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Complete List of Authors:	Porter, Caitlin; Saint Mary's University, Biology Lundholm, Jeremy; Saint Mary's University, Biology Bowron, Tony; CBWES, Lemieux, Ben; CBWES, van Proosdij, Danika; Saint Mary's University, Geography Neatt, Nancy; CBWES, Graham, Jennie; CBWES,
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**Classification and environmental correlates of tidal wetland vegetation in Nova Scotia,
Canada.**

Caitlin Porter¹, Jeremy Lundholm¹ Tony Bowron², Ben Lemieux², Danika van Proosdij³, Nancy
Neatt², and Jennie Graham²

¹. Porter, C. (caitlinjimporter@gmail.com) & Lundholm, J. (jlundholm@smu.ca): Department of Biology,
Saint Mary's University, 923 Robie St., Halifax, NS B3H 3C3². Bowron, T. (Tony.Bowron@gmail.com),
Lemieux, B. (ben.d.lemieux@gmail.com), Neatt, N. (nancy.neatt@gmail.com) & Graham, J.
(jen.m.graham@gmail.com): CB Wetlands and Environmental Specialists (CBWES Inc.), 331 Newbury
Road, Hammonds Plains, Halifax, NS B4B 0C6. ³. van Proosdij, D. (dvanproo@smu.ca): Department of
Geography and Environmental Studies, Saint Mary's University, 923 Robie St., Halifax, NS B3H 3C3

Corresponding author: Caitlin Porter. Address: Department of Biology, Saint Mary's University, 923
Robie St., Halifax, NS B3H 3C3. Phone: (902) 719-4815. Email: caitlinjimporter@gmail.com,

Abstract: We numerically classified tidal wetland vegetation and determined the relationships between variation in plant species composition and environmental factors. Sampling was conducted at eight sites along a range of tidal magnitudes (<2 to >14 m). Cluster analysis revealed seven distinct salt or brackish marsh plant associations, usually dominated by a single graminoid species. Redundancy analysis showed continuous variation among community units and identified inundation time, elevation, soil salinity and organic matter content as key correlates of plant community patterns. Associations detected were similar to those found in New Brunswick Bay of Fundy and Northumberland Strait wetlands, and to those farther south in northern New England, but two new brackish associations were also identified within this study (*Juncus balticus*-*Festuca rubra* and *Spartina pectinata*). Although elevation is understood to drive vegetation types in salt marshes in the region, here we show that salinity can differentiate vegetation types at the same elevation. These data provide a quantitative baseline and allow for better predictions of tidal wetland ecological restoration trajectories in Nova Scotia.

Key words: Plant communities, Tidal wetland, Salt marsh, Salinity, Inundation, *Spartina*

33 **Introduction**

34 Tidal wetlands comprise some of the most fertile and valuable coastal habitats globally and are important
35 features of the north-eastern Atlantic coastline of North America. Tidal wetlands provide many ecosystem
36 services including buffering of coastal zones from storm damage, and provision of habitat for ecologically
37 significant and commercially important species (Fernald 1920, McAloney 1981, Roberts and Robertson
38 1986, Hicklin 1987, Fielding 2001, Craft et al. 2009). Tidal wetlands are regularly inundated and
39 characterized by a salinity gradient (Ewanchuk and Bertness 2004). Within eastern North America, the
40 salinity gradient is represented by freshwater marshes at higher elevations and salt marshes at relatively
41 lower elevations. These tidal wetlands are dominated by highly productive graminoids, mainly grasses
42 (Poaceae), sedges (Cyperaceae) and rushes (Juncaceae) (Zoltai and Vitt 1995, Warner and Rubec 1997).
43 Past works indicate that the zonation is maintained by biotic interactions between plant species, resulting
44 in the dominance of competitive species in more benign conditions, and stress-tolerant subordinate
45 species in areas subjected to increased inundation and salinity (Bertness and Ellison 1987, Bertness
46 1991a, Pennings and Callaway 1992, Pennings et al. 2005).

Development pressures have historically resulted in losses of European (e.g., Tonis et al. 2002) and North American (e.g., Neckles et al. 2002) tidal wetlands. In the three Maritime Provinces of Canada (Nova Scotia, New Brunswick, and Prince Edward Island), approximately 70% of the historical area of salt marsh has been lost, primarily due to dyking (Hanson and Calkins 1996). Nova Scotia contains over 50% of remaining salt marsh in the region (Bowron et al. 2012) divided among three distinct coastlines: the Atlantic Coast, the Bay of Fundy and the Northumberland Strait/Gulf of St. Lawrence.

There is a need for more robust quantitative classification and description of ecological conditions of tidal wetlands since restoration projects have become more prevalent in Maritime Canada over the past 30 years, and are increasingly important because climate change-associated sea level rise pressures marsh ecosystems (Olsen et al. 2005, Singh et al. 2007). Awareness of the loss of fish habitat and the threats to shoreline stability posed by relative sea level rise now prompt efforts to restore the ecological functioning of tidal wetlands (Bowron et al. 2011).

Research quantifying environmental factors and statistical analysis of vegetation-environment relationships of tidal wetlands in eastern Canada is limited. Previous accounts of salt marsh community composition and environmental drivers for tidal wetlands in Nova Scotian are largely either qualitative or

assess only a limited number of sites (Ganong 1903, Chapman 1937, 1974, Pielou and Routledge 1976, Thannheiser 1984, Roberts and Robertson 1986). Nova Scotian tidal wetlands have many of the same communities recognized further south in New England (Bertness and Ellison 1987, Jacobson and Jacobson 1989) including a low marsh zone dominated by *Spartina alterniflora* Loisel. and a mid- to high marsh zone dominated by *Spartina patens* (Aiton) Muhl.. Despite broad similarities between tidal vegetation in Nova Scotia and the other Maritime Provinces (e.g., Chmura et al. 1997, Olsen et al. 2005), and the well-studied tidal vegetation in New England, it is also known that species with a more northerly distribution can be common in the plant communities in the Bay of Fundy (Jacobson and Jacobson 1989, Chmura et al. 1997) and very little of the literature covers the brackish areas higher in the tidal frame which are quite common in many Nova Scotia marshes. The goals of this study were to classify tidal wetland vegetation, including brackish communities, in Nova Scotia using multivariate statistical and ordination methods, and to determine the environmental drivers of plant community composition.

Materials and Methods

Study region

Nova Scotia's climate is broadly categorized within the humid continental type, warm summer subtype according to the Koppen Climate Classification (Peel et al. 2007)(Appendix A6). Eight sites were selected to represent three distinctive coastal areas of Nova Scotia (Table 1; Fig. 1) (Bowron et al. 2012): the Bay of Fundy Region, the Atlantic Coast, and the Carboniferous Lowlands of the Gulf of St. Lawrence/Northumberland Strait Region. The sites (Table 1) serve as reference sites for ecological restoration activities in the region (e.g., van Proosdij et al. 2010); six from the Bay of Fundy, one Atlantic coast and one from the Northumberland Strait (Appendix A6). The Bay of Fundy region has the majority of tidal marsh habitat in the province and currently hosts the most established salt marsh ecological restoration projects in the region (van Proosdij et al. 2010, Bowron et al. 2011, 2012).

