

Ecohydrology of wetland plant communities along an estuarine to tidal river gradient

AMY B. BORDE ,[†] HEIDA L. DIEFENDERFER , VALERIE I. CULLINAN ,
SHON A. ZIMMERMAN , AND RONALD M. THOM 

Pacific Northwest National Laboratory, Coastal Sciences Division, Marine Sciences Laboratory, 1529 West Sequim Bay Road, Sequim, Washington 98382 USA

Citation: Borde, A. B., H. L. Diefenderfer, V. I. Cullinan, S. A. Zimmerman, and R. M. Thom. 2020. Ecohydrology of wetland plant communities along an estuarine to tidal river gradient. *Ecosphere* 11(9):e03185. 10.1002/ecs2.3185

Abstract. Abiotic filters that interact with wetland plant communities along tidal–fluvial gradients are highly dynamic, and understanding their quantitative thresholds and relationships to interspecific competition is important during an era of sea-level rise and watershed hydrologic change. Yet, landscape-scale studies of major coastal rivers from the river mouth to the head of tide, such as this study, remain rare. Here, we develop a new predictive framework for estuarine–tidal river research and management using a river-specific low-water datum and the wetland inundation indicator SEV_g , the growing-season sum exceedance value of hourly surface-water depth. The distribution and variability of the wetland species pool ($n = 203$) on the 234 river kilometer (rkm) lower Columbia River and estuary floodplain are described for the first time. 4,940 quadrats at 50 marshes were surveyed (2005–2016). Throughout the estuarine–tidal river system, SEV_g was well suited to describe the wetland inundation regime and its variability based on the combination of longitudinal river position and elevation. SEV_g increased significantly landward. Two primary wetland inundation regimes were identified: the seaward-tidal, usually greatest during the winter months, and landward-fluvial, greatest during the growing season. Nearest the ocean, salinity is the abiotic factor limiting species richness and non-native species. Farther upriver, the daily, seasonal, and interannual variability of the wetting and drying cycle encourage disturbance-tolerant species and non-natives and limit the number of hydrophytes and total vegetative cover. Hence, the average between-year similarity of site-scale areal cover significantly decreased landward. Hierarchical cluster analysis indicated five vegetative groups and five ecohydrologic zones between rkm 0 and 234 were discriminated with 76 significant species–zone associations. All zones had unique indicator species. Species with high indicator values were *Carex lyngbyei* throughout the estuarine zones, and *Eleocharis palustris*, *Sagittaria latifolia*, and the invasive non-native *Phalaris arundinacea* in the upper estuarine and lower, middle, and upper tidal river zones ($IV > 0.90$). Competition from *C. lyngbyei* nearest the ocean and *P. arundinacea* in the tidal river was associated with reduced species richness when total cover was $>65\%$. This framework of filters informs the design and prediction of future wetland plant communities on coastal river floodplains.

Key words: abiotic filter; community assembly; ecohydrology; hydrological regime; regulated river; species pool; terrestrial–aquatic interface; tidal freshwater; tidal river; wetland.

Received 16 August 2019; **accepted** 30 August 2019; **final version received** 22 May 2020. **Corresponding Editor:** Debra P. C. Peters.

Copyright: © 2020 The Authors. This is an open access article under the terms of the Creative Commons Attribution License, which permits use, distribution and reproduction in any medium, provided the original work is properly cited.

[†] **E-mail:** Amy.Borde@pnnl.gov

INTRODUCTION

Large tidal rivers present a challenging spatiotemporal gradient of abiotic filters on wetland

plant community assembly, which must be understood for effective conservation and restoration planning, and for management of multiple uses including shipping, industrial

development, agriculture, and human habitation. River floodplains have complex processes and spatial patterns of interconnected flora, fauna, and flow regimes along environmental gradients both longitudinal and lateral to the mainstem river channel (Welcomme 1979, Naiman and Décamps 1997, Bunn and Arthington 2002). The plant communities arrayed along wetland gradients are affected by disturbance processes that may cause both flooding and desiccation, and species are adapted to fluctuations in water level (Strayer and Findlay 2010) and salinity (Crain et al. 2004). In low-elevation areas near coasts, tides and salinity make the hydrological controls on river–floodplain ecosystems complex, and variations in river discharge, coastal upwelling and downwelling, and hydropower operations all affect water surface elevations (Jay et al. 2016, Jones et al. 2020).

While estuarine wetlands have been extensively studied, landscape-scale studies of the wetland complexes of major coastal rivers spanning the estuarine-to-tidal freshwater wetland gradient from river mouth to the head of tide are scarce, perhaps due to the persistence of interdisciplinary schisms noted by Odum (1988). Studies in the Chesapeake Bay region have documented wetland vegetation patterns along the estuarine gradient (Sharpe and Baldwin 2009, Sharpe and Baldwin 2013). A few studies of narrower scope have encompassed both estuarine and tidal freshwater wetlands of tidal rivers; for instance, a review article from the Fraser River estuary of western Canada summarized localized wetland studies along the estuarine gradient (Adams and Williams 2004). More commonly, tidal–fluvial forcing and sediment redistribution within major channels have been examined over these extensive aquatic–terrestrial regions where tidal influence may extend hundreds of kilometers inland, for example, the Amazon River in Brazil (Gallo and Vinzon 2005), Saint Lawrence River of eastern Canada (Godin 1999), Thames River in England (Amin 1983), Yangtze River in China (Yu et al. 2014), Elbe River in western Europe (Doerffer et al. 1989), and Columbia River in the western United States (Jay et al. 2015). On this basis, we argue that a more universally applicable and comprehensive approach to understanding the physical drivers on plant community distribution and potential migration in

major tidal rivers is needed to frame the successive thresholds of changes in major abiotic filters between the river mouth and the head of tide relative to plant tolerances and the zonation thereby produced.

Tidal rivers and the tidal freshwater wetlands upstream of estuaries have long been subject to intensive human activities, for example, from 800 BC onward in Europe (Zonneveld and Barendregt 2009). In many regions of Africa, the Americas, Asia, the Middle East, and Europe, impacts on tidal rivers and estuaries have intensified in recent centuries as the effects of agricultural and industrial developments interact with effects of upstream river regulation on hydrodynamics, sedimentary processes, and water temperatures (Lotze et al. 2006, Latrubesse et al. 2017). Direct land reclamation also reduces the areal extent of floodplain ecosystems (e.g., Kiviat 2009, Struyf et al. 2009, Tian et al. 2015). Tidal wetlands are very sensitive to water surface elevation and sediment deposition, and their survival and migration during an era of marine transgression with increasing rates of sea-level rise depends on complex feedbacks with geomorphology, plant establishment, and growth (Kirwan and Megonigal 2013).

In recent decades, the intrinsic values of tidal freshwater wetlands have been recognized and initiatives for their conservation and restoration have been made (Jacobs et al. 2009, Zonneveld and Barendregt 2009). Knowledge of the spatial distribution and temporal variability of plant communities is a foundation for ecosystem management and is particularly important for the restoration of native coastal plant communities (Sullivan 2001). Although natural hydrologic processes and patterns must be understood as a guide for ecological restoration plans (Poff et al. 1997), restoration to historical or prehistorical conditions cannot always serve as an overriding restoration goal as it did in the early years of practice (Stanford et al. 1996, Ward et al. 2001, Jackson and Hobbs 2009). This is clearly the case when river flow is regulated by dams. Given the highly dynamic nature of tidal rivers, a reasonable restoration goal may be to restore native plant communities to conditions similar to nearby reference wetlands, which are a foundation of the reference models used for planning (Clewett and Aronson 2013). In restoration, the

features of reference wetlands are frequently the basis of design elements, including wetland elevation, vegetation planting plans, microtopography, and tidal channel morphology, as well as the management of invasive plant species (Zedler 2001).

On the Pacific Coast of the continental United States, tidal freshwater wetlands of the Columbia River floodplain are very well developed, comparable to rivers on the Atlantic Coastal Plain (Pratolongo et al. 2019). Fifteen years ago, we began developing a network of tidal wetland reference sites along the 234 river kilometer (rkm) lower Columbia River and estuary (Fig. 1; hereafter referred to as the “study area”), similar to existing networks in tidal freshwater wetlands on the Hudson River and in coastal Louisiana (Findlay et al. 2002, Steyer et al. 2003). The large concentration of tidal freshwater wetlands in the study area is unique on the West Coast of North America (Callaway et al. 2012), and most similar to the tidal wetland and estuarine complex on the Fraser River of Canada (Ward et al. 1992). However, recent reviews of tidal freshwater wetlands have shown that the plant communities within the complex environmental mosaic in our study area have not been definitively characterized (Leck et al. 2009, Pratolongo et al. 2019), although valuable documentation exists in earlier reports (Christy and Putera 1993, Kunze 1994) and we have since published preliminary data (Callaway et al. 2012). To date, most research in the study area has focused on the estuary (Fox et al. 1984, Small et al. 1990), not on the extensive fluvially dominated tidal freshwater reaches (Jay et al. 2016). Thus, we sought to characterize the composition and distribution of plant communities along the full estuarine–tidal river gradient and to develop easily measured predictive hydrologic variables, appropriately defined in space and time, to enable future analyses of the effects of sea-level and river-flow changes under climate change (National Research Council 2012). The reference site network spans the Pacific Ocean to the Cascade Range, the focal area of the Columbia Estuary Ecosystem Restoration Program (CEERP; Ebberts et al. 2018), and it is intended to provide the program with fundamental information about ecosystem structure and function to inform restoration program planning and project design. It has now grown to

>60 tidal wetland research sites including emergent marshes, shrub-dominated wetlands, and forested wetlands.

We hypothesized that the hydrological regime and salinity associated with the *x*, *y*, *z* position of a wetland in the floodplain explain aspects of the spatiotemporal variability of plant community composition, richness, and cover along a tidal–fluvial gradient of the hydrological regime. Through analysis of data on 50 emergent marshes in the CEERP network of reference sites and additional documentation, we investigated the requirements for abiotic filtering outlined by Kraft et al. (2015): the observed pattern along the environmental gradient, lack of limitations to dispersal, environmental filtering, and competitive exclusion. Although the value of the environmental filtering concept has been widely examined in recent years (Cadotte and Tucker 2017), it is reasonable to expect transitions between plant communities along mixohaline–freshwater gradients and floodplain elevation gradients because of direct abiotic effects on plant physiology and indirect effects through competition and other mechanisms. It is well known that both salinity and flooding have the capacity to prevent the establishment and persistence even of wetland plants (Leck 1996, Engels et al. 2011, Janousek and Folger 2013, Lichvar et al. 2014). The seed bank, seedlings, and vegetation of tidal freshwater wetlands can fluctuate significantly year to year (Leck and Simpson 1995). In fact, the hydrological regime of a shore zone wetland is a master variable for the distribution of vegetation, and the effects of hydrological processes are in turn controlled by elevation (Keddy and Reznicek 1986, Strayer and Findlay 2010). Overall, our research objectives were to:

1. Determine the spatial patterns of wetland vegetation cover and composition, relative to physical controlling factors (potential abiotic filters) and competition by the dominant plant species in both mixohaline and freshwater regions, in three dimensions (lateral and longitudinal relative to the mainstem river, plus elevation).
2. Validate a metric of wetland surface-water inundation and evaluate the interannual variability in areal cover relative to

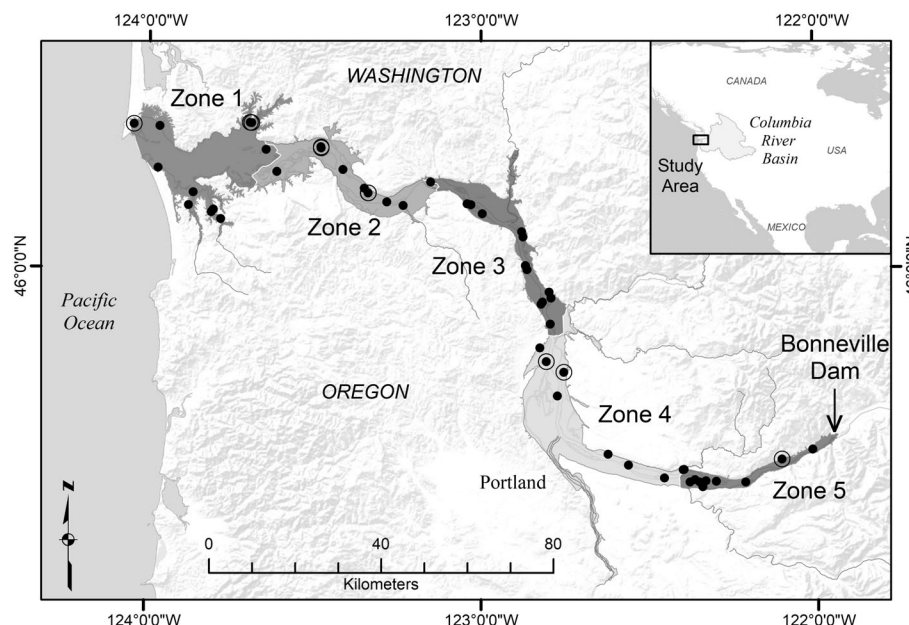


Fig. 1. Map of study area showing zonation and locations of wetland study sites (solid dots). Circled sites represent long-term monitoring sites; two sites, high and low elevation, are located at the eastern site in zone 1. Ecohydrologic zones 1–5 incorporate characteristics of the wetland plant communities and the hydrologic regime: tidally dominated zones—(1) Lower Estuary and (2) Upper Estuary; and fluvially dominated zones—(3) lower tidal river, (4) middle tidal river, and (5) upper tidal river (Jay et al. 2016). The maximum surface extent of salinity intrusion at low flow is seasonally and interannually variable to ~rkm 39, the upper extent of zone 1 (Jay and Smith 1990), above which the river is tidal freshwater.

hydrological regime for the dominant vegetation species.

3. Develop distinctive plant community descriptions associated with major thresholds in abiotic transitions along the tidal–fluvial gradient, with associated indicator species and floristic quality assessments.

Thus, in this paper, we develop the fundamental scientific basis for a widely applicable approach to measuring successive filters on plant communities along and across the tidal–fluvial gradients of coastal river floodplains. This approach enables disturbance-caused change to be predicted. The foundation of the approach to predicting future plant assemblages and distributions lies in indexing the relationships between vegetation, elevation, salinity, and hydrologic regime. Thus, we present the empirical basis for the wetland vegetation component of a longitudinal zonation of ecohydrologic zones from the river mouth to the head of tide at Bonneville Lock and Dam (Jay et al. 2016; Fig. 1). Findings will

further inform the reference models used by planners and engineers for designing wetland restoration on the lower Columbia River and estuary.

MATERIALS AND METHODS

Study area

The 1468-km² floodplain of the study area extends from the mesotidal, polyhaline reaches near the Pacific Ocean through coastal mountain ranges to the broad trough around the confluence of the Willamette River, and ends in the narrow Columbia River Gorge where Bonneville Dam is located at rkm 234 (Fig. 1). The hydrologic regime shifts from tidally to fluvially dominated along the landward gradient, and climate variability and river-flow management contribute to its seasonal and interannual variability (Jay et al. 2015). Columbia River flows measured since 1878 at The Dalles (located at rkm 310 and constituting approximately 75% of the flow at the mouth) indicate that flows ranged from ~1000 to 35,000 m³/s historically (Jay et al. 2015). Recent

regulated flows (2007–2016) measured at a gauge closer to the mouth (located at rkm 87 and representing 97% of flow to the ocean; Jay et al. 2015) range from 2350 to 17,190 m³/s with an average of 6880 m³/s. The salt wedge advances and retreats, and the degree of stratification vs. mixing varies with seasonal flows, neap-spring tide transitions, and ebb vs. flood tides, but usually extends between 20 and 40 km from the river mouth (Jay and Smith 1990). Tidal amplitudes range from approximately 3 m near the mouth to <1 meter in the upper tidal river reaches (Jay et al. 2015). Historically, most of the floodplain of this estuary was dominated by tidal freshwater wetlands because of the strong fluvial influence. Recent land cover change analysis estimates conclude that 68% of tidal marshes have been lost since 1870 to the combined effects of changes in Columbia River discharge and diking, leaving 4606 ha (Marcoe and Pilon 2017). This extensive loss of wetland land cover reduced friction against river flow to the extent that the river surface slope and maximum water levels have been altered since the late 1800s (Helaire et al. 2019).

