate change effects including sea-level rise (SLR), extreme storm events, and increased salinity are projected to increase and greatly reduce the extent of existing salt marsh areas. While sea-level rise is projected to rise linearly through the mid-century (NRC 2012), extreme storm events may increase in severity more rapidly (Cayan et al. 2008).

With increasing sea level rise, changes in hydrologic regime and salinity levels will exert greater physical stresses, particularly on those species that may already be at their upper limits (i.e. in transition zones), so that they are more susceptible to competitive displacement (Mahall and Park 1976a, 1976b, 1976c; Pennings and Callaway 1992; Callaway and Zedler 1998). SLR projections of a few centimeters can cause inundation effects large enough to alter plant communities (McKee and Mendelssohn 1989, Adam 1990, Zedler et al. 1999, Baldwin et al. 2001). Increased salt water intrusion upestuary can shift the composition and structure of freshwater marshes to brackish plant communities (McKee and Mendelssohn 1989, Spalding and Hester 2007, Watson and Byrne 2009). Furthermore, fostering rapid rates of sedimentation by encouraging early development of plant communities may be particularly important for restoration projects conducted along the Pacific coast in the next few decades. Thus, earlier colonization of plant communities in tidal salt marshes may improve the longevity of newly restored marshes in light of climate change, and better understanding of how tidal salt marsh communities respond to elevation and salinity are the first steps in developing restoration strategies that create resiliency to rapid environmental changes.

Acknowledgments

Support for the study was provided by the U. S. Geological Survey Western Ecological Research Center, U. S. Fish and Wildlife Service (D. Roster, G. Nakai, M. Mahaffy), Nisqually Indian Tribe, Ducks Unlimited, and the Nisqually River Foundation. This work was also supported by interns (USGS Students in Support of Native American Relations, Evergreen College). We thank H. Minnella, M. Holt, H. Allgood-Tucker, USGS technicians, and Nisqually National Wildlife Refuge volunteers for their assistance. K. Lovett and C. Janousek provided helpful editorial comments. The use of trade, product or firm names in this publication is for descriptive purposes only and does not imply endorsement by the U.S. Government.

Literature Cited

Adam, P. 1990. Saltmarsh Ecology. Cambridge University Press, New York.

Apostol, D., and M. Sinclair. 2006. Restoring the Pacific Northwest: The Art and Science of Ecological Restoration in Cascadia. Island Press, Washington, DC.

Baldwin, A. H., M. S. Egnotovich, and E. Clarke. 2001. Hydrologic change and vegetation of tidal freshwater marshes: field, greenhouse, and seed-bank experiments. Wetlands 21:519-531.

Bertness, M. D. 1991. Zonation of *Spartina patens* and *Spartina alterniflora* in a New England salt marsh. Ecology 72:138-148.

Bertness, M. D., and S. W. Shumway. 1993. Competition and facilitation in marsh plants. American Naturalist 142:718-724.

Bertness, M. D., L. Gough, and S. W. Shumway. 1992. Salt tolerances and the distribution of fugitive salt marsh plants. Ecology 73:1842-1851.

Boumans, R. M. J., D. M. Burdick, and M. Dionne. 2002. Modeling habitat change in salt marshes after tidal restoration. Restoration Ecology 10:543-555.

Burg, M. E., D. R. Tripp, and E. S. Rosenburg. 1980. Plant Associations and primary productivity of the nisqually salt marsh on Southern Puget Sound, Washington. Northwest Science 54:222-236.

Callaway, J. C., and J. B. Zedler. 1998. Interactions between a salt marsh native perennial (*Salicornia virginica*) and an exotic annual (*Polypogon monspeliensis*) under varied salinity and hydroperiod. Wetlands Ecology and Management 5:179-194.

Cayan, D. R., P. D. Bromirski, K. Hayhoe, M. Tyree, M. D. Dettinger, and R. E. Flick. 2008. Climate change projections of sea level extremes along the California coast. Climatic Change 87:57-73.