Vegetation was systematically sampled throughout July and August (peak biomass) along transects oriented perpendicular to the primary watercourse. Transect plot sampling was used rather than subjectively placed releve plots since this method may be particularly important for detecting fine-scale patterns in marshes by avoiding assumptions frequently made about stand homogeneity (Zedler 1999). Transects were oriented from a benchmark at the upland edge of each marsh, delineated by the distinct hydrological, vegetation and elevation boundary associated with wetlands. For most of the sites, this

boundary corresponded with the discrete toe of a steep slope. The upland edge of marshes was included in the sampling design mainly to support ongoing long-term monitoring of these sites, but also to maintain sampling consistency in the grid pattern between sites and to capture a wide gradient in elevation and zonal vegetation. Transects spanned the breadth of each marsh from the upland edge to the primary watercourse. The interval distances between transects and between samples along each transect were consistent within sites but varied between sites dependent upon site size.

Long-term data from vegetation plots over the last 10 years at these sites indicate vegetation was stable over the course of monitoring save for variation in the size and location of small unvegetated salt water pannes or natural site disturbances including ice scarification and creek bank erosion. The salinity and sediment sampling methodology was updated in 2009; therefore the analysis used 2010 vegetation, salinity and sediment data for consistency, with the exception of Smith Gut at which all variables were sampled in 2009.

Plant species composition and abundance were sampled from 1m² quadrats using the point-intercept method (e.g., Roman et al. 2002). Each quadrat was divided into 25 grid squares (20 cm x 20 cm) and sampling was conducted at the intercept points using a wooden dowel (3mm diameter, 1m length).

106 Vegetation height was measured to the nearest 0.01m for the most abundant species in each plot. The
107 number of pins contacting a species was used as a measure of abundance of that species within the plot;
108 species rooted in the plot but not contacting a pin were assigned a value of 0.05. All plants were identified
109 to species level. Scientific nomenclature is provided according to the International Taxonomic
110 Information System database (ITIS 2015), but common names follow the Atlantic Canada Conservation
111 Data Centres database (ACCDC 2015).

112 *Environmental variables*

113 All sample plots were surveyed using a Trimble R8 GNSS RTK GPS surveying system which has a
114 reported accuracy of 9 mm horizontal and 15 mm vertical. In 2010, surveys were processed by a third
115 party and accuracy reports were not provided. However, accuracy reports for subsequent surveys in the
116 same region made with the same equipment had a horizontal precision of 12 ± 13 mm, vertical precision
117 of 19 ± 19 mm, and position (3D) dilution of precision of 1.51 ± 0.51 . Elevations are reported relative to
118 the Canadian Geographic Vertical Datum of 1928 (CGVD28), which is referenced from Mean Water
119 Level (MWL) measurements made in 1928 at tide gauges across Canada. To incorporate tidal range into
120 analyses, hydroperiod was determined for each sample plot. Inundation frequency and mean inundation

121 time for all study sites was determined using plot elevations and predicted tide heights. Predicted tidal
122 signal (5 minute interval) and high tide elevations were obtained for Canadian Hydrographic Service
123 (CHS) tide stations at Chezzetcook Inlet (CHS tide station #43), Merigomish (CHS tide station #1620),
124 and Hantsport (CHS tide station #282) using Tides and Currents Pro v2.5. The data were then converted
125 from Chart Datum (CD) to CGVD28 using reference benchmarks provided by CHS to allow comparison
126 to surveyed plot elevations. Inundation frequency was calculated by determining the percentage of
127 predicted high tides within the year that exceed the plots elevation and result in tidal flooding. Mean
128 inundation time was calculated by using the tidal signal to determine the total amount of time each plot
129 was flooded and dividing by the number of high tide events that resulted in tidal inundation.

130 Interstitial pore water salinity was sampled three times in July, August and September, from a subset
131 of the vegetation sampling stations representative of tidal and elevation range of each marsh (Table 1).
132 Samples were collected at low tide when there was no precipitation. At each sampling location a shallow
133 (15 cm) and a deep (45 cm) pore water sample was taken using a soil probe sipper constructed according
134 to the design specified in Roman et al. (2002), with larger diameter tubing (4 mm) to accommodate the
135 minerogenic conditions experienced on marshes in the Minas Basin. The sample design is intended to

capture variability in pore water samples observed seasonally and spatially, both within the rooting zone and across the marsh platform. Pore water samples were stored until suspended particles settled, after which a refractometer (nearest 2 ppt) reading was collected. Salinity data were averaged to provide a single mean value per location for use in analyses.

Paired sediment cores were collected from a subset of vegetation plots using a stratified random sampling procedure to ensure that different elevations were sampled (Table 1). Sample size varied between sites depending on sampling design and intensity at any given site (Table 1). The first of the two cores was collected by inserting a 30 ml syringe (26 mm diameter; 53 mm depth) for bulk density and the second collected by pressing a metal tube (10.16 cm long and 3.81 cm diameter) to level with sediment surface and ensuring that the interior and exterior surface levels were equal. Bulk density (g/cm^3) was determined by drying and weighing a known volume of the sample. The second core was removed from the ground using a knife and trowel to minimize compaction and individually capped, sealed in a plastic bag, labelled and frozen. The top 2 cm of this core was removed, sectioned into two equally sized sub-samples. One sub-sample was weighed and placed in a crucible for drying at 105 °C for 24 hrs to determine water content. Once dried, each sample was weighed and placed in a muffle furnace for two

151 hours at 550 °C. These subsamples were then cooled in a desiccating jar and weighed again to calculate
152 loss on ignition (LOI) of organic material. Coarse organic material was removed using tweezers from the
153 second sub-sample destined for grain size analysis. Remaining organic fraction was removed by digestion
154 using 30% hydrogen peroxide in order to prevent fusing the fine fraction. The resultant mineral sediment
155 of the second sub-samples were then processed through a Coulter Laser Multisizer 3, merged using a
156 customized script in Matlab and analyzed using Gradistat (Blott and Pye 2001). Size classes were
157 determined using a modified Udden-Wentworth scale (Blott and Pye 2001).

158 *Statistical analyses*

159 To explore multivariate relationships in plant species composition, a Principal Components Analysis
160 (PCA) was conducted on Hellinger's transformed species abundance data to overcome limitations related
161 to linear assumptions (Legendre and Gallagher 2001). Though more traditional ordination techniques can
162 provide similar projections of species coordinates in multivariate space, PCA was best suited for these
163 analyses because of its high resolution (lack of distortion), solution (outcome of analyses) stability
164 (Legendre and Legendre 1998, Wildi 2010) and because it avoids the risk of uncontrolled alteration to the
165 similarity pattern inherent within detrending procedures (Legendre and Legendre 1998, Wildi 2010,

Borcard et al. 2011). Axes with eigenvalues greater than one were considered significant and used for interpretation.

Redundancy Analysis (RDA) was used to determine relationships between plant species composition and measured environmental variables describing sediment, topographic and hydrological characteristics of the vegetation sampling plots (list of variables used in Appendix A1). Prior to analysis, species abundance data were Hellinger transformed. Environmental variables were first standardized to zero mean and unit variance. A forward selection procedure was used to identify which of those environmental variables explained the most variance in species composition and abundance. Three separate analyses were performed: all plots included; only plots where sediment variables were sampled (Table 1); only plots where salinity variables were sampled (Table 1).