Sampling sites

This paper analyzes and synthesizes environmental and marsh plant community data sets from research in the study area from 2005 to 2016. We sampled a total of 51 emergent marshes (site location details and descriptions in Appendix S1: Table S1). All data are from a suite of reference wetlands (hereafter “sites”) and eight long-term monitoring sites that were selected from among the best remaining emergent marshes in the system. Random selection of sampling sites was not possible because of logistical and ownership constraints, but we sampled a broad and relatively even spatial distribution of sites representing the range of hydrogeomorphic settings (Fig. 1). The six most seaward sites are exposed to surface water salinity: Baker Bay, Chinook (high and low marsh), Trestle Bay, Lewis and Clark River Mouth, and Fort Clatsop (the latter site only in fall during low river flows). Submerged aquatic vegetation data are not included in these analyses.

The emergent marsh types were estuarine–intertidal or riverine–tidal wetlands as broadly classified according to Cowardin et al. (1979). A subset of the sites is known to have a history of

dredged-material placement over part or all of the site as a result of channel-management activities since the early 1900s, however recently disturbed sites were excluded from this analysis. Three sites in this analysis had been diked, but were breached and thus passively restored ~10, 50, and 60 yr prior to sampling. Areal plant cover and composition at a previously diked site in the region have been shown to reach equilibrium within 10 yr (Thom et al. 2002). A subset of 26 sites, or about half of the sampled sites, was used for selected analyses identified below, termed “least-disturbed sites,” because during the course of the study, historical disturbances were identified at the remaining 25 sites (Appendix S1: Table S1). For comprehensive sampling and long-term trends analysis, we selected the fringing emergent marsh along the upper extent of the extremely shallow Cunningham Lake on Sauvie Island in ecohydrologic zone 4 (rkm 145), because it is strongly influenced by the fluvial–hydrological regime and therefore has greater interannual variability than more tidal sites.

Data collection

From 2005 to 2016, we collected vegetation data at 47 marsh sites along the mainstem Columbia River on 230 transects totaling 1523 1-m² quadrats with vegetation, and at an additional four marsh sites along tributaries to the mainstem river (23 transects totaling 64 quadrats with plant cover; Fig. 1). Eight sites selected for trends analysis, which spanned the tidal–fluvial gradient, were monitored for 5–12 yr and the remainder for 1–2 yr, for a total of 4,940 quadrats evaluated. All sites were sampled during summer when vegetation biomass was at its peak. Data were collected according to protocols we established for the CEERP (Roegner et al. 2009), with some additions. At multiple sites in the study area, we calculated species–area curves as the basis for the sample-size recommendations in the protocols and re-checked those assumptions for additional sites in this study. The monitored indicators reported here are herbaceous plant species areal cover and the surveyed elevation of land and water surface in the wetlands.

At each site, we used systematic sampling with multiple random starts to establish herbaceous vegetation monitoring locations. First, transects were established at equal intervals along a

baseline established with a random start point near a wetland channel, and then, 1-m² sample plots were spaced at equal intervals from randomly selected starting points on each transect. Shrub and tree species were only included in the cover if stems emerged from the soil within the quadrat. Additional field notes and elevation measurements were taken to characterize the upper and lower emergent marsh boundaries; that is, shrub and tree species defined the upper boundary, and the edge of emergent vegetation marked the lower boundary. Percent cover for each plant species present in a given 1-m² plot was determined visually by estimating percent cover in 5% increments. Additional features such as bare ground, open water, wood, and drift wrack identified in the plots were also recorded. When plant identification could not be determined in the field, a specimen was collected for later identification using taxonomic keys or manuals at the laboratory. If an accurate identification could not be resolved, the plant remained unidentified in the database.

We delineated major vegetation communities at each trends analysis site using Trimble GeoXT and GeoXH handheld global positioning system (GPS) units (Trimble, Sunnyvale, California, USA). We input these data into a geographic information system (ArcGIS 10; Esri, Redlands, California, USA) used to create maps of each site showing major communities. Initially, sites were mapped annually but little change was observed so this was discontinued in favor of remapping only when change was visually observed during the annual vegetation plot sampling.

We collected elevation data using Trimble real-time kinematic global positioning system (RTK GPS) methods. Data prior to 2010 were collected with a Trimble 5800 GPS receiver (rover) and Trimble 5700 GPS receiver (base), using data collection software Trimble Survey Controller v11.05. Since 2010, we have used a Trimble R8 GNSS receiver system with Trimble Survey Controller v12.45. All elevation surveys were referenced to the North American Vertical Datum of 1988 (NAVD88). At each site, we used a benchmark to reference all survey data, preferably an established local benchmark if one could be located. We imported and reviewed data collected from the RTK GPS using Trimble Geomatics Office v1.63 software, which was replaced with Trimble

Business Center v2.81 software midway through the study; points with a high root-mean-square value were flagged by the processing software and removed from the survey data set. We exported survey data in a GIS shapefile format and visually checked the data for validity.

We collected hourly absolute pressure data in channels at all marshes using HOBO model U20 series water-level loggers (Onset Computer, Bourne, Massachusetts, USA) that were deployed for one year or longer. Pressure data were corrected for atmospheric pressure, and the RTK GPS-surveyed elevation of the instrument casing and measured offset to the sensor were used to calculate water levels reported in NAVD88. At the most seaward site, in Baker Bay, we collected salinity data in the tidal channel from August 2011 to September 2013 using a HOBO model U24 series conductivity/salinity logger (Onset Computer). Samples were collected and analyzed using a YSI Pro30 conductivity meter (YSI, Inc., Yellow Springs, Ohio, USA) at the beginning and end of each 6-month sample period to validate data logger measurements.

Data and statistical analysis

Elevation.—To compare plant communities along the tidal–fluvial gradient, we converted land-surface and water elevation data in NAVD88 to reference a fixed low-water reference plane, the non-tidal Columbia River Datum (CRD) originally developed and periodically updated by the U.S. Army Corps of Engineers (Hickson 1912), which is the station datum identified by National Oceanic and Atmospheric Administration (NOAA) Tides and Currents (above river mile 23). In effect, this removed the gradient of the river bottom from the survey data allowing direct comparison of wetland elevations.

Inundation.—Sum exceedance value (SEV), a derived variable incorporating magnitude, timing, and duration of surface-water flooding, is useful for evaluating the effect of variable water levels on vegetation (Simon et al. 1997, Gowing et al. 2002, Araya et al. 2011). In effect, the SEV indexes the two key elements of interaction between water-flow and coastal wetlands identified by Möller and Christie (2019), magnitude and duration. We calculated the SEV for given elevations using the following equation:

$$SEV = \sum_{i=1}^n (h_{\text{elev}}) \quad (1)$$

where n is the number of hours present in the time period evaluated, and h_{elev} is the hourly water depth above a given elevation. The units are meter hours per time period. The elevations used in this study were (1) the average land elevation of vegetation plots sampled at a site and (2) the average land elevations at which a given species occurs. The time periods evaluated were the annual deployment period and the growing season (SEV_g), which was based on the number of frost-free days for the region ($>0^\circ\text{C}$), as determined by the Agricultural Applied Climate Information System for Clark County, Washington, USA (NOAA 2018). Both periods were standardized to include the same days in each year, accounting for different deployment and retrieval dates, as follows: the growing season including 22 April–22 June and 20 August–13 October (115 d), and the annual deployment period, 20 August–22 June of the next year (306 d). SEV is independent of datum because it is the sum of the hourly depth. SEV_g was calculated for all years for which data were available, at each elevation used in the study. We developed regressions of wetland site on channel station and identified two equations based on water year type (high or moderate; $R^2 = 0.99$ for both). At long-term trends analysis sites, in years lacking wetland water surface elevation data (i.e., because of sensor malfunction), we calculated SEV_g from the nearest station data (e.g., NOAA at St. Helens), by using the appropriate regression equation.

Salinity.—Conductivity and temperature data from the HOBO U24 data logger were processed using HOBOWare Conductivity Assistant, which calculates the specific conductivity and salinity using the Practical Salinity Scale of 1978. To extend the data record, we downloaded data from May 2013 to September 2016 from the National Science Foundation Science and Technology Center, Center for Coastal Margin Observation and Prediction (C-MOP 2019) Saturn-07 station, located at 1-m depth and approximately 3 km from the Baker Bay site. The C-MOP data were considered preliminary, so the data were evaluated for outliers prior to use and were not used in statistical analyses. The mean, minimum,

maximum, and range were calculated at daily, monthly, and annual intervals.

Plant cover and elevation.—The plant cover data were summarized to determine the most abundant species, defined as those having both the greatest cover in a quadrat and percent cover $>20\%$ in at least 20 quadrats. Similarly, the most frequent plants were defined as those with a probability of occurrence $>15\%$ with at least one quadrat with $\geq 5\%$ cover. We report the surveyed elevation ranges for observations of the most abundant and frequent plant species in the study region.

Data used in statistical analyses.—Where appropriate, only the subset of wetlands with no known historical localized disturbance factors were included in analyses, because the Columbia is a regulated river with a major navigation channel and floodplain land uses including agriculture, forestry, industry, and urbanization. All quality control-checked data that met the criteria for analysis (e.g., specific water years, least disturbed marshes, and concurrent hydrology and vegetative data) were used in every analysis. However, because different combinations of data were required for each analysis, such as vegetation and hydrology or multiple years, the sample size differed for many analyses (Appendix S1: Table S3). The 2009–2010 water surface elevation data were used in several analyses to represent moderate-flow years.

Regression analysis.—Simple linear and segmented regressions were conducted on average site and water elevations, SEV , and average number of species per quadrat as a function of river kilometer. Additionally, the average relative cover of *Phalaris arundinacea*, an invasive non-native species, and average number of species were calculated for each zone, elevation (rounded to the tenth place in m, CRD), and level of *P. arundinacea* (none, low if cover $\leq 20\%$, moderate if cover is $>20\%$ and $\leq 60\%$, and high if cover is $>60\%$). For those averages based on *P. arundinacea* levels, residuals from a quadratic regression of the $\log_{10}$ number of species on elevation were observed to be a function of cover. Thus, a segmented regression was fit to the residuals as a function of the cover of *P. arundinacea* to determine the level of cover associated with a greater impact on the number of species. However, for the averages based on *Carex lyngbyei*, a dominant native species, the linear and quadratic slopes for elevation

were not significant; thus, the $\log_{10}$ number of species was regressed on the relative cover of *C. lyngbyei* using both a quadratic and a segmented regression model. A plot of the total number of species by elevation and zone for each cover class of *P. arundinacea* and *C. lyngbyei* was created for all quadrats with >60% cover to facilitate examination of the effects of competition on overall cover.

Trends in hydrology and vegetation community.—We developed a coarse index to compare flow years by summing the monthly mean flow as measured at The Dalles Dam for the months of April–October between 1987 and 2016. The range of the growing-season flow index from 1987 to 2016 (30 yr) was 796,730–1,989,700 m³. The first quartile provided the cutoff boundaries between low- and moderate-flow years (1,100,000 m³), and the third quartile was used between moderate- and high-flow years (1,500,000 m³). Extreme values for this data set (2015 was below 1,000,000 m³ and 2011 was above 1,900,000 m³) were included with the low and high categories, respectively. Thus, the study years were categorized as low, moderate, or high with respect to river-flow effects on wetland hydrology.

Similarity analyses on the eight trends sites, using the Bray-Curtis similarity coefficient (*S'*) as a measure of distance between years (described by Clarke and Warwick 2001), were performed on average percent cover data using PRIMER (Quest Research Limited, Auckland, New Zealand). Percent cover data were arc-sine, square-root-transformed, but were not standardized, prior to analyses. The similarity matrix was converted to a dendrogram by using the hierarchical, unweighted pair-group mean-averaging method of clustering. Clusters combined at greater linkage distances are more dissimilar than those combined at smaller linkage distances.

In addition to the range of percent cover at eight trends analysis sites, we also report a 12-year time-series analysis of percent cover at one site to illustrate how the within-year and among-year fluctuations of water levels affect shoreline plant communities along both regulated and unregulated rivers (Hill et al. 1998, Jay et al. 2015). The Cunningham Lake site was evaluated for the effects of inundation as measured by SEV on vegetation cover. A change analysis in ArcGIS (version 10.4; Esri) compared the earliest plant

community maps with the most recent plant community maps for each trends analysis site (except Secret River, which was only mapped once due to the large size of the site and little observed change during annual sampling). We compared the following site-years: Baker Bay (2012, 2015); Welch Island (2012, 2015); White's Island (2009, 2015); Cunningham Lake (2006, 2015); Campbell Slough (2005, 2015); and Franz Lake (2008, 2012, 2015). (Three years were compared at the Franz Lake site because different mapping areas were covered and extensive changes had occurred.) Comparable mapped areas were intersected, the area for each plant community type was calculated, and the difference in area for each community was calculated.

Hierarchical cluster analysis.—Average percent cover for 141 species (occurring at 2 or more sites) at 76 site-year combinations (2005–2012) was analyzed by hierarchical cluster analysis with complete linkage using pairwise community dissimilarity between site and years. Species data were reduced by combining species that were difficult to distinguish in the field in four cases and submerged aquatic species. A minimum of five groups was achieved by cutting the dendrogram at 95% dissimilarity. Analysis was performed using the R package *vegan* in R version 3.5.1 (R Core Team 2018).

Discriminant analysis.—Five zones within contiguous sections of the river, first described by Jay et al. (2016), were defined based on hydrology, salinity, vegetation observations, and geophysical features of the river. To determine whether the zones could be discriminated based on vegetation cover data, we used 45 plant species that represented 90% of the cumulative average site-year relative cover, from 26 less-disturbed marshes between rkm 12 and rkm 228 (2005–2016; 74 site-year combinations). Discrimination using the standardized average relative cover successfully discriminated all sites into five zones. Four discriminant scores (score 1–score 4) were calculated for all sites and plotted against each other, providing a visual indication of the distinctive zones. Analysis was performed using Statistica, version 12 (StatSoft, Tulsa, Oklahoma, USA).

Indicator species analysis.—The average percent cover for 141 species at 76 site-year combinations (2005–2012; the same data used for the cluster

analysis) was analyzed to determine which species have significant associations with each zone. Species are associated with a zone based on the maximum indicator value, which is a function of the relative abundance (specificity) and relative frequency (fidelity) within a zone (Dufrêne and Legendre 1997). The statistical significance of the association was determined by a permutation test. Analysis was performed using the R package *indicspecies* (De Cáceres and Legendre 2009, R version 3.5.1; R Core Team 2018).

Floristic quality assessment.—A floristic quality assessment (FQA; Freyman et al. 2016) was conducted for each trends analysis site in 2016. The coefficient of conservatism (C) values were previously developed for most native species found at the sites and represent the collective opinion of botanical and ecological experts from the region (Rocchio and Crawford 2013). The floristic quality index (FQI), the adjusted FQI (which eliminates the sensitivity of the FQI to species richness and incorporates the effect of non-native species; Miller and Wardrop 2006), and other associated community assessment metrics were calculated using the Western Washington Floristic Quality Assessment Index Calculator (version 2.1, 27 June 2013; Washington State Department of Natural Resources, Olympia, Washington, USA).

RESULTS

Spatial patterns of plant species and abiotic factors along tidal–fluvial and elevation gradients

As expected, the average site elevation of emergent marshes in meters, NAVD88, significantly increases with river kilometer in the landward direction (regression, $n = 47$, $P < 0.001$). However, the simple linear model does not fit well ($R^2 = 70\%$, nonparametric goodness of fit, $P = 0.022$). A segmented regression using two linear models with a single join point fit the data well ($R^2 = 81\%$, nonparametric goodness of fit, $P = 0.12$; Fig. 2a). The join point was estimated at rkm 111 (95% confidence interval [CI]: 96–127); the first slope from rkm 0 to rkm 111 was not significantly different from zero ($P = 0.09$), and the second slope from rkm 111 to 228 was significantly different from zero ($P < 0.001$). In contrast, the slope of the simple linear regression of the average site elevation

after data were converted to meters, CRD, for marshes above rkm 37 and to mean lower low water (MLLW) below rkm 37, against the distance from the mouth of the Columbia River (km) was not significant (regression, $n = 38$ above rkm 36, $P = 0.59$), which illustrates the effect of correcting elevations to datums based on low-water elevation (Fig. 2b, c). Inundation as measured by the $\log_{10}$ SEV_g at 2-m, CRD, elevation for the years 2009 and 2010 ($n = 32$) increases upstream of rkm 139 (regression, $n = 14$, $P = 0.001$), whereas the slope downstream of rkm 139 was not significantly different from zero (regression, $n = 18$, $P = 0.73$), indicating lower and less variable SEV_g downstream of rkm 139 (Fig. 2d). Regardless of the differences in inundation throughout the study area, the average annual water level relative to CRD, at sites in moderate flood years, was consistent along the tidal river continuum (Fig. 2c).

