

4-21-2017

Pore Water Salinity Drives Brackish Vegetation Change in Salt Marsh Tidal Restoration

Shri Andrea L. Verrill MS
University of Southern Maine

Follow this and additional works at: <https://digitalcommons.usm.maine.edu/etd>

 Part of the [Biology Commons](#)

Recommended Citation

Verrill, Shri Andrea L. MS, "Pore Water Salinity Drives Brackish Vegetation Change in Salt Marsh Tidal Restoration" (2017). *All Theses & Dissertations*. 311.
<https://digitalcommons.usm.maine.edu/etd/311>

This Open Access Thesis is brought to you for free and open access by the Student Scholarship at USM Digital Commons. It has been accepted for inclusion in All Theses & Dissertations by an authorized administrator of USM Digital Commons. For more information, please contact jessica.c.hovey@maine.edu.

Pore Water Salinity Drives Brackish Vegetation Change in Salt Marsh Tidal Restoration

Shri Andrea L. Verrill

A Thesis

Submitted in Partial Fulfillment of the
Requirements for the Degree of Masters of Science in Biology

At the
University of Southern Maine

Advisor:

Dr. Curtis Bohlen

University of Southern Maine Department of Biological Sciences

Committee Members:

Dr. Karen Wilson¹, Dr. Jeff Walker²

Dr. Doug Currie²

¹University of Southern Maine, Department of Environmental Science

²University of Southern Maine, Department of Biological Science

**The University of Southern Maine
Department of Biological Science**

Date: 4-21-17

We hereby recommend that the thesis of Shri Andrea L. Verrill, entitled:

***Pore Water Salinity Drives Brackish Vegetation Response
to Salt Marsh Tidal Restoration***

Be accepted in partial fulfillment of the requirements for the degree of

Masters of Science in Biology

Signatures:

Author: Shri Andrea L. Verrill Date: 4-21-17

Advisory Committee:

Robert L. Bohl Date: 4-21-17
(Graduate Advisor)

[Signature] Date: 4-21-17

[Signature] Date: 4/24/17

[Signature] Date: 4/24/17
Chair of the Department of Biological Sciences

[Signature] Date: 4/25/17
Dean of the College of Science, Technology and Health

Table of Contents

Acknowledgements.....	iii
Abstract.....	iv
List of Tables	vi
List of Figures.....	vii
Introduction.....	8
Basic <i>Typha</i> physiology and ecology.....	11
Study Goals	13
Research Objectives.....	13
Hypotheses.....	13
Field Site Description.....	14
Methods and Statistical Analysis.....	15
Results.....	23
Discussion.....	27
Conclusions.....	31
References.....	32
Tables.....	37
Figures.....	40

Acknowledgements

I would like to thank my advisor Dr. Curtis Bohlen for his encouragement, guidance, expertise, humor, and kindness; Casco Bay Estuary Partnership staff Matt Craig and Beverly Bailey-Smith for sharing much of my Graduate school journey. Much gratitude goes to my steadfast committee member Dr. Karen Wilson for invaluable insight to my experimental design, data collection methods, and thesis edits. I was fortunate to benefit from knowing Dr. Tom Knight, Dr. Lou Gainey, and Dr. Mike Mazurkiewicz who each spent some time on my committee before passing from this life. I am grateful to Dr. Doug Currie and Dr. Jeff Walker for stepping onto my committee to allow me to finish.

Many hands make light work and I was blessed with a huge number of people who offered many forms of help: Dr. Hilary Neckles, Dr. Dave Burdick, Dr. Susan Adamovitch, Dr. Andy Reeves, Dr. David Champlain, Dr. Matt Lieberman, Dave Rocque, Dave Wilkinson, Lena Champlain, Amanda Pratt, Bethanny Araujo, Matt Burke, Kari Beaulieu, Sean Rafe, Leticia Smith, Molly Payne-Wynn, Brandon Braden, Abby Pearson; colleagues on the Society for Ecological Restoration, New England Chapter and the Maine Association of Wetland Scientists.

Research cost money, and I'm grateful to the USM Department of Biological Studies, Maine Association of Wetland Scientists, and Sigma Xi for helping to fund my project.

I would like to thank my family for their support and my loving partner Alex Jackimovicz for providing endless inspiration. I dedicate this thesis in loving memory of my dear friend Steve Solms. Here's the doughnut.

Abstract

Salt marsh vegetation plays an important role in building and maintaining elevation on the marsh surface. For marshes to persist as sea-level-rise (SLR) occurs, the marsh accretion process must increase elevation at a rate greater than or equal to the rate of SLR. If salt marshes do not maintain elevation above sea level, salt marshes will drown, and associated benefits to humans, fish, and wildlife, and their contribution to the health of estuarine and marine ecosystems will be lost. Salt tolerant plant species are adapted to frequent and prolonged periods of inundation with seawater and typically maintain elevation where they persist along the seaward edge of salt marshes. Brackish and freshwater species often occur along the marsh's landward margins. It is not well understood how these brackish and freshwater species respond to SLR. Monitoring vegetation before and after tidal restoration can provide insight into how vegetation responds to hydrologic change and thus may help to predict response of tidal marsh vegetation to SLR. To better understand the mechanisms responsible for changes in vegetation, this study looked at the effects of increased inundation and pore water salinity on the brackish species *Typha angustifolia* and the freshwater species *Typha latifolia* one year following tidal restoration.

Long Marsh is a Northern New England salt marsh, which underwent culvert enlargement in 2014. It was monitored one year before (2013) and one year after (2014) tidal restoration to document environmental changes associated with increased tidal flux. Twelve vegetation transects, stretching perpendicular from the tidal creek to the upland, were established on the marsh, each with 10 to 14 evenly distributed sampling plots. One transect downstream of Long Reach Lane, which never experienced tidal restriction, was

used as a reference. The remaining 11 transects were located upstream of Long Reach Lane.

I conducted a descriptive study that looked at the roles salt and flood tolerance play in structuring vegetation response to changes in tidal flux. Results strongly suggest that a change in pore water salinity was the primary driver for vegetation change at this site and that the significant mortality of *T. angustifolia* occurred because of increased pore water salinity, not inundation. This implies that salt exposure must be considered to effectively evaluate how vegetation may respond to SLR in the narrow coastal wetlands of Casco Bay.

List of Tables

Table 1	Plants identified during 2013 and 2014 MDOT vegetation monitoring
Table 2	Plant Species in Vegetation Zones Determined by Salinity Index
Table 3	Plant Species in Vegetation Zones Determined by Inundation Index

List of Figures

Figure 1	Sea Level Trend at Portland Maine
Figure 2	Long Marsh Soil/Peat Profile
Figure 3	Transect and Sub-study Locations on Long Marsh.
Figure 4	<i>Typha</i> Border Shift
Figure 5	Total Vegetation Cover Before and After Tidal Restoration
Figure 6	Total <i>Spartina</i> Cover Before and After Tidal Restoration
Figure 7	Total <i>Typha</i> Change Before and After Tidal Restoration
Figure 8	Mean Transect Changes in Salinity Indicator Score
Figure 9	NMDS Ordination with Dominant Species Patterns
Figure 10	Relationship between Salinity Index and NMDS Ordination Axis 1
Figure 11	Randomization: Assessment of the Salinity Index's Vulnerability to Misclassification of Individual Species
Figure 12	Vegetation Zones on Elevation Profile: Transect 4
Figure 13	Vegetation Zones on Elevation Profile: Transect 6
Figure 14	Vegetation Zones on Elevation Profile: Transect 9
Figure 15	2014 Mean Pore Water Salinity in <i>Typha</i> Biomass Plots
Figure 16	2014 Brackish Zone Pore Water Salinity Levels
Figure 17	2014 <i>Typha</i> Robustness
Figure 18a	2013 Green <i>Typha</i>
Figure 18b	2014 Brown/Dead <i>Typha</i>
Figure 19	Aboveground (Living and Dead) <i>Typha</i> Biomass

Introduction

Tidal marshes provide significant ecosystem services, which help maintain estuarine ecosystem health that benefits humans, fish and wildlife. Primary producers in New England salt marshes help maintain marine ecosystems through a trophic relay of nutrients (Deegan et al. 2002). These salt marshes also provide spawning habitat (Rountree et al. 2007) for economically important fish and shellfish species, habitat for shorebirds to wade, nest and feed; and hunting grounds for game species such as duck and deer (Roman et al. 2002). Marsh macrophytes help filter pollution and nutrient runoff from adjacent uplands, acting as a buffer zone to help maintain estuarine water quality. Roots and senesced plant material on the marsh surface also accumulate biomass by trapping tidally deposited sediment, increasing elevation. This strengthens the shoreline and helps control erosion (Nyman et al. 2006; Gedan et al. 2009; 2008 Gulf of Maine Council on the Marine Environment), which is increasingly an issue as symptoms of climate change such as sea-level-rise (SLR) and storm surges threaten shoreline stability.

SLR and climate change are a problem for tidal marshes. Rising sea levels and frequency of extreme weather are stress factors that contribute to salt marsh disturbance. The sea level off Maine's coast has been rising at a rate of 1.8 ± 0.1 mm/year since 1912 (Slovinsky 2015). In 2009 – 2010, an extreme SLR event occurred along the Northeast coast of North America. Within this two year time period the coastal sea level north of New York City increased by 128 mm, an event that may be linked to human induced climate change (Goddard et al. 2015; Fig. 1). It is not known if salt marsh accretion rates can keep pace with SLR associated with climate change (Cahoon and Guntenspergen 2007; Scavia et al. 2002; Morris et al. 2002). Accretion rates must match or exceed sea

level rise SLR in order for the salt marsh ecosystem to survive. Extreme weather events such as prolonged drought and intense rainfall also affect the inundation and salinity levels to which salt marsh macrophytes are exposed. If accretion rates are slower than SLR and if the marsh macrophytes cannot adapt to increasingly extreme disturbances caused by extreme weather then the salt marshes drown and their ecosystem services are lost.

Hydrologic conditions structure salt marsh ecological zones (Thibodeau et al. 1998; Hemond et al. 2011; Moffett et al. 2012; Silvestri et al. 2005), which are comprised of multiple interacting gradients that create microhabitat heterogeneity (Bockelmann et al. 2002; Smith et al. 2009). Plants commonly found in southern New England salt marshes all grow better in fresh water but stronger competitors push these subordinate species out of the fresh water zone and into the more stressful, saline environment where tolerance to salt determines persistence (Grace and Wetzel 1981; Wilson and Keddy 1986; Crain et al. 2004).

Soil salinity is a major stressor to marsh vegetation (Wilson and Keddy 1986; Allakhverdiev et al. 2000) and greatly influences vegetation response to salt marsh restoration (Roma et al. 2002). For this reason, salinity is among the most important parameters in determining the structure and continuance of vegetation after restoration (Odum 1988; Mitsch and Gosselink 2007).

Typically, salt marsh vegetation is organized in distinct zonation patterns (Miller and Egler 1950) generated by plant physiological tolerance, physical disturbance, and interspecific competition (Bertness 1991) with species occupying well-defined locations along an inundation gradient. This spatial pattern is controlled by the interplay of stress-

tolerant species (which occur in flooded areas near the tidal creek) with more competitive, but less-salt tolerant species that occur in less stressful microhabitats (Koninsky and Burdick 2004).

Plant exposure to tidal inundation period and frequency is largely regulated by elevation; proximity to tidal channels, micro topography, and other factors have less influence. These complex interacting factors make it difficult to estimate the impact that SLR will have on marsh ecosystems.

The inundation gradient is not the only factor contributing to variation in pore water salinity. In brackish marshes where both inundation and salinity vary across the marsh surface, it is not readily understood how the two gradients interact. The spatial gradient of pore water salinity is partially shaped by lateral distance from the tidal creek to the uplands, and partially by longitudinal distance from the downstream estuary to the freshwater inputs upstream. Groundwater flow and the hydrology of adjacent uplands control pore water geochemistry and therefore shape marsh macrophyte zonation (Wilson et al. 2015).

Due in part to the effect of interacting inundation and salinity gradients, plants in intertidal wetlands are expected to modify their distribution in response to altered hydrology (Roman et al. 1984; Smith et al. 2009; Baldwin and Sharpe 2009). Although static plant zonation has been well studied in southern New England salt marshes, the mechanism of vegetation readjustment to new hydrologic conditions is not well understood (Crain et al. 2004).

Tidal restoration projects provide an opportunity to assess how systems respond to hydrologic alteration that may mimic some impacts of SLR. Long narrow coastal

marshes, which are widespread in Casco Bay, Maine, remain relatively unstudied. These wetlands, termed “Fluvial Minor marshes” (Kelley 1987; Kelley et al. 1988) are deep, narrow, elongate estuaries parallel to adjacent bedrock peninsulas. Local geohydrology plays an important role in vegetation patterns (Boumans 2002). Runoff from adjacent uplands, including very small streams, contributes significant freshwater to the terrestrial borders of the salt marsh and greatly influences plant zonation (Jacobson and Jacobson 1989).

Tidal restrictions reduce salt-water delivery to the high marsh, thus reducing inundation frequency and surface and pore water salinity upstream (Anisfield 2012). The effect of tidal restrictions on salt marshes depends on the restriction’s type, size, longevity, and severity (Anisfield 2012). Dams, plugs, and road and railway crossings with inadequate culverts reduce tidal flooding, salinity, drainage, and intertidal habitat. Many salt marshes have been filled, drained, or permanently diked to make room for development (Neckles et al. 2002).

Hydrologic alterations can decrease the area dominated by salt tolerant species (halophytes), opening the system to expansion of brackish species that do not survive in full salinity. It has been hypothesized that disturbance makes the perimeter of the tidal wetland more suitable to invasive species, such as phragmites (*Phragmites australis*), purple loosestrife (*Lythrum salicaria*), and cattails (*Typhacea*).

Basic *Typha* physiology and ecology

Typhacea are a family of herbaceous perennial, rhizomatous, monoecious, emergent macrophytes with a spike of wind-pollinated flowers (male above and female below) commonly found in wet or saturated soils throughout a broad range of habitat,

spanning from early to late successional in the U.S. and Canada (Grace and Harrison 1986; Simpson 2006). *Typha* reproduce through both vegetative clonal growth and seed dispersal (Grace and Harrison 1986) and have well developed aerenchyma that provides a flow of oxygen to rhizomes even when submerged (Jordan and Whigham 1988). This contributes to their ability to persist in disturbed and saline conditions (McNaughton 1966; McNaughton et al. 1974; Jones et al. 1979; Olson and Freeland (2009).

Cattails found in Maine typically occupy ecological niches along salinity and inundation gradients, with Narrow Leaved Cattail (*Typha angustifolia*) located in more saline and more dry areas, Broad Leaved Cattail (*Typha latifolia*) in less saline and more wet areas, and their sterile hybrid *Typha x glauca* somewhere in between the two (McMillan 1959; Grace and Harrison 1986; Mcmillan 2013). These two *Typha* species and their hybrid were documented at Long Marsh in expected zonation patterns. *T. angustifolia* occurred seaward and closer to the tidal channel than *T. latifolia*. This pattern is thought to be shaped by the respective tolerance to salt and moisture exhibited by each of the species. *T. x. glauca* is intermediate between its two parent species in both respects (Shih and Finkelstein 2008; Grace 1982).

T. angustifolia is commonly found in both brackish and fresh water tidal marshes (Farnsworth and Meyerson 2003). It is considered a disturbance species frequently found in brackish, estuarine marshes, at the high marsh and upland edges and in partially drained wetlands (Burdick et al. 1999, Warren et al. 2001; Konisky and Burdick 2004) where it is often the dominant species (Smith 1967; Grace and Harrison 1986). Although it is native to North America, rapid range expansion coinciding with European settlement and its ability to outcompete and displace other native species has caused it to be deemed

an invasive species in brackish water environments (Grace and Harrison 1986; Selbo and Snow 2000; Alpert et al. 2004; Shih and Finkelstein 2008, Konisky and Burdick 2004). As such, it may be considered an indicator of anthropogenic change in wetland hydrology (Wilcox 1995; Farnsworth and Meyerson 2003). While *T. angustifolia* may be found in many of the same places as *T. latifolia*, it can tolerate more saline and more alkaline environments than *T. latifolia* (Grace 1987). *T. latifolia* is a native of North America (Rafinesque 1836; Grace 1987), may be found in all types of wetland communities (Grace and Harrison 1986) and can tolerate some salinity and acidity (Kuehn et al. 1999).

I conducted a descriptive study that evaluated vegetation response to the increase in inundation and salinity after tidal restoration with *T. angustifolia* selected as the primary vegetative indicator for ecosystem change. This analysis looked at the response of vegetation to tidal restoration to help clarify the mechanisms of vegetation response to hydrologic change in the context of interacting inundation and salinity gradients. The goal was to describe vegetation changes in the year following tidal restoration in order to better understand why vegetation zones may shift in response to tidal restoration.