To identify distinct plant associations, a floristic cluster analysis was performed on standardized species abundance data using the Ward's minimum variance clustering method (Ward 1963), which seeks to minimize the sum of squared distances within clustered groups. This technique avoids several problems associated with the more popular TWINSpan or average-linkage clustering methodologies (see Legendre and Legendre 1998). Formal agglomerative hierarchical clustering, combined with random

181 sampling avoids bias of initial assumptions made about community structure inherent with many other
182 classification methodologies (Wildi 2010).

183 A meaningful level of dendrogram cutting (i.e., identifying split points among clusters which would
184 differentiate groups) was determined quantitatively. To establish the first criteria for cutting, fusion levels
185 were plotted and the range where clear jumps between levels occurred was identified (Legendre and
186 Legendre 1998, Borcard et al. 2011). Next, silhouette widths were plotted and the optimal number of
187 clusters was determined according to the Rousseeuw quality index (Rousseeuw 1987). Then a silhouette
188 plot of the final partition was created. Group membership and misclassifications were assessed through
189 associated Si values; a measure of grouping validity and relative strength. The square roots of fusion
190 levels were plotted to avoid distension of the dendrogram without altering topology, as recommended by
191 Borcard et al. (2011). Communities were named based on dominance according to CNVC standards at the
192 hierarchical level of the association (CNVC 2013). Indicator Species Analysis was applied to pre-
193 classified vegetation units to determine indicator species. Indicator species are defined as those expressing
194 either dominance (high frequency and abundance) or exclusivity to a given association (Dufrêne and
195 Legendre 1997). To evaluate the adequacy of the sampling methods to detect associations and species,

196 sampling effort curves were calculated to determine whether the number of associations or species
197 detected reached an asymptote (indicating capture of all associations or species in the sampled areas).
198 Associations and species accumulation were summarized by plots, transects, and sites using 1000
199 randomizations each. All analyses were performed using the open source software R, version 2.15.0 (R
200 Core Team 2013); packages used included "vegan" for PCA, RDA and cluster analyses, "PACKFOR" for
201 forward selection of environmental variables in RDA, "labdsv" for indicator species analysis, and
202 "specaccum" for sampling effort curves.

203

204 **Results**

205 *Overall species richness, frequency, and abundance*

206 Eighty-three vascular plant species were identified across all eight study sites; including 28 graminoids,
207 54 forbs and one shrub species (Appendix A2). Forbs contributed the largest percent of species richness,
208 but graminoids were the most frequent and abundant growth form encountered. The only shrub species,
209 *Myrica gale* L., was identified within two sample plots.

210 *Plant species composition patterns*

211 Five clonal graminoid species account for most of the differentiation in species composition and
212 abundance between plots (Fig. 2). *Spartina alterniflora* and *Spartina patens* are closely associated in
213 positive score on Axis 1 in the PCA diagram, but widely separated on Axis 2 (Fig. 2a). *Carex paleacea*
214 Schreb. Ex Wahlenb. exhibits the lowest negative score on Axis 1, followed by centroids of *Juncus*
215 *gerardii* Loisel. (high on Axis 3) and *Spartina pectinata* Link, also projected negatively on Axis 1. *C.*
216 *paleacea* and *S. pectinata* are both at the low end of Axis 3 (Fig. 2b). The rest of the species are not
217 strongly associated with any of the main axes of variation (Appendix A4), so the main community types
218 may be expected to differ mainly in the abundance of these five main graminoid species. Plots at different
219 sites are spread throughout the ordination space, thus there were no plant communities distinct to
220 particular sites. The St. Croix site stands out in being deficient in plots characterized by *S. patens* and *S.*
221 *alterniflora* (Fig. 2a), and plots with abundant *J. gerardii* (high scores on Axis 3) are concentrated at Bass
222 Creek, Cogmagun, and Smith Gut sites (Fig. 2b)

223 *Vegetation classification and environmental variables*

224 Seven distinctive plant associations were identified using Ward's minimum variance clustering (Fig. 3;
225 detailed descriptions are in Appendix A7). All but two of these associations are characterized by a single
226 dominant clonal graminoid species, after which the associations are named (Fig. 3, Tables 2 and 3).
227 Species richness varied between six and 40 species per association. The associations generally sort out
228 over gradients of elevation, salinity and inundation (Fig. 4, Table 3). The *S. alterniflora* association was
229 found at the lowest elevations, with high inundation durations and relatively high salinity (Table 3). The
230 *S. patens* association was next higher up in elevation and also characterized by relatively long inundation
231 and high soil salinity. Both *Distichlis spicata* (L.) Greene and *Juncus gerardii* associations occurred in
232 areas with relatively high elevations and salinities, and low inundation durations; The *Carex paleacea*
233 association was found in high elevations with low salinity and intermediate inundation durations; the
234 *Spartina pectinata* association was at similar elevations to the previous, but with lower inundation
235 duration and salinity. The *J. balticus*-*Festuca rubra* association had highly variable inundation durations
236 depending on the site and occurred at relatively high elevations and low salinities. Finally, the upland-
237 miscellaneous vegetation was mainly comprised of sample plots located on the upland edge, these often
238 had very low salinity but intermediate inundation frequencies.

239 The RDA model including all plots explains 16.6% of variance expressed by species in response to
240 environmental factors (Fig. 4, Appendix A3). Positive RDA axis 1 scores are associated with the tallest
241 measured vegetation heights and the species *S. pectinata*, *C. paleacea*, *Symphyotrichum novi-belgii* (L.)
242 G.L. Nesom. and *Agrostis stolonifera* L. (Fig. 4a). Negative RDA 2 scores are associated with short
243 inundation time and the species *J. gerardii*, *C. paleacea*, *S. pectinata*, *Potentilla anserina* ssp. *anserina*
244 L., *Festuca rubra* L. and *Solidago semprevirens* L. Positive RDA 2 scores are associated with long
245 inundation times and the species *S. alterniflora*. Areas dominated by *S. patens* are thus higher in elevation
246 and have shorter inundation times than areas dominated by *S. alterniflora* (Fig. 4a, Table 3). The four
247 plots dominated by *D. spicata* are associated with higher elevations and shorter inundation times
248 compared with *S. patens* (Fig. 4b). *J. gerardii* is projected at negative RDA 1 and 2 scores, associated
249 with relatively high elevation. When plot subsets where salinity or sediment data were collected were
250 analyzed, patterns in the RDAs were largely consistent with those presented in Table 3 (Appendix A5).

251 Association accumulation curves level off indicating that sampling approximately five sites, 30
252 transects or 75 plots, if selected at random, was necessary to capture all the community types
253 (associations) in the region (Fig. 5). Species accumulation curves show no levelling off at the sampling

intensity in this study (Fig. 5), suggesting that more species may be detected with higher sampling effort within these sites.