The hydrograph of the tidal river is most strongly influenced by the seasonal effects of spring snowmelt. The hydrograph of the estuary is also strongly affected by tides and the winter flooding of rain-dominated tributary watersheds west of the Cascade Mountains, producing clear seasonal differences persisting through low-, average-, and high-flow years (Fig. 3). Thus, the SEV_g at the average elevation of each wetland increases significantly with increasing river kilometer (Fig. 2d; regression on $\log_{10}$ -transformed data, $n = 18$, $P = 0.004$ below and $n = 14$, $P = 0.02$ above rkm 139). The SEV_g varies inversely with elevation (e.g., the outliers at rkm 37 are for the lowest marsh in the sample set) and directly with flow. Moreover, most marsh inundation occurs during the growing season in the tidal river above rkm 104, while downstream of this point, greater inundation occurs in the winter months (non-growing season) and to higher elevations at the sites, driven by winter high tides and winter flooding (Fig. 4a), though this was variable between years (Fig. 4b).

Salinity in zone 1 was variable on daily, monthly, seasonal, and annual scales. Just as tides and river flow affect the hydrograph, these drivers also affect salinity. Monthly means are provided in Appendix S1: Table S2. The daily range of salinity varies depending on the neap-spring tide cycle and river flow.

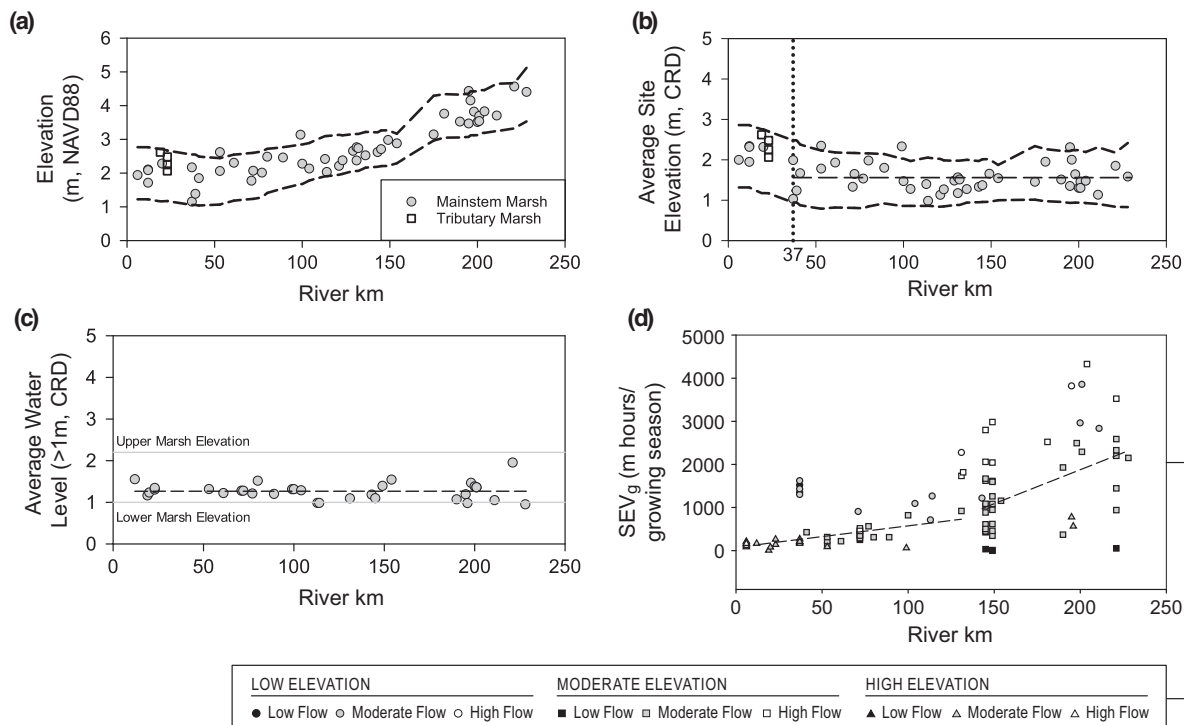


Fig. 2. Longitudinal patterns on the tidal-fluvial gradient. (a) Average site elevation of marshes on the mainstem and tributary rivers in m, NAVD88, and (b) converted to m, CRD, above rkm 37 and m, MLLW, below rkm 37; tributaries remain m, NAVD88. The dashed lines in (a) and (b) represent the running average of the upper and lower marsh elevations within a 20-rkm window. (c) Average annual water-surface elevation when marshes are inundated (>1 m, CRD) in moderate-flow years (2009–2010). The gray lines represent the upper and lower marsh elevations. (d) The growing-season SEV during low-, moderate-, and high-flow years at the average site elevation. Regression lines are back-transformed $\log_{10}$ SEV at average site elevation for moderate-flow years 2009–2010.

We observed 203 plant species in the emergent marshes (see species list, Appendix S1: Table S4), and found evidence of variation by elevation and position along the tidal-fluvial gradient. Most species are native (158), but many are introduced (45). The overall elevation extent of these marshes was 0.5–3.8 m, CRD, for mainstem river marshes (though typically >0.9 m, CRD) and 0.8–2.8 m, NAVD88, on tributary marshes (Table 1). The average elevations of quadrats in each vegetation study plot on mainstem river marshes were tightly clustered around the average annual water levels recorded in each marsh (average of hourly water level), 1.3 m, CRD, in average water years (2009, 2010; Fig. 2b, c). Some species have a higher affinity for the tidally dominated areas closer to

the mouth, and others have a higher affinity for the more fluvially dominated areas, and more overlap between these species occurs in zones 2–4 (Table 1). Sites in the estuarine-to-tidal river section associated with the peak of the quadratic curve (zone 2, rkm 39–87; Fig. 5) had significantly greater species richness than the upper portions of the river (zones 4 and 5, rkm 132–228; ANOVA, $n = 22$, $P = 0.005$).

The most abundant plant species in zone 1 was the native, monoculture-forming hydrophyte *C. lyngbyei*. The proportion of quadrats with >65% cover of *C. lyngbyei* in zone 1 was 0.32 and in zone 2 was 0.15, but it was not present in zones 3–5. The invasive non-native hydrophyte, *P. arundinacea*, was present in 51–58% of all quadrats sampled in tidal freshwater zones 2–5.

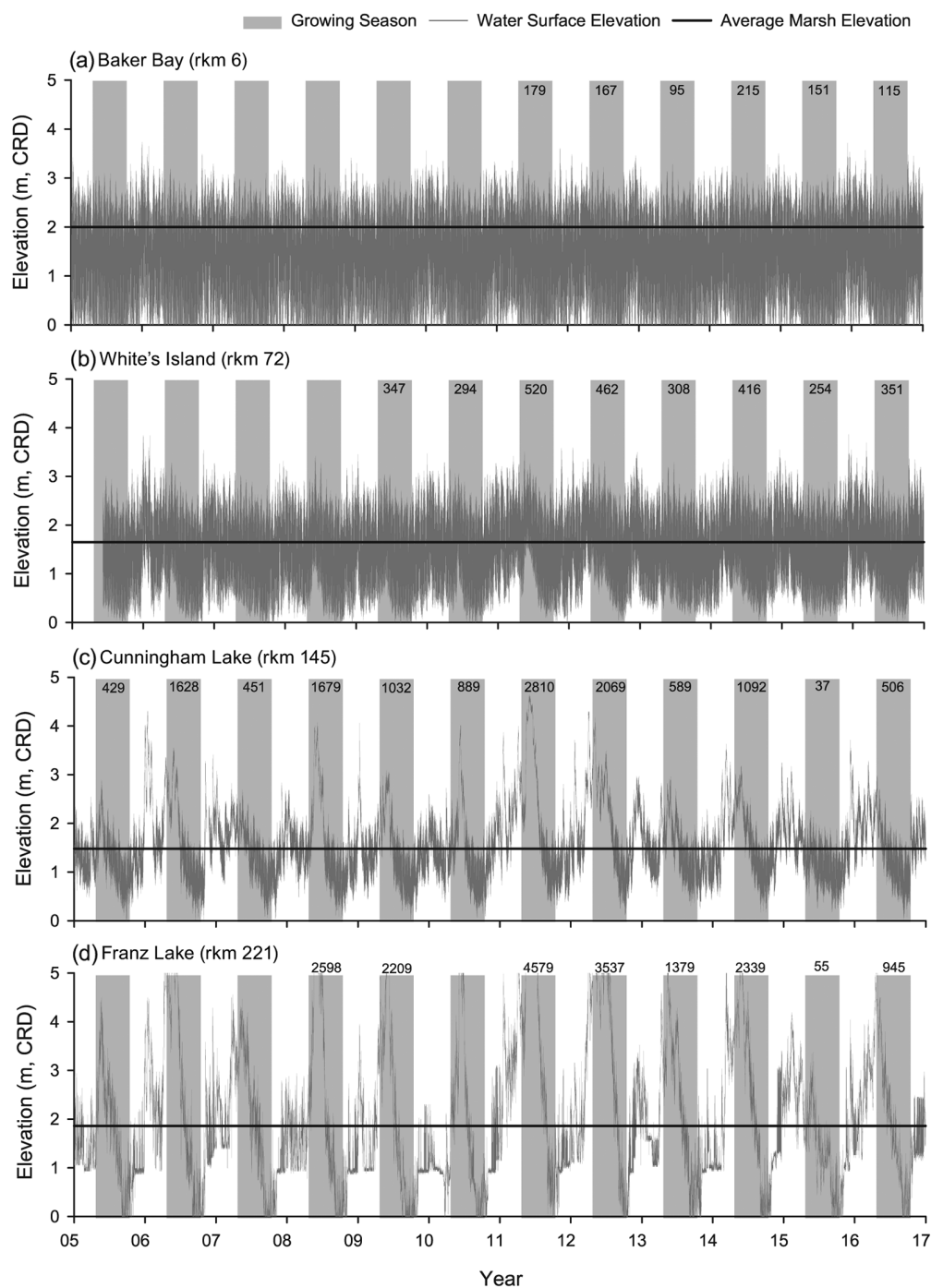


Fig. 3. The tidal wetland hydrograph at locations representing variable surface hydrology along the tidal–fluvial gradient, 2005–2016. For each growing season (gray box) in which vegetation was sampled, sum exceedance values (SEVs), calculated as the sum of hourly water depths over average wetland elevation (black horizontal line), are given at the top of the box. SEVs were calculated using on-site water-level data. Continuous water-level data shown are from the nearest published tide station: NOAA stations at (a) Astoria, OR (rkm 28), (b) Skamokawa, WA (rkm 54), and (c) St. Helens, OR (rkm 139); and USGS station (d) below Bonneville Dam (rkm 233).

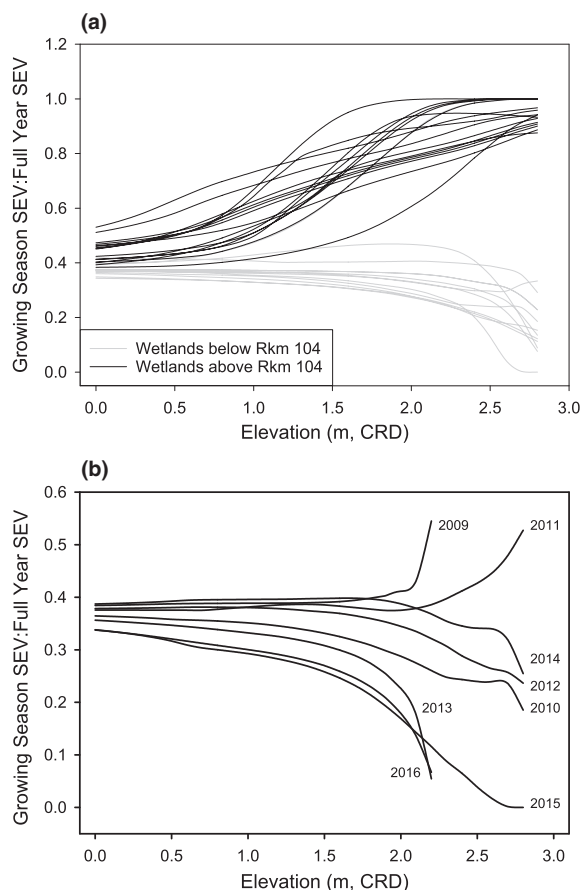


Fig. 4. The ratio of growing-season SEV to annual SEV, showing (a) the relative influence of rain-dominated winter flows (below rkm 104) vs. snow-dominated spring-freshet flows (above rkm 104) on wetland inundation regimes for wetlands sampled in water years 2009 and 2010, and (b) the interannual variability of the ratio for an upper estuarine site, White's Island (rkm 72), which is also shown in (a) using 2010 water year data.

The proportion of quadrats with >65% cover of *P. arundinacea* was 0.05, 0.25, 0.20, 0.26, and 0.05 in zones 1–5, respectively. In zone 1, *P. arundinacea* was not present below rkm 15, and between rkm 15 and 35, it was found only at higher marsh elevations (>1.9 m, CRD) (Table 1). Its average cover remained low (generally < 20%) seaward of rkm 60 and landward of rkm 195 in zone 5. In zone 2, *C. lyngbyei*, an obligate wetland species, and *P. arundinacea*, a facultative wetland species (Lichvar et al. 2014),

overlap in their elevation range however, *C. lyngbyei* occurred slightly lower in the tidal frame.

The $\log_{10}$ -transformed number of species was a function of the relative cover of *C. lyngbyei* both as a quadratic ($R^2 = 54\%$) and as a segmented regression ($R^2 = 59\%$). *C. lyngbyei* and *P. arundinacea* cover below 65% had no impact on the number of species ($P = 0.23$ and $P = 0.09$, respectively). However, *C. lyngbyei* and *P. arundinacea* cover greater than or equal to 65% had a significant impact on the number of species observed, indicated by a significant slope ($P < 0.001$; $R^2 = 64\%$ and $R^2 = 54\%$, respectively). Visual examination of the number of species by elevation, for quadrats with >60% total vegetative cover, also indicates that wetlands with higher cover of *C. lyngbyei* or *P. arundinacea* tend to have fewer total species (Fig. 6).

Interannual variability of plant community with inundation along the tidal–fluvial gradient

Change analysis using our plant community maps and similarity analysis of quadrat-scale data indicated that the six sites all exhibited some level of change in both boundaries and areal cover. A weighted similarity analysis of vegetation cover between years at each site demonstrated that average similarity between years significantly decreased moving up river (regression, $P < 0.001$; Fig. 7); the three most landward sites averaged 67% similarity compared to 75% at the five most seaward sites. In addition, successive high-water years appeared to have a sustained cumulative effect on plant communities in the tidal river, particularly in the low-marsh community; for example, lower cover in 2013 and 2014 followed floods associated with the spring freshets in the high-flow years 2011 and 2012 (Figs. 3 and 8).

In general, areal plant cover was reduced by increased inundation (Fig. 9). Total percent cover decreased significantly as a function of the SEV_g measure of inundation (linear regression, $n = 60$, $P < 0.001$) using 28 sites located between rkm 6 and rkm 221 with 1–12 yr of data (Fig. 9a). At Cunningham Lake, *P. arundinacea* percent cover decreased significantly as a function of SEV_g (linear regression, $n = 12$, $P = 0.003$; Fig. 9b); *E. palustris* percent cover had a decreasing trend as a function of SEV_g (linear regression, $n = 12$, $P = 0.10$; Fig. 9c); and *S. latifolia* percent cover

Table 1. Elevation extent observed for the most abundant and/or most frequent plants in emergent marshes of the lower Columbia River and estuary. All elevations are in meters, relative to CRD (except those on tidal tributaries are in meters, NAVD88).

