



# Vertical Zonation and Niche Breadth of Tidal Marsh Plants Along the Northeast Pacific Coast

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Received: 26 October 2017 / Revised: 8 May 2018 / Accepted: 21 May 2018 / Published online: 23 July 2018  
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## Abstract

The distribution patterns of sessile organisms in coastal intertidal habitats typically exhibit vertical zonation, but little is known about variability in zonation among sites or species at larger spatial scales. Data on such heterogeneity could inform mechanistic understanding of factors affecting species distributions as well as efforts to assess and manage coastal species and habitat vulnerability to sea-level rise. Using data on the vertical distribution of common plant species at 12 tidal marshes across the US Pacific coast, we examined heterogeneity in patterns of zonation to test whether distributions varied by site, species, or latitude. Interspecific zonation was evident at most sites, but the vertical niches of co-occurring common species often overlapped considerably. The median elevation of most species varied across marshes, with site-specific differences in marsh elevation profiles more important than differences in latitude that reflect regional climate gradients. Some common species consistently inhabited lower or higher elevations relative to other species, but others varied among sites. Vertical niche breadth varied more than twofold among species. These results indicate that zonation varies by both site and species at the regional scale, and highlight the potential importance of local marsh elevation profiles to plant vertical distributions. Furthermore, they suggest that coastal foundation species such as marsh plants may differ in their vulnerability to sea-level rise by being restricted to specific elevation zones or by occurring in narrow vertical niches.

**Keywords** Realized niche · Salt marsh · Sea-level rise · Species distribution · Tidal datums

## Introduction

Through direct and indirect effects, tides and atmospherically driven variation in water levels affect the vertical distribution of plants, algae, and invertebrates in coastal ecosystems (Doty 1946; Bertness 1991b; Chappuis et al. 2014). The patterns and

underlying mechanisms of vertical zonation of plant species in temperate salt marshes have long interested ecologists (Hinde 1954). Tidal inundation gradients affect a number of key aspects of plant community structure and function in coastal wetlands, including seedling recruitment (Engels et al. 2011), species composition and richness (Janousek and Folger 2014), primary productivity (Snedden et al. 2015), and litter decomposition (Kirwan et al. 2013).

At local scales (e.g., within a single site), experiments have shown that the vertical distribution of tidal marsh species is set by variable tolerance to abiotic gradients and by biological interactions among neighboring species (Bertness and Ellison 1987; Bertness 1991a; Pennings and Callaway 1992; Pennings et al. 2005). One common paradigm, proposed initially from observation (Chapman 1939) and later confirmed experimentally (Bertness and Ellison 1987; Bertness 1991b), is that interspecific competition sets the upper limits of marsh plant distributions, while physiological intolerance of abiotic stressors such as prolonged inundation determine lower limits (Castillo et al. 2000; Fariña et al. 2009). Other geomorphic characteristics of tidal wetlands that may vary with elevation such as presence or

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Communicated by John C. Callaway

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**Electronic supplementary material** The online version of this article (<https://doi.org/10.1007/s12237-018-0420-9>) contains supplementary material, which is available to authorized users.

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absence of tidal creeks (Zedler et al. 1999), or proximity to pools, creeks, or upland habitat (Niering and Warren 1980; Griffin et al. 2011; Kim et al. 2012), may also affect species distribution and composition across tidal wetland landscapes.

The importance of factors such as elevation, salinity, and species interactions to plant zonation has been well established (Pennings et al. 2005; Fariña et al. 2009; Engels et al. 2011). However, these factors may not be predictive for zonation within specific wetlands or across multiple estuaries in a larger geographic region because of spatial turnover in species composition, local abiotic gradients, or successional history. Variation in climate or tidal amplitude at increasingly larger spatial scales could impact zonation patterns in wetlands within and among estuaries (McKee and Patrick 1988). For instance, while competition plays a role in structuring zonation in many salt marshes, competitive relationships among dominant plants can shift with changes in nutrient availability (Levine et al. 1998) or along tidal gradients (Bertness and Hacker 1994; Noto and Shurin 2017). Chapman (1940) observed that distributions for many plant species relative to inundation varied between two different New England marshes. Silvestri et al. (2005) also found that mean species elevation differed among four marshes within a single Mediterranean estuary. Mechanistically, abiotic stress can set the lower and upper elevation limits of some intertidal species (Pennings and Callaway 1992; Osland et al. 2017), or the lower limits of some species can be set by competition (Bockelmann and Neuhaus 1999; van de Koppel et al. 2006; Fariña et al. 2009). Given multiple interacting factors potentially affecting species distributions and varying climatic conditions among sites, the specific mechanisms underlying zonation patterns may not be readily transferrable from one tidal wetland to another (Fariña et al. 2009).