Crain, C. M., B. R. Silliman, S. L. Bertness, and M. D. Bertness. 2004. Physical and biotic drivers of plant distribution across estuarine salinity gradients. Ecology 85:2539-2549.

Dean, T., Z. Ferdaña, J. White, and C. Tanner. 2001. Identifying and Prioritizing Sites for Estuarine Habitat Restoration in Puget Sound's Skagit River Delta. Puget Sound Research. People for Puget Sound and U.S. Fish and Wildlife Service.

Ellings, C. 2011. Nisqually National Wildlife Refuge estuary restoration project monitoring framework. Unpublished draft report on file with the Nisqually National Wildlife Refuge, Olympia, WA.

Engels, J. G., and K. Jensen. 2010. Role of biotic interactions and physical factors in determining the distribution of marsh species along an estuarine salinity gradient. Oikos 119:679-685.

Flora of North America Editorial Committee. 1993. Flora of North America. Oxford University Press, New York and Oxford.

Fofonoff, N. P. 1985. Physical Properties of Seawater: A New salinity scale and equation of state for seawater. Journal of Geophysical Research. 90: 3332-3342.

Foxgrover, A. C., D. P. Finlayson, and B. E. Jaffe. 2011. 2010 Bathymetry and digital elevation model of Coyote Creek and Alviso Slough, south San Francisco Bay, California: U.S. Geological Survey Open-File Report 2011-1315. Available online at http://pubs.usgs.gov/of/2011/1315 (accessed June 2014).

Hinkle, R. L., and W. J. Mitsch. 2005. Salt marsh vegetation recovery at salt hay farm wetland restoration sites on Delaware Bay. Ecological Engineering 25:240-251.

Hitchcock, C. L., and A. Cronquist. 1973. Flora of the Pacific Northwest. University of Washington Press, Seattle, WA.

Hutchinson, I. 1988. Salinity Tolerance of Plants of Estuarine Wetlands and Associated Uplands. Simon Fraser University, Burnaby, BC.

Janousek, C. N., and C. L. Folger. 2014. Variation in tidal wetland plant diversity and composition within and among coastal estuaries: assessing the relative importance of environmental gradients. Journal of Vegetation Science 25:534-545.

Kruckeberg, A. R. 1991. The Natural History of Puget Sound Country. University of Washington Press, Seattle, WA.

Kentula, M. E. 2000. Perspectives on setting success criteria for wetland restoration. Ecological Engineering 15:199-209.

Levine, J. M., J. S. Brewer, and M. D. Bertness. 1998. Nutrient competition and plant zonation in a New England salt marsh. Journal of Ecology 86:285-292.

Lortie, C. J., R. W. Brooker, P. Choler, Z. Kikvidze, R. Michalet, F. I. Pugnaire, and R. M. Callaway. 2004. Rethinking plant community theory. Oikos 107:433-38.

Mahall, B. E., and R. B. Park. 1976a. The ecotone between *Spartina foliosa* Trin. and *Salicornia virginica* L. in salt marshes of northern San Francisco Bay. I. Biomass and production. Journal of Ecology 64:421-433.

Mahall, B. E., and R. B. Park. 1976b. The ecotone between *Spartina foliosa* Trin. and *Salicornia virginica* L. in salt marshes of northern San Francisco Bay. II. Soil water and salinity. Journal of Ecology 64:793-809.

Mahall, B. E., and R. B. Park. 1976c. The ecotone between *Spartina foliosa* Trin. and *Salicornia virginica* L. in salt marshes of northern San Francisco Bay. III. Soil aeration and tidal immersion. Journal of Ecology 64:811-819.

McKee, K. L, and I. A. Mendelssohn. 1989. Response of a freshwater marsh plant community to increased salinity and increased water level. Aquatic Botany 34:301-316.

Mitsch, W. J., and R. F. Wilson. 1996. Improving the success of wetland creation and restoration with

know-how, time and self-design. Ecological Applications 6:77-83.