The examinations undertaken in this study were designed to test specific hypotheses about the influence of salinity and inundation on brackish vegetation. To provide contextual and descriptive data, halophytic and glycophytic responses were compared to those of brackish vegetation. *Two primary hypotheses* were made with regard to expected vegetation changes.

- Increased inundation causes mortality of brackish species;
- Increased pore water salinity levels cause mortality of brackish species.

Secondary hypotheses:

- Halophytes will increase in percent cover.
- Halophytes will expand their footprint toward the upland border.
- *T. angustifolia* will decrease in percent cover.
- The brackish zone dominated by *T. angustifolia* will shrink in size.
- The border of robust *T. angustifolia* will retract toward the upland border.

Field Site Description

Field Site. All fieldwork and observational studies were conducted in Long Marsh (43°50'26. 40"N, 69°55'12. 65"W) off Long Reach Lane in the town of Harpswell, just south of Brunswick in Cumberland County, Maine. The Maine Department of Transportation (MDOT) removed an undersized culvert beneath Long Reach in February of 2014 and replaced it with a much larger box culvert as compensatory mitigation for impact to wetlands during bridge building activity on Route 1 at Martin's Point.

The tidal restriction at Long Reach Lane existed for 70 - 100 years before the tidal restoration project began, caused by construction of a road and causeway across the lower reaches of the marsh sometime in the early 1900s (USGS Topographical maps 1910-1945). The culvert placed in the causeway to allow the ebb and flow of the tide was only 38 inches in diameter, which created a significant hydrologic restriction. Over time, the restriction created by the narrow culvert triggered a suite of changes in the upstream marsh, including reduced tidal inundation, increased sedimentation, reduced salinity and altered vegetation.

Because of the importance of longitudinal and lateral salinity gradients on-site, Long Marsh exhibits a broad brackish swath between the typical high marsh zone and fresh water margin at the adjacent uplands. As one moves perpendicular from the tidal

creek toward the upland border, brackish and then freshwater plant communities replace halophytic vegetation. This vegetation is atypical because New England salt marshes are usually covered > 95% by emergent perennial halophytic vegetation (Bertness and Ellison 1987). Near the tidal channel, salt tolerant vegetation develops typical salt marsh zonation indicative of a range in tolerance to salt and inundation. Species with intermediate tolerance for salt occur next, while freshwater vegetation inhabits the wetland ecotone downslope of terrestrial borders (Emery et al. 2001). The expansive freshwater plant communities found not only at the upstream end of the wetland but also on the lateral margins of the marsh were likely maintained pre-restoration by freshwater input from adjacent uplands.

The hydrology of Long Marsh is complex because of the interplay between seawater from tidal flooding and fresh water from adjacent uplands, which is mediated by a complex belowground sedimentary environment. Glacial marine deposits and till overlay the bedrock floor of this long narrow valley. Sediment input from upland runoff, and tidally deposited minerals and detrital layers comprise much of the salt marsh substrate in the root zone. The three-dimensional underground structure of glacially deposited marine clay (Penobscot Formation), secondary silt-clay deposits and peats shape the dynamics of water flow, and thus shape ecological processes (Fig 2). Belowground hydrology influences pore water salinity in the root zone, soil oxygen levels, oxidation-reduction reactions, and decomposition processes.

Methods

MDOT vegetation transects. In the 2013 field season, twelve vegetation transects were established as the foundation for an observational study and long-term restoration

monitoring program (Fig. 3). Transects run roughly perpendicular to the long axis of the wetland valley from the tidal creek, and extend to the upland border. The downstream reference transect and upstream transects 4, 6, and 9 were selected for the basis of this study in part because they contain *Typha angustifolia*, and in part because of access and relatively homogeneous substrate.

Transects were designed to be permanent so that nearly identical locations could be sampled from year to year. Position of transects on the marsh surface were established by placing stakes adjacent to the channel, spots of paint on trees at the upland margin, and linking the two with a measuring tape extending in a recorded compass direction toward the marked tree. The position of each end of each transect was recorded using a hand-held GPS receiver and documented to relocate the transects in the future.

Plots (1m x 1m) were evenly spaced along each transect to fit between 10 and 14 plots between the channel and the upland, with a minimum spacing between plots of 2 meters on center. Plots were not permanently marked, but were approximately re-located in 2014 based on the distance from the tidal channel marked on the measuring tape.

In practice, stakes along the channel were often lost over the winter, presumably because they were torn out of the sediment by ice. Nevertheless, all transects were successfully relocated in 2014 using the GPS coordinates and compass direction. Transect 1, used as the reference, was changed slightly in 2014 (based on a small change in compass direction) to pick up additional vegetation along the freshwater margin for use in future years. The transect change resulted in moving some plots laterally (within vegetation zones) by less than 2 meters.

Plants occurring in each 1m x 1m plot were identified to the species level in July

of 2013 and 2014. Taxonomy follows usage in Haines and Vining (1990). Abundance and frequency of each species was estimated visually using a modified Braun-Blanquet relevé method. The same observers were involved with estimating percent cover in both 2013 and 2014. Bryophytes were noted, but not identified to species, and have been omitted from this analysis. Change in vegetation was studied by looking at differences in percent cover between 2013 (before restoration) and 2014 (the year immediately post restoration).

Salinity Index. Relative salinity tolerance of each common plant species was estimated for this study based on narrative descriptions of species-by-species habitat preferences in Tiner (2009). A Salinity Index score of 3 was assigned to salt tolerant species, brackish plants were assigned a score of 2 and freshwater plants, a score of 1. For example, the description of *T. angustifolia* habitat was “Brackish and tidal fresh marshes (regularly and irregularly flooded zones) (Tiner 2009), therefore I gave it a score of 2, and whereas the description of *T. latifolia* habitat was “Tidal fresh marshes” equaling a score of 1.

Inundation Index. Flood tolerance was estimated by using the standard U.S. Army Corps of Engineers (ACE) “Wetland Indicator Status”, which is a measure of the relative frequency each plant is found in wetlands (U.S. Army Corp of Engineers, 2013). This was used to roughly estimate the species response to increased inundation. Obligate wetland (OBL) species were given an index of 4, facultative wetland (FACW) species, an index of 3, facultative (FAC) species, an index of 2, facultative upland (FACU) species, an index of 1. One species, *Juncus arcticus*, was not listed in the ACE list of plant species for the Northeast, but was only listed in the list for Alaska. We used the indicator status

for the species from the Alaska list (OBL).

For each year, every plot was then characterized in relationship to the inundation gradient by calculating a weighted average *flood tolerance score* and in relation to the salinity gradient by deriving a weighted average *salinity score*. These scores were averages of the indexes for each plant species found in the plot, weighted by their percent cover. For purposes of this calculation, species that were present in plots, but with an estimated percent cover of less than 1% were treated as though they had a cover of 1%.

Statistical analysis of vegetation data. Vegetation data was analyzed in R (R Core Team 2012) using ordination and cluster analysis functions from the “vegan” data analysis package (Oksanen et al. 2013). Graphics were produced in R using tools included in the MASS package and others (Venables and Ripley 2002).

Several strategies were employed to understand the nature of vegetation response to hydrologic change. First, dimensionality of vegetation data was reduced for visualization using a non-metric multidimensional scaling ordination based on a Bray-Curtis distance metric (using the *vegdist* and *metaMDS* functions from the *vegan* package). The distance metric was calculated on unnormalized percent cover data, because many plots showed significant plant mortality, but only modest change in abundance of the few plant species that survived. Uncommon plant species were pooled to a single pseudo-species.

Second, an objective vegetation classification was developed based on the same distance metric using hierarchical cluster analysis relying on Ward’s minimum variance criterion to define cluster membership (using the *hclust* function in *vegan*).

Third, vegetation in each plot was characterized in terms of *flood tolerance* and

salinity tolerance by calculating weighted averages (based on percent cover) of the flood tolerance and salinity tolerance of all plant species present. To account for the possibility of mis-identifying species, which may subsequently influence the weighted averages, a bootstrap randomization of the salinity index data was done.

The plot by plot salinity scores and the NMDS scores are both derived from the same vegetation data. NMDS scores are derived from NMDS analysis and salinity scores are based on the relative salinity score given to the individual species in each plot. The resulting marginal distribution of salinity scores is far from normal. Thus it may be inappropriate to rely on conventional tests for statistical significance of the correlation coefficient to assess the significance. A bootstrap test confirms the low probability that the correlation would arise by chance. Of 1,000 bootstrap samples (in which salinity scores were drawn with replacement from the observed marginal distribution), none showed correlation coefficient with the NMDS scores higher than 0.018.

The question also arises as to whether results are robust in terms of the salinity scores assigned to individual species. A randomization method was used to assess how rapidly the correlation coefficient drops as the quality of the species-by-species salinity index declines. The algorithm involves gradually degrading the quality of information contained in the species-by-species salinity score, and observing the effect lower quality information has on the conclusions. While this does not allow a quantitative estimate of the impact of assignment errors, it does allow a qualitative understanding of the effect errors might have. Analysis was carried out using custom built functions in R. Steps of the analysis are as follows:

- (1) Draw a random subsample (of a particular size) of the plant species observed;

- (2) Assign those plant species (and only those plant species) random Salinity Index values, based on the relative frequency of Salinity Index values in the entire plant; species list. This simulates a “error” in assigning the salinity index to those particular species;
- (3) Recalculate plot-level index scores, based on these partially randomized index scores;
- (4) Repeat (1) through (3) 1,000 times;
- (5) Repeat (1) through (4) with several different sized samples of plant species;
- (6) Graph the results.

Typha border. The border of the high marsh brackish zone dominated by *T. angustifolia* was walked twice with a GeoXT handheld Trimble unit with sub meter accuracy. The 2013 border was estimated by walking the border of the cattail stands early in 2014 (April), before new plant growth. The border was readily discernable because of the persistence of standing dead cattails from the previous growing season. The 2014 border was documented by walking the border again later in the 2014-growing season (September), based on presence of living plants. The geospatial data was transferred from the unit with Trimble data transfer software and uploaded into ArcMap as two separate line shape files (Fig. 4).

Typha Green Index. An index was established to measure the robustness of *Typha* along the spatial gradient from the tidal creek and the upland border. Sampling quadrats were spaced a minimum of two meters apart along three replicate transects. Measurements began in the high marsh-brackish transition zone where dominant percent

cover changed from high marsh species to standing *Typha* from previous growing seasons, and continued in a compass direction toward the marsh margins at the upland border. Transects were located near MDOT vegetation transects where *Typha* was documented in 2013, i.e., transects 4, 6, 9 and at the downstream reference site.

The Green Index estimates the relative health of the cattails by combining data on the size of the tallest three living cattails in the quadrat with the proportion of each leaf that was still green. Leaf height and width were measured on the three tallest living cattails in each plot. A five-point robustness scale (RS) based on percent green was assigned to each plant (0% to 20% = 1; 21% to 40% = 2; 41% to 60% = 3; 61% to 80% = 4; 81% to 100% = 5). Then this RS score was multiplied by the height (h) and width (w) to provide a 'gi' score for each plant. The mean of three individual plant scores resulted in a 'gI' score for each plot. Finally, a mean GI plot score was calculated from similarly placed plots in each of three replicate transects.

$$\text{Individual } Typha \text{ gi} = w \times h \times (20 \times (5 + RS) + 10)$$

$$\text{Mean plot gI} = \frac{(gi1+gi2+gi3)}{3}$$

$$\text{Mean of three replicates GI} = \frac{(gI1+gI2+gI3)}{3}$$

Vegetation and elevation. Elevation of the marsh surface referencing the NAVD_88 tidal datum was surveyed and recorded along transects 4, 6, and 9 using a Total Station in 2013. An average of three data points were collected at each horizontal distance from tidal creek, one in the center of the transect and one each an arm's length apart on either side. Dominant vegetation was also classified and recorded at each sample point by noting the top two species with the highest percent cover. The combined distance, elevation, and vegetation data was mapped in ArcGIS as a shape file.

Pore water salinity. Pore water salinity wells were installed in May of 2014 in paired transects near the MDOT vegetation transects where Narrow Leaved Cattail was present in 2013, i.e., transects 4, 6, 9 and at the reference site downstream. Three paired wells were placed within the 2013 brackish zone dominated by *T. angustifolia*. One pair was installed closer to the tidal channel, in the adjacent high marsh zone, and one pair closer to the uplands, where *T. latifolia* was dominant in the freshwater zone in 2013.

Pore water salinity measurements were collected with a handheld refractometer at approximately two hours before or after high tide, over five sampling dates during the growing season. Average pore water salinity along this transect was calculated to establish the mean pore water salinity for the high marsh-brackish transition zone.

Pore water salinity data was also collected in the locations where *Typha* aboveground biomass was harvested. Three pore water wells were installed at the front, middle, and back of the plots. Salinity was recorded using the same methods and on the same dates the salinity data was collected along paired transects where vegetation was characterized.

Typha aboveground biomass. In both 2013 and 2014, all standing *Typha*, living and dead was clipped to the marsh surface from 1 m² plots. Plots were located parallel to the tidal creek within the 2013 high marsh brackish transitional zone that was, at that time, dominated by *T. angustifolia*. (See Fig. 3: R, A, B, C, D, & E for plot locations). Clipped material was then placed in a drying room and drying oven at a consistent temperature until fully desiccated. The dried plant material was weighed with a Pesola spring scale to establish aboveground biomass (Bertness and Ellison 1987; Sharpe and Baldwin 2011; Janousek and Mayo 2013).

Results

Vegetation transects

Vegetation sampling across Long Marsh in 2013 and 2014 resulted in 72 vascular plants identified to the species level (Table 1). When the salinity index was applied to these species, 22.1% were found to be halophytes, 25% brackish, and 52.9% glycophytic (Table 2). The inundation score revealed that 50.7% are plants that almost always occur in wetlands (99% of the time); 31.9% usually occur in wetlands but occasionally are found in non-wetlands (67-99% of the time); 11.6 % of the species were equally likely to occur in wetlands and non-wetlands (34-66% of the time); and 5.8% of the species almost always occur in non-wetlands in our region (ACOE 2012) (Table 3).

Change in total vegetation percent cover

Overall there was a decrease in total percent cover of vegetation at upstream restoration sites, whereas percent cover remained relatively unchanged at the downstream reference site. Changes in percent cover were modest close to the tidal channel along transects 4 and 6, but extensive in the areas further from the channel that were dominated by brackish and freshwater vegetation in 2013. At transect 9, changes were minimal adjacent to the tidal channel and again adjacent to the uplands, but were much more significant in between in the brackish zone (Fig. 5). These changes are consistent with the hypothesis that there would be widespread brackish vegetation mortality, thinning the width of the brackish zone as a result of restored tide.

Change in *Spartina* percent cover

Spartina species did not increase in percent cover post-restoration nor did they expand their footprint appreciably toward the upland (Fig. 6).

Change in *Typha* percent cover

Percent cover of the total of all three *Typha* species was reduced at 2014 upstream transects (Fig. 7). Changes in *Typha* cover at transect 4 and 9 were highly statistically significant (paired student's t-test: $p = 0.007$) and ($p = 0.006$) respectively. The change at transect 6 was not statistically significant ($p = 0.228$). The reference site did not have any *Typha* present in the first year. (Note that the apparent increase in *Typha* near the upland border in 2014 reflects the decision to re-align the transect in 2014). As was true for total plant cover, changes in *Typha* cover were small near the channel and near the uplands, and greater in between.

Mean change in salinity and inundation indices

Overall, the upstream restoration plots' mean scores shifted to indicate less salt tolerant vegetation ($t = 5.9065$, $df = 119$, $p < 0.001$) but the mean score for flood tolerance did not change ($t = 1.642$, $df = 119$, $p = 0.1032$). The downstream reference area showed no statistically significant change in either index (Salinity Index: $t = -0.0533$, $df = 11$, $p = -0.9584$; Inundation Index: $t = 0.1775$, $df = 11$, $p = 0.8624$). The amount of change toward salt tolerance varied between transects, with transect 4 actually showing a shift toward less salt tolerant vegetation and transect 12 showing no change (Figure 8).

Systematic variation in vegetation

NMDS ordination of data from MDOT sampling plots for 2013 and 2014 produced a two dimensional representation of the plant community data (Fig. 9). Results of the ordination are rotated so that NMDS axis 1 aligns with the greatest systematic variation in community structure. Species typically found in specific vegetation zones were clustered in a gradient from most salt tolerant to least salt tolerant. These clusters are similar to the dominant species cover observed and recorded when documenting

elevation along the MDOT vegetation transects.