Discussion

Salt Marsh Ecology

The three main salt marsh communities found (those dominated by *S. alterniflora*, *S. patens*, or *J. gerardii*) are commonly found in low, intermediate and high elevations in New England and New Brunswick (eg., Chmura et al. 1997, Olsen et al. 2005). *S. alterniflora* is the dominant low marsh species throughout the north-western Atlantic, and is considered to be restricted to high salinity, long inundation conditions due to its competitive inferiority to *S. patens* and other high marsh species (Bertness and Ellison 1987). However, *S. alterniflora* has been shown experimentally to succeed across the elevation/inundation gradient when competitors are removed (Bertness and Ellison 1987), and was found frequently in plots classified as belonging to the *S. patens* association (Figure 4a). This may reflect wrack or ice disturbance within the *S. patens* zone, leading to small bare patches that can be colonized by *S.*

268 *alterniflora*. *S. patens* is dominant at intermediate elevations, and cannot penetrate lower in the tidal
269 frame due to its inability to oxygenate soils and tolerate longer flooding (Bertness 1991b, Kirwan and
270 Guntenspergen 2012), but is usually kept out of higher elevations as it is outcompeted there by *J. gerardii*
271 (Bertness 1991a), considered to be a later successional species (Patriquin 1981, Thannheiser 1984) and
272 thought to have a competitive advantage as it begins growth much earlier in the year (Bertness 1991a). *J.*
273 *gerardii* may also facilitate other species, as shade resulting from its canopy reduces evaporation, keeping
274 the salt concentration from rising and allowing colonization by less salt-tolerant species (Hacker and
275 Bertness 1999). For these communities, most of the subordinate species we found are also present in other
276 marshes further south in the US (Bertness and Ellison 1987, Jacobson and Jacobson 1989).

277 Although the *D. spicata* community was only detected at four plots, it was a distinctive community
278 type characterized by similar environmental conditions to the *J. gerardii* community: high elevations,
279 high salinities and low inundation times. This species may colonize disturbances due to ice or wrack
280 deposition in high marsh areas when dominant competitors are killed off (Bertness et al. 1992). Despite
281 intolerance of flooding (Lonard et al. 2013), *D. spicata* also colonizes areas disturbed by submergence

relating to sea-level rise (Fox et al. 2012). In turn, *D. spicata* is known to facilitate *J. gerardii* and *S.*

patens via reducing substrate salinity (Crain et al. 2008).

Although many studies from the east coast of the US report the presence of a distinct vegetation type

occurring in pannes created by disturbance to high marsh vegetation (Ewanchuk and Bertness 2004,

Griffin et al. 2011), no comparable communities were identified in any of the sites in this study. In

general, forb pannes are largely absent from marshes in all three regions of the province, despite the

occurrence of large amounts of sea ice causing disturbances in the Bay of Fundy region. We have

observed patches of the earlier successional species, *Salicornia maritima* S.L. Wolff & Jefferies, but only

at disturbed sites. Studies on an outer Bay of Fundy marsh in New Brunswick report widespread *Plantago*

maritima L. in disturbed high marsh areas (Chmura et al. 1997, van Proosdij et al. 1999), but this species

was uncommon in sample plots in the current study. Pools containing *Zostera marina* L. and *Ruppia*

maritima L. have been also found on salt marsh restoration sites in Nova Scotia (Bleakney and Meyer

1979, Patriquin 1981). Chapman (1974) considers these to be an early successional stage of the forb

pannes found in New England. Patriquin (1981) similarly considers pannes to be a feature of an immature

marsh, occurring where poor drainage conditions created by uneven sediment distribution result in the

297 replacement of *S. alterniflora*. Of three sample plots included in this study that contained open standing
298 water, one contained *R. maritima* and was numerically allocated to the miscellaneous grouping of plots
299 that were otherwise associated with upland conditions.

300 Less is known about the distribution and environmental relationships of brackish communities. *Juncus*
301 *balticus* is reported as occurring at the terrestrial edge of the high marsh (*S. patens*, *J. gerardii*
302 communities) in Bay of Fundy sites (Chapman 1974, Chmura et al. 1997), and occurred in all three study
303 regions, but is seldom mentioned as a component of tidal marshes in other studies. This may represent a
304 community that is more common in more northern, west Atlantic tidal marshes (Thannheiser 1984). *C.*
305 *paleacea* is found in Maine tidal marshes with significant freshwater influence, as is *S. pectinata*
306 (Jacobson and Jacobson 1989), but that study did not detect *J. balticus* at all. While previous work in
307 Nova Scotia identifies the *C. paleacea* community as a high marsh community type (Pielou and Routledge
308 1976, Thannheiser 1984), there is almost no mention of *S. pectinata*, which is a common component of
309 brackish areas in the marshes studied. Here it appears that, while the "brackish" communities identified
310 are all characterized by intermediate salinities (9-12 ppt), the *C. paleacea* community is characterized by
311 longer inundation times than *S. pectinata*, and the *J. balticus*-*F. rubra* community appears at the highest

elevations/shortest inundation times of the three. The *C. paleacea* community is also characterized by the highest organic matter content (Table 3), which likely reflects high rates of peat production. Carbon storage by tidal marshes is determined in part by the net rate of organic matter production in the soil (Chmura 2013) and thus the persistence of this plant association may be important to the overall value of tidal marshes in the province. Further studies of belowground productivity are warranted to compare the potential of these different community types as carbon sinks.

We were able to differentiate between distinct associations documented at the same elevation and relate these to salinity and inundation. In tidal freshwater wetlands and marsh edges, tidal variability is high and the influence of freshwater input also varies seasonally thus affecting transport of sediments and nutrients, as well as salinity and acts as a constraint on plant growth (Flynn et al. 1995, Pont et al. 2002, Neubauer 2013). Gradients of inundation and salinity appear to be at least partially independent, with high salinities occurring at a range of inundation times. For example, the *J. gerardii* association is found at relatively short inundation durations similar to *S. pectinata*, but with much higher substrate salinity (Table 3). This is consistent with literature in which *J. gerardii* is considered to be species typical of high salt marsh (polyhaline) (eg., Chapman 1974), whereas *S. pectinata* and *C. paleacea* are considered

327 brackish or mesohaline species. Plant species also show independent variation to both gradients. For
328 example, Egan and Unger (2000) found that highly salt-tolerant species differed greatly in their tolerance
329 to inundation. Given the scarcity of published literature on marsh edge and brackish communities (*J.*
330 *balticus* - *F. rubra* and *S. pectinata*), and because salinity did not always correlate with elevation and
331 inundation time, restoration managers in the region are recommended to incorporate more salinity
332 sampling into their monitoring programs in order to predict vegetation dynamics.

333 Sediment variables show similar patterns to those reported in other studies (DeLaune et al. 1979,
334 Crooks et al. 2002, van Proosdij et al. 2010), with relatively fine particles and high bulk density
335 associated with low marsh (*S. alterniflora* associations), and brackish associations with greater organic
336 content and lower bulk densities. Vegetation height was included as an environmental variable in the
337 redundancy analysis as an index of productivity, but this may be valid only within a species (Fox et al.
338 2012) and using these results only as descriptors of the communities is recommended. Other variables
339 such as redox potential and nutrient levels may also affect plant community composition (Bertness and
340 Ellison 1987, Davy et al. 2011, Fox et al. 2012), but were not measured in this study and may provide
341 further resolution to the plant community patterns detected here. Likewise, disturbances caused by

342 grazing, ice scour and deposition of vegetation mats could also affect distribution of species (Schröder et
343 al. 2002, Hulzen et al. 2006), especially subordinates, which did not respond strongly to the measured
344 environmental gradients here.