Mofjeld, H. O., A. J. Venturato, V. V. Titov, F. I. González, and J. C. Newman. 2002. Tidal Datum Distributions in Puget Sound, Washington, Based on a Tidal Model. NOAA Technical memorandum OAR PMEL-122. Pacific Marine Environmental Laboratory, Seattle.

National Ocean and Atmospheric Administration (NOAA). Dupont Warf station ID: 9446828 (http://tidesandcurrents.noaa.gov/data_menu.shtml?type=Superseded+Bench+Mark&mstn=9446828). Accessed March 2011.

NRC (National Research Council). 2012. Sea-Level Rise for the Coasts of California, Oregon, and Washington: Past, Present, and Future. National Academy Press, Washington, DC.

Pennings, S. C., M. B. Grant, and M. D. Bertness. 2005. Plant zonation in low-altitude salt marshes: disentangling the roles of flooding, salinity and competition. Journal of Ecology 93:159-167.

Pennings, S. C., and R. M. Callaway. 1992. Salt marsh plant zonation: the relative importance of competition and physical factors. Ecology 73:681-690.

Pojar, J., and A. MacKinnon. 1994. Plants of the Pacific Northwest Coast: Washington, Oregon, British Columbia and Alaska. Lone Pine Publishing, Vancouver.

Rasser, M. K., N. L. Fowler, and K. H. Dunton. 2013. Elevation and plant community distribution in a microtidal salt marsh of the western Gulf of Mexico. Wetlands 33:575-583.

Redondo-Gómez, S., J. M. Castillo, C. J. Luque, T. Luque, M. E. Figueroa, and A. J. Davy. 2007. Fundamental niche differentiation in subspecies of *Sarcocornia perennis* on a salt marsh elevational gradient. Marine Ecology Progress Series 347:15-20.

Roman, C. T., M. J. James-Pirri, and J. F. Heltshe. 2001. Monitoring salt marsh vegetation. A protocol for the long-term coastal ecosystem monitoring program at Cape Cod National Seashore. Wellfleet, MA.

Sanderson, E. W., S. L. Ustin, and T. C. Foin. 2000. The influence of tidal channels on the distribution of salt marsh plant species in Petaluma Marsh, CA, USA. Plant Ecology 146:29-41.

Scavia, D., J. C. Field, D. F. Boesch, R. W. Buddemeier, V. Burkett, D. R. Cayan, M. Fogarty, M. A. Harwell, R. W. Howarth, C. Mason, D. J. Reed, T. C. Royer, A. H. Sallenger, and J. G. Titus. 2002. Climate change impacts on U.S. coastal and marine ecosystems. Estuaries 25:149-164.

Scholten, M., and J. Rozema. 1990. The competitive ability of *Spartina angilica* on Dutch saltmarshes. *In* A. J. Gray and P. E. M. Benham (editors), *Spartina angilica*: a research review. Institute of Terrestrial Ecology Research Publication 2, London, UK. Pp. 39-47.

Silliman, B. R., and J. C. Zieman. 2001. Top-down control of *Spartina alterniflora* production by periwinkle grazing in a Virginia salt marsh. Ecology 82:2830-2845.

Simenstad, C. A., and J. R. Cordell. 2000. Ecological assessment criteria for restoring anadromous salmonid habitat in Pacific Northwest estuaries. Ecological Engineering 15:283-302.

Smith, C. R., M. C. Austen, G. Boucher, C. Heip, P. A. Hutchings, G. M. King, I. Koike, P. John, D. Lambshead, and P. Snelgrove. 2000. Global change and biodiversity linkages across the sediment-water interface. BioScience 50:1108-1120.

Snedden, G. A., and G. D. Steyer. 2013. Predictive occurrence models for coastal wetland plant communities: Delineating hydrologic response surfaces with multinomial logistic regression. Estuarine, Coastal and Shelf Science 118:11-23.