Salinity tolerance vegetation patterns

NMDS ordination revealed clear patterns in the vegetation, which correspond with plant zonation (Fig. 9). NMDS axis 1 was highly correlated with the salinity score of associated vegetation (Correlation coefficient: $r = -.902$, $p < 0.001$, Fig. 10), but uncorrelated with inundation ($r = -.003$, $p = 0.965$). NMDS axis 2 was uncorrelated with the salinity index, and weakly correlated with the Wetland Indicator Score, but the latter correlation was only marginally significant ($r = -0.105$, $p = 0.087$) suggesting that inundation was not a strong influence in determining the dominant vegetation patterns on-site. A bootstrap sample confirms that the correlation between the NMDS score and the Salinity Index Correlation was statistically significant ($p < 0.001$).

The randomization method used to assess the vulnerability of the salinity index to misclassification of individual species (Fig. 11) revealed that even numerous errors are likely to have only a limited effect on the results. If mistakes are made in assigning index scores they are most likely to be made with rare species. However, rare species have relatively little effect on the plot indexes, so most classification errors will have little influence on calculation of the correlation coefficient.

Vegetation patterning along an elevation gradient

Elevation change was evident at transitions between halophytic and brackish vegetation but not clear between the brackish and glycophytic zones. There was a clear elevation difference between the *S. alterniflora* (low marsh) zone and *S. patens* (mid marsh) zone, between the *J. gerardii* (high marsh) zone and the *T. angustifolia* (brackish zone) but not obvious between the transition between *T. angustifolia* and *T. latifolia*

(glycophytic zone) (Figures 12-14).

Pore water salinity.

Pore water salinity upstream was significantly higher than in the downstream reference in the plots where *Typha* biomass was harvested and coincided with *Typha* mortality ($t = 17.6418$, $df = 4$, $p = 0.0001$, Fig. 15). Levels recorded in the high marsh-brackish transition zone were also much higher upstream than at the downstream reference ($t = 55.1595$, $df = 4$, $p < 0.0001$, Fig. 16).

Typha Green Index (GI)

The *green index* indicates that *Typha* robustness was lowest at midstream transects 4 and 6 (Fig 17). At the reference site, peak robustness was similar to that at transect 9, which is the furthest upstream.

***Typha* changes**

In 2014 the *T. angustifolia* border retracted dramatically away from the tidal creek towards the upland and the width of the brackish vegetation zone decreased (Fig. 4). Mortality of *Typha* was documented with photos before and after (Figs. 18a and 18b). Except immediately adjacent to the uplands, individual plants remaining after tidal restoration tended to be short, brown or some combination of the two.

Typha aboveground biomass

Change in total *Typha* aboveground biomass (living and dead) was minimal between 2013 and 2014 (Fig. 19). Biomass at upstream locations was consistent with the downstream reference levels and showed no significant change from one year to the next ($N = 24$, $Z = 0.9279$, $p = 0.35238$; not significant at $p \leq 0.05$).

Discussion

Vegetation change was drastic in the first growing season following tidal restoration. Mortality of *T. angustifolia* was widely observed in the brackish zone. Previous studies conducted in New England salt marshes have often concluded that flooding is the more important physical stress determining vegetation zones (Bertness 1991b; Shumway et al. 1992) and not salinity (Pennings et al. 2005). However, changes observed in this study are consistent with the hypothesis that vegetation change was driven principally by increased pore water salinity. Increased inundation did not appear to have as much influence on vegetation pattern or change. As temperatures rise due to global warming, evapotranspiration (ET) rates are likely to increase. This may result in pore water salinity patterns similar to those in low latitude marshes where salinity levels often increase to a peak in the middle or high marsh where increased ET concentrates salts in the soil (Pennings and Bertness 1999, 2001). The proposal by Pennings et al. (2005) that there is a need to test for geographical differences in the role of salinity was confirmed by this study.

Findings in this study suggest that exposure to increased pore water salinity is a major factor influencing the response of vegetation to changing hydrology. Much of the literature on Northeastern US salt marshes discusses marsh vulnerability to SLR principally in terms of elevation, and thus inundation. The literature is full of reports suggesting that sediment accretion may not be able to keep pace with accelerating rates of relative sea level rise (RSLR). Such studies implicitly assume that vegetation changes will be influenced primarily through increased inundation (Warren and Niering 1993; Orsen et al. 1998; Wigand et al. 2014; Smith et al. 2015; Jarrell et al. 2016). The results

of this study suggest that a focus on differences in elevation capitol (Cahoon and Guntenspergen 2010; Watson et al. 2014) alone may not be sufficient to predict community shifts in response to RSLR, especially over the short and medium term.

Vegetation response to hydrologic alteration was strongest where brackish species were present in 2013, exactly as would be expected if changes in salinity were driving vegetation change. The most drastic decrease in plant cover occurred in the middle of transects 4,6, and 9 where *Typha* was present in 2013. The salinity index also revealed that the greatest change in the salt tolerance of vegetation occurred in the brackish areas. Tidal restoration had less effect on pore water salinity at the marsh margins and further upstream, where robust *Typha* was present after restoration. This is likely due to higher levels of fresh water input from the uplands and less frequent tidal inundation. Thibodeau et al. (1998) and Gardner and Reeves (2002b) describe how uplands discharge fresh groundwater through the high marsh. Hemond et al. (2011) found that subsurface hydrology plays an important role in governing the behavior of plant zonation.

An ecological zone model created by Xin et al. (2013) describes three distinct salt marsh zones: 1) zone near the tidal creek, which fills and drains on a semi-diurnal tidal cycle; 2) a middle zone that drains on the spring-neap tidal cycle; and 3) a zone distal from the tidal creek where drainage during the neap tide is less than or equal to the rate of evapotranspiration. While the spring-neap tidal cycles principally control plant zonation in the halophytic salt marsh (Wilson et al. 2016), groundwater flow patterns, including upward seepage, form Xin et al.'s "ecological zones" (Wilson et al. 2011; Moffett et al. 2012).

Three distinct vegetation zones were observed on Long Marsh, and were

described in term of their dominant vegetation: 1) a halophytic zone closest to the tidal creek; 2) a brackish vegetation zone in the middle; and 3) a glycophytic zone distant from the tidal creek and proximate to adjacent upland. These zones are similar, but not identical to Xin et al.'s three "ecological zones". The similarities reflect hydrological interactions between tidal salt water, and the fresh groundwater influence along the tidal margins. The differences may reflect the cooler climate of Maine tidal wetlands, where evapotranspiration is lower, and hypersaline conditions less likely to develop. Or the dissimilarities may be due to the thick layers of glacially deposited marine clay that create containing layers at this site, which are much different than the sand beneath Xin et al.'s salt marshes. It is not known how subsurface groundwater moves through the organic horizon at Long Marsh, and no data has been collected on evapotranspiration at this site. Further research would be needed to provide understanding of the mechanism underlying the ecological zones and thus how they may affect vegetation zonation.

It is telling that plants in the genus *Spartina*, which are salt tolerant, did not show significant declines in percent cover in response to restoration, while the members of the genus *Typha*, which are less salt tolerant, did. Contrary to expectation, salt tolerant *Spartina* species and other salt tolerant plants did not increase in percent cover in the areas where extensive *Typha* mortality occurred. This is most likely due to the large standing dead *Typha*, which shades out any seedlings and/or prevents vegetative spread. It may take several more years for halophytes to populate the marsh surface where brackish vegetation was present in 2013.

Stunted and highly stressed *Typha* were widespread, as characterized by the green index in the 2014-growing season. Mortality of almost all brackish species at transect 4

left only a few cattails as the last remaining live plants. This explains the counter-intuitive results of an overall shift toward less salt tolerant vegetation at that site. It is likely that their survival was due to a couple of factors. First, energy stored in the rhizomes of what was a well-established stand, permitted plants to grow early in the season based not on accumulation of new biomass, but on reallocation of reserves to leaf tissue (Boyd and Hess 1970). Second, fresh water input from spring precipitation may have made local growing conditions temporarily suitable for growth of even some salt-intolerant species. However, as the temperature increased during the growing season, rain events became less frequent, and groundwater became depleted in the adjacent uplands, dilution of salt water decreased, and pore water salinity increased, stressing the plants, and eventually leading to their death.

Robust *Typha* were observed upstream, at plot set E, even though the average recorded salinity at that site was more than double ($12.4 \pm .61$ ppt SE) than at the reference site (5.8 ± 1.1 ppt SE). It appears that *Typha* are able to withstand short periods of pore water salinity around 12 parts per thousand and persist, but not at sites with higher salinity (Sites A-D with means ranging from 17.5 to 26.7).

Although cattail were obviously stressed, and mortality widespread, measurements of *Typha* aboveground biomass showed little change one year after restoration, with significant declines observed at only one location (Fig. 19). This apparently paradoxical result occurred because total biomass measurements included both living and dead material. One year after restoration, standing dead material was still sufficiently abundant to mask declines in live biomass. Measuring the living and dead plant parts separately would have likely yielded a stronger signal.

Conclusions

It is essential to understand the potentially wide range of biological responses to SLR in order to make well-informed decisions. Studies conducted during this tidal restoration project provided an opportunity to build our knowledge base with regard to environmental changes that occur with the associated increased inundation and salinity. Physiochemical changes caused by increased pore water salinity on this site may create population level shifts in salt intolerant vegetation on the marsh surface. It is unknown what the consequences this altered wetland community structure will have on ecosystem functions such as nutrient export to deeper waters, shellfish, fish, and bird spawning, nesting, and feeding grounds, shoreline stabilization, and buffering runoff from adjacent uplands. While much has been done to evaluate vegetation response to SLR in terms of inundation based on elevation gradients, this study clearly supports the need to consider salt as a major factor influencing vegetation response to tidal restoration in the long narrow tidal wetland, Long Marsh.

As cities and municipalities along the coast of Maine prepare for impacts related to Climate change, resiliency in the face of SLR is a priority. Coastal managers and planners are becoming increasingly aware of the need to plan for infrastructure and utilities that can withstand higher high tides, storm surges, and extreme weather events (Fernandez 2015). However, very little is known about how increased salinity exposure will affect built systems. Thus including salinity data in coastal models for expected SLR scenarios may prove useful.

References

- Allakhverdiev, S. I., Sakamoto, A., Nishiyama, Y., Inaba, M., & Murata, N. (2000). Ionic and osmotic effects of NaCl-induced inactivation of photosystems I and II in *Synechococcus* sp. *Plant physiology*, 123(3), 1047-1056.
- Anisfeld, S. C. (2012). Biogeochemical responses to tidal restoration. *Tidal Marsh Restoration* (pp. 39-58). Island Press/Center for Resource Economics.
- Baldwin, A. H., McKee, K. L., & Mendelssohn, I. A. (1996). The influence of vegetation, salinity, and inundation on seed banks of oligohaline coastal marshes. *American Journal of Botany*, 470-479.
- Sharpe, P. J., & Baldwin, A. H. (2009). Patterns of wetland plant species richness across estuarine gradients of Chesapeake Bay. *Wetlands*, 29(1), 225-235.
- Bertness, M. D., & Ellison, A. M. (1987). Determinants of pattern in a New England salt marsh plant community. *Ecological Monographs*, 57(2), 129-147.
- Bertness, M. D., & Shumway, S. W. (1993). Competition and facilitation in marsh plants. *The American Naturalist*, 142(4), 718-724.
- Boumans, R. M. J., Burdick, D. M., & Dionne, M. (2002). Modeling habitat change in salt marshes after tidal restoration. *Restoration Ecology*, 10(3), 543-555.
- Boyd, C. E., & Hess, L. W. (1970). Factors influencing shoot production and mineral nutrient levels in *Typha latifolia*. *Ecology*, 51(2), 296-300.
- Cahoon, D. R., & Guntenspergen, G. R. (2010). Climate change, sea-level rise, and coastal wetlands. *National Wetlands Newsletter*, 32(1), 8-12.
- Cao, M., Xin, P., Jin, G., & Li, L. (2012). A field study on groundwater dynamics in a salt marsh—Chongming Dongtan wetland. *Ecological Engineering*, 40, 61-69.
- Crain, C. M., Silliman, B. R., Bertness, S. L., & Bertness, M. D. (2004). Physical and biotic drivers of plant distribution across estuarine salinity gradients. *Ecology*, 85(9), 2539-2549.
- Deegan, L. A., Hughes, J. E., & Rountree, R. A. (2002). Salt marsh ecosystem support of marine transient species. In *Concepts and controversies in tidal marsh ecology* (pp. 333-365). Springer Netherlands.

- Emery, N. C., Ewanchuk, P. J., & Bertness, M. D. (2001). Competition and salt-marsh plant zonation: stress tolerators may be dominant competitors. *Ecology*, 82(9), 2471-2485.
- Farnsworth, E. J., & Meyerson, L. A. (2003). Comparative ecophysiology of four wetland plant species along a continuum of invasiveness. *Wetlands*, 23(4), 750-762.
- Fernandez, I. J., Schmitt, C., Stancioff, E., Birkel, S. D., Pershing, A., Runge, J., ... & Mayewski, P. A. (2015). Maine's Climate Future: 2015 Update.
- Gardner, L. R., & Reeves, H. W. (2002). Seasonal patterns in the soil water balance of a *Spartina* marsh site at North Inlet, South Carolina, USA. *Wetlands*, 22(3), 467-477.
- Gedan, K. B., Silliman, B. R., & Bertness, M. D. (2009). Centuries of human-driven change in salt marsh ecosystems. *Annual Review of Marine Science*, 1, 117-141.
- Goddard, P. B., Yin, J., Griffies, S. M., & Zhang, S. (2015). An extreme event of sea-level rise along the Northeast coast of North America in 2009–2010. *Nature communications*, 6.
- Grace, J. B. (1987). The impact of preemption on the zonation of two *Typha* species along lakeshores. *Ecological Monographs*, 57(4), 283-303.
- Grace, J. B., & Harrison, J. S. (1986). The biology of Canadian weeds.: 73. *Typha latifolia* L., *Typha angustifolia* L. and *Typha xglauca* Godr. *Canadian Journal of Plant Science*, 66(2), 361-379.
- Grace, J. B., & Wetzel, R. G. (1981). Habitat partitioning and competitive displacement in cattails (*Typha*): experimental field studies. *The American Naturalist*, 118(4), 463-474.
- Grace, J. B., & Wetzel, R. G. (1982). Niche differentiation between two rhizomatous plant species: *Typha latifolia* and *Typha angustifolia*. *Canadian Journal of Botany*, 60(1), 46-57.
- Haines, A. & Vining, T. F. (1990). *Flora of Maine: a manual for identification of native and naturalized vascular plants of Maine*. Bar Harbor, Maine: VF Thomas Co. 847p.
- Hemond, H. F., & Fifield, J. L. (1982). Subsurface flow in salt marsh peat: A model and field study. *Limnology and Oceanography*, 27(1), 126-136.
- Jacobson, H. A., Jacobson, G. L., & Kelley, J. T. (1987). Distribution and abundance of tidal marshes along the coast of Maine. *Estuaries and Coasts*, 10(2), 126-131.
- Keddy, P. A. (2010). *Wetland ecology: principles and conservation*. Cambridge University Press.

- Kelley, J. T., Belknap, D. F., Jacobson Jr, G. L., & Jacobson, H. A. (1988). The morphology and origin of salt marshes along the glaciated coastline of Maine, USA. *Journal of Coastal Research*, 649-666.
- Kelley, J. T. (1987). Inventory of Coastal Environments and Classification of Maine's Glaciated Shoreline. *Glaciated Coasts. Academic Press, Inc New York. 1987. p 151-176, 12 fig, 2 tab, 32 ref.*
- Konisky, R. A., & Burdick, D. M. (2004). Effects of stressors on invasive and halophytic plants of New England salt marshes: a framework for predicting response to tidal restoration. *Wetlands*, 24(2), 434-447.
- Kuehn, M. M., Minor, J. E., & White, B. N. (1999). An examination of hybridization between the cattail species *Typha latifolia* and *Typha angustifolia* using random amplified polymorphic DNA and chloroplast DNA markers. *Molecular Ecology*, 8(12), 1981-1990.
- McMillan, C. (1959). Salt tolerance within a *Typha* population. *American Journal of Botany*, 521-526.
- Miller, W. R., & Egler, F. E. (1950). Vegetation of the Wequetequock-Pawcatuck Tidal-Marshes, Connecticut. *Ecological Monographs*, 20(2), 143-172.
- Mitsch, W. J., & Gosselink, J. G. (2007). *Wetlands*. Hoboken. ed: John Wiley & Sons, Inc.
- Moffett, K. B., & Gorelick, S. M. (2016). Relating salt marsh pore water geochemistry patterns to vegetation zones and hydrologic influences. *Water Resources Research*, 52(3), 1729-1745.
- Morris, J. T., Sundareshwar, P. V., Nietch, C. T., Kjerfve, B., & Cahoon, D. R. (2002). Responses of coastal wetlands to rising sea level. *Ecology*, 83(10), 2869-2877.
- Neckles, H. A., Dionne, M., Burdick, D. M., Roman, C. T., Buchsbaum, R., & Hutchins, E. (2002). A monitoring protocol to assess tidal restoration of salt marshes on local and regional scales. *Restoration Ecology*, 10(3), 556-563.
- Nyman, J. A., Walters, R. J., Delaune, R. D., & Patrick, W. H. (2006). Marsh vertical accretion via vegetative growth. *Estuarine, Coastal and Shelf Science*, 69(3), 370-380.
- Roman, C. T., Niering, W. A., & Warren, R. S. (1984). Salt marsh vegetation change in response to tidal restriction. *Environmental Management*, 8(2), 141-149.
- Odum, W. E. (1988). Comparative ecology of tidal freshwater and salt marshes. *Annual Review of Ecology and Systematics*, 19(1), 147-176.