345 *Regional Variation*

346 In general, many of the same associations were found on all three coastlines within the region, despite
347 large differences in elevation and tidal characteristics between Fundy and the other two coasts (Table 3).
348 The association accumulation curves suggest that the sampling methods were adequate to detect all
349 associations at the sites. Both the Atlantic and Northumberland Strait Regions are characterized by much
350 lower tidal amplitude than the Bay of Fundy but the relative position of the different associations along
351 the elevation gradient is similar across all three coasts (Table 3), suggesting that the dominant plant
352 species are responding to the same ecological processes in all the regions. In general, more sampling of
353 Northumberland Strait and Atlantic wetlands is necessary to confirm the generality of patterns we
354 observed in this study.

355 *Succession and Implications for Restoration Monitoring*

356 The sites sampled here are representative of reference conditions for tidal marshes in the region.
357 Succession in tidal marshes has been described in the region (Chapman 1974, Patriquin 1981), but not
358 quantitatively studied in Nova Scotia, with the exception of recovery trajectories in restored marshes
359 (Byers and Chmura 2007, Van Proosdij et al. 2010). The sites described here represent mature
360 communities where vegetation zonation is relatively stable due to the lack of current anthropogenic
361 disturbances. These communities have been recognized as relatively stable over hundreds of years in New
362 England (Miller and Egler 1950).

363 Primary succession in salt marshes in the region is considered to consist of colonization of a site by *S.*
364 *alterniflora* followed by accretion of sediment, and later differentiation into low marsh (dominated by *S.*
365 *alterniflora*) and high marsh (dominated by *S. patens*). We have now recognized other high marsh types
366 as separate associations, but their successional trajectories are not known. The occurrence of these
367 different salt marsh types may relate to ecological factors such as the relative ability to colonize after
368 disturbances (e.g. Bertness and Ellison 1987) and the relative frequency of small disturbances caused by
369 ice or wrack deposition, which were not quantified in our study. Secondary succession in these systems
370 has been hypothesized to consist of salt marsh annuals, followed by recolonization by *S. alterniflora* or

371 high marsh species at higher elevations. We did not detect communities dominated by annuals in this
372 study, but have observed these at restoration sites, where bare mud is much more common. In New
373 England, such patches are usually recolonized by perennials within three years (Bertness and Ellison
374 1987).

375 Ecological restoration of tidal wetlands in Nova Scotia has proceeded using a paired-reference site
376 approach, where each site under restoration is compared with an intact or reference marsh nearby
377 (Bowron et al. 2012). When the nearest intact marsh has a different range of environmental conditions
378 than the restoration site, this can complicate predictions of vegetation zonation and the relative proportion
379 of plant associations as recovery proceeds (van Proosdij et al. 2010). Now that the elevation ranges have
380 been quantified and other environmental characteristics of the tidal wetland communities described it may
381 be possible to build a reference condition model for tidal wetlands in each region. This would enable
382 restoration efforts to progress to a multiple-reference site approach where vegetation plots from a regional
383 set of pre-established reference sites can be matched with plots at restoration sites that have similar
384 environmental conditions (Reynoldson et al. 1997, Westhead 2005), resulting in cost savings.

385 Sea level rise will likely shift zonation of tidal marshes to higher elevations relative to current-day
386 upland communities. The ability for tidal marsh communities to migrate landward and persist depends on
387 sediment supply, the tidal range of the site and the distribution of elevations (Chmura 2013) and lack of
388 anthropogenic barrier (e.g. road or dyke) (Ponte 2013). This study presents baseline information (e.g.
389 ranges of environmental variables) describing plant communities and their environmental correlates,
390 needed to predict response to climate change (Warren and Niering 1993, Gedan and Bertness 2009,
391 Hladic and Alber 2014). In the face of sea level rise and increasing inundation, we can predict that these
392 communities will shift inland, with the relative extent of different zones depending to a large extent on
393 site-specific elevation distributions, the existence of natural habitats (as opposed to built structures) into
394 which tidal march communities can migrate, and hydrological influences (Byers and Chmura 2014),
395 including the amount of freshwater influencing the marsh in its new tidal range.

396 This paper was the first to use quantitative methods to classify Nova Scotia tidal wetland communities
397 and link plant community composition with environmental gradients. This study provides resolution of
398 the brackish associations at the oligohaline ends of the salinity gradients. This information can facilitate

399 adoption of a multiple reference site approach, with a strong baseline for studies on the restoration,
400 monitoring and management of coastal wetlands in the region.

401

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407

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578 **Tables**579 **Table 1.** Study site location, site elevation and sample size.

Site	GPS Location (UTM)	Site Elevation (m)		Sample Size		
		Mean	Range	Vegetation	Salinity	Sediment
Cogmagun River*	412096E, 4992816N	6.68	4.86-7.25	23	8	7
Walton River*	421950E, 5008087N	6.18	4.62-7.25	28	5	3
Walton Fringe*	422407E, 5007824N	5.62	4.28-6.95	13	0	0
Bass Creek*	410990E, 5005715N	5.77	4.22-6.57	25	5	17
Smith Gut †	547844E, 5055018N	0.72	0.22-0.89	20	5	6
Lawrencetown ‡	472402E, 4943514N	0.58	0.37-0.77	24	6	5
St. Croix*	419838E, 4984888N	7.42	5.31-8.74	19	6	6
St. Croix Fringe*	418642E, 4980339N	6.38	4.84-8.06	13	0	1
				(n=165)	(n=35)	(n=45)

580 *Bay of Fundy, †Northumberland, ‡Atlantic Coast, GPS coordinates are provided in UTM, Zone

581 20NNAD 84

582

583 **Table 2.** Indicator Species of tidal marsh vegetation associations.

Association	Indicator Species	Indicator value*	p	Frequency %
<i>Spartina alterniflora</i> Salt Marsh	<i>Spartina alterniflora</i>	0.68	0.001	100
<i>Spartina patens</i> Salt Marsh	<i>Spartina patens</i>	0.50	0.001	100
<i>Distichlis spicata</i> Salt Marsh	<i>Distichlis spicata</i>	0.92	0.001	100
<i>Juncus gerardii</i> Salt Marsh	<i>Juncus gerardii</i>	0.75	0.001	100
<i>Carex paleacea</i> Brackish Marsh	<i>Carex paleacea</i>	0.61	0.001	100
<i>Juncus balticus</i> - <i>Festuca rubra</i> Brackish Marsh	<i>Juncus balticus</i>	0.68	0.001	67
	<i>Festuca rubra</i>	0.56	0.001	80
	<i>Anthoxanthum nitens</i>	0.29	0.01	40
	<i>Scutellaria galericulata.</i>	0.26	0.006	27
	<i>Myrica gale</i>	0.14	0.03	13
	<i>Carex hormathodes</i>	0.14	0.042	13
	<i>Spartina pectinata</i> Brackish Marsh	0.83	0.001	100
	Upland-Miscellaneous			
	<i>Taraxacum officinale</i>	0.40	0.002	40
	<i>Galium palustre</i>	0.34	0.008	45
	<i>Equisetum arvense</i>	0.28	0.014	35
	<i>Poa pratensis</i>	0.24	0.003	20
	<i>Solidago canadensis</i>	0.19	0.014	35
	<i>Solidago gigantea</i>	0.19	0.038	20
	<i>Bromus inermis</i>	0.14	0.05	10
	<i>Centaurea nigra</i>	0.14	0.042	15

584 * Dufrêne-Legendre Indicator Species values; large indicator values (upper limit is 1.0) indicate high
585 levels of specificity and fidelity to a particular association; low p values express significance ($\alpha= 0.05$)

586 **Table 3.** Summary of environmental characteristics of tidal marsh vegetation associations.