Scientific name	River extent (rkm)	Observed elevation extent within marshes†					
		Zone 1 tributary	Zone 1	Zone 2	Zone 3	Zone 4	Zone 5
<i>Agrostis</i> spp.	6–149	NA	1.6–2.5	1.8–1.9	NA	NA	NA
<i>Alisma triviale</i>	37–201	NA	1.0–1.1	1.3–1.9	1.1–1.2	1.3	NA
<i>Argentina egedii</i> ssp. <i>Egedii</i>	6–221	2.3–2.7	1.8–2.7	0.8–2.3	2.3	2.0	1.3–2.0
<i>Athyrium filix-femina</i>	19–23	2.4–2.8	NA	NA	NA	NA	NA
<i>Bidens cernua</i>	37–195	NA	1.0–2.1	0.8–1.9	1.4	1.5	NA
<i>Callitriche heterophylla</i>	20–221	0.8–2.4	1.0–1.9	0.8–1.9	1.1–1.4	1.3–1.7	1.9–2.3
<i>Caltha palustris</i>	37–72	NA	1.8–2.2	1.5–2.4	NA	NA	NA
<i>Carex lyngbyei</i>	6–89	1.0–2.7	1.0–2.7	0.9–2.1	NA	NA	NA
<i>Carex obnupta</i>	19–221	1.7–2.7	NA	1.6–2.4	1.3–2.4	1.1–2.7	1.3–2.2
<i>Eleocharis acicularis</i>	6–221	NA	1.0–2.4	0.8–1.1	0.9–1.7	1.0–1.8	1.7–2.1
<i>Eleocharis palustris</i>	6–228	0.9–2.5	1.0–2.2	0.8–2.4	0.6–2.4	0.9–2.3	0.6–2.5
<i>Elodea canadensis</i>	37–201	NA	0.9–1.2	0.7–1.9	0.6–1.2	0.7–1.4	0.6–2.1
<i>Epilobium ciliatum</i>	37–228	2.5–2.6	2.0–2.2	1.3–2.4	1.8–3.4	2.1–2.6	NA
<i>Equisetum fluviatile</i>	37–221	NA	1.8–2.1	1.5–2.1	1.3–1.6	1.4–2.1	1.5–1.9
<i>Galium trifidum</i> var. <i>pacificum</i>	20–221	2.5–2.7	1.8–2.1	1.6–2.4	1.6–2.4	NA	NA
<i>Impatiens capensis</i> , <i>I. noli-tangere</i> ‡	20–221	NA	2.1	1.6–2.4	1.5–2.4	NA	NA
<i>Iris pseudacorus</i>	12–149	NA	2.7	1.1–2.4	1.1–1.9	NA	NA
<i>Juncus oxymeris</i>	37–203	NA	1.2	1.3–1.9	1.0–1.7	1.5–2.0	1.3–1.6
<i>Leersia oryzoides</i>	53–221	NA	NA	1.5–2.4	1.1–2.0	1.4–2.0	1.3–2.5
<i>Lilaeopsis occidentalis</i>	6–149	NA	0.9–2.3	NA	0.9–1.7	NA	NA
<i>Ludwigia palustris</i>	12–221	NA	NA	1.4–1.6	1.2–1.9	1.0–2.1	1.3–3.3
<i>Lythrum salicaria</i>	37–175	NA	1.3–2.1	1.4–2.1	1.4–1.8	1.1–2.0	NA
<i>Mentha arvensis</i>	53–228	NA	NA	0.9–2.4	1.2–1.8	1.7–2.1	1.5–2.1
<i>Mimulus guttatus</i>	53–221	NA	NA	1.3–1.9	1.7–1.9	NA	NA
<i>Myosotis laxa</i> , <i>M. scorpioides</i> ‡	12–201	0.8–0.9	1.3–2.2	1.1–2.4	0.6–2.0	NA	0.6–1.2
<i>Oenanthе sarmentosa</i>	20–77	2.3–2.7	1.8–2.7	1.3–2.3	NA	NA	NA
<i>Phalaris arundinacea</i>	20–228	2.1–2.7	1.9–2.7§	1.1–2.4	1.1–3.2	1.2–3.8	1.3–2.7¶
<i>Polygonum amphibium</i>	145–221	NA	NA	NA	NA	1.1–2.5	1.3–2.4
<i>Polygonum hydropiper</i> , <i>P. hydropiperoides</i> ‡	23–221	2.4–2.6	2.1–2.2	1.1–1.9	1.1–2.2	1.4–1.7	1.5–2.2
<i>Sagittaria latifolia</i>	37–221	NA	1.9–2.2	0.7–2.4	0.5–1.8	0.8–1.7	0.6–1.9
<i>Salix</i> spp.	19–228	2.5–2.7	NA	2.2	1.1–2.2	1.2–2.9	1.3–3.8
<i>Schoenoplectus tabernaemontani</i>	20–221	1.3–2.6	0.9–2.2	1.8–2.3	0.5–1.6	NA	0.9–1.8
<i>Sium suave</i>	20–113	NA	1.2–2.1	1.4–1.9	1.4	NA	NA
<i>Symphyotrichum subspicatum</i>	6–203	2.4–2.7	1.2–2.5	1.5–1.9	NA	NA	NA
<i>Triglochin maritima</i>	6–12	NA	1.7–2.4	NA	NA	NA	NA
<i>Typha angustifolia</i>	6–123	NA	1.9–2.2	1.3–2.1	1.3–1.4	NA	NA
<i>Typha latifolia</i>	20–100	2.4–2.7	1.7–2.6	NA	1.4–1.9	NA	NA
<i>Vicia americana</i>	20–89	2.5–2.7	NA	NA	1.9	NA	NA

† Extreme high and low elevations may not have been included in the wetland sampling area.

‡ These two species were often indistinguishable in the field and generally occurred at the same elevation and were therefore combined.

§ There was one occurrence of a lower elevation in one quadrat, but it did not persist in subsequent years.

¶ <1.3 m in elevation, reed canary grass is extremely sparse.

decreased significantly as a function of SEV_g (linear regression, $n = 12$, $P = 0.03$; Fig. 9d).

The apparent replacement of plant species dominants was documented by the change analysis in several communities. For example, at the

most estuarine site, Baker Bay, we observed a 16% decline in the area of the *C. lyngbyei*-dominated community and an 8% increase in communities dominated by *Agrostis stolonifera* from 2011 to 2015, as well as increases in bare ground/pans

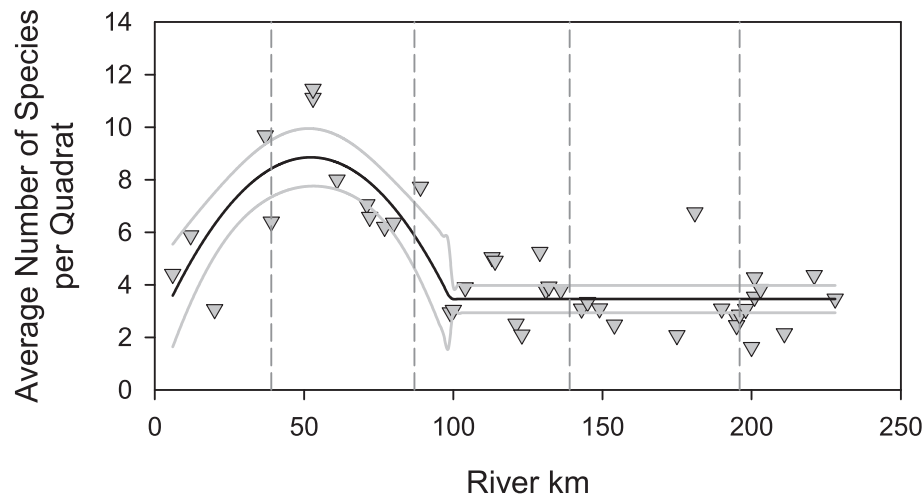


Fig. 5. Average number of species per quadrat in the mainstem sites, with segmented regression and 95% confidence intervals. Vertical dashed lines indicate zones.

and *Typha angustifolia*. Similarly, we observed a 4% shift of *C. lyngbyei* to *P. arundinacea* between 2009 and 2015 at White's Island. Franz Lake, the most fluvially dominated trends analysis site, was the only site where a decrease in *P. arundinacea* was observed; the area of the mixed *P. arundinacea*/*Polygonum amphibium* community declined 58%, whereas *P. amphibium* developed into a monoculture covering 63% of the area between 2008 and 2015.

The plant species composition at the trends analysis site, Cunningham Lake (rkm 145), had a mean between-year similarity in cover of 68.7% over 11 yr based on 66 year-to-year comparisons (min 51.4%, Q1 63.9%, median 68.8%, Q3 73.9%, max 86.5%; Fig. 7). The vegetation at Cunningham Lake graded from *S. latifolia* at the lowest marsh elevation upward to *Eleocharis palustris*, with high marsh typically dominated by *P. arundinacea* above that. Although the boundaries of the plant community zonation are somewhat static, our change analysis indicated that the communities often overlap at the boundaries where they form mixed communities that change over time. For instance, at Cunningham Lake between 2006 and 2015, 45% of the area of herbaceous communities changed; much of this change occurred at the edges of communities. The lowest elevation marsh community at Cunningham Lake changed the most, where 53% of the area became unvegetated.

Within the *E. palustris*-dominated community, 25% cover of this species was displaced by *S. latifolia* at the lower extent and 25% was replaced by *P. arundinacea*-dominated communities at the upper boundary.

Discrimination of plant communities and indicator species

Indicator species analysis.—Seventy-six significant species–zone associations ($P < 0.05$) were identified. Zone 2 had the greatest number of significant species–zone associations (44 species), and zone 4 had the least number of significant species–zone associations (10 species), either alone or in combination with other zones. Species with high indicator values (IV) were *Carex lyngbyei* throughout the zones 1–2 ($IV > 0.7$), and *Eleocharis palustris*, *Sagittaria latifolia*, and the invasive non-native *Phalaris arundinacea* in zones 2–5 ($IV > 0.90$). These tended to be the species of greatest coverage in the study area. Other species with high IV (> 0.70) included *Sium suave* and *Iris pseudacorus* associated with zone 2, and *Lilaeopsis occidentalis* associated with zones 1 and 3. All the remaining species had indicator values less than 0.68, and 75% of the values were < 0.345 . Species associated with a single zone tended to have either high specificity (the probability of a site belonging to a zone given that the species was observed there) or high fidelity (the probability of finding a species in sites belonging to a zone),

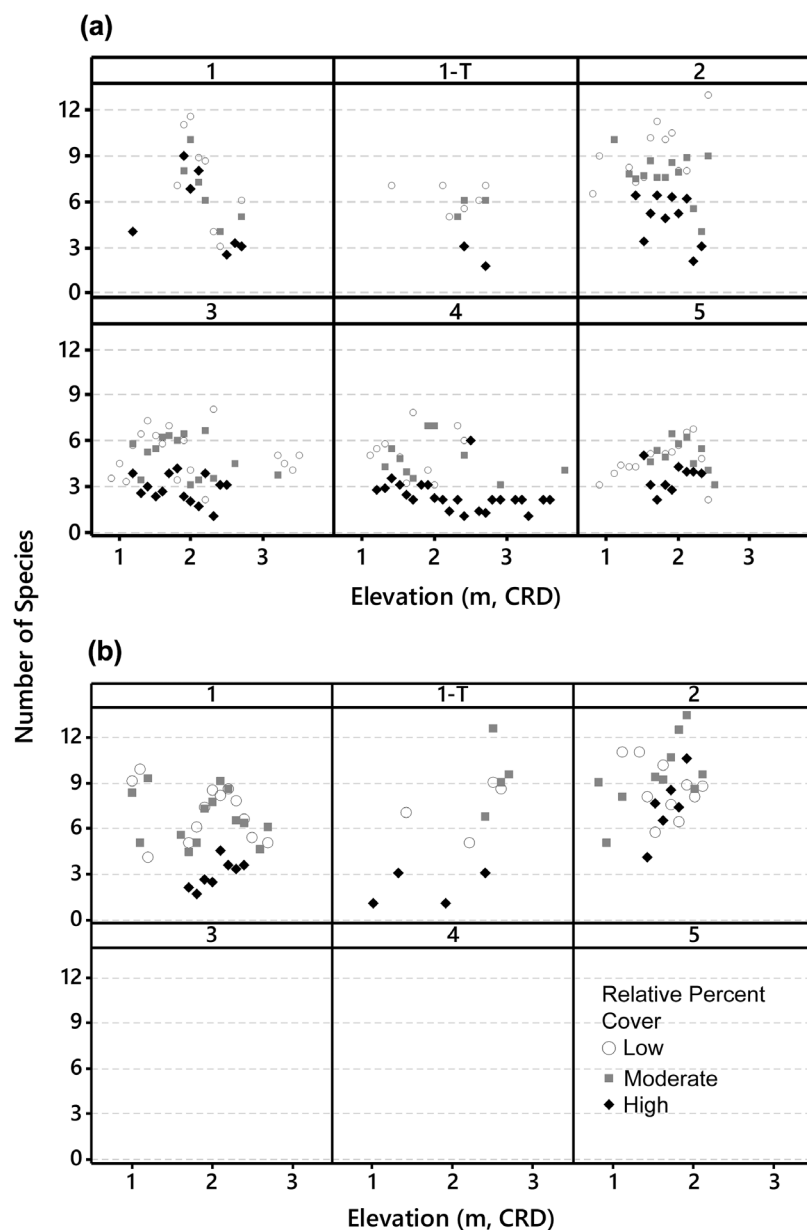


Fig. 6. The average number of species per quadrat by elevation distribution for low, medium, and high relative percent cover of (a) *P. arundinacea* in zones 1–5, and (b) *C. lyngbyei* in zones 1–2 (species not present in zones 3–5). Wetlands on tributaries to zone 1 within the Columbia River floodplain are also shown (1-T).

but not both. The species with highest fidelity and specificity are provided in Table 2. The average value of specificity for those species with significant species–zone associations was 0.92 ($Q1 = 0.88$ and $Q3 = 1.0$). Fidelity values were

generally low with the average value equal to 0.46 ($Q1 = 0.27$ and $Q3 = 0.62$).

Environmental tolerance traits.—Among the trends analysis sites, the two most landward sites had slightly fewer hydrophytic species than the

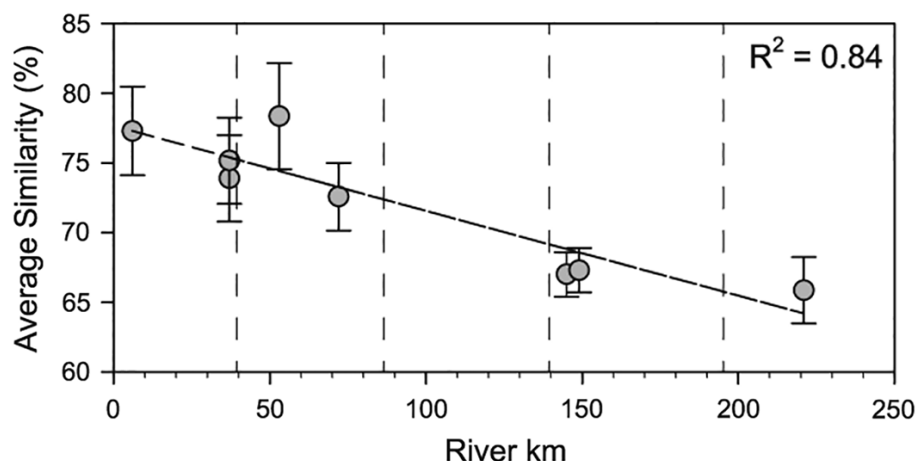


Fig. 7. Average pairwise vegetation community similarity at sites through time and the associated 95% confidence interval. Vertical dashed lines indicate zones.

six more seaward sites (Table 3). The majority (91%) of the 203 species in the study area were hydrophytes. The wetland indicator status on the National Wetland Plant List for the United States is obligate for 98 species, facultative wetland for 53, facultative for 34, and facultative upland or undefined for the remaining species (Appendix S1: Table S4; Lichvar et al. 2014). Of the species with high fidelity to zone 1 (Table 2), all six are known to be tolerant of salt in the ranges present in the estuarine portion of the Columbia River (Westley 1962, Piggott 1969, Smith 1976, Knudson and Woodhouse 1982, MacDonald 1984, Woodell 1985, Hutchinson 1988). Of the six salt-tolerant species with high fidelity to zone 1, two indicator species also have high specificity to zone 1 and high fidelity and specificity to zone 2, *Carex lyngbyei* and *Oenanthе sarmentosa* (Table 2). *Castilleja ambigua* had high specificity to zone 1 and is typically found in saline soils in our region (Janousek and Folger 2013). Three other species with high specificity to zone 1 had low tolerance to salt (Hutchinson 1988, MacDonald 1984), and they were only found in parts of zone 1 without surface salt intrusion: *Athyrium felix-femina* was in the tributaries, whereas *Sparganium eurycarpum* and *Caltha palustris* were located at the more landward sites in the zone. Two of the known salt-tolerant species with high fidelity to zone 1, *Callitriche heterophylla* and *Lilaeopsis occidentalis*, also have high fidelity to zone 3. No other

salt-tolerant species have high fidelity to zone 3, or have high fidelity or specificity to zones 4 or 5. The freshwater dominants with very high fidelity to zones 2–4 or 2–5 are known to have no to low salt tolerance: *E. palustris*, *S. latifolia*, and *P. arundinacea* (McElgunn and Lawrence 1973, Howard and Mendelssohn 1999, Martin and Shaffer 2005).