- Oksanen, J., Blanchet, F. G., Kindt, R., Legendre, P., Minchin, P. R., O'hara, R. B., ... & Oksanen, M. J. (2013). Package 'vegan'. *Community ecology package, version, 2*(9).
- Olson, A., Paul, J., & Freeland, J. R. (2009). Habitat preferences of cattail species and hybrids (*Typha* spp.) in eastern Canada. *Aquatic Botany*, 91(2), 67-70.
- Pennings, S. C., & Bertness, M. D. (2001). Salt marsh communities. *Marine community ecology*, 289-316.
- Rafinesque, C. S. (1836). *Flora telluriana*. Philadelphia, PA: Murray Printing Company.
- R Core Team (2012). *R: A language and environment for statistical computing*. R Foundation for Statistical Computing. Vienna, Austria. URL <http://www.R-project.org/>.
- Roman, C. T., Raposa, K. B., Adamowicz, S. C., James-Pirri, M. J., & Catena, J. G. (2002). Quantifying vegetation and nekton response to tidal restoration of a New England salt marsh. *Restoration Ecology*, 10(3), 450-460.
- Rountree, R. A., & Able, K. W. (2007). Spatial and temporal habitat use patterns for salt marsh nekton: implications for ecological functions. *Aquatic Ecology*, 41(1), 25-4
- Scavia, D., Field, J. C., Boesch, D. F., Buddemeier, R. W., Burkett, V., Cayan, D. R., ... & Reed, D. J. (2002). Climate change impacts on US coastal and marine ecosystems. *Estuaries*, 25(2), 149-164.
- Selbo, S. M., & Snow, A. A. (2004). The potential for hybridization between *Typha angustifolia* and *Typha latifolia* in a constructed wetland. *Aquatic Botany*, 78(4), 361-369.
- Shen, C., Jin, G., Xin, P., Kong, J., & Li, L. (2015). Effects of salinity variations on pore water flow in salt marshes. *Water Resources Research*, 51(6), 4301-4319.
- Shih, J. G., & Finkelstein, S. A. (2008). Range dynamics and invasive tendencies in *Typha latifolia* and *Typha angustifolia* in eastern North America derived from herbarium and pollen records. *Wetlands*, 28(1), 1-16.
- Shumway, S. W., & Bertness, M. D. (1994). Patch size effects on marsh plant secondary succession mechanisms. *Ecology*, 75(2), 564-568.
- Silvestri, S., Defina, A., & Marani, M. (2005). Tidal regime, salinity and salt marsh plant zonation. *Estuarine, coastal and shelf science*, 62(1), 119-130.

Slovinsky, P. (2015). Potential sea level rise, storm surge, marsh migration, and hurricane impacts in Biddeford, ME. Department of Agriculture, Conservation and Forestry. Maine Geological Survey.

Smith, L. M., & Kadlec, J. A. (1983). Seed banks and their role during drawdown of a North American marsh. *Journal of Applied Ecology*, 673-684.

Smith, S. M., Roman, C. T., James-Pirri, M. J., Chapman, K., Portnoy, J., & Gwilliam, E. (2009). Responses of Plant Communities to Incremental Hydrologic Restoration of a Tide-Restricted Salt Marsh in Southern New England (Massachusetts, USA). *Restoration Ecology*, 17(5), 606-618.

Taylor, Peter H. (2008). Gulf of Maine Ecosystem-Based Management Toolkit Survey Report. Gulf of Maine Council on the Marine Environment. 35 p.

Thibodeau, P. M., Gardner, L. R., & Reeves, H. W. (1998). The role of groundwater flow in controlling the spatial distribution of soil salinity and rooted macrophytes in a southeastern salt marsh, USA. *Mangroves and Salt Marshes*, 2(1), 1-13.

Tiner, R. W. (2009). *Field guide to tidal wetland plants of the northeastern United States and neighboring Canada: vegetation of beaches, tidal flats, rocky shores, marshes, swamps, and coastal ponds*. Univ of Massachusetts Press.

United States Army Corp of Engineers, (2013). National Wetland Plant List. URL http://wetland_plants.usace.army.mil

Venables, W. N. & Ripley, B. D. (2002) *Modern Applied Statistics with S. Fourth Edition*. Springer, New York.

Wilcox, D. A. (1995). Wetland and aquatic macrophytes as indicators of anthropogenic hydrologic disturbance. *Natural Areas Journal*, 15(3), 240-248.

Wilson, A. M., Evans, T., Moore, W., Schutte, C. A., Joye, S. B., Hughes, A. H., & Anderson, J. L. (2015). Groundwater controls ecological zonation of salt marsh macrophytes. *Ecology*, 96(3), 840-849.

Wilson, S. D., & Keddy, P. A. (1986). Species competitive ability and position along a natural stress/disturbance gradient. *Ecology*, 67(5), 1236-1242.

Xin, P., Li, L., & Barry, D. A. (2013). Tidal influence on soil conditions in an intertidal creek-marsh system. *Water Resources Research*, 49(1), 137-150.

Xin, P., Zhou, T., Lu, C., Shen, C., Zhang, C., D'Alpaos, A., & Li, L. (2017). Combined effects of tides, evaporation and rainfall on the soil conditions in an intertidal creek-marsh system. *Advances in Water Resources*, 103, 1-15.

Tables

Table 1. Plant species identified during 2013 and 2014 vegetation monitoring, with salinity and inundation scores assigned to each species.

Salinity score	Inundation score	Genus	Species	Common name
3	4	<i>Argentina</i>	<i>anserina</i>	Silverweed
3	4	<i>Glaux</i>	<i>maritima</i>	Saltwort
3	4	<i>Juncus</i>	<i>gerardii</i>	Saltmarsh Rush
3	4	<i>Ruppia</i>	<i>maritima</i>	Beaked Ditch-Grass
3	4	<i>Salicornia</i>	<i>depressa</i>	Common Glasswort
3	4	<i>Spartina</i>	<i>alterniflora</i>	Saltwater Cord Grass
3	4	<i>Suaeda</i>	<i>maritima</i>	Herbaceous Seepweed
3	4	<i>Triglochin</i>	<i>maritima</i>	Seaside Arrow-Grass
3	3	<i>Distichlis</i>	<i>spicata</i>	Coastal Salt Grass
3	3	<i>Juncus</i>	<i>arcticus</i>	Artic Rush
3	3	<i>Plantago</i>	<i>maritima</i>	Goosetongue
3	3	<i>Puccinellia</i>	<i>tenella</i>	Tundra Alkali Grass
3	3	<i>Solidago</i>	<i>sempervirens</i>	Seaside Goldenrod
3	3	<i>Spartina</i>	<i>patens</i>	Salt-Meadow Cord Grass
3	2	<i>Atriplex</i>	<i>prostrata</i>	Hastate Orache
3	2	<i>Hordeum</i>	<i>jubatum</i>	Fox-Tail Barley
2	4	<i>Bolboschoenus</i>	<i>maritima</i>	Sea Club-Rush
2	4	<i>Calamagrostis</i>	<i>canadensis</i>	Bluejoint
2	4	<i>Cladium</i>	<i>mariscoides</i>	Smooth Saw-Grass
2	4	<i>Lythrum</i>	<i>salicaria</i>	Purple Loosestrife
2	4	<i>Schoenoplectus</i>	<i>acutus</i>	Hard-Stem Club-Rush
2	4	<i>Schoenoplectus</i>	<i>maritimus</i>	Sea Club-Rush
2	4	<i>Schoenoplectus</i>	<i>pungens</i>	Three-Square
2	4	<i>Typha</i>	<i>angustifolia</i>	Narrow-Leaf Cat-Tail
2	3	<i>Agrostis</i>	<i>stolonifera</i>	Spreading Bent Grass
2	3	<i>Elymus</i>	<i>pycnanthus</i>	Tick Quackgrass
2	3	<i>Spartina</i>	<i>pectinata</i>	Freshwater Cord Grass
2	3	<i>Symphyotrichum</i>	<i>novi-belgii</i>	New Belgium American-Aster
2	3	<i>Thinopyrum</i>	<i>pycnanthum</i>	Tick Quackgrass
2	2	<i>Calystegia</i>	<i>sepium</i>	Hedge False Bindweed
2	2	<i>Euthamia</i>	<i>graminifolia</i>	Grass-leaved Goldenrod
2	2	<i>Panicum</i>	<i>virgatum</i>	Wand Panic Grass
2	2	<i>Toxicodendron</i>	<i>radicans</i>	Eastern Poison Ivy
2	1	<i>Elymus</i>	<i>repens</i>	Creeping Wild Rye
2	1	<i>Festuca</i>	<i>rubra</i>	Red Fescue
2	4	<i>Typha</i>	<i>x glauca</i>	Hybrid Cattail
1	4	<i>Carex</i>	<i>crinita</i>	Fringed Sedge
1	4	<i>Carex</i>	<i>hystericina</i>	Porcupine Sedge
1	4	<i>Carex</i>	<i>lacustris</i>	Lakebank Sedge
1	4	<i>Carex</i>	<i>lurida</i>	Shallow Sedge
1	4	<i>Carex</i>	<i>paleacea</i>	Chaffy Sedge
1	4	<i>Carex</i>	<i>stipata</i>	Stalk-Grain Sedge
1	4	<i>Carex</i>	<i>utriculata</i>	Northwest Territory Sedge
1	4	<i>Dryopteris</i>	<i>cristata</i>	Crested Wood Fern

Salinity score	Inundation score	Genus	Species	Common name
1	4	<i>Dulichium</i>	<i>arundinaceum</i>	Three-Way Sedge
1	4	<i>Galium</i>	<i>asprellum</i>	Rough Bedstraw
1	4	<i>Glyceria</i>	<i>canadensis</i>	Rattlesnake Manna Grass
1	4	<i>Lycopus</i>	<i>americanus</i>	Cut-Leaf Water-Horehound
1	4	<i>Lycopus</i>	<i>uniflorus</i>	Northern Water-Horehound
1	4	<i>Lysimachia</i>	<i>terrestris</i>	Swamp candle
1	4	<i>Osmunda</i>	<i>regalis L. var spectabilis</i>	Royal Fern
1	4	<i>Persicaria</i>	<i>sagittata</i>	Arrow-leaved Tearthumb
1	4	<i>Proserpinaca</i>	<i>palustris</i>	Marsh Mermaidweed
1	4	<i>Rosa</i>	<i>palustris</i>	Swamp Rose
1	4	<i>Scutellaria</i>	<i>galericulata</i>	Hooded Skullcap
1	4	<i>Typha</i>	<i>latifolia</i>	Broad-Leaf Cat-Tail
1	4	<i>Vaccinium</i>	<i>macrocarpon</i>	Large Cranberry
1	3	<i>Alnus</i>	<i>incana</i>	Speckled Alder
1	3	<i>Carex</i>	<i>scoparia</i>	Pointed Broom Sedge
1	3	<i>Equisetum</i>	<i>pratense</i>	Meadow Horsetail
1	3	<i>Galium</i>	<i>trifidum</i>	Three-Petal Bedstraw
1	3	<i>Hypericum</i>	<i>mutilum</i>	Dwarf St. John's-Wort
1	3	<i>Ilex</i>	<i>verticillata</i>	Common Winterberry
1	3	<i>Impatiens</i>	<i>capensis</i>	Spotted Touch-Me-Not
1	3	<i>Onoclea</i>	<i>sensibilis</i>	Sensitive Fern
1	3	<i>Panicum</i>	<i>dichotomiflorum</i>	Fall Panic Grass
1	3	<i>Spiraea</i>	<i>alba</i>	White Meadowsweet
1	3	<i>Spiraea</i>	<i>tomentosa</i>	Steeplebush
1	3	<i>Thelypteris</i>	<i>palustris</i>	Eastern Marsh Fern
1	2	<i>Abies</i>	<i>balsamea</i>	Balsam Fir
1	2	<i>Acer</i>	<i>rubrum</i>	Red maple
1	1	<i>Quercus</i>	<i>rubra</i>	Northern Red Oak
1	1	<i>Solidago</i>	<i>altissima</i>	Tall Goldenrod
2		<i>Scirpus</i>	sp.	
1		<i>Carex</i>	sp.	
1		<i>Ribes</i>	sp	
1		<i>Rubus</i>	sp.	
1		<i>Viola</i>	sp.	
		<i>Eleocharis</i>	sp	
		Unknown	Forb	
		Unknown	Grass	
		Unspecified	Unspecified	

Table 2 Plant Species in Vegetation Zones Determined by Salinity Index

Score	Vegetation Zone	Number of species with score	%
3	Halophytes	16	22%
2	Brackish	20	28%
1	Glycophytes	36	50%

Table 3 Plant Species in Vegetation Zones Determined by Inundation Index. Typical habitats used in wetland delineation were given a numerical value in similar fashion, with the highest score equating to the most flood tolerant. Inundation score: OBL (4), FACW (3), FAC (2), FACU (1); Salinity score: Halophyte (3), Brackish (2), Glycophyte (1).

Score	ACOE Wetland Indicator	Number of species with score	%
4	OBL	38	52.8%
3	FACW	22	30.6%
2	FAC	8	11.1%
1	FACU	4	5.6%

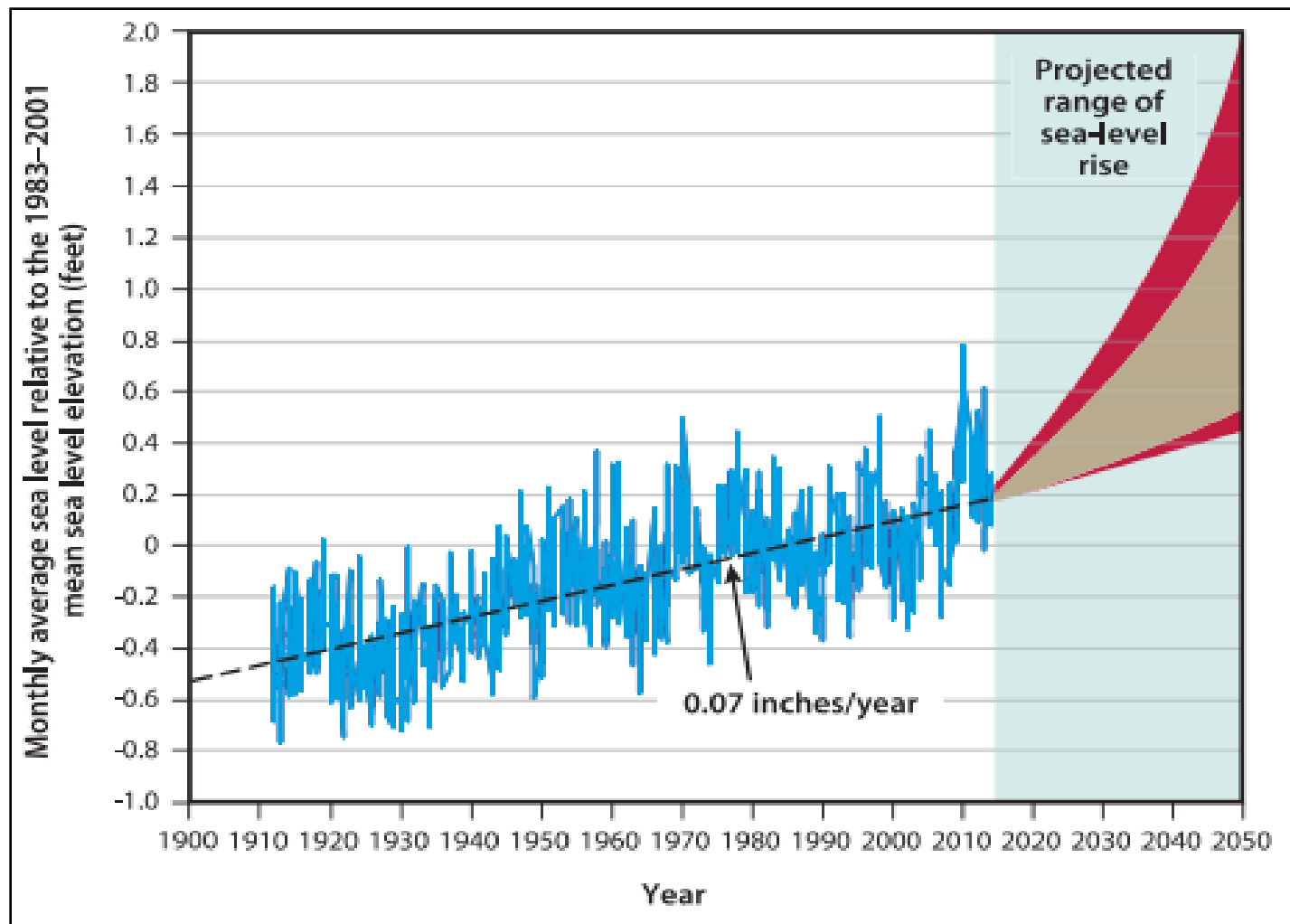


Figure 1. Sea Level Trend at Portland Maine. Relative rate of SLR on Maine's coast from the early 1900s to 2013 (blue). (Fernandez et al. 2015).