		Salt Marsh				Brackish Marsh			Upland
Association		<i>Spartina alterniflora</i>	<i>Spartina patens</i>	<i>Distichlis spicata</i>	<i>Juncus gerardii</i>	<i>Carex paleacea</i>	<i>Spartina pectinata</i>	<i>Juncus balticus-Festuca rubra</i>	Upland and miscellaneous
Mean elevation (m relative to CGVD28 vertical datum±SE)	Fundy	5.15±0.13	6.05±0.10	6.24±0.34	6.73±0.11	6.54±0.21	6.49±0.23	7.13±0.17	6.98±0.43
	Atl.	0.42±0.02	0.58±0.02			0.62±0.02	0.67	0.70±0.02	
	North.	0.33±0.11				0.71±0.03	0.82±0.03	0.78±0.02	
Elevation range (m)	Fundy	4.22-6.32	4.32-6.68	5.36-6.65	5.7-7.19	5.24-7.366	5.18-7.48	6.48-7.72	4.84 - 8.74
	Atl.	0.37-0.49	0.49-0.64			0.59-0.67		0.66-0.77	
	North.	0.22-0.44				0.52-0.81	0.66-0.89	0.74-0.79	
Mean inundation time (minutes* ±SE)	Fundy	143.2±5.5	111.2±4.0	105.2±11.0	80.6±5.3	91.6±9.0	85.7±8.3	57.5±12.3	101.3±31.8
	Atl.	416.2±10.3	351.7±9.5			330.5±8.4	314.7	301.1±8.3	
	North.	366.2±51.1				182.1±15.8	139±10.5	153.2±5.2	
Mean pore water salinity (±SE)	(ppt)	18.2±1.7	20.0±1.7	21.6	21.6±3.0	12.4±1.3	9.54±1.24	9.3±4.5	0.7±0.4
Mean particle size (±SE)	(microns)	8.86±0.32	9.50±0.56	8.19	9.84±0.90	16.73±5.79	30.17±16.6	17.45±6.23	8.20±0.09
Mean sediment organic matter	(%)	6.66±0.40	19.40±4.67	15.42	14.61±1.35	31.72±7.10	15.87±4.83	24.82±7.82	14.13±5.83

Mean sediment dry bulk density	(g*cm-3)	0.81±0.04	0.49±0.10	0.83	0.66±0.07	0.31±0.07	0.65±0.15	0.44±0.15	0.72±0.30
Mean vegetation height	(cm)	106±7	52±2	59±5	44±2	87±7	142±9	75±13	96±14

* Average number of minutes plot is flooded during flooding events (ie., hydroperiod in minutes divided by inundation frequency in number of events).

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Figure Captions

Figure 1. Map showing locations of study sites. Redrawn from data provided by Natural Resources Canada; no permission required, see: <https://www.nrcan.gc.ca/terms-conditions/10847> ; information licensed under the Open Government Licence – Canada. <http://open.canada.ca/en/open-government-licence-canada>

Figure 2. Principal components analysis of species abundance in tidal marsh plots. Axes 1-3 explain 25%, 18% and 12% of the variance in species composition/abundance respectively. a) Axes 1 and 2; *Spartina alterniflora* and *S. patens* centroids are found at the coordinates (0.998,0.978), and (0.978, 1.01) respectively; central polygon contains all other species' centroids (Fig. S3) b) Axes 1 and 3; *S. alterniflora*, *S. patens* and *J. gerardii* centroid coordinates: (0.998,0.0535), (0.978, -0.217), (-0.309,0.998) respectively; Species' centroids indicated by abbreviations (Table S1). Major species: car.pal = *Carex paleacea*; jun.ger = *Juncus gerardii*; spa.alt = *Spartina alterniflora*; spa.pat = *Spartina patens*; spa.pec = *Spartina pectinata*.

Figure 3. Classification of tidal marsh vegetation. Height represents the dissimilarity index of the Ward's minimum variance clustering method. General descriptions of environmental characteristics represent a synthesis of RDA results (see Fig. 4) and average values of environmental variables described in the text (Table 3). Right side contains association names in bold, followed by the number of plots classified into each group (n), Si is the silhouette value, an index of within-group similarity (stronger positive scores = more similar), and total number of species (spp.) found in the plots classified into each group.

Figure 4. Redundancy analyses of species abundance in tidal marsh plots, with environmental variables; plots labelled using plant associations determined using Ward's minimum variance clustering. All plots, environmental variables included: elev = plot elevation; unin.time = amount of time plot is inundated; veg.height = height of vegetation; Axes 1-3 explain 9.8%, 5.6% and 2.2% of the variance in species composition in response to environmental variables, respectively. a) Axes 1 and 2; b) Axes 1 and 3. Central polygons contain all other species centroids. Major species: car.pal = *Carex paleacea*; jun.ger = *Juncus gerardii*; spa.alt = *Spartina alterniflora*; spa.pat = *Spartina patens*; spa.pec = *Spartina pectinata*; hie.odo = *Anthoxanthum nitens*; fes.rub = *Festuca rubra*; pot.ans = *Potentilla anserina*; sym.nov = *Symphotrichum novi-belgii*; agr.sto = *Agrostis stolonifera*

Figure 5. Sampling effort-association accumulation curves ((a)-(c)) for sites, transects and plots. Sampling effort-species accumulation curves ((d)-(f)). Polygons show 95% confidence intervals.

Appendix A1. Detailed climate and site descriptions.

Climate along the Atlantic coast is characterized by a long cool growing season and a winter that is more moderate in comparison with other parts of Nova Scotia. July temperatures are typically below 15°C, and January temperatures are on average above -5°C. Precipitation is on average 1200mm – 1400mm annually, except 1400mm – 1600mm in northern Halifax County. The Bay of Fundy is similar climatically. The Bay of Fundy region receives shelter from the North Mountain and Cobequid hills. The Atlantic coast is comparatively cooler in summer in comparison with the Bay of Fundy, and also frequently exposed to high winds. On the Northumberland Strait, annual precipitation averages less than 1000mm. Mean July temperatures are 17°C, and <6°C in January. Fog is common on the Atlantic Coast in the summer and fall, the summer in the Bay of Fundy and early spring on the Northumberland coast (Davis and Browne 1996). Salt marshes in all of these areas experience ice and snow for a minimum of four months of the year (Bowron et al. 2012).