Hierarchical cluster analysis.—The five groups resulting from the cluster analysis at 95% dissimilarity indicated that a gradient of the vegetative community occurs with increasing distance from the mouth and a boxplot was used to visually describe the variability in location (rkm) among groups (Fig. 10a). Cluster group 3, which was made up of low-marsh sites, overlaps groups 1 and 2. Despite the overlap in river kilometers between groups, the median distances (rkm) for the members of each group increased significantly with group number in the landward direction (simple linear regression, $P = 0.024$, $R^2 = 86\%$).

Discriminant function analysis.—Five contiguous sections of the river, proposed as a wetland vegetation component of a longitudinal zonation for the study area by Jay et al. (2016; Fig. 1), were successfully discriminated (Wilk's lambda < 0.00001, $P < 0.0001$) with four significant roots (chi-square, $P < 0.0001$). Eigenvalues for each function were greater than 3. Roots 1 and 4 explained 93% of the variance and separated all five groups. The plot of discriminant scores

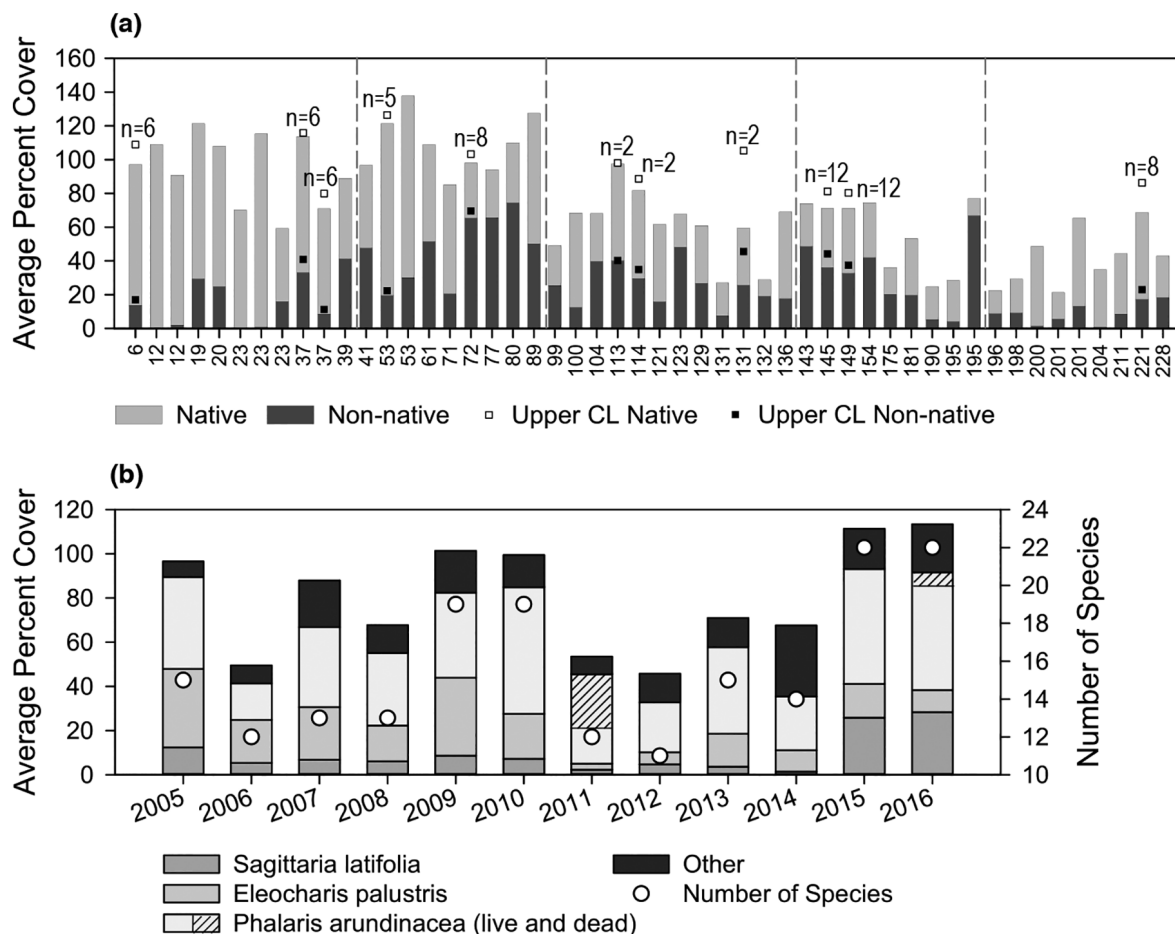


Fig. 8. (a) Average percent native and non-native cover for the 50 wetland study sites arrayed along rkm (x-axis); vertical dashed lines indicate zones. Multiple years of data are represented by the mean of all years, with the number of years (n) provided with the upper confidence limit (CL). (b) An example of the interannual variability of average percent cover and number of identified species at one long-term monitoring site, Cunningham Lake (rkm 145). Cover of standing dead *P. arundinacea* was included if it was >5% and is indicated by slashed lines.

(score 1 and score 4) for all sites provides a visual indication that all five zones are distinguishable (Fig. 10b).

Floristic quality assessment.—The mean coefficient of conservation (C) and the FQI of the eight trends analysis sites both had narrow ranges at the estuarine sites ($C = 3.1\text{--}4.8$; $FQI = 19.0\text{--}21.8$) and at the tidal river sites ($C = 2.4\text{--}3.1$; $FQI = 14.6\text{--}16.7$) (Table 3). The tidal river site values are indicative of species with broader ecological niches that are tolerant of disturbance. Three of four estuarine sites were >20 FQI (Secret River high marsh, Welch Island, and White's Island) indicating high quality. Only 24–25% of species

at the two most seaward estuarine sites were adapted for extreme anthropogenic or natural stressors ($C \leq 3$), in contrast to 40–51% of species at the six more upriver sites. Of the 203 species identified in the entire study, and of the natives, only nine had low tolerance for disturbance and 102 were highly tolerant of disturbance.

Synthesis of abiotic factors and community assemblage on the tidal–fluvial gradient

Following Cadotte and Tucker (2017), we evaluated a characteristic of the plant community, areal species cover, relative to an environmental

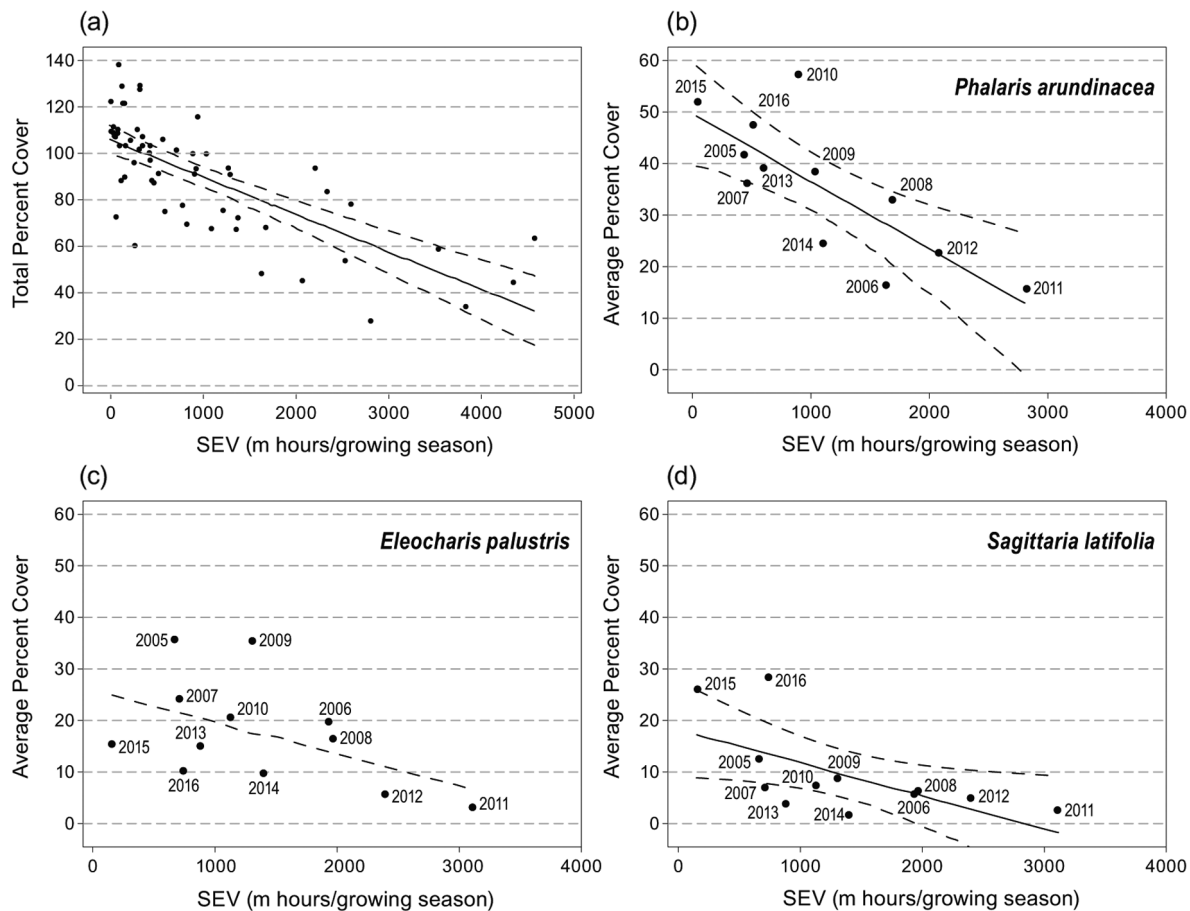


Fig. 9. (a) Total annual site average percent vegetation cover related to annual growing-season inundation (SEV_g), calculated at the average site elevation for 60 site-year combinations throughout the estuary. Annual average percent vegetation cover related to SEV_g for the dominant species at a single site, Cunningham Lake (rkm 145), calculated at the average elevation of each species: (b) *Phalaris arundinacea* (1.5 m, CRD), (c) *Eleocharis palustris* (1.3 m, CRD), and (d) *Sagittaria latifolia* (1.3 m, CRD).

gradient. We used elevation as a surrogate for inundation, and the wetland indicator status ratings, which incorporate herbaria records, botanical literature review, and frequency assessments (Lichvar et al. 2014). In all zones, facultative upland and facultative species had extremely low cover across the elevation gradient, the cover of facultative wetland species was 0% at the highest inundation levels, and obligate wetland species cover was 0% at the lowest inundation levels (Fig. 11). In summary, the abiotic factors and plant community characteristics vary predictably along the tidal-fluvial hydrologic and mixohaline-freshwater gradients represented by the five zones (Fig. 12).

DISCUSSION

Although it has long been understood that physical disturbance controls species richness in many ecosystems (e.g., Levin and Paine 1974, Connell 1978, Bertness and Ellison 1987), elucidating the interacting effects of the hydrologic regime and salinity on species assembly in wetlands along estuarine-to-tidal river gradients remains an important challenge, especially with rising sea levels affecting tidal freshwater floodplains (Baldwin et al. 2009). Furthermore, understanding these factors provides the scientific underpinnings necessary to predict the effects of defragmenting and enhancing resilience of

Table 2. The plant species with the highest (a) fidelity and (b) specificity in each of five zones in the lower Columbia River and estuary.

Species name	Zone				
	1	2	3	4	5
(a) Fidelity >0.6					
<i>Argentina egedii</i> ssp. <i>Egedii</i>	✓				
<i>Deschampsia cespitosa</i>	✓				
<i>Carex lyngbyei</i>	✓	✓			
<i>Oenanthе sarmentosa</i>	✓	✓			
<i>Lilaeopsis occidentalis</i>	✓		✓		
<i>Callitriche heterophylla</i>	✓	✓	✓		
<i>Mimulus guttatus</i>		✓			
<i>Lotus corniculatus</i>		✓			
<i>Myosotis laxa</i> , <i>M. scorpioides</i>		✓			
<i>Sium suave</i>		✓			
<i>Iris pseudacorus</i>		✓			
<i>Epilobium ciliatum</i> ssp. <i>watsonii</i>		✓			
<i>Elodea canadensis</i>		✓	✓		
<i>Sagittaria latifolia</i>		✓	✓	✓	
<i>Eleocharis palustris</i>		✓	✓	✓	✓
<i>Phalaris arundinacea</i>		✓	✓	✓	✓
<i>Equisetum fluviatile</i>		✓	✓	✓	✓
<i>Leersia oryzoides</i>		✓	✓	✓	✓
<i>Ludwigia palustris</i>			✓	✓	✓
(b) Specificity = 1.0					
<i>Athyrium filix-femina</i> ssp. <i>cyclosorum</i> †	✓				
<i>Castilleja ambigua</i> ssp. <i>ambigua</i>	✓				
<i>Sparganium eurycarpum</i>	✓				
<i>Triglochin maritima</i>	✓				
<i>Carex lyngbyei</i>	✓	✓			
<i>Oenanthе sarmentosa</i>	✓	✓			
<i>Caltha palustris</i> var. <i>palustris</i>	✓	✓			
<i>Glyceria grandis</i>		✓			
<i>Salix sitchensis</i>		✓			
<i>Galium triflorum</i>		✓			
<i>Juncus effusus</i>		✓			
<i>Potamogeton richardsonii</i>		✓			
<i>Glyceria striata</i>		✓			
<i>Platanthera dilatata</i>		✓			
<i>Trifolium wormskoldii</i>		✓			
<i>Mimulus lewisii</i>			✓		
<i>Schoenoplectus triqueter</i>			✓		
<i>Potamogeton natans</i>			✓	✓	

† Found in the uppermost tributary site only.

physically disturbed landscapes. In this study, we sought to develop a predictive framework for the research, measurement, modeling, management, and restoration of tidal wetland plant communities along estuarine-to-tidal river gradients in the context of river flows regulated by a system of dams. In light of the advances in the understanding of functional traits,

phylogenetics, and microbial interactions in recent decades, it has been argued that stricter criteria for verification of environmental filtering would benefit the science of plant communities (Kraft et al. 2015).

We broadly addressed these criteria using plant species cover and environmental data collected in 50 wetlands in the Columbia River, USA, where brackish wetlands are imperiled (ranked S2) and tidal freshwater wetlands are critically imperiled (ranked S1; Rocchio and Crawford 2015a). Additionally, we validated the utility of a metric of wetland inundation (SEV_g) for evaluating the interacting effects of elevation and longitudinal river position on multiple types of measurements of wetland plant communities on the continuum, including their interannual variability. The successful discrimination of five zones (Fig. 10b), made up of wetland sites that clustered by distance from the river mouth (Fig. 10a), provided evidence of a longitudinal gradient defined by the environmental filters associated with geophysical and hydrologic regimes in the river (Jay et al. 2016).

Framework for estuarine–tidal river research and management

Along the estuarine-to-tidal river gradient, the abiotic and biotic characteristics of the river–floodplain system each showed strong longitudinal trends, whether increasing, decreasing, or mixed (Fig. 12). The elevation of wetlands, regardless of longitudinal position, affected their inundation during the growing season (SEV_g ; Fig. 2d), which in turn dictates the proportion of facultative wetland vs. obligate wetland plant species (Fig. 11). Interannual differences in Columbia River runoff affect growing-season inundation and are predictive of the percent cover of dominant species and the total plant community percent cover in high-, moderate-, and low-flow years in the tidal river (Fig. 9). Species richness was suppressed by abiotic conditions in the lower estuary and the tidal river (Fig. 5) and correlated with the percent cover of dominant species *P. arundinacea* cover in freshwater zones 2–5 and *C. lyngbyei* cover in mixohaline zone 1 (Fig. 6).