Understanding the distribution of tidal wetland species with elevation is critical for management of estuarine wetlands including assessment of sea-level rise (SLR) effects on wetland structure and function. For example, vulnerability to SLR is likely to differ among species depending on their relative position within the tidal frame, how wide or narrow their realized niches are with respect to tidal inundation (Russell et al. 1985), and how tolerant they are to increasing inundation or salinity (Janousek et al. 2016). Zonation patterns also may provide insight into fundamental mechanisms structuring species distributions, such as the relative importance of abiotic versus biotic factors, which will inform predictions of future vegetation composition with a changing climate (Zavaleta et al. 2003) or with invasion by non-native species (Castillo et al. 2000). Finally, understanding local- to regional-scale variation in zonation along latitudinal or climate gradients is important for planning wetland restoration (Zedler et al. 1999).

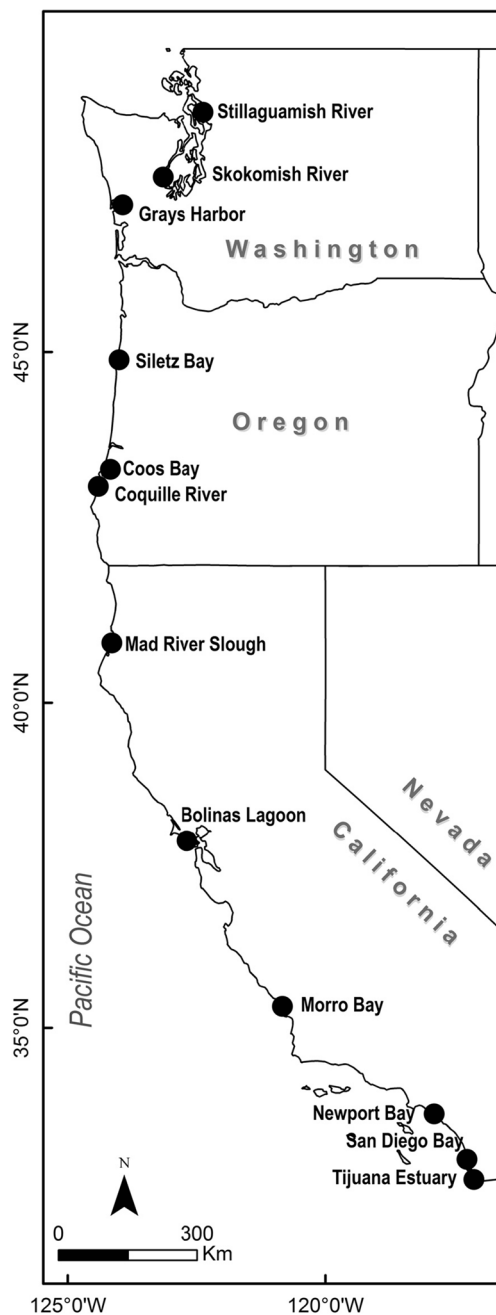
We used extensive field data on the distribution of common tidal marsh plants in 12 estuaries along the Pacific coast of the continental USA to evaluate zonation at site-specific and coast-wide scales. The sites spanned a region of the northeast Pacific

that varies in tidal range, species composition, and climate including precipitation and temperature. We assessed how multiple aspects of plant zonation varied spatially within and among the sites, and whether species differed consistently in their distribution patterns along the Pacific coast. Specifically, we examined six hypotheses: (1) species distributions differ from the overall vertical distribution of intertidal marsh habitat (i.e., factors other than overall habitat space constrain species distributions), (2) common species are vertically separated from each other along the intertidal elevation gradient, (3) the order of individual species from low marsh to high marsh is consistent relative to co-occurring species across sites suggesting species-specific affinities for particular inundation regimes, (4) median elevations of individual species differ among sites, (5) common species differ in overall vertical range (niche size) suggesting variation in abiotic tolerance or species interactions, and (6) median elevations of occurrence or niche size of three common coast-wide species vary with latitude associated with climate gradients along the Pacific coast (e.g., Russell et al. 1985).

## Materials and Methods

Vegetation and elevation data (Thorne 2015; Thorne et al. 2015a) were collected from tidal marshes along the Pacific coast of the continental USA between 2011 and 2014 as part of efforts to model potential sea-level rise impacts to coastal wetlands (Thorne et al. 2014, 2015b, 2016). Vegetation data were used from 12 sites along a latitudinal gradient (Fig. 1 and Table 1) with sampling at each site conducted along the full elevation range of emergent marsh habitat (from the mudflat-marsh boundary to the highest elevation of marsh vegetation). All sites in the study were in continuously open estuaries, with the exception of Tijuana Estuary which is sometimes partially connected to the ocean when a sand bar mutes tidal influence. At each site, elevation and vegetation data were collected over a sampling grid with plots spaced along parallel transects (Thorne et al. 2014, 2015b, 2016; Supplementary Fig. 1). Transects extended from the upland edge to the lower elevation marsh-mudflat boundary. The distance between transects and plot spacing within transects was generally 50 m. Sample sizes ranged from  $n = 126$  at Siletz to  $n = 621$  at Morro, depending on the size of the tidal wetland area surveyed at each site.