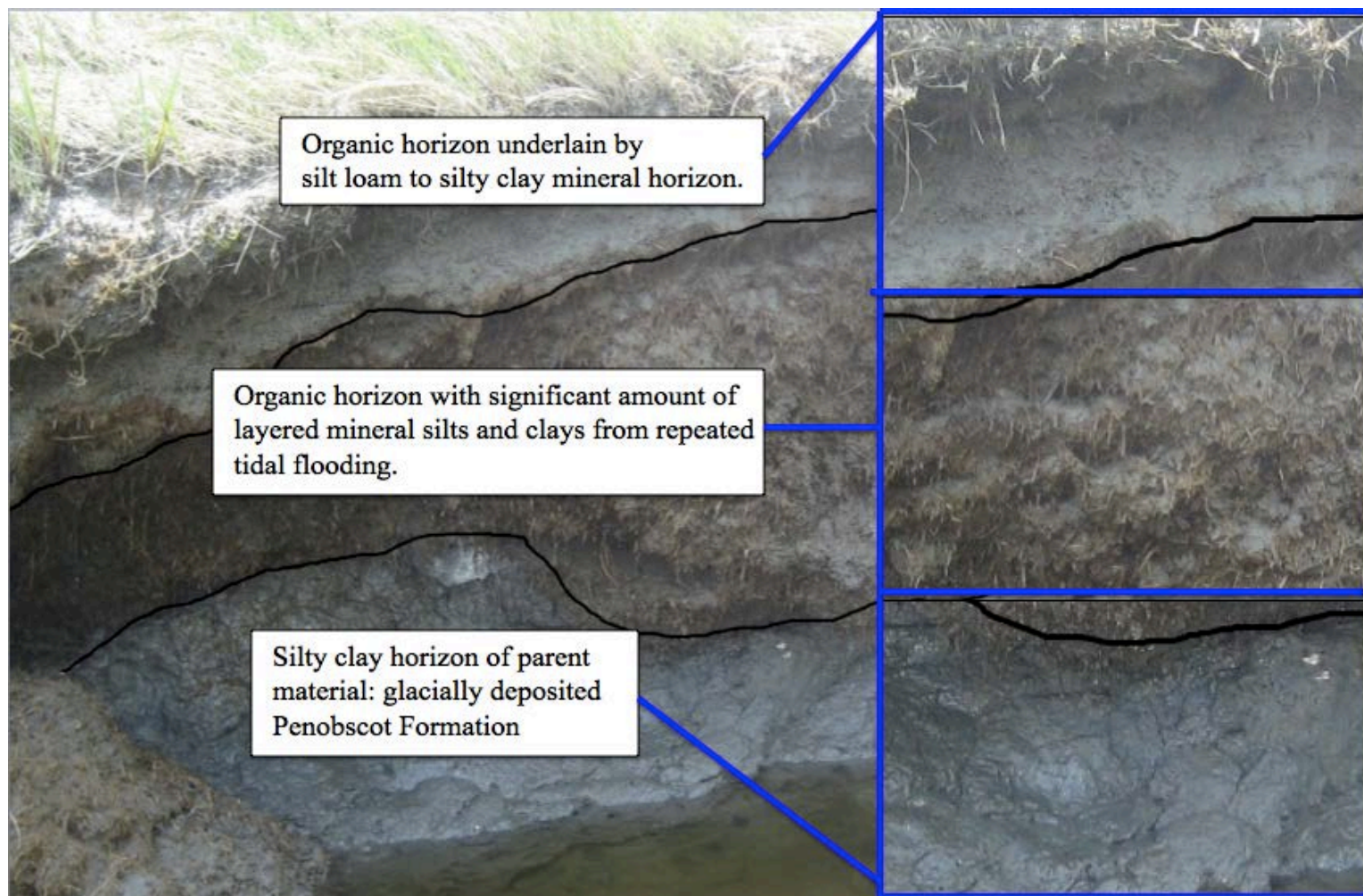


Figure 2. Long Marsh Soil/Peat Profile. Soil layers revealed in 2014 after tidal restoration eroded away the low marsh area near MDOT transect 2. Soil classification lines and descriptions were added to the photo (credit Matt Craig) by USDA soil scientist Dave Wilkinson.



Figure 3. Transect and Sub-study Locations on Long Marsh. Image shows 10 of the 12 MDOT vegetation transects (red). This study focused on changes occurring along transects 4, 6, and 9 (labeled). A-E marks the locations of plots used in the *Typha* aboveground biomass sub-study (purple). R marks the downstream reference (red). The entire project area is approximately 2 kilometers long.



Figure 4 *Typha* border shift. Shift in position of the border between *Typha* and other vegetation reflects extensive mortality following tidal restoration.

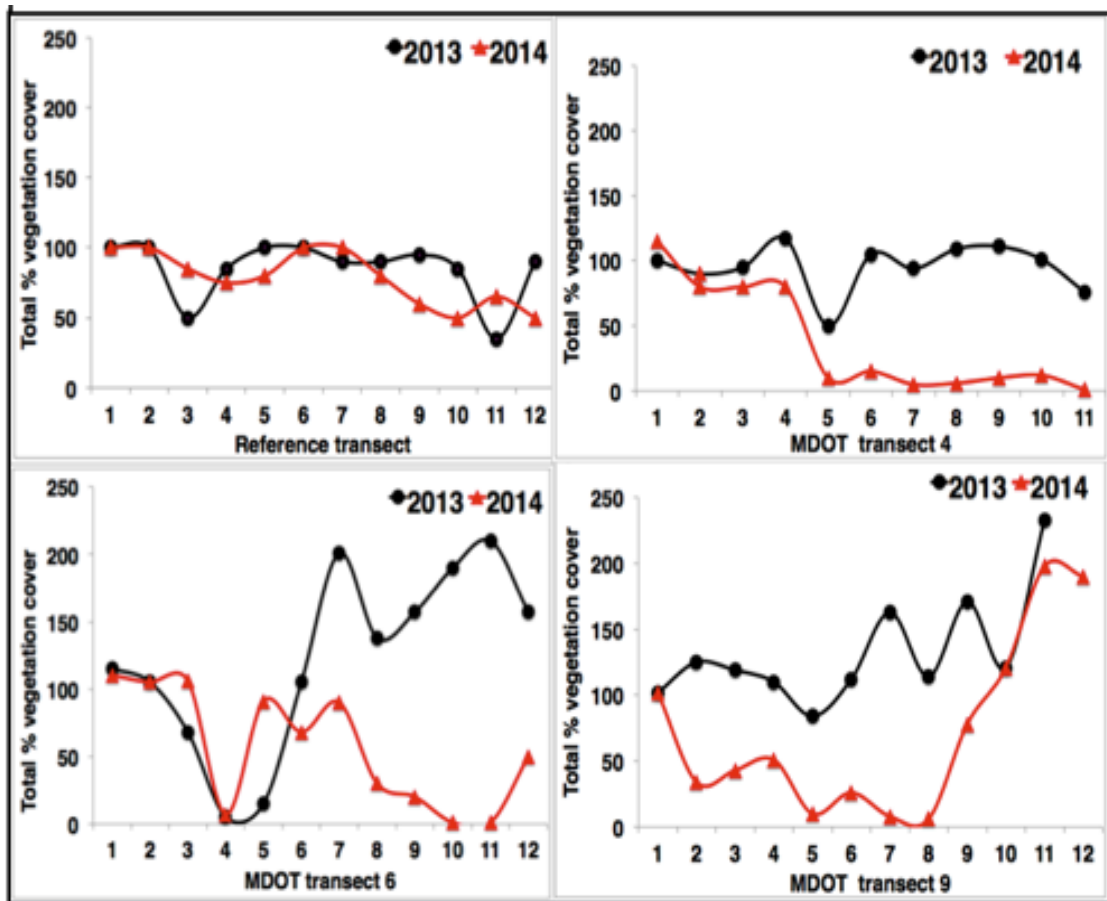


Figure 5 Total Vegetation Cover Before and After Tidal Restoration. The x-axis shows plots in order along the transects, from the tidal creek (Plot 1) to the uplands (on the extreme right). The y-axis shows total percent cover of vegetation present in each plot. Values can exceed 100% because some plant species overtop others, allowing for multiple layers of vegetation. The lines provide visual continuity for data collected in each respective year but smoothing is not indicative of actual data.

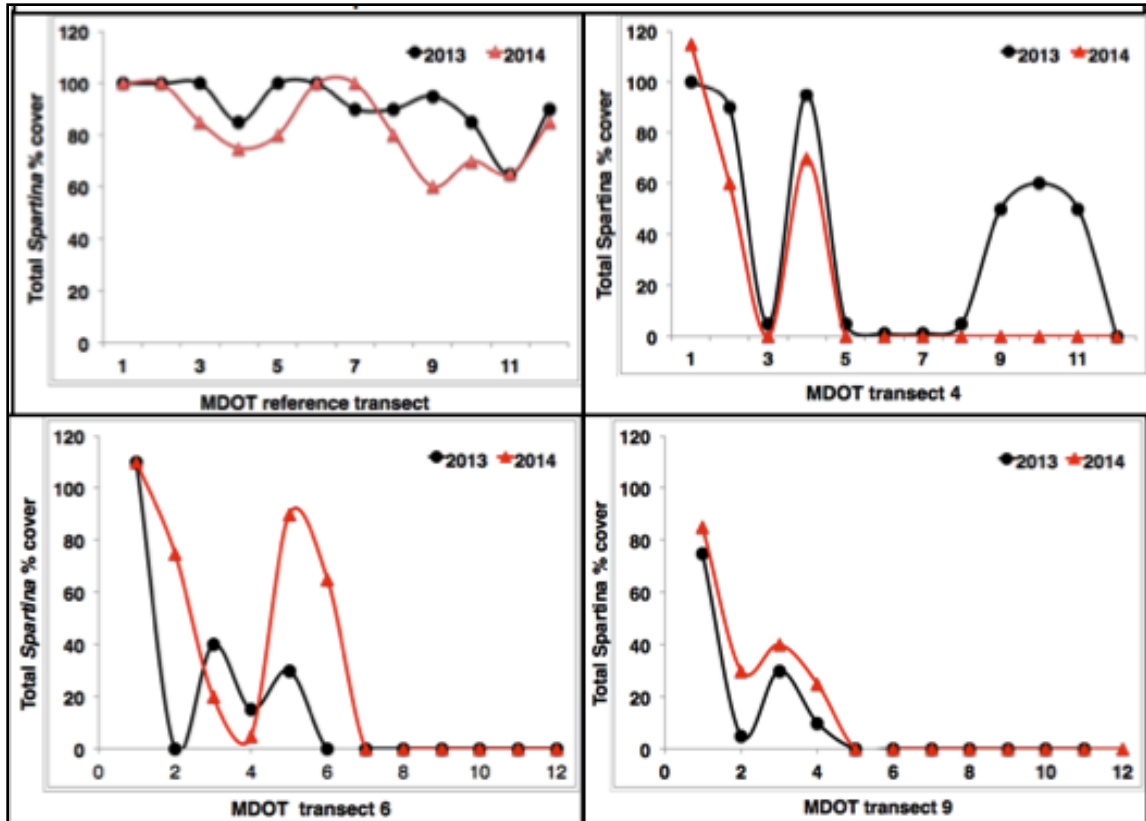


Figure 6. Total *Spartina* Cover Before and After Tidal Restoration. The x-axis shows plots in order along the transects, from the tidal creek (Plot 1) to the uplands (on the extreme right). The y-axis shows total percent cover of vegetation present in each plot. Values can exceed 100% because some plant species overtop others, allowing for multiple layers of vegetation. The lines provide visual continuity for data collected in each respective year but smoothing is not indicative of actual data.

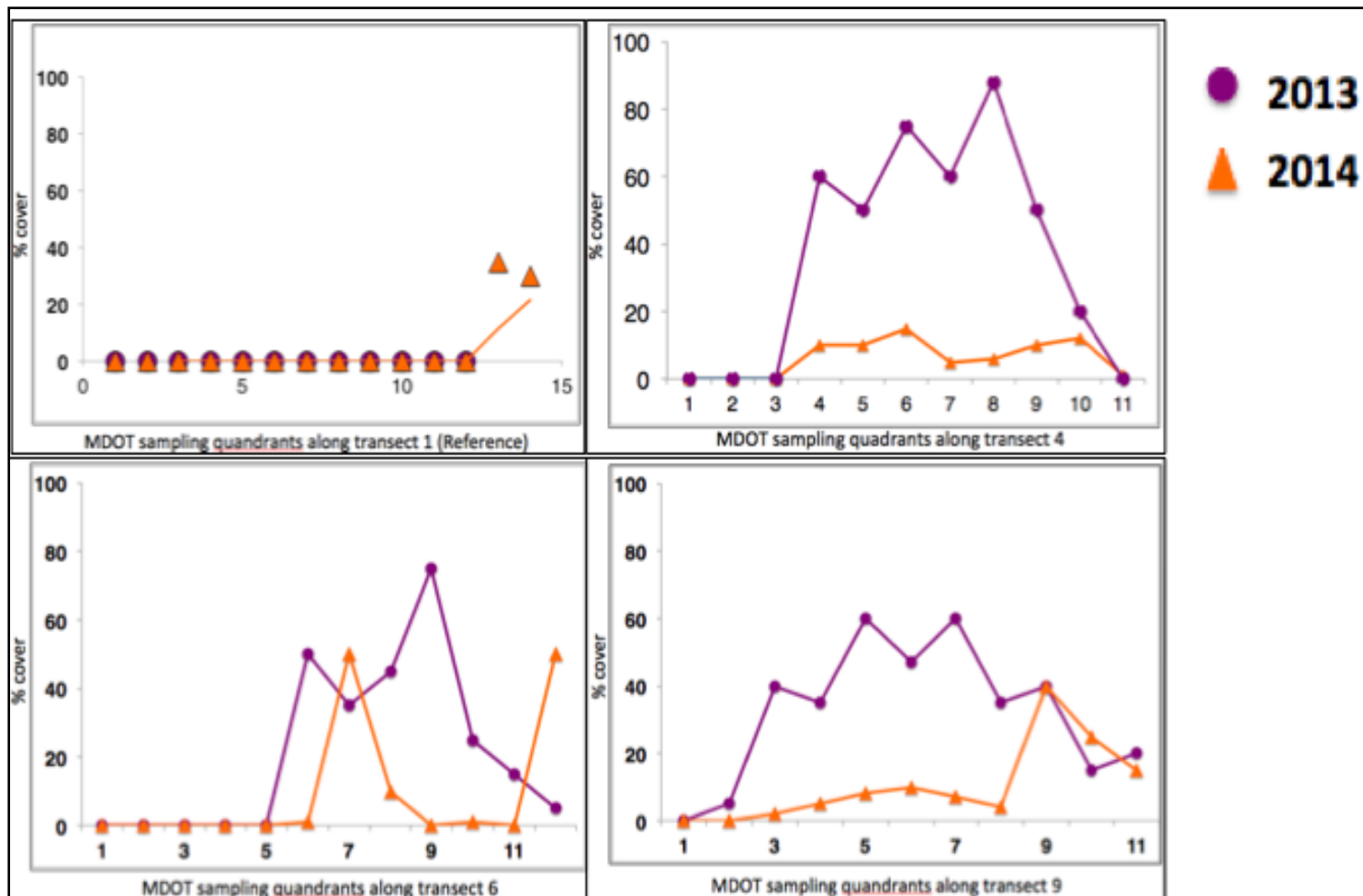


Figure 7 Total *Typha* Cover Change Before and After Tidal Restoration. Purple circles indicate the total percent cover of *Typha* along MDOT sampling transects in 2013, and the orange triangles 2014. On the x-axis are plots along the transects, from the tidal creek on the left to the uplands on the right. On the y-axis is the percent cover of total *Typha* species present.