The SEV_g metric is a useful measure of wetland inundation that is sensitive to lateral (elevation) and longitudinal (rkm) river position and

Table 3. Floristic Quality Assessment metrics for the long-term emergent marsh monitoring sites. Sites are ordered left to right, starting at the Columbia River mouth, from the estuary through the upper tidal river. Abbreviations are C, coefficient of conservatism, and FQI, floristic quality index; hydrophyte, is defined as plants with obligate or facultative wetland indicator status (Rocchio and Crawford 2013).

Metric	Baker Bay	Secret River (low)	Secret River (high)	Welch Island	White's Island	Cunningham Lake	Campbell Slough	Franz Lake
Relative distance (rkm)	6	37	37	53	72	145	149	221
Mean C (all species)	4.8	3.8	3.2	3.4	3.1	3.1	2.4	3.0
Percentage intolerant (C value ≥ 7)	13	4	7	5	2	5	5	6
Percentage tolerant (C value ≤ 3)	25	24	49	40	47	45	51	48
FQI (all species)	19.1	19.0	20.2	21.8	20.0	14.6	14.8	16.7
Adjusted FQI	46.5	36.7	33.9	36.3	33.4	32.5	29.1	32.1
% hydrophyte	75	76	66	76	74	68	62	55

interannual variability in river flow (Figs. 2d, 12). The elevation range for emergent marshes within a given zone is on the order of a few meters, but the range changes with zone, so the use of a regional low-water datum (in our case the CRD) permits the normalized comparison of abiotic or biotic metrics along the tidal–fluvial gradient. The following ecological explanations of these gradients of abiotic factors and biological characteristics by zone and elevation, and the validation of the measurement metrics, suggest that they will have utility as a more universal framework for the research and the management of natural resources on terrestrial–aquatic gradients.

Species richness was highest in the upper estuary, similar to findings for the Nanticoke River in Chesapeake Bay and suggestive of the effect of intermediate disturbance levels (Fig. 5; Connell 1978, Sharpe and Baldwin 2009). The upper estuary has an intermediate level of disturbance between the lower estuary, where salinity constrains the number of species, and the tidal river, where seasonal flooding and competition from non-natives limit the number of species. Relative native plant cover was highest in the lower estuary, moderately high in the upper tidal river, and moderately low in the sections of the river between them (Figs. 8a, 12). Overall, the total vegetative cover, percent of hydrophytic plants, and floristic quality decrease in the landward direction (Table 3 and Fig. 12). The adjusted floristic quality index (FQI) reduces the sensitivity to species richness and considers the effect of non-native species (Miller and Wardrop 2006) and is perhaps a better indication of floristic

quality in the upper estuary and tidal river where non-native species are more prevalent. Despite the lower native species richness in the mixohaline lower estuary, where species tend to be salt-adapted (Janousek and Folger 2013), the higher native cover in this zone produces a higher adjusted floristic quality index than the upper zones. Near-surface salinity and the presence of salt-tolerant plants decrease sharply near the transition from the lower to the upper estuary. Germination of most coastal marsh plants in this region, even plants commonly found in saline wetland soils, is highly sensitive to soil salinity ≥ 10 ppt; most plants achieve maximum seedling length and germination under fresh to oligohaline conditions (0–5 ppt; Janousek and Folger 2013).

Generally speaking, several factors increase in the landward direction including inundation of wetlands during the growing season, interannual and seasonal variability of the hydrologic regime, interannual variability of the vegetative cover, and percent disturbance-tolerant plant species (Fig. 12). Disturbance-tolerant species increase in the upper estuary to a level equal to that of the tidal river, indicating that although the hydrological regime in the upper estuary is predominantly tidal, the lack of salinity allows for the establishment of more disturbance-tolerant and non-native species (C value = 0). In addition, the muted interannual and seasonal variability of the hydrological regime in the upper estuary zone (Fig. 3) may result in a greater number of species because the stress of seasonal flooding is reduced (Fig. 5). We infer

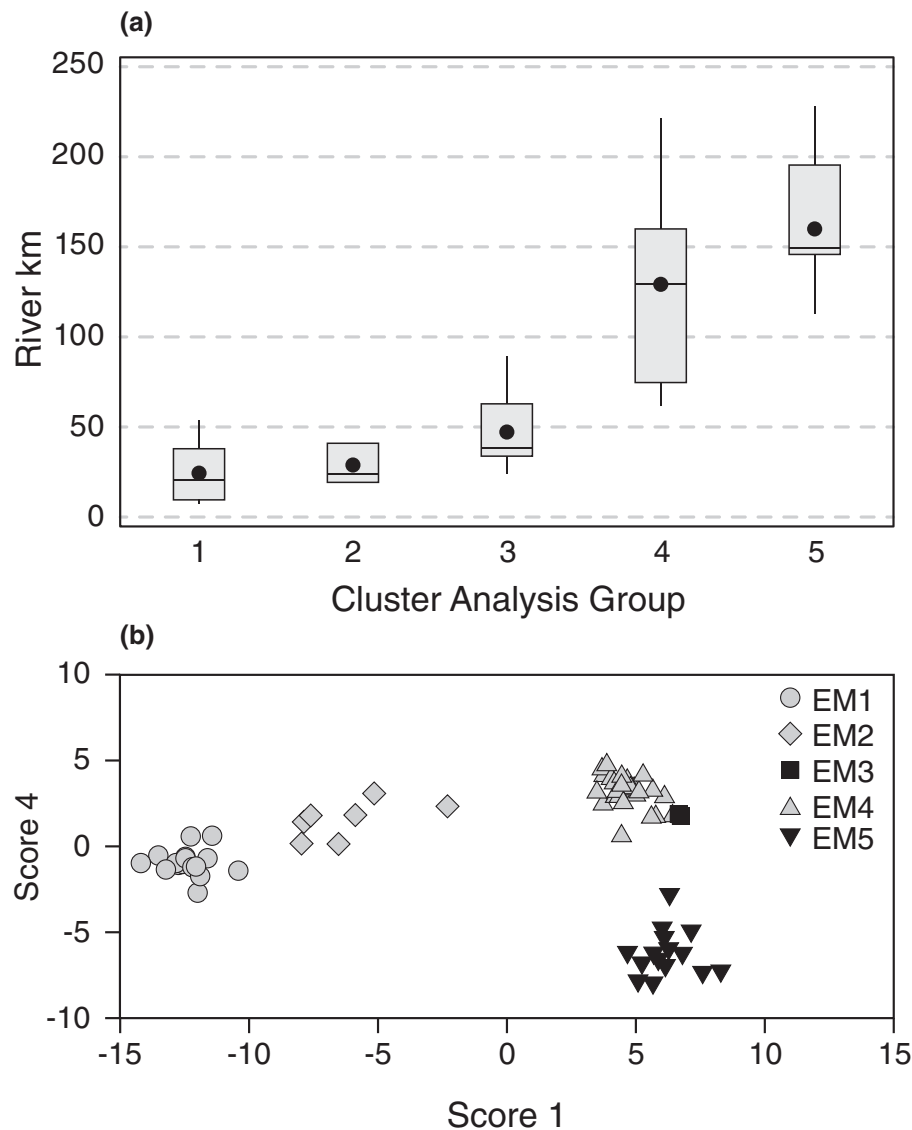


Fig. 10. (a) Results of cluster analysis seeded with five categories, box plots represent river kilometers where the clustered sites occurred and (b) scatter plot of the discriminant scores for ecohydrologic zones 1–5.

that hydrophytes are suppressed in the tidal river (Fig. 12) because they likely cannot withstand the interannual variability and seasonal variability of the hydrologic regime or the daily wetting and drying effects of dam operations. At upriver sites in flood years, many plant species, including hydrophytic obligate wetland species, were reduced to very low percent cover (Fig. 9b–d), presumably because their tolerance of inundation was exceeded by spring freshets during a portion of the growing season.

Our findings indicated that both salinity and cumulative surface-water depth in wetlands during the growing season (SEV_g) are strong abiotic filters driving plant community assembly. Further, variability of inundation is also important. In turn, these factors vary by longitudinal river position, while inundation also varies by elevation or the lateral river axis (Bunn and Arthington 2002). These abiotic filters, along with competitive dominance of certain plant species, influence the outcomes of ecological restoration

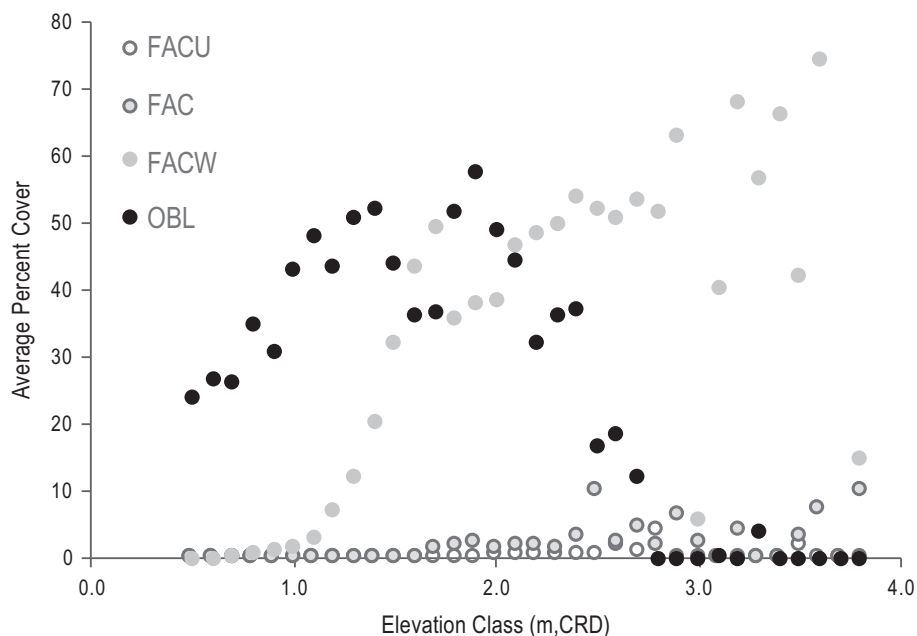


Fig. 11. Average percent cover of plant species in wetland indicator status categories on the elevation gradient (binned into 10-cm elevation classes). Data from the 46 mainstem river wetlands (108 site-year combinations; tributary sites excluded). Wetland indicator status abbreviations are OBL, obligate wetland; FACW, facultative wetland; FAC, facultative; and FACU, facultative upland (Lichvar et al. 2014).

(Funk et al. 2008). The relationships between distance from the river mouth, hydrology, elevation, and species composition and competition will continue to provide valuable information for designing study strata, predicting the effects of climate change-related hydrologic changes in sea level and basin-scale hydrology on plant communities, informing the managers and policymakers who are determining future Columbia River system operations, and improving ecological restoration and adaptive management of the estuary and tidal river (Ebberts et al. 2018). At the regional scale, the spatial gradients of relationships between environmental factors, plant community structure, and associated wetland functions are critical for improving coastal Earth system models (Ward et al. 2020).

Community assembly and dynamics along estuarine–tidal river gradients

The inundation tolerance ranges, which were strongly indicated by elevation limits on species' occurrence (Table 1) and the reduction of cover with increased SEV_g (Fig. 9), may be explained by plant traits. Some 13 plant traits are involved

in resistance to the effects of inundation and desiccation from short- and long-duration soil waterlogging and shallow or deep submergence of plant shoots (Colmer and Voesenek 2009). In tidal freshwater marsh species, seed size is related to the success of germination under inundation, but overall germination is lower with flooding or soil saturation than in drained samples and germination success is generally enhanced by light (Leck 1996). Inundation also indirectly impacts plants by limiting the penetration of light (Keddy and Reznicek 1986). The physiological effects of salinity result in a small number of salt-tolerant species in the pool, including all six species with high fidelity to zone 1, which presumably have a competitive advantage (Table 2; Hutchinson 1988). Few of these species also have high fidelity or specificity to zones 2 or 3, and none are important in zones 4 or 5.

Two species most frequently had high percent cover: *C. lyngbyei* had high fidelity and specificity to ecohydrologic zones 1 and 2, and *P. arundinacea* had high fidelity to zones 2–5 and low specificity to any zone (Table 2).

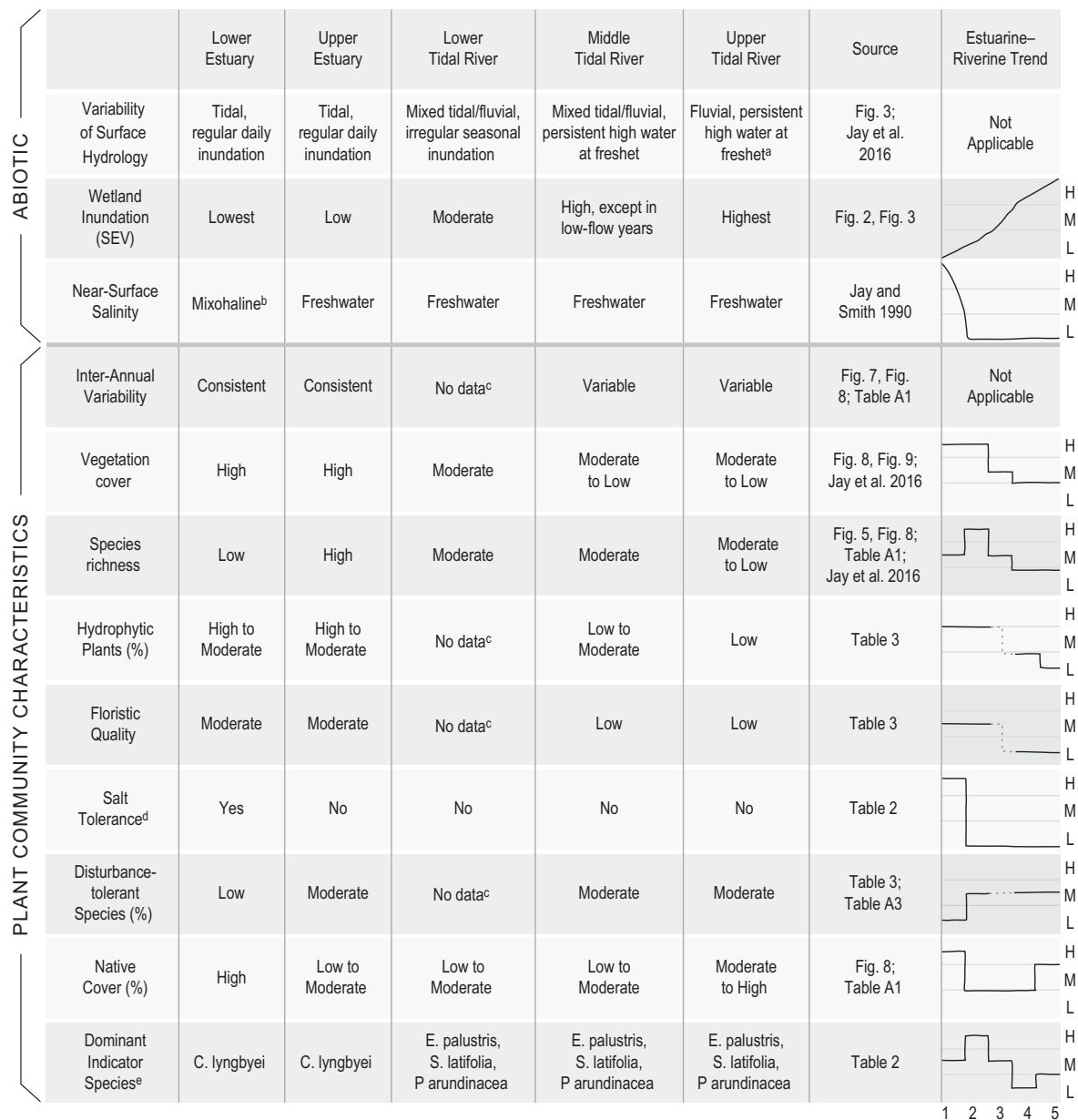


Fig. 12. Abiotic factors and plant community characteristics along the ecohydrologic gradients from the estuary through the tidal river. The estuarine-to-riverine trends from zone 1 to zone 5 are summarized in the right-most column. Relative ranks are qualitative and were developed from the data and information in the sources. Ranks are abbreviated as H, high; M, medium; and L, low. In the Lower Estuary, near-surface salinity is spatiotemporally variable, and plant species may be termed “euryhaline” to describe the ability to tolerate a wide range of salinity (0–25 ppt maximum salinity at MLLW, low river flow, and neap tide [Jay and Smith 1990]). In the Lower Tidal River, multi-year trend sites were absent; however, several sites were sampled a second time and the variability of vegetative cover with flow year was observed. In the Upper Tidal River, the variability of surface hydrology is also affected by the Federal Columbia River Power System. The evaluation of salt tolerance was based on plant species with high fidelity to zone 1 (>0.6) and very high fidelity (>0.96) to zones 2–5. The trend line for dominant indicator species is based on total number of indicator species per zone.