The Bay of Fundy Region is a macro-tidal embayment with semi-diurnal (twice daily) tides ranging from 3 m at the mouth of the Bay to a maximum of 16.3 m at the head (Desplanque and Mossman 2004). It is characterized by high suspended sediment concentrations, causing high rates of sediment deposition in intertidal environments (Chmura et al. 2001, Bowron et al. 2012). In the Atlantic Coastal Region, coastal wetlands experience micro-tidal conditions (0.2 – 2.1 m) twice daily, and are subject to higher wave energy (Bowron et al. 2012) due to ocean swells (Davis and Browne 1996). Tidal range within the Northumberland Strait varies from 0.3 m to 2.4 m (Davies 2012) from west to east, although mean water levels and tidal constituents are variable due to the presence of an amphidromic point on the eastern boundary of the Strait (Davidson-Arnott 2010). This results in diurnal tides at the western entrance of the

Strait changing to larger semi-diurnal tides to the east along the NS shore (Desplanque and Mossman, 2004).

Relatively intact and regionally representative sites were selected. Current anthropogenic disturbance is largely absent from all of the study sites, which occur within a mixed forested, residential and agricultural context. Most of the sites are associated with transportation infrastructure (e.g., the upland edge of the Lawrencetown site is adjacent to a roadway), representing a vector for exotic species and limiting future landward migration in response to rising sea levels. Although the transportation infrastructure may influence hydrology and species composition, tidal flow and sediment input are unrestricted at all of these sites. In contrast with many New England marshes, a large portion of tidal wetlands in the Bay of Fundy are, or had historically been, dyked for agriculture (Ganong 1903). Remnant dykes are present at the St. Croix Fringe Marsh and also the Walton Fringe marsh. Although only the marshland outside of these dykes was sampled, agricultural activities including hay production would likely have taken place here as recently as 1900. At Cogmagun, historical agricultural use is evident by the presence of ditches that have been assimilated into a hybrid tidal creek network system. Previous studies in nearby regions have found that these historic agricultural disturbances are reflected in the vegetation communities (e.g., Jacobson and Jacobson 1989, Millard et al. 2013). While it could be argued that these study sites do not represent a pristine condition, the absence of current disturbance and the time elapsed since agriculture use is typical of this region, and therefore suitable as reference sites for restoration efforts.

Additional References:

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Appendix A2. Detailed descriptions of vegetation associations.

The ***S. alterniflora* Salt Marsh** association was found in 28 plots across seven sites ($Si=0.88$). The silhouette index (Si) is a measure of how distinct an association is, such that the closer Si is to 1, the more similar plots within the group are to one another, and the stronger the fit as a cluster. Weakly positive Si scores indicate elements in common with other associations and negative Si scores indicate a poorly clustered group.

This association's namesake *S. alterniflora* was found in every plot with high mean abundance (cover: $93.9\% \pm 22\%$). *S. patens* was found in fewer plots; with relatively lower abundance (cover: $29.3\% \pm 16.7\%$). No other species was found in more than three plots or 10.7% of sample plots in this association which is characterized by low species richness in general: six species total (mean: 1.5 species/m²). This association was found across all study sites except St. Croix fringe, and only one plot belonging to the association was found at St. Croix, and only two plots were found at Smith Gut. The indicator species *S. alterniflora* and sample plots in the association occur in areas with low elevation and with high inundation time (Figure 4a,b), intermediate salinity (Supplementary Figure S2) (although the average salinity across all plots in the association is quite high (Table 3), sediment of low organic content, small size and high bulk density (Fig. 4, Supplementary Figure S2). This association had the longest inundation times (Table 3). In terms of sediment, particle size was much lower than average and third smallest in comparison with other associations. Bulk density of sediment was greatest in comparison with other groups. Organic matter content of sediment were the lowest in comparison with other associations.

The ***S. patens* Salt Marsh** association was found at 37 plots across five sites ($Si=0.65$), with high abundance of the dominant *S. patens* present in every sample plot ($92.1\% \pm 24.1\%$ cover). *S. alterniflora* was identified in 26/37 sample plots with a mean of $32\% \pm 25.2\%$ cover. *A. glabriuscula* was found within 9/37 plots with a low mean cover of $6.3\% \pm 8.4\%$. No other species was found in greater than 4/37 sample plots. This association also shares *Limonium carolinum* and *Salicornia maritima* in common with the *C. paleacea* association, but lacks *Suaeda maritima* that is present in that association. As well, the *S. patens* association is slightly more species-rich than the *C. paleacea* one, with 13 species in total (mean: 2.4 species/m²). Plots in this association were found at five of eight study sites: Bass Creek, Lawrencetown, Walton, Walton-fringe and just one plot at Cogmagun. The indicator species *S. patens* and sample plots are most closely associated with relatively high inundation durations, high salinity, intermediate elevations and sediments of low bulk density, small particle size, low organic composition (Figure 4 Supplementary Figure S2; Table 3). Mean pore water salinity of this association is high (Table 3).

Although the ***Distichlis spicata* Salt Marsh** association was only found in four plots across three sites, it is a distinct association ($Si = 0.64$) characterized by high abundance of *D. spicata* ($95\% \pm 5\%$ cover). *S. patens* was also found within every plot, with lower mean abundance ($70\% \pm 24.1\%$ cover). *S. alterniflora* was found within three plots where its abundance comprised $68.3\% \pm 2.2\%$ cover. Three other species were identified within one sample plot only, for a total of 6 species belonging to this association (mean: 3.5 species/m²). Two sample plots were found at the Walton reference site, one at Walton Fringe and one at Bass Creek. The indicator *D. spicata*

and the four sample plots are associated with relatively high elevation, low inundation time, high salinity and bulk density of sediment (Table 3). Salinity/sediment characteristics are based on measurements from one plot only but this plot had very high salinity, comparable to that in the *J. gerardii* association (Table 3).

The ***J. gerardii* Salt Marsh** association was found in 19 plots at two sites ($Si=0.51$). The main species *J. gerardii* was present in all plots at high abundance (cover: $94.1\% \pm 9.8\%$). *S. patens* was found in about half of plots (9/19 plots) with variable abundance (mean of $36.5\% \pm 32.9\%$ cover). *S. sempervirens* and *Atriplex glabriuscula* were each found in 6/19 sample plots with mean covers of $36.7\% \pm 30.1\%$ and $1.5\% \pm 2\%$ respectively. No other species were found within more than three sample plots. *Plantago major* and *S. pectinata* occurred in relatively high abundance within the single sample plots where they were found. Total richness of the association was 17 species (mean: 3.05 species/m²). This association was found only at Bass Creek and Cogmagun study sites, and although Smith Gut had relatively high abundances of *J. gerardii* (Fig. 2), none of the plots at that site were classified to this type. The indicator species *J. gerardii* and the majority of sample plots in this association tend to occur in areas with high salinity, high elevation, and short inundation times (Supplementary Figure S2). Mean elevation is second greatest of the associations and inundation time is the lowest (Table 3). Sediment characteristics are intermediate for most variables, and pore water salinity was the highest measured (Table 3).