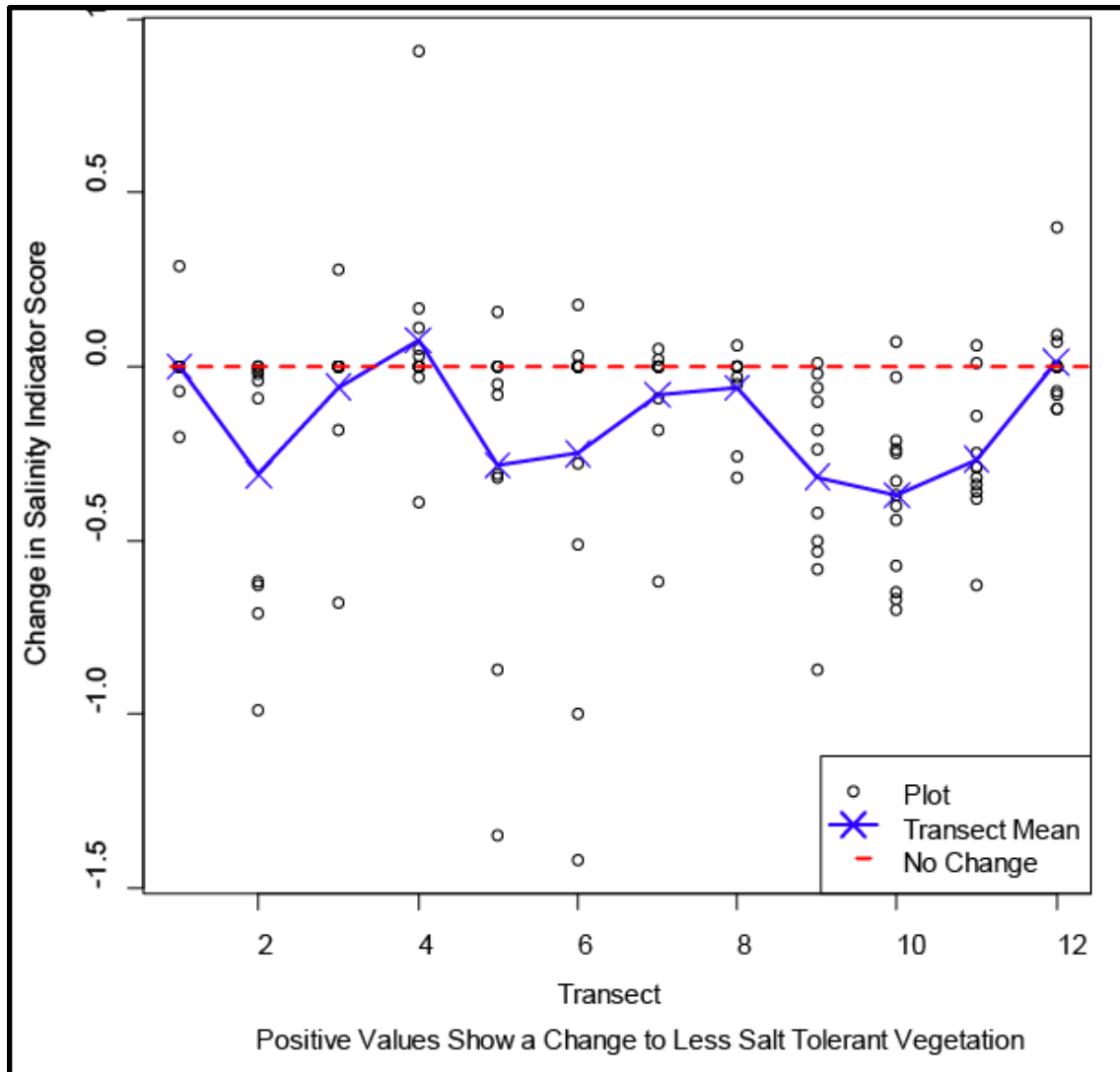


Figure 8 Mean Transect Changes in Salinity Indicator Score. The red dotted line indicates no change from 2013 to 2014. The y-axis reflects the amount of change in salinity index score for each sampling plot at all of the 12 MDOT vegetation sampling transects (shown on the x axis). The blue markings show the mean change in salinity index score for each transect.

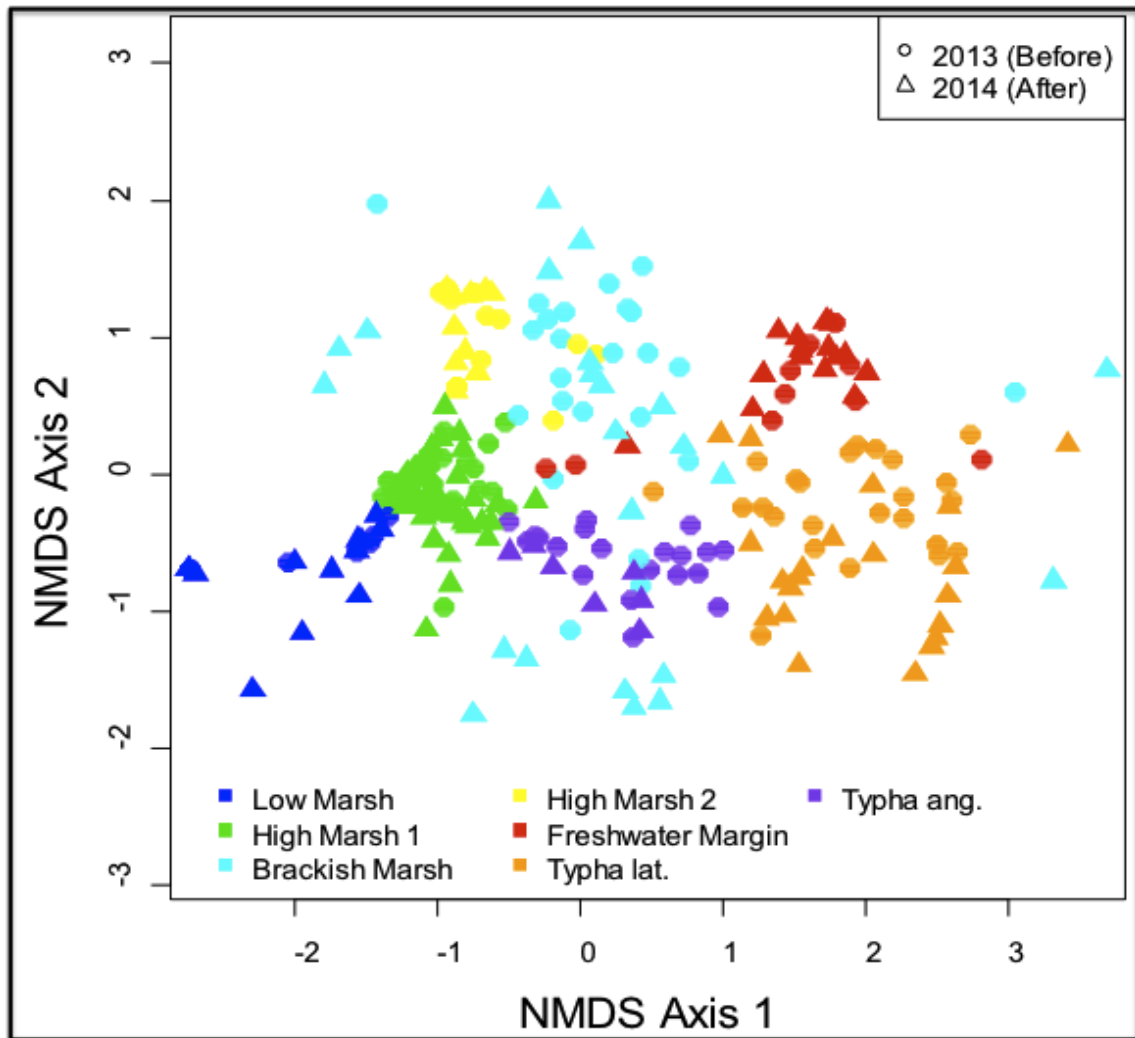


Figure 9 Nonmetric Multidimensional Scaling (NMDS) Ordination with Dominant Species Pattern. NMDS scaling plot based on analysis of data from both 2013 and 2014. Colors reflect results of the cluster analysis. Colors depict categories assigned by the cluster analysis; names reflect interpretation based on which species dominate the plots.

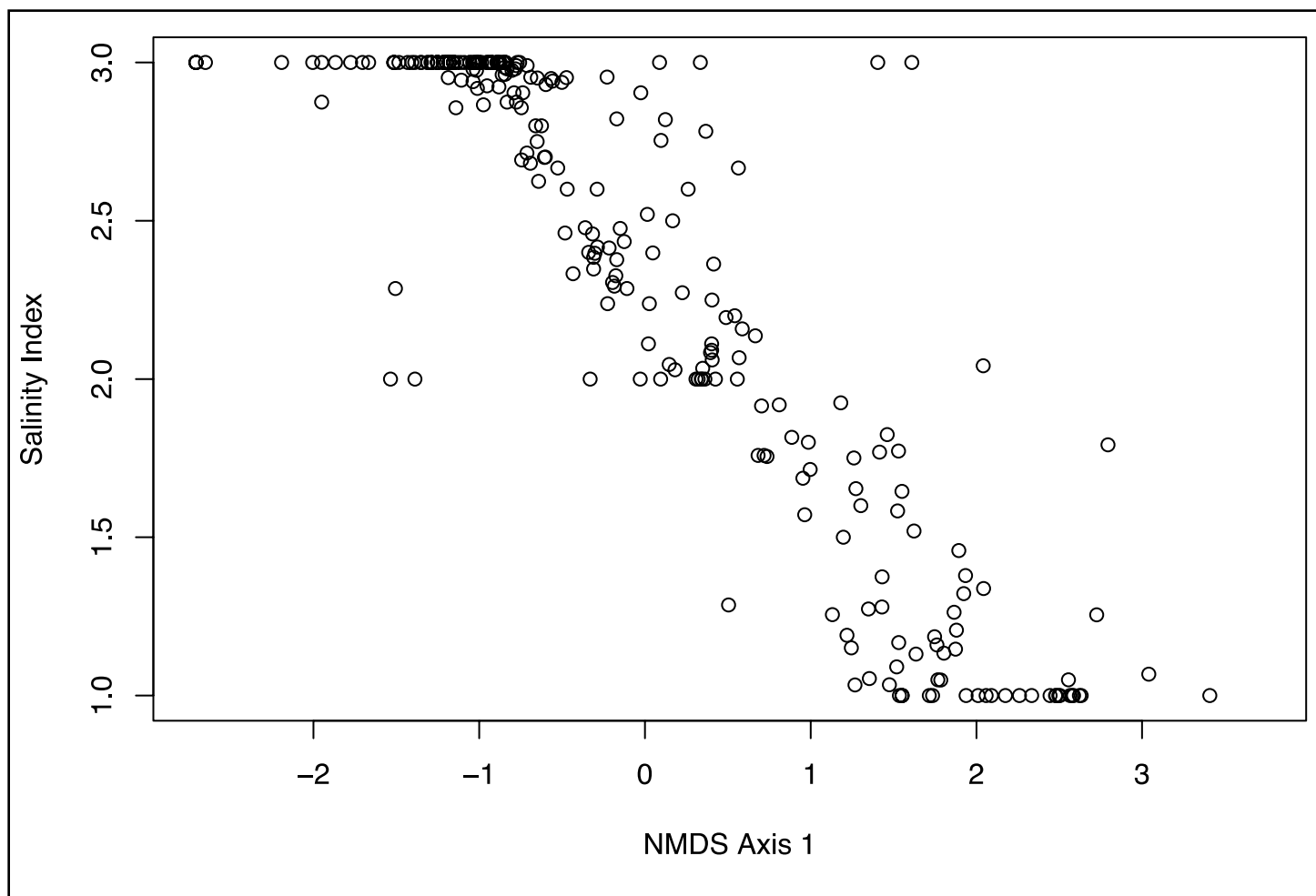


Figure 10 Relationship between Salinity Index and NMDS Ordination Axis 1. The correlation between NMDS Axis 1 and the Salinity Index is highly statistically significant ($p < 0.001$).

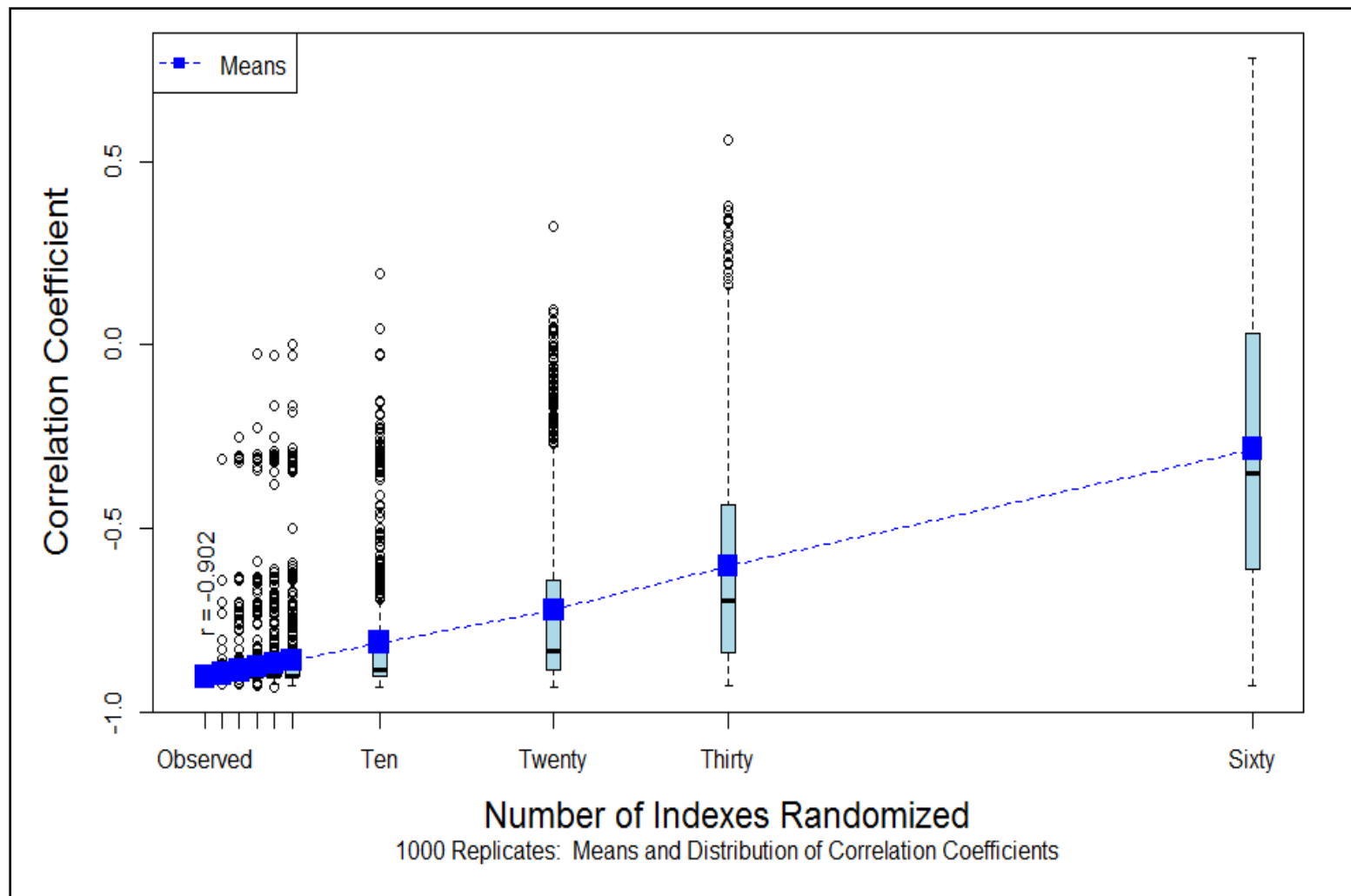


Figure 11 Randomization: Assessment of the Salinity Index's Vulnerability to Misclassification of Individual Species.