P. arundinacea was found only at the higher elevations in zone 1 (Table 1). There was a significant impact on species richness when either plant's relative cover in a quadrat was >60% (Fig. 6). Thus, we cannot infer that the low number of species tolerant of environmental conditions at upper and lower ends of the tidal–fluvial gradient reduces competition (Fig. 12).

The native brackish plant community in the Pacific Northwest with a high percent cover of *C. lyngbyei*, documented in the U.S. National Vegetation Classification (Rocchio and Crawford 2015b), is present in zone 1. However, we observed higher diversity in the *C. lyngbyei* communities in zone 2 tidal freshwater wetlands than previously described (Fig. 5). *P. arundinacea* is highly invasive in freshwater wetlands of the Pacific Northwest including tidal wetlands such as those on the lower Columbia River floodplain (Lavergne and Molofsky 2004). Cover of *P. arundinacea* is lower in zone 5, likely because of its low tolerance for high inundation (Miller and Zedler 2003), steeper slopes such that less area at optimum elevations is available, and competition with species, such as *P. amphibium*, that are more adapted to higher and more variable inundation.

In some cases, flood years coincided with species shifts. For instance, the 2012 species shift at Franz Lake occurred during the second of two consecutive years of high inundation. The former dominant species was *P. arundinacea*, a facultative wetland species that can tolerate some level of tidal and seasonal inundation. The replacement species, *P. amphibium*, is an obligate wetland species that is often found on shorelines, in shallow water, and along streams and lakes (Washington Department of Ecology 2001). To survive high inundation levels, the plant grows very tall (>2 m) developing aerenchyma in the leaves and stems to facilitate floating on the surface of the water (Partridge 2001). When the water recedes, the plant is prostrate on the ground. The species has persisted at the site since the high inundation years, despite very low inundation during the spring and summer in 2015. Persistence may have been aided by the species' ability to change its morphology, becoming smaller (~1 m), with narrow stems and more upright growth habit in response to changing inundation (Partridge 2001). This adaptable plant is currently outcompeting *P. arundinacea* at the site, and given its wide tolerance for changing

hydrology, we believe it is likely to continue to do so.

Like Keddy and Reznicek (1986) showed for the Great Lakes, high water levels appear to create gaps that are colonized by other species. In another example of a species shift, the decline in overall cover at Cunningham Lake associated with 2011–2012 high-flow years (Fig. 3c) persisted in 2013–2014. During the low-water years of 2015–2016, the average cover of low-marsh plant *S. latifolia* increased over that observed in the preceding decade (Fig. 8b). It appears that the *S. latifolia* expanded into the low-elevation niche previously filled by *E. palustris*.

In contrast to the tidal river, in estuarine portions of the river there is less interannual variability. The change analysis suggested that interaction between flow and salinity may also play a role in plant community shifts. At the most seaward site, Baker Bay, an increase in non-native species *A. stolonifera* and *T. angustifolia* was coincident with reduction in cover of *C. lyngbyei*. In the warmer low-water year, 2015, we observed reduced cover and early senescence of *C. lyngbyei* at Baker Bay, which could have been related to high salinity levels during summer months (Appendix S1: Table S2). However, upriver of maximum salinity intrusion at White's Island, *C. lyngbyei* also decreased in the 2015 change analysis coincident with an increase in *P. arundinacea*. The widespread occurrence of *P. arundinacea* in the study area may facilitate its rapid spread when gaps become available.

Limitations and future research needs

This study developed the hydrologic regime–plant species relationships underpinning community distribution and will inform future research bearing on adaptation to altered salinity and hydrologic regimes, that is, trait-based, functional group, and soil microbiome studies. Anthropogenic features of the study area that should be considered when transferring this framework to other coastal river systems are the jetty system near the river mouth, the navigation channel, urban development on the middle tidal river floodplain, forest harvest in the watersheds, agriculture in the floodplains, and the effects of the hydropower system and water withdrawals on wetland inundation, particularly in the middle and upper tidal river. The zones identified

here may be viewed as strata for future research. Despite sampling 50 wetlands over a 234-rkm region, however, sampling was sparse for such a dynamic and spatially complex region. The conclusions of statistical tests reported here may be either strengthened or altered once additional data are collected, affecting the zonation. In eco-hydrologic zone 3, for example, the less-disturbed wetlands, that were the basis of the zonation analysis (Fig. 10b), are rare due to land conversion and dredged-material placement (Marcoe and Pilson 2017). Similarly, the low number of sites in the seaward vicinity of the boundary between zones 1 and 2 means that further data collection could refine the boundary location.

Strict environmental filtering is difficult to ascertain through observational studies (Cadotte and Tucker 2017). In addition to abiotic conditions, another factor in the species assemblage could be variability in the species pool available for colonization of sites (Aarssen and Schamp 2002), particularly at locations farther from the mainstem river. That said, the high aquatic connectivity shown by the influence of zone (Fig. 2) and elevation (Fig. 4) on SEV_g and wetland indicator status (Fig. 11) facilitates the dispersal of plant propagules and lessens limitations on the species pool in the study area. Evaluation of major factors that structure species composition and abundance, including competitive exclusion and other biotic interactions (Engels et al. 2011), colonization, and other environmental stressors and disturbances (Grime 2001), is recommended. Further analysis is also needed to identify individual plant associations and situate them within the U.S. National Vegetation Classification System (Jennings et al. 2009). Similar to other tidal freshwater ecosystems, such as the Hudson River, in which wetlands are major generators of particulate organic carbon to the estuarine carbon budget with seasonally variable exchange rates (Hunsinger et al. 2010), the combined storm surge and rain events in the fall and winter, in tributaries to the estuary zones, mobilize and transport marsh plant matter (Thom et al. 2018). The degree to which similar patterns of export occur during the spring freshet in the tidal river and the importance of plant species composition is uncertain.

CONCLUSION

Multidisciplinary methods supporting a landscape-scale approach to ecological research in tidal–fluvial transition zones are important because sea-level rise and other climate-driven hydrologic changes are affecting coasts and tidal rivers worldwide. This study design built on prior regional-scale studies in tidal freshwater or coastal areas (Findlay et al. 2002, Steyer et al. 2003) and in turn the framework for research and management described here will be transferrable to other coastal rivers. The utility of the SEV_g , which integrates water surface elevation dynamics and the elevation of a plant species, community, or wetland site is notable. Taken together, our findings provide a robust set of factors to consider when designing restoration projects and predicting changes in floristic composition.

The flora of tidal wetland plant communities of the lower Columbia River and estuary described here is strongly controlled by abiotic filters, which in turn are directly associated with the vertical, lateral, and longitudinal position of wetlands on the river floodplain. Two plant species with high areal cover, which are significantly associated with lower species richness, transition in their dominance along the tidal–fluvial gradient. Unlike classification, which assumes discontinuous groups, our findings show that there is gradual change across elevation gradients both within wetlands and along the mainstem river, based on the distance from the influence of salt and regular tidal regimes at the coast and from the dominance of the variable river-flow regime at the head of tide. Nevertheless, five vegetation zones were discriminated, arrayed from the river mouth to the head of tide, associated with indicator species and unique patterns of salinity and inundation, which will provide the basis for future study designs and analysis of individual plant associations on this dynamic tidal–fluvial gradient.

Species moderately tolerant of disturbance were widespread in the tidal river and upper estuary (Fig. 12), indicating a potential for resilience of the tidal wetlands. The longitudinal gradients of tidal–fluvial hydrology and mixohaline–freshwater salinity (Fig. 12), together with the elevation gradients (Fig. 11), were important abiotic controls on plant community development and resistance

to interannual variability on coastal river floodplains. The areal extent of these abiotic environmental gradients will vary in every coastal river system, yet this general framework and the SEV_g metric should be widely applicable to the extraction of abiotic filters, effects of plant species competition, and distinct ecohydrologic zones.

ACKNOWLEDGMENTS

Data collection and analysis were mostly funded through the CEERP: four studies by the Bonneville Power Administration (BPA) and three studies by the U.S. Army Corps of Engineers (USACE) Portland District. We are grateful to J. Karnezis and B. Zelinsky, BPA, and C. Studebaker and the late B. Ebberts, USACE, for supporting a scientific foundation for the CEERP. We also thank C. Corbett (preceded by S. McEwen) of the Lower Columbia Estuary Partnership (LCEP), and G. E. Johnson of Pacific Northwest National Laboratory, who administered six of the seven studies in which data were collected and assisted us at many decision points. G.E. Johnson and K. L. Sobocinski were instrumental to initiating this research. We also thank program coordinators at LCEP including J. Leary, E. Haas, K. Jones, J. Sagar, A. Hanson, and M. Schwartz, and numerous individuals who assisted in field data collection and data processing over the years, particularly N. Sather, R. Kaufmann, C. Wright, and C. Trostle. J. Rocchio kindly discussed plant community classification in the Washington State Natural Heritage Program with us. At PNNL, we are grateful for support by N. Johnson for graphics, H. Stewart for data analysis, and S. Ennor for editing. Comments from anonymous reviewers improved and focused the manuscript. Lastly, we are grateful to the many public and private landowners who allowed and facilitated access to their wetlands for this research. AB is the principal investigator; AB, VC, HD, and RT designed the study; AB, HD, SZ, and RT contributed to site selection; AB, SZ, HD, and RT collected the data; AB, VC, HD, RT, and SZ analyzed the data; AB, VC, HD, and SZ contributed to figures and tables; AB and HD reviewed the literature; and AB, HD, VC, and RT synthesized and wrote the manuscript.

LITERATURE CITED

Aarssen, L. W., and B. S. Schamp. 2002. Predicting distributions of species richness and species size in regional floras: applying the species pool hypothesis to the habitat templet model. *Perspectives in Plant Ecology, Evolution and Systematics* 5:3–12.

- Adams, M. A., and G. L. Williams. 2004. Tidal marshes of the Fraser River estuary: composition, structure, and a history of marsh creation efforts to 1997. B. J. Groulx, D. C. Mosher, J. L. Luternauer and D. E. Bilderback, Fraser River Delta, British Columbia: Issues of an Urban Estuary. Geological Survey of Canada Bulletin. 567:147–172.
- Amin, M. 1983. On perturbations of harmonic constants in the Thames estuary. *Geophysical Journal of the Royal Astronomical Society* 73:587–603.
- Araya, Y. N., J. Silvertown, D. J. Gowing, K. J. McConway, H. P. Linder, and G. Midgley. 2011. A fundamental, eco-hydrological basis for niche segregation in plant communities. *New Phytologist* 189:253–258.
- Baldwin, A. H., A. Barendregt, and D. F. Whigham. 2009. Tidal freshwater wetlands – An introduction to the ecosystem. Pages 1–10 in A. Barendregt, D. Whigham and A. Baldwin, editors. *Tidal freshwater wetlands*. Backhuys Publishers, Leiden, The Netherlands.
- Bertness, M. D., and A. M. Ellison. 1987. Determinants of pattern in a New England salt marsh plant community. *Ecological Monographs* 57:129–147.
- Bunn, S. E., and A. H. Arthington. 2002. Basic principles and ecological consequences of altered flow regimes for aquatic biodiversity. *Environmental Management* 30:492–507.
- Cadotte, M. W., and C. M. Tucker. 2017. Should environmental filtering be abandoned? *Trends in Ecology and Evolution* 32:429–437.
- Callaway, J. C., A. B. Borde, H. L. Diefenderfer, V. T. Parker, J. M. Rybczyk, and R. M. Thom. 2012. Pacific Coast tidal wetlands. Pages 103–116 in D. P. Batzer and A. H. Baldwin, editors. *Wetland habitats of North America: Ecology and conservation concerns*. University of California Press, Berkeley, California, USA.
- Center for Coastal Margin Observation and Prediction (C-MOP). 2019. Salinity data from Saturn-07 station; May 2013 to September 2016. Downloaded 12/26/19 from http://www.stccmop.org/datamart/observation_network
- Christy, J. A., and J. A. Putera. 1993. Lower Columbia River Natural Area Inventory: 1992. Report to The Nature Conservancy, Washington Field Office, Seattle, Washington. Oregon Natural Heritage Program, Portland, Oregon, USA.
- Clarke, K. R., and R. M. Warwick. 2001. Change in marine communities: an approach to statistical analysis and interpretation. Second edition. PRIMER-E Ltd., Plymouth, UK.
- Clewell, A. F., and J. Aronson. 2013. Ecological restoration: principles, values, and structure of an

- emerging profession. Second edition. Island Press, Washington, D.C., USA.
- Colmer, T. D., and L. A. C. J. Voesenek. 2009. Flooding tolerance: suites of plant traits in variable environments. *Functional Plant Biology* 36: 665–681.
- Connell, J. H. 1978. Diversity in tropical rain forests and coral reefs. *Science* 199:1302–1310.
- Cowardin, L. M., V. Carter, F. C. Golet, and E. T. LaRoe. 1979. Classification of wetlands and deep-water habitats of the United States. FWS/OBS 79/31. U.S. Department of the Interior Fish and Wildlife Service. Office of Biological Services, Washington, D.C., USA.
- Crain, C. M., B. R. Silliman, S. L. Bertness, and M. D. Bertness. 2004. Physical and biotic drivers of plant distribution across estuarine salinity gradients. *Ecology* 85:2539–2549.
- De Cáceres, M., and P. Legendre. 2009. Associations between species and groups of sites: indices and statistical inference. *Ecology* 90:3566–3574.
- Doerffer, R., J. Fischer, M. Stössel, C. Brockmann, and H. Grassl. 1989. Small scale patches of suspended matter and phytoplankton in the Elbe River estuary, German Bight and tidal flats. *Advanced Space Research* 9:191–200.
- Dufrêne, M., and P. Legendre. 1997. Species assemblages and indicator species: the need for a flexible asymmetrical approach. *Ecological Monographs* 67:345–366.
- Ebberts, B. D., B. D. Zelinsky, J. P. Karnezis, C. A. Studebaker, S. Lopez-Johnston, A. M. Creason, L. Krasnow, G. E. Johnson, and R. M. Thom. 2018. Estuary ecosystem restoration: implementing and institutionalizing adaptive management. *Restoration Ecology* 26:360–369.
- Engels, J. G., F. Rink, and K. Jensen. 2011. Stress tolerance and biotic interactions determine plant zonation patterns in estuarine marshes during seedling emergence and early establishment. *Journal of Ecology* 99:277–287.
- Findlay, S. E. G., E. Kiviat, W. C. Nieder, and E. A. Blair. 2002. Functional assessment of a reference wetland set as a tool for science management and restoration. *Aquatic Sciences* 64:107–117.
- Fox, D. S., S. Bell, W. Nehlsen, and J. Damron. 1984. The Columbia River Estuary: atlas of physical and biological characteristics. Columbia River Estuary Data Development Program, Astoria, Oregon, USA.
- Freyman, W. A., L. A. Masters, and S. Packard. 2016. The Universal Floristic Quality Assessment (FQA) Calculator: an online tool for ecological assessment and monitoring. *Methods in Ecology and Evolution* 7:380–383.
- Funk, J. L., E. E. Cleland, K. N. Suding, and E. S. Zavaleta. 2008. Restoration through reassembly: plant traits and invasion resistance. *Trends in Ecology & Evolution* 23:695–703.
- Gallo, M., and S. Vinzon. 2005. Generation of overtides and compound tides in Amazon estuary. *Ocean Dynamics* 55:441–448.
- Godin, G. 1999. The propagation of tides up rivers with special considerations on the upper Saint Lawrence River. *Estuarine, Coastal and Shelf Science* 48:307–324.
- Gowing, D. G., C. S. Lawson, E. G. Youngs, K. R. Barber, J. S. Rodwell, M. V. Prosser, H. L. Wallace, J. O. Mountford, and G. Spoor. 2002. The water regime requirements and the response to hydrological change of grassland plant communities. Project BD1310 for the Department of Environment, Food, and Rural Affairs by Institute of Water and Environment, Bedford, UK.
- Grime, J. P. 2001. Plant strategies, vegetation processes, and ecosystem properties. Second edition. John Wiley and Sons Ltd, Chichester, UK.
- Helaire, L. T., S. A. Talke, D. A. Jay, and D. Mahedy. 2019. Historical changes in Lower Columbia River and estuary floods: a numerical study. *Journal of Geophysical Research: Oceans* 124:7926–7946.
- Hickson, R. E. 1912. A report on the establishment of river gages on lower Columbia & Willamette rivers. Report to Major J. F. McIndoc, U.S. Army Corps of Engineers, July 1, 1912. Portland District, Portland, Oregon, USA.
- Hill, N. M., P. A. Keddy, and I. C. Wisheu. 1998. A hydrological model for predicting the effects of dams on the shoreline vegetation of lakes and reservoirs. *Environmental Management* 22:723–736.
- Howard, R. J., and I. A. Mendelsohn. 1999. Salinity as a constraint on growth of oligohaline marsh macrophytes. I. Species variation in stress tolerance. *American Journal of Botany* 86:785–794.
- Hunsinger, G. B., S. Mitra, and S. E. G. Findlay. 2010. Wetland-driven shifts in suspended particulate organic matter composition of the Hudson River estuary, New York. *Limnology and Oceanography* 55:1653–1667.
- Hutchinson, I. 1988. Salinity tolerance of plants of estuarine wetlands and associated uplands. Contract No. C0088137, Washington State Shorelands and Coastal Zone Management Program: Wetlands Section, Olympia, Washington.
- Jackson, S. T., and R. J. Hobbs. 2009. Ecological restoration in the light of ecological history. *Science* 325:567–569.
- Jacobs, S., O. Beauchard, E. Struyf, T. Cox, T. Maris, and P. Meire. 2009. Restoration of tidal freshwater vegetation using controlled reduced tide (CRT)