The ***Carex paleacea* Brackish Marsh** association was assigned to 21 plots across seven sites ($Si = 0.25$) (Figure 3; Table 3), and is characterized by dominance of *C. paleacea*, which was present in every plot and of greatest abundance (mean cover $\pm$ standard deviation: $97\% \pm 6.6\%$) within the association. 21 species were identified within this group (mean plot richness: 4.5 species/m²). In addition to the dominant sedge, several other species occurred with notable abundance and frequency. *Agrostis stolonifera* was identified within almost half of sample plots (10), with a mean abundance of $16.2\% \pm 3.3\%$. *Festuca rubra* was found in eight/21 plots with a mean abundance of $6.3\% \pm 9.95\%$. *S. patens*, *J. gerardii* and *Argentina anserina* were found within 7/21 sample plots with mean abundances of $5.14\% \pm 3.5\%$, $4.29\% \pm 3.7\%$, and $1.4\% \pm 1.4\%$ respectively. *S. alterniflora* and *S. sempervirens* were the only other species found in more than five sample plots. They each had small mean abundances: $2.6\% \pm 1.8\%$, and $1.9\% \pm 1.6\%$ respectively. The indicator species *C. paleacea* and the majority of sample plots in this community are associated with higher inundation time and greater sediment size (Supplementary Figure S2). Mean pore water salinity was intermediate and indicative of brackish conditions (Table 4). Sediments were slightly larger than average in particle size, low in bulk density and had the highest organic matter content (Table 3).

The ***J. balticus* – *F. rubra* Brackish Marsh** association was found in 14 plots across seven sites ($Si=0.13$), and is one of the most species rich, with 40 species identified in total (mean: 7.7 species/m²). Six indicator species characterize this association (Table 3). The strongest indicator species is *J. balticus* (Table 3): 10 of 14 plots containing this species belong to this association and it is represented in relatively high abundance where found: $90.4\% \pm 13.4\%$ cover. *F. rubra* is next strongest indicator and the most frequent species, present in all but two sample plots this association (12/14 plots). *F. rubra* occurred in high abundance: $90.3\% \text{ cover} \pm 23.7\%$.

Though not an indicator species, *C. paleacea* was identified in more than half (9) of sample plots, where it had relatively high cover values: $42\% \pm 27\%$. No other species were found in greater than six plots in the association, but several species were exclusive to the *J. balticus*-*F. rubra* association and represent indicator species (Table 3). *Hierochloa odorata* was relatively uncommon throughout the study (16 sample plots with $41\% \pm 27.5\%$ cover), but was found in six sample plots belonging to this association, expressed in higher abundance than elsewhere outside the association: cover = $64.7\% \pm 13.2\%$. *Scutellaria galericulata* was found five times throughout this study, with four occurrences belonging to the *J. balticus*-*F. rubra* association (cover = $27.1\% \pm 30.5\%$). *Myrica gale* was found only within two sample plots; both belong to this association (cover = $22\% \pm 25.4\%$). *Carex hormathodes* was found within only three sample plots throughout the study, two of which belong to this association (cover = $6.1\% \pm 8.3\%$). Both indicator species *J. balticus* and *F. rubra* and sample plots in the association tend to occur in areas with large particle size, high organic matter, high inundation time, low elevation and relatively low salinity (Figure 4; Supplementary Figure S2; Table 3).

The ***S. pectinata* Brackish Marsh** association was found at 21 plots across seven sites ($S_i=0.26$). The dominant *S. pectinata* was present in every plot with mean of $91\% \pm 10.7\%$ cover. *C. paleacea* was the second most frequent species, present within most (12/21 or 80.9%) sample plots at $44.5\% \pm 32.7\%$ cover. *S. novi-belgii*, *A. stolonifera*, and *S. sempervirens* were found in eight, seven and six plots respectively, comprising $11.9\% \pm 24.2\%$, $13.4\% \pm 37.2\%$, and $46.7\% \pm 10.3\%$ cover respectively. Total species richness of this association is 39 species (mean: 6.1 species/m²). *S. pectinata* and plots classified into this association were found in areas with relatively high elevation, intermediate to low salinity and low inundation duration (Table 3; Figure 4; Supplementary Figure S2). Sediment particle size was relatively high on average, but also had great variability (Table 3).

The remaining 21 plots could not be classified and form a "miscellaneous" group ($S_i=-0.006$). All of these plots were found at the St. Croix-reference and St. Croix-fringe sites. This group contained the highest number of misclassifications: seven plots, representing 33% of plots within the group. Other plots maintained weakly positive S_i scores. Total species richness is 54 species, larger than any other association (mean: 7.3 species/m²). The strongest indicator species of this group of plots is *Taraxacum officinale*; a non-native, weedy upland species found in 8/21 plots with abundance of $13.5\% \pm 14\%$ cover. *Galium palustre* was the most abundant species of the group, found in 9/21 plots with a mean abundance of $46.2\% \pm 32.5\%$ cover and represents the second strongest indicator value. All other indicator species were uncommon throughout this study or entirely exclusive to the upland/miscellaneous plots. Seven of ten occurrences of *Equisetum arvense* within this study were found within this association. Four of five study occurrences of *Poa pratensis* occur within this association. Seven of eight occurrences of *Solidago canadensis* belong to this association. Two of three occurrences of *Bromus inermis* were found within this association. All four occurrences of *Solidago gigantea* and all three occurrences of *Centaurea nigra* belong to this association. This group of indicator species form an assemblage of species absent from all other tidal wetland associations identified. Plots and indicator species are associated with high elevation, low salinity and low inundation time (Figures 3,4 Supplementary Figure S2; Table 3).

Upland and Miscellaneous: Cluster analyses show 21 sample plots do not significantly fit into the classification hierarchy. Indicator species analysis reveals these plots are largely characterized by presence of upland, freshwater wetland associated and exotic forbs and graminoids. The weakly negative Si score suggests that these plots share floristic similarities with other associations. Some of the miscellaneous sample plots represent transition with the upland edge of the marsh. It may also be the case that a few of these sample plots represent distinctive community types that were underrepresented on the eight study sites surveyed.

Forb dominated communities, such as those panne areas described in Northern New England (eg., Ewanchuk and Bertness 2004), or alluded to by other studies in Nova Scotia (eg., Thannheiser 1984) were not a conspicuous feature of the marshes sampled for this study. The authors did however observe shallow pools of permanent standing water on the marshes that in some cases supported living aquatic vegetation. Numerical classification did not reveal a statistically significant plant association here. This may be due to their limited representation and therefore small sample size. Of three sample plots that contained open standing water, one contained the species *Ruppia maritima* L. (Sea Ditchgrass) and was numerically allocated to the miscellaneous grouping of plots. Two additional sample plots were collected from pools that contained no vegetation but were fringed by the *Spartina alterniflora* and *Carex paleacea* associations. Other studies in the region also identify shallow water pools colonized by the submergent aquatic *Ruppia maritima* or that are fringed by dominant graminoids found in this study, especially *Spartina alterniflora* (Bleakney et al. 1979, Patriquin 1981, Chmura et al. 1997, Millard et al. 2013). Shallow pools of standing water contribute to overall marsh biodiversity, and are worthy of mention because they are more common on northern marshes (Noel and Chmura 2011) and because their habitat value is well recognized (Bleakney et al 1979, Roberts and Robertson 1986).