Spalding, E. A., and M. W. Hester. 2007. Interactive effects of hydrology and salinity in oligohaline plant species productivity: implications of relative sea-level rise. Estuaries and Coasts 30:214-225.

Takekawa, J. Y., K. Thorne, K. Buffington, K. Spragens, K. Swanson, J. Drexler, D. Schoellhamer, C. Overton, and M. Casazza. 2013. Final report for sea-level rise response modeling for San Francisco Bay estuary tidal marshes. U.S. Geological Survey Open-File Report 2013-1081.

Tanner, C. 2000. Estimating the relationship between elevation and estuarine habitats: lessons from other puget sound estuarine restoration sites. Unpublished report on file with the Nisqually National Wildlife Refuge, Olympia, WA.

Thom, R., R. Zeigler, and A. B. Borde. 2002. Floristic development patterns in a restored Elk River estuarine marsh, Grays Harbor, Washington. Restoration Ecology 10:487-496.

Thorne, K. M. , D. Elliott-Fisk, G. Wylie, W. Perry, and J. Y. Takekawa. 2014. Importance of biogeomorphic and spatial properties in assessing a tidal salt marsh vulnerability to sea-level rise. Estuaries and Coasts 37:941-951.

USFWS (U.S. Fish and Wildlife Service). 2005. Nisqually National Wildlife Refuge: Comprehensive Conservation Plan and Environmental Impact Statement.

Valiela, I., J. M. Teal, S. D. Allen, R. Vanetten, D. Goehringer, and S. Volkmann. 1985. Decomposition in salt-marsh ecosystems—the phases and major factors affecting disappearance of above-ground organic-matter. Journal of Experimental Marine Biology and Ecology 89:29-54.

Watershed Sciences. 2011. LiDAR coverage for the Nisqually River Delta: Data and metadata report to USGS Pacific Coastal and Marine Geology and US Fish and Wildlife Service.

Watson, E. B., and R. Byrne. 2009. Abundance and diversity of tidal marsh plants along the salinity gradient of the San Francisco Estuary: implications for global change ecology. Plant Ecology 205:113-128.

Weilhoefer, C. L., W. G. Nelson, P. Clinton, and D. M. Beugli. 2012. Environmental determinants of emergent macrophyte vegetation in Pacific Northwest estuarine tidal wetlands. Estuaries and Coasts 36:377-389.

Weinnman, F., M. Boulé, K. Brunner, J. Malek, and V. Yoshino. 1984. Wetland Plants of the Pacific Northwest. U.S. Army Corps of Engineers, Seattle, WA.

Williams, P., and P. Faber. 2001. Salt marsh restoration experience in San Francisco Bay. Journal of Coastal Research 27:203-211.

Wolters, M., A. Garbutt, R. M. Bekker, J. P. Bakker, and P. Carey. 2008. Restoration of salt-marsh vegetation in relation to site suitability, species pool and dispersal traits. Journal of Applied Ecology. 45:904-912.

Woo, I., and J. Y. Takekawa. 2012. Will inundation and salinity levels associated with projected sea level rise reduce the survival, growth, and reproductive capacity of *Sarcocornia pacifica* (pickleweed)? Aquatic Botany 102:8-14.

Woo, I, K. L. Turner, and J. Y. Takekawa. 2011. Monitoring and Evaluation of the Nisqually Delta Restoration Project. Unpublished project progress report to Nisqually National Wildlife Refuge, Olympia, WA.

Zedler, J. B. 2001. Handbook for Restoring Tidal Wetlands. CRC Press LLC, Boca Raton, FL.

Zedler, J. B., J. C. Callaway, J. S. Desmond, G. Vivian-Smith, G. D. Williams, G. Sullivan, A. E. Brewster, and B. K. Bradshaw. 1999. California salt-marsh vegetation: An improved model of Spatial Pattern. Ecosystems 2:19-35.

Received 24 March 2014
Accepted for publication 02 December 2014