- along the Schelde Estuary (Belgium). *Estuarine, Coastal and Shelf Science* 85:368–376.
- Janousek, C. N., and C. L. Folger. 2013. Inter-specific variation in salinity effects on germination in Pacific Northwest tidal wetland plants. *Aquatic Botany* 111:104–111.
- Jay, D. A., A. B. Borde, and H. L. Diefenderfer. 2016. Tidal–fluvial and estuarine processes in the lower Columbia River: II. Water level models, floodplain wetland inundation, and system zones. *Estuaries and Coasts* 39:1299–1324.
- Jay, D. A., K. Leffler, H. L. Diefenderfer, and A. B. Borde. 2015. Tidal–fluvial and estuarine processes in the lower Columbia River: I. along-channel water level variations, Pacific Ocean to Bonneville Dam. *Estuaries and Coasts* 38:415–433.
- Jay, D. A., and J. D. Smith. 1990. Residual circulation in shallow estuaries 1. Highly stratified, narrow estuaries. *Journal of Geophysical Research* 95:711–731.
- Jennings, M. D., D. Faber-Langendoen, O. L. Louckes, R. K. Peet, and D. Roberts. 2009. Standards for associations and alliances of the U.S. National Vegetation Classification. *Ecological Monographs* 79:173–199.
- Jones, A. E., A. K. Hardison, B. R. Hodges, J. W. McClelland, and K. B. Moffett. 2020. Defining a riverine tidal freshwater zone and its spatiotemporal dynamics. *Water Resources Research* 56: e2019WR026619.
- Keddy, P. A., and A. A. Reznicek. 1986. Great Lakes vegetation dynamics: the role of fluctuating water levels and buried seeds. *Journal of Great Lakes Research* 12:25–36.
- Kirwan, M. L., and J. P. Megonigal. 2013. Tidal wetland stability in the face of human impacts and sea-level rise. *Nature* 504:53–60.
- Kiviat, E. 2009. Human uses of tidal freshwater wetlands on the USA East Coast. Pages 21–30 in A. Barendregt, D. Whigham, and A. Baldwin, editors. *Tidal freshwater wetlands*. Backhuys Publishers, Leiden, The Netherlands.
- Knudson, P., and W. W. Woodhouse Jr. 1982. Pacific coastal marshes. Pages 111–130 in R. R. Lewis III, editors. *Creation and restoration of coastal plant communities*. CRC Press, Boca Raton, Florida.
- Kraft, N. J. B., P. B. Adler, O. Godoy, E. C. James, S. Fuller, and J. M. Levine. 2015. Community assembly, coexistence and the environmental filtering metaphor. *Functional Ecology* 29:592–599.
- Kunze, L. M. 1994. Preliminary classification of native, low elevation, freshwater wetland vegetation in Western Washington. Washington State Department of Natural Resources, Olympia, Washington, USA.
- Latrubesse, E., et al. 2017. Damming the rivers of the Amazon Basin. *Nature* 546:363–369.
- Lavergne, S., and J. Molofsky. 2004. Reed canary grass (*Phalaris arundinacea*) as a biological model in the study of plant invasions. *Critical Reviews in Plant Sciences* 23:415–429.
- Leck, M. A. 1996. Germination of macrophytes from a Delaware River tidal freshwater wetland. *Bulletin of the Torrey Botanical Club* 123:48–67.
- Leck, M. A., A. H. Baldwin, V. T. Parker, and I. Schile. 2009. Plant communities of tidal freshwater wetlands of the continental USA and southeastern Canada. Pages 41–58 in A. Barendregt, D. Whigham and A. Baldwin, editors. *Tidal freshwater wetlands*. Backhuys Publishers, Leiden, The Netherlands.
- Leck, M. A., and R. L. Simpson. 1995. Ten-year seed bank and vegetation dynamics of a tidal freshwater marsh. *American Journal of Botany* 82:1547–1557.
- Levin, S. A., and R. T. Paine. 1974. Disturbance, patch formation, and community structure. *Proceedings of the National Academy of Sciences of the United States of America* 71:2744–2747.
- Lichvar, R. W., M. Butterwick, N. C. Melvin, and W. N. Kirchner. 2014. The national wetland plant list: 2014 update of wetland ratings. *Phytoneuron* 41:1–42.
- Lotze, H. K., H. S. Lenihan, B. J. Bourque, R. H. Bradbury, R. G. Cooke, M. C. Kay, S. M. Kidwell, M. X. Kirby, C. H. Peterson, and J. B. C. Jackson. 2006. Depletion, degradation, and recovery potential of estuaries and coastal seas. *Science* 312:1806–1809.
- Marcoe, K., and S. Pilson. 2017. Habitat change in the lower Columbia River estuary, 1870–2009. *Journal of Coastal Conservation* 21:505–525.
- Martin, S. B., and G. P. Shaffer. 2005. *Sagittaria* biomass partitioning relative to salinity, hydrologic regime, and substrate type: implications for plant distribution patterns in coastal Louisiana, United States. *Journal of Coastal Research* 21:167–174.
- MacDonald, K. B. 1984. Tidal marsh plant production in the Columbia River Estuary. Columbia River Estuary Data Development Program, Columbia River Estuary Study Taskforce, Astoria, Oregon.
- McElgunn, J. D., and T. Lawrence. 1973. Salinity tolerance of Altai wild ryegrass and other forage grasses. *Canadian Journal of Plant Science* 53:303–307.
- Miller, R. C., and J. B. Zedler. 2003. Responses of native and invasive wetland plants to hydroperiod and water depth. *Plant Ecology* 167:57–69.
- Miller, S. J., and D. H. Wardrop. 2006. Adapting the floristic quality assessment index to indicate anthropogenic disturbance in central Pennsylvania wetlands. *Ecological Indicators* 6:313–326.

- Möller, I., and E. Christie. 2019. Hydrodynamics and modeling of water flow in coastal wetlands. Pages 289–323 in G. M. E. Perillo, E. Wolanski, D. R. Cahoon, and C. S. Hopkinson, editors. *Coastal Wetlands: An integrated ecosystem approach*. Second edition. Elsevier, Amsterdam, The Netherlands.
- Naiman, R. J., and H. Décamps. 1997. The ecology of interfaces: riparian zones. *Annual Review of Ecology and Systematics* 28:621–658.
- National Research Council [Ocean Studies Board]. 2012. *Sea-level rise for the coasts of California, Oregon, and Washington: past, present, and future*. National Academies Press, Washington, D.C., USA.
- NOAA [National Ocean and Atmospheric Administration]. 2018. Regional Climate Center AgACIS (Agricultural Applied Climate Information System) WETS Tables. <http://agacis.rcc-acis.org/>
- Odum, W. E. 1988. Comparative ecology of tidal freshwater and salt marshes. *Annual Review of Ecology and Systematics* 19:147–176.
- Partridge, J. W. 2001. *Persicaria amphibia* (L.) Gray (*Polygonum amphibium* L.). *Journal of Ecology* 89:487–501.
- Poff, N. L., J. D. Allan, M. B. Bain, J. R. Karr, K. L. Prestegard, B. D. Richter, R. E. Sparks, and J. C. Stromberg. 1997. The natural flow regime: a paradigm for river conservation and restoration. *BioScience* 47:769–784.
- Piggott, C. D. 1969. Influence of mineral nutrition on the zonation of flowering plants in coastal salt-marshes. Pages 25–35 in I. Rorison, editor. *Ecological aspects of the mineral nutrition of plants*. Blackwell Publishing, Oxford, United Kingdom.
- Pratolongo, P., N. Leonardi, J. R. Kirby, and A. Plater. 2019. Temperate coastal wetlands: morphology, sediment processes, and plant communities. Pages 105–152 in G. M. E. Perillo, E. Wolanski, D. R. Cahoon and C. S. Hopkinson, editors. *Coastal Wetlands: An Integrated Ecosystem Approach*. Second edition. Elsevier, Amsterdam, The Netherlands.
- R Core Team. 2018. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.
- Rocchio, F. J., and R. C. Crawford. 2013. Floristic quality assessment for Washington vegetation. Report 2013–03. Washington State Department of Natural Resources Natural Heritage Program, Olympia, Washington, USA.
- Rocchio, F. J., and R. C. Crawford. 2015a. Conservation Status Ranks for Washington's Ecological Systems. Report 2015–03. Washington State Department of Natural Resources Natural Heritage Program, Olympia, Washington, USA.
- Rocchio, F. J., and R. C. Crawford. 2015b. Ecological systems of Washington state: a guide to identification. Report 2015–04. Washington State Department of Natural Resources Natural Heritage Program, Olympia, Washington, USA.
- Roegner, G. C., H. L. Diefenderfer, A. B. Borde, R. M. Thom, E. M. Dawley, A. H. Whiting, S. A. Zimmerman, and G. E. Johnson. 2009. Protocols for monitoring habitat restoration projects in the lower Columbia River and estuary. National Oceanic and Atmospheric Administration Technical Memorandum NMFS-NWFSC-97. U.S. Department of Commerce, Seattle, Washington, USA.
- Sharpe, P. J., and A. H. Baldwin. 2009. Patterns of wetland plant species richness across estuarine gradients of Chesapeake Bay. *Wetlands* 29: 225–235.
- Sharpe, P. J., and A. H. Baldwin. 2013. Wetland plant species richness across estuarine gradients: the role of environmental factors and the mid-domain effect. *Aquatic Botany* 107:23–32.
- Simon, S. D., M. E. Cardona, B. W. Wilm, J. A. Miner, and D. T. Shaw. 1997. The sum exceedance value as a measure of wetland vegetation hydrologic tolerance. Pages 195–210 in K. B. Macdonald and F. Weinmann, editors. *Wetland and Riparian Restoration: Taking a Broader View*. Proceedings of the Society for Ecological Restoration International Conference, Seattle, Washington, September 14–16, 1995. EPA 910-R-97-007, U.S. Environmental Protection Agency, Region 10, Seattle, Washington, USA.
- Small, L. F., C. D. McIntire, K. B. Macdonald, J. R. Lara-Lara, B. E. Frey, M. C. Amspoker, and T. Winfield. 1990. Primary production, plant and detrital biomass, and particle transport in the Columbia River Estuary. *Progress in Oceanography* 25:175–210.
- Smith, J. L., D. R. Midd, and L. W. Messmer. 1976. Impact of dredging on the vegetation in Grays Harbor. Appendix F in *Maintenance Dredging and the Environment of Grays Harbor*, Washington. U.S. Army Corps of Engineers, Seattle District, Seattle, Washington.
- Stanford, J. A., J. V. Ward, W. J. Liss, C. A. Frissell, R. N. Williams, J. A. Lichatowich, and C. C. Coutant. 1996. A general protocol for restoration of regulated rivers. *Regulated Rivers: Research & Management* 12:391–413.
- Steyer, G. D., C. E. Sasser, J. M. Visser, E. M. Swenson, J. A. Nyman, and R. C. Raynie. 2003. A proposed coast-wide reference monitoring system for evaluating wetland restoration trajectories in Louisiana. *Environmental Monitoring and Assessment* 81:107–117.

- Strayer, D. L., and S. E. G. Findlay. 2010. Ecology of freshwater shore zones. *Aquatic Science* 72:127–163.
- Struyf, E., S. Jacobs, P. Meire, K. Jensen, and A. Barendregt. 2009. Plant communities of European tidal freshwater wetlands. Pages 59–70 in A. Barendregt, D. Whigham, and A. Baldwin, editors. *Tidal freshwater wetlands*. Backhuys Publishers, Leiden, The Netherlands.
- Sullivan, G. 2001. Establishing vegetation on restored and created coastal wetlands. Pages 119–156 in J. Zedler, editor. *Handbook for restoring tidal wetlands*. CRC Press, Boca Raton, Florida, USA.
- Thom, R. M., S. A. Breithaupt, H. L. Diefenderfer, A. B. Borde, G. C. Roegner, G. E. Johnson, and D. L. Woodruff. 2018. Storm-driven particulate organic matter flux connects a tidal tributary floodplain wetland, mainstem river, and estuary. *Ecological Applications* 28:1420–1434.
- Thom, R. M., R. Zeigler, and A. B. Borde. 2002. Floristic development patterns in a restored Elk River estuarine marsh, Grays Harbor, Washington. *Restoration Ecology* 10:487–496.
- Tian, B., Y. X. Zhou, R. M. Thom, H. L. Diefenderfer, and Q. Yuan. 2015. Detecting wetland changes in Shanghai, China using FORMOSAT and Landsat TM imagery. *Journal of Hydrology* 529:1–10.
- Ward, J. V., K. Tockner, U. Uehlinger, and F. Malard. 2001. Understanding natural patterns and processes in river corridors as the basis for effective river restoration. *Regulated Rivers: Research and Management* 17:311–323.
- Ward, N., et al. 2020. Representing the function and sensitivity of coastal interfaces in Earth system models. *Nature Communications*. <https://doi.org/10.1038/s41467-020-16236-2>
- Ward, P., K. Moore, and R. Kistritz. 1992. *Wetlands of the Fraser lowland, 1989: an inventory* Technical Report Series 146, Ministry of the Environment Canadian Wildlife Service, Delta, British Columbia, Canada.
- Washington Department of Ecology. 2001. *An aquatic plant identification manual for Washington's freshwater plants*. Washington Department of Ecology, Olympia, Washington, USA.
- Welcomme, R. L. 1979. *Fisheries ecology of floodplain rivers*. Longman, London, UK.
- Westley, R. 1962. *Physical and chemical data, Grays Harbor 1956–1962*. Washington Department of Fisheries Hydrographic Data Vol. II No. 2, Olympia, Washington.
- Woodell, S. R. J. 1985. Salinity and seed germination patterns in coastal plants. Pages 223–229. In *Ecology of coastal vegetation*. Springer, Dordrecht, The Netherlands.
- Yu, S., J. Yang, and G. Liu. 2014. Impact assessment of Three Gorges Dam's impoundment on river dynamics in the north branch of Yangtze River estuary, China. *Environmental Earth Sciences* 72:499–509.
- Zedler, J. B. editor. 2001. *Handbook for restoring tidal wetlands*. CRC Press, Boca Raton, Florida, USA.
- Zonneveld, I. S., and A. Barendregt. 2009. Human activities in European tidal freshwater wetlands. Pages 11–20 in A. Barendregt, D. Whigham, and A. Baldwin, editors. *Tidal freshwater wetlands*. Backhuys Publishers, Leiden, The Netherlands.

SUPPORTING INFORMATION

Additional Supporting Information may be found online at: <http://onlinelibrary.wiley.com/doi/10.1002/ecs2.3185/full>