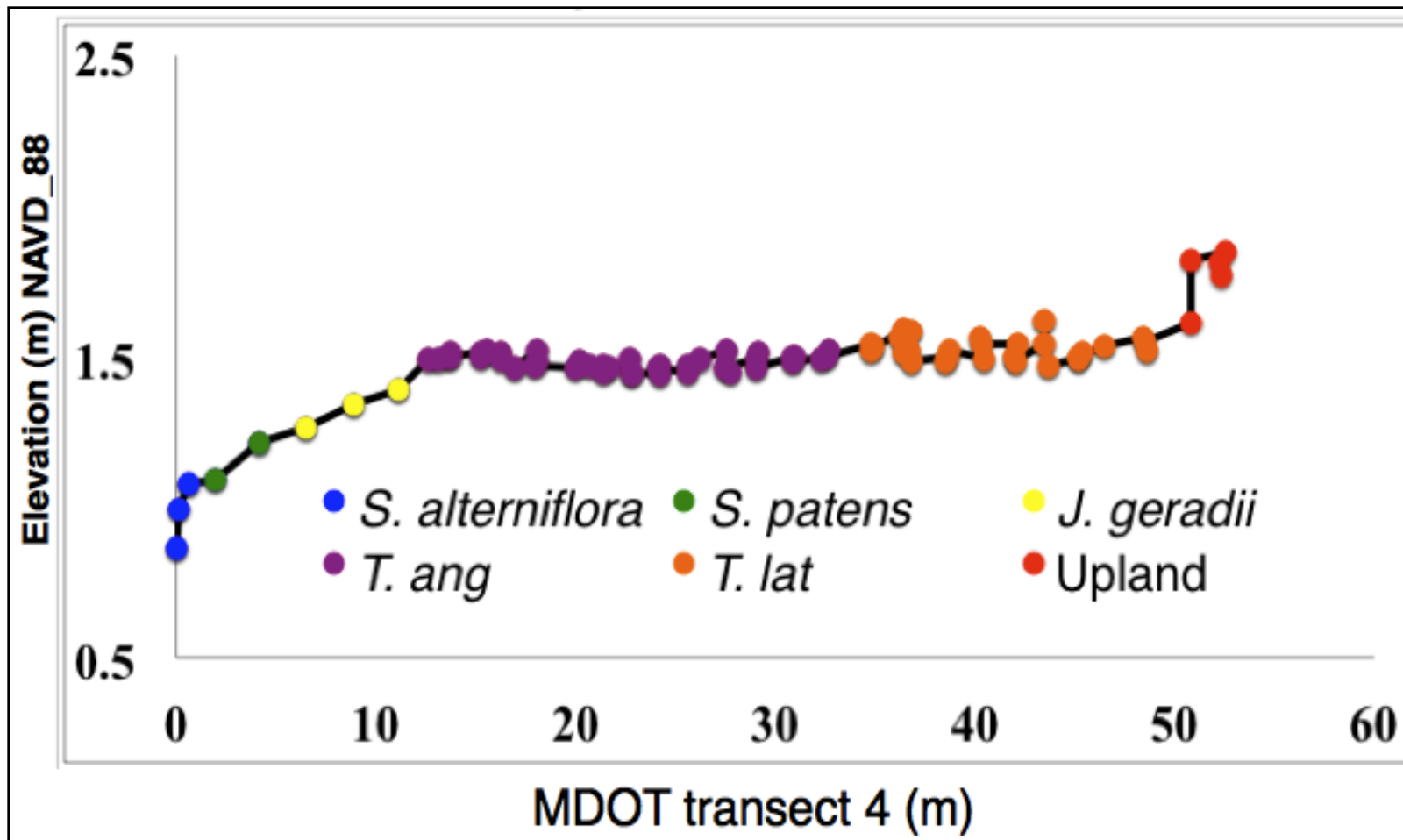


Figure 12 Vegetation Zones on Elevation Profile: Transect 4 in meters NAVD 88. The x-axis shows the distance from the tidal creek. The y-axis shows elevation. Colors indicate the dominant plant species, as listed in the image (*T. ang* = *Typha angustifolia*; *T. lat* = *T. latifolia*; red indicates presence of upland vegetation).

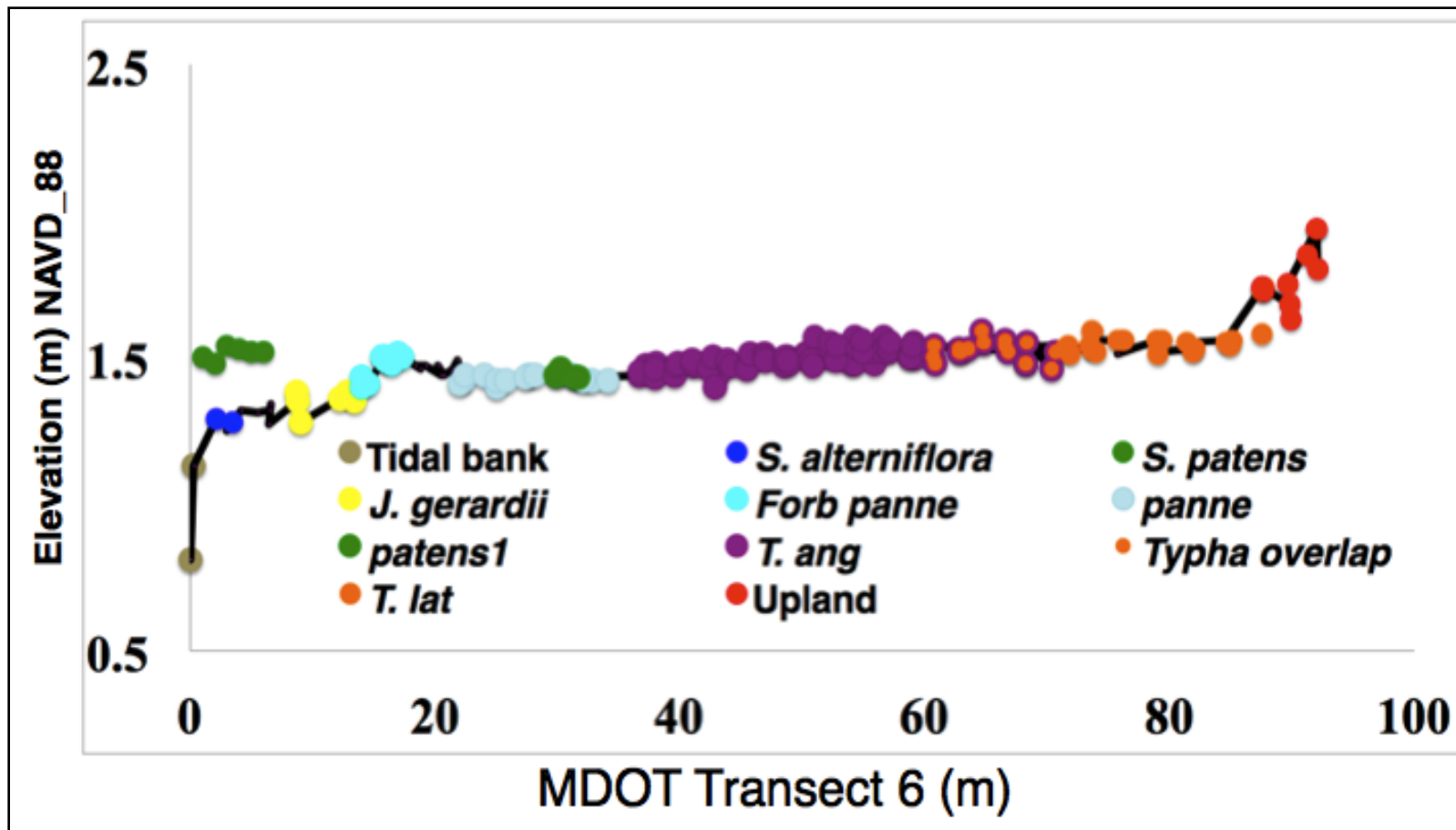


Figure 13 Vegetation Zones on Elevation Profile: Transect 6 in meters NAVD 88. The x-axis shows the distance from the tidal creek. The y-axis shows elevation. Colors indicate the dominant plant species, as listed in the image (*T. ang* = *Typha angustifolia*; *T. lat* = *T. latifolia*; red indicates presence of upland vegetation; brown shows unvegetated bank of the tidal creek.).

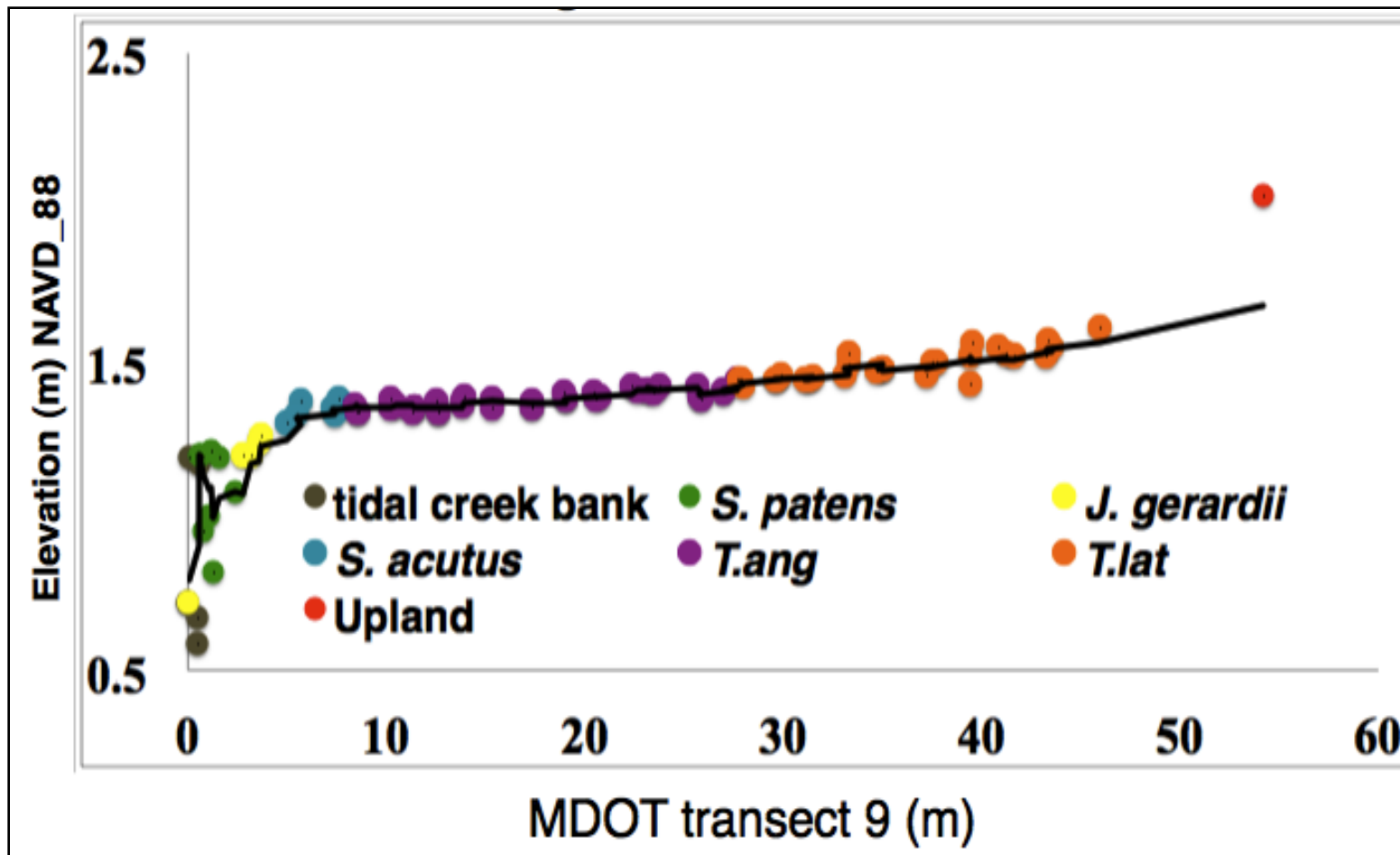


Figure 14 Vegetation Zones on Elevation Profile: Transect 9 in meters NAVD 88. The x-axis shows the distance from the tidal creek. The y-axis shows elevation. Colors indicate the dominant plant species, as listed in the image (*T. ang* = *Typha angustifolia*; *T. lat* = *T. latifolia*; red indicates presence of upland vegetation; brown shows unvegetated bank of the tidal creek).

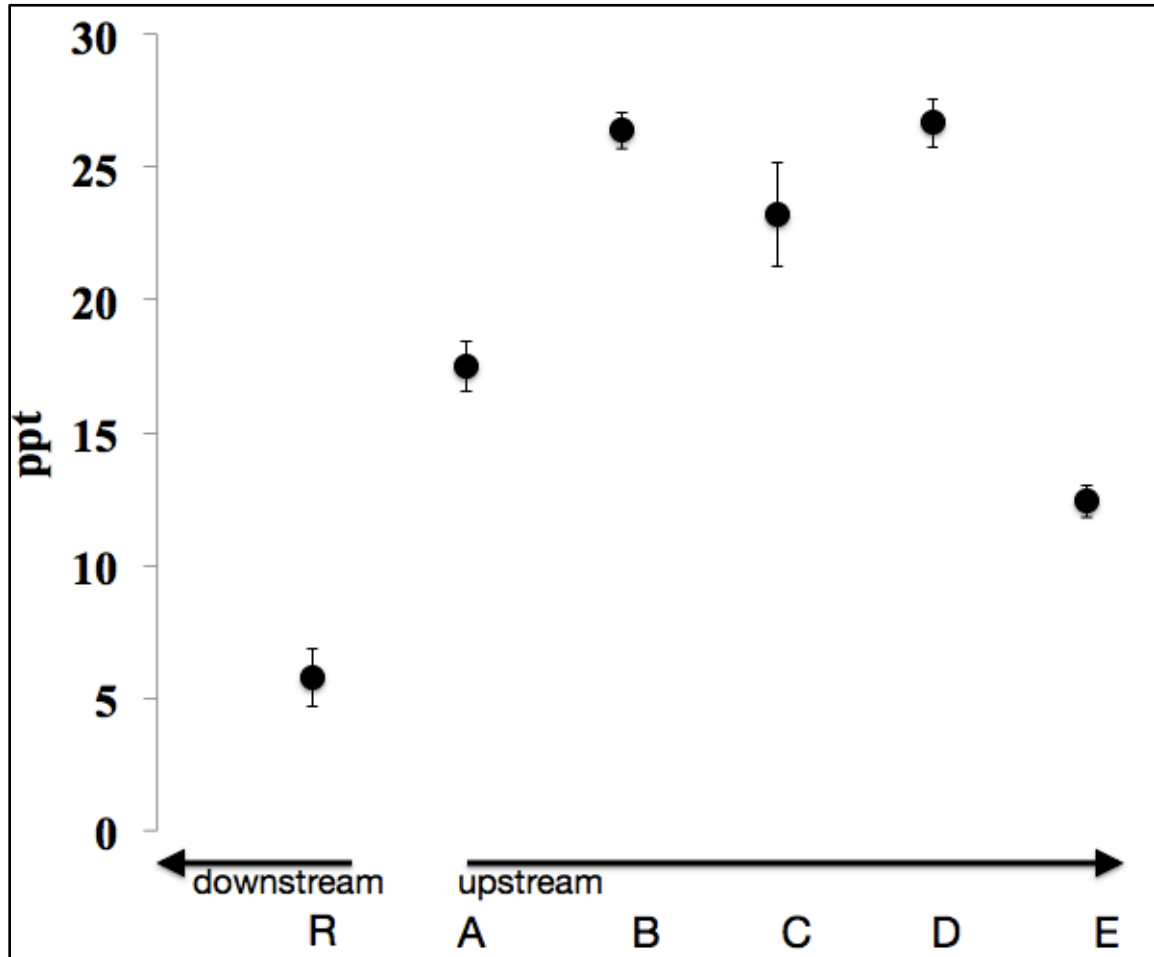


Figure 15 2014 Mean Pore Water Salinity in *Typha* Biomass Plots. Downstream reference mean (R) 5.8 ± 1.10 SE; Upstream plot means (A) $17.5 \pm .95$ SE; (B) $26.4 \pm .69$ SE; (C) 23.2 ± 1.95 SE; (D) $26.7 \pm .91$ SE; (E) $12.4 \pm .61$ SE. Pore water salinity was taken within two hours of predicted low tide on June 28, July 19, August 4, August 14, and September 18 in 2014 at the same location where aboveground biomass was collected. Points are shown with 1 SE bar.

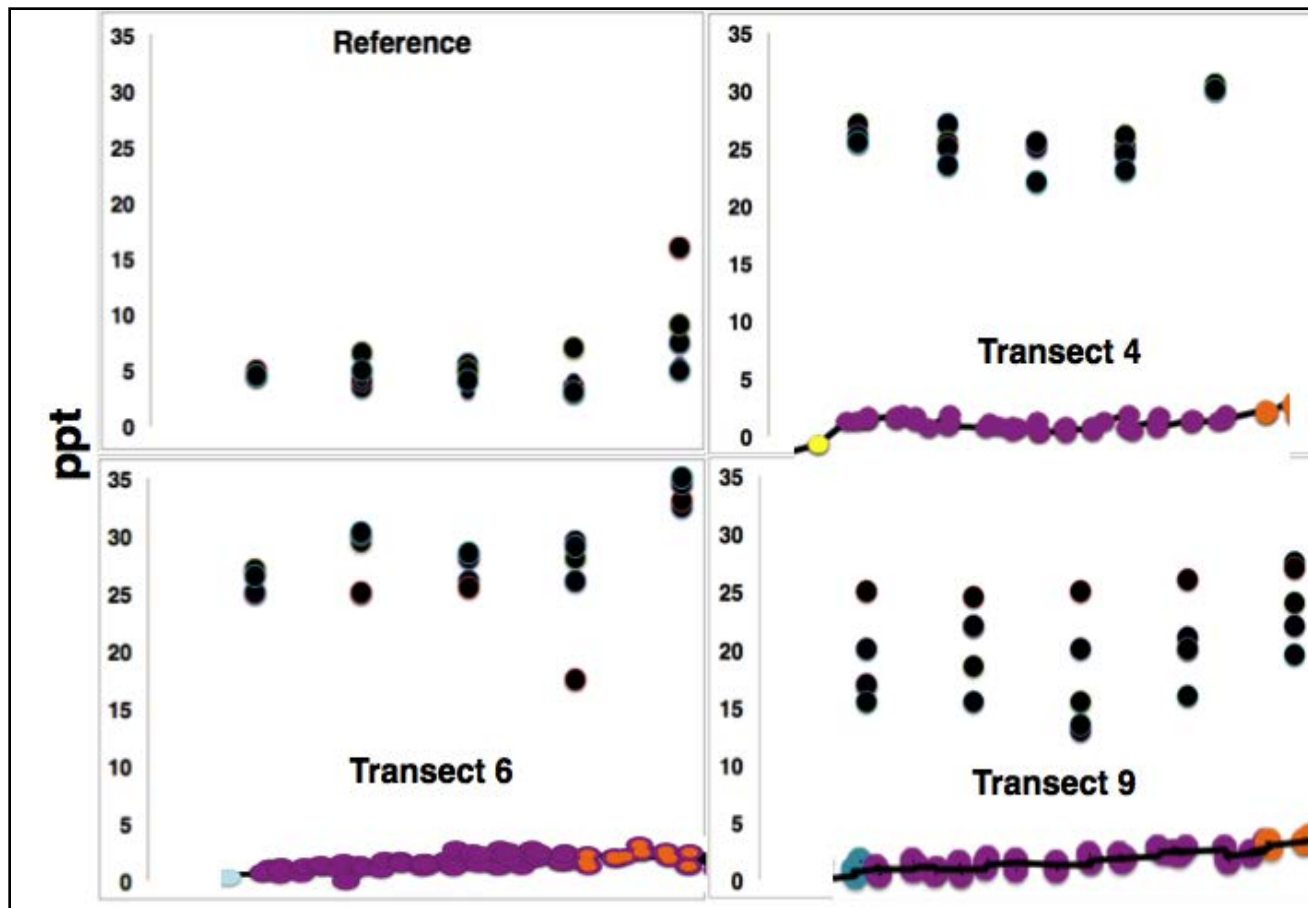


Figure 16 2014 Brackish Zone Pore Water Salinity Levels. Pore water salinities along vegetation transect are consistent with *Typha* survival at the reference ((1)(mean = 5.28 ppt \pm 1.19 SD)) and *Typha* mortality upstream: ((4)(mean = 26.27ppt \pm 2.17 SD)); ((6) = 28.27 ppt \pm 3.31 SD)); ((9)(mean = 20.28 ppt \pm 2.60 SD)). Dominant species and elevations along the x-axis for transects 4, 6, and 9 indicate spatial context of pore water wells. For each transect, one well was in the high marsh halophyte zone (yellow or blue), three were inside the 2013 brackish zone (purple), and one was located in the glycyphytic zone (orange). Horizontal scale varies.

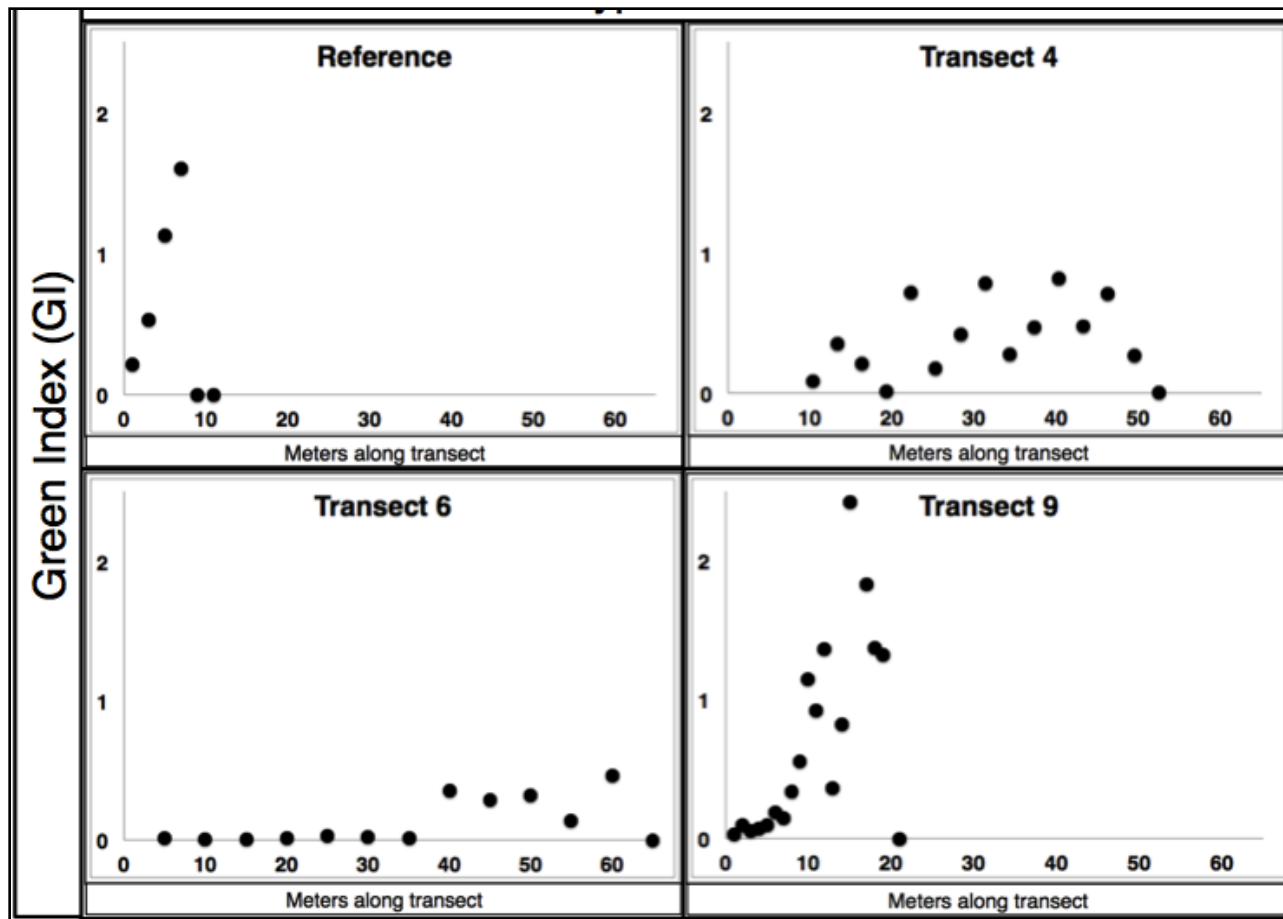


Figure 17 2014 *Typha* Robustness. Each black dot represents the mean green index (GI) score in sampling quadrants along three replicate transects located near to MDOT transects. On the x-axis the distance along the transect from the high marsh to the upland are shown. The reference transect and transect 9 are much shorter than transects 4 and 6 and are shown to scale. This demonstrates the respective thin or thickness of the brackish zone dominated by *Typha*. On the y-axis the green index (GI) indicates robustness of *Typha* plants at each transect.

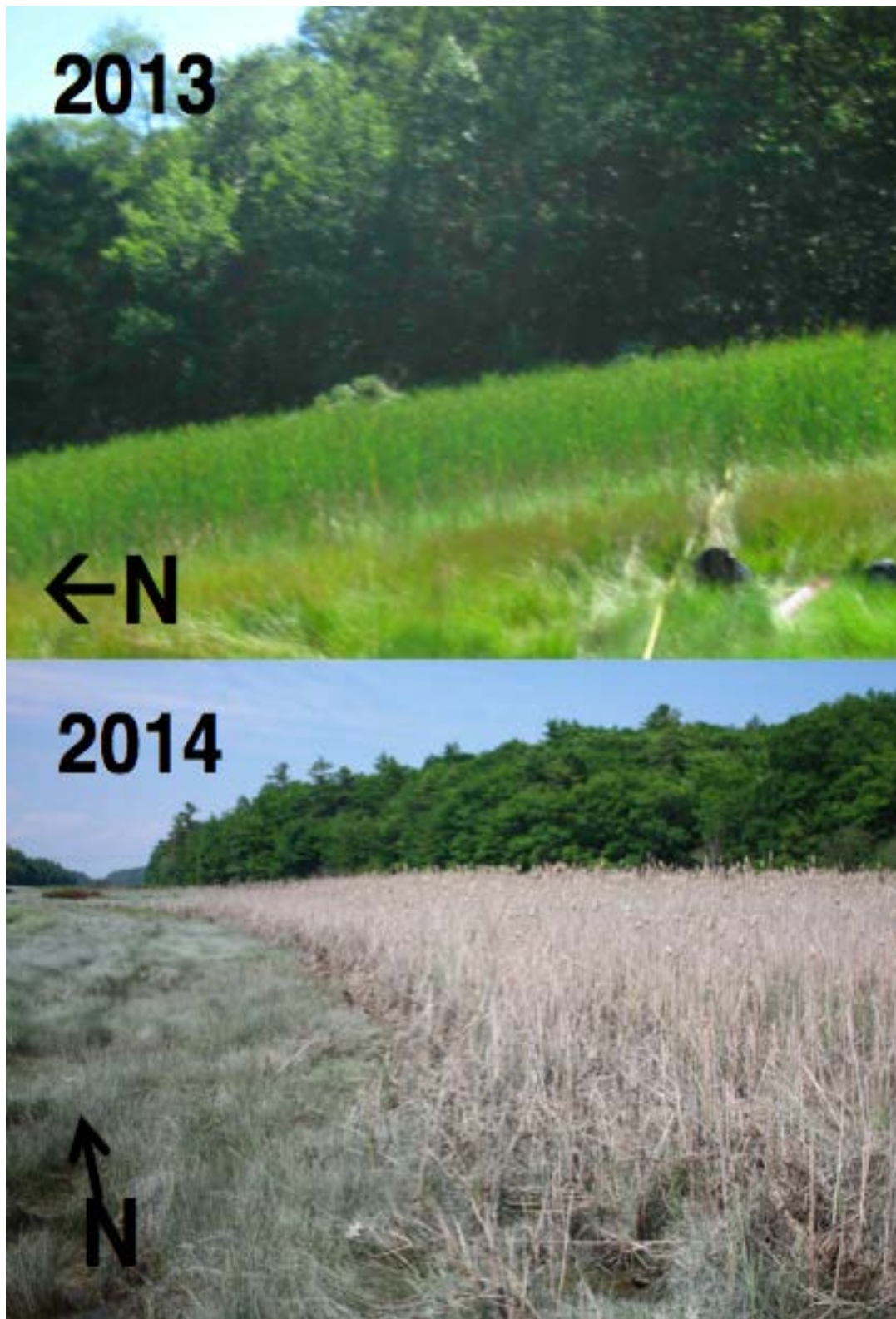


Figure 18a 2013 Green *Typha* and **Figure 18b** 2014 Brown/Dead *Typha*. Bright green robust *T. angustifolia* at transect 4 in 2013 is shown above in contrast with dead brown standing *Typha* remaining in the same location in 2014 below.

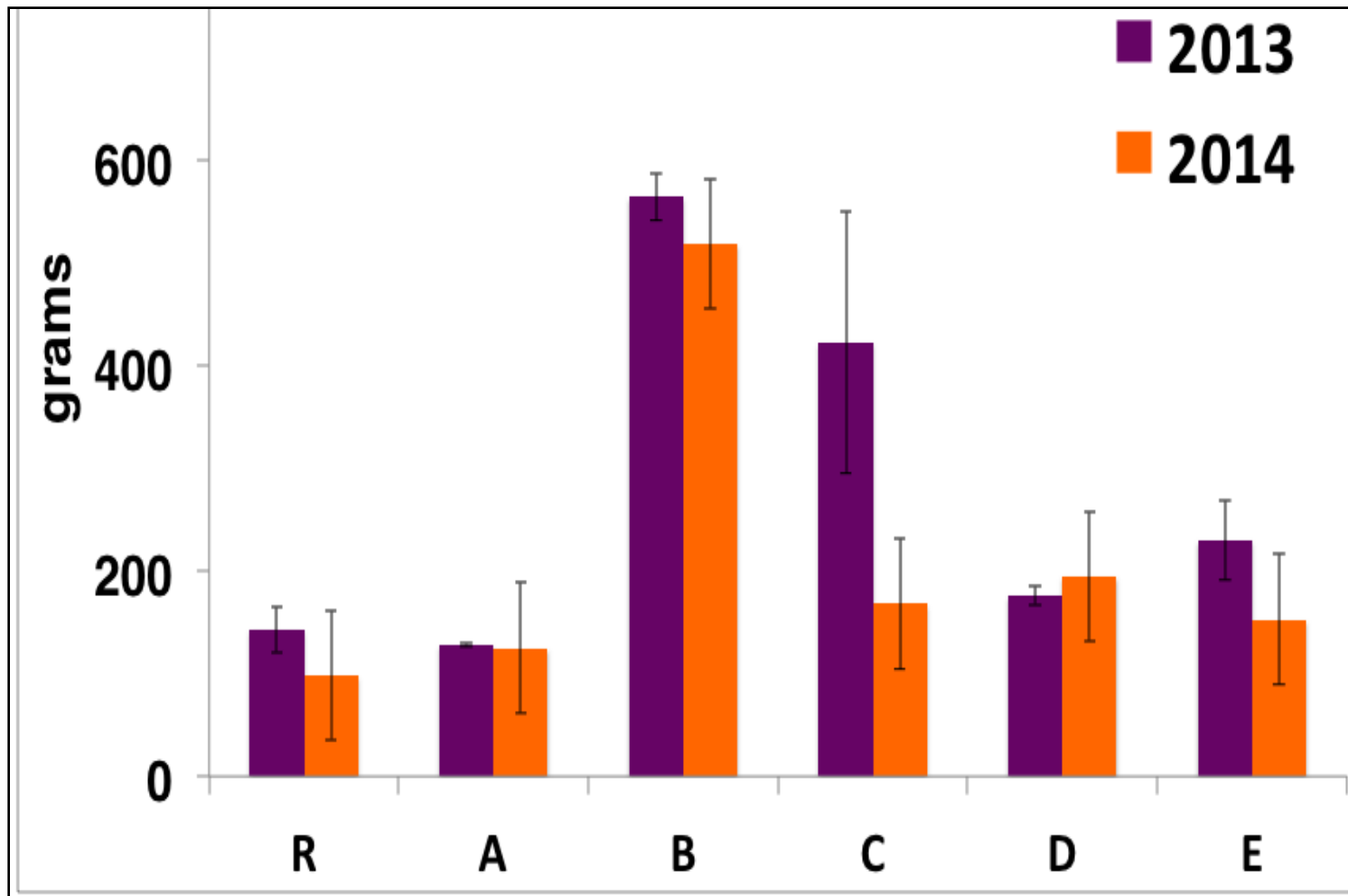


Figure 19 *Typha* Aboveground (Living and Dead) Aboveground Biomass. Change in *Typha* aboveground biomass between 2013 and 2014 at the high marsh brackish transitional zone, which was dominated by robust *Typha* in 2013. Locations of plots are indicated in Figure 3.