At each sampling point, the percent cover of all vascular plant species was visually assessed in  $0.5 \times 0.5$ -m plots. Species were treated as either present ( $>0\%$  cover) or absent in each plot. Botanical nomenclature generally follows Baldwin et al. (2012) (Table 2). All occurrences of perennial pickleweed (*Salicornia perennis* in Oregon and Washington; *S. perennis* and *S. pacifica* in California) were treated as the same species (hereafter *S. pacifica*; Piirainen et al. 2017), although these taxa may not be conspecific across the whole coast (see Baldwin et al. 2012).



**Fig. 1** Map of tidal marsh study sites on the Pacific coast of North America

Adjacent to each plot, the geodetic elevation of the marsh surface was determined with a Leica survey-grade GNSS rover (Viva GS15 and RX1250X models) using real-time kinematic (RTK) corrections. Data corrections were streamed to the rover via internet connections to GNSS base-station networks (Leica Smartnet, [www.smartnetna.com](http://www.smartnetna.com), in southern California and Puget Sound, Washington; Oregon Real-Time GNSS Network, [www.oregon.gov/ODOT/ORGN/pages/index.aspx](http://www.oregon.gov/ODOT/ORGN/pages/index.aspx), in Oregon), or by radio connection to a single Leica base station co-located at the site during surveys. The rovers had field-tested accuracies at tidal benchmarks

typically  $\leq 0.06$  m (Thorne et al. 2015b, 2016). Ellipsoid heights of the marsh surface were processed with Leica Geomatics software to determine orthometric heights using the North American Vertical Datum of 1988 (NAVD88). All NAVD88 elevations were referenced to the geoid 12A model.

Orthometric heights of the marsh surface were scaled by local tidal range to compare plant distributions within and among sites for most analyses. This facilitated comparison among sites because both tidal amplitude and NAVD88 relationships with local tidal datums vary among Pacific coast estuaries (Table 1 and Supplementary Table 1). A unitless metric,  $z^*$ , was used that scales plot elevations to local tidal range:

$$z^* = (z - \text{MTL}) / (\text{MHHW} - \text{MTL})$$

where  $z$  is the plot elevation, MTL is the mean tide level, and MHHW is local mean higher high water with all values in meters relative to the NAVD88 geodetic datum (Swanson et al. 2014). Standardized tidal datums are proportional to inundation frequency and duration regardless of total tidal amplitude, because Pacific coast marsh flooding is principally tidally driven. Emergent tidal marsh vegetation typically begins at, or somewhat above, local MTL ( $z^* = 0$ ) and extends to the upper limit of tidal influence at approximately  $z^* = 1.7$ .

To estimate local tidal ranges and NAVD88 relationships with tidal datums at each site, several sources of data were used (Supplementary Table 1). For Tijuana, San Diego Bay, Newport, Bolinas, Mad River, Coquille, Coos, Grays, Skokomish, and Stillaguamish, tidal datum positions relative to NAVD88 were obtained from NOAA (<https://tidesandcurrents.noaa.gov>) since water-level stations were located near the study sites ( $\leq 10$  km). For Bolinas, a NOAA tide station provided relative tidal datums, and the relationship between NAVD88 and datums was derived from high-accuracy GPS survey data published for a nearby stable tidal benchmark (<https://www.ngs.noaa.gov/OPUS>). At Siletz, NOAA's VDATUM model of vertical transformations (v.3.4) was used to estimate MTL and MHHW relative to NAVD88 (<https://vdatum.noaa.gov>). At Morro, VDATUM was used to estimate MTL while water-level data from an intertidal logger was used to determine MHHW as described in Thorne et al. (2016). Our conversion of NAVD88 geodetic values to local tidal datums did not account for potential errors in tidal datum estimates, such as SLR effects on NAVD88-tidal datum relationships since the last computed tidal epoch, local vertical land motion, or higher uncertainty in tidal estimates based on shorter water-level time series. However, any such errors are likely to be on the order of several centimeters.

At each site, the data sets contained plots from the low marsh to the highest observed plots estimated to be within tidal influence. The upland-wetland boundary was defined as the  $z^*$  value ( $z^*_{\text{upland}}$ ) predicted to flood only once per year

**Table 1** Summary of site information including site name and three-letter site code, site latitude and longitude (from Thorne et al. 2014, 2015b, 2016), number of vegetated quadrats sampled ( $n$ ), elevation range

of vegetated quadrats, and estimated marsh-upland boundary and NOAA reference station used to estimate upper extent of tidal influence

Site (abbreviation)	Latitude, longitude	Vegetation plots		Marsh-upland boundary	
		$n$	Elevation range ( $z^*$ )	Reference NOAA station	$z^*$
Tijuana Estuary (TIJ)	32° 33' 09"N, 117° 06' 38"W	279	0.631 to 1.731	San Diego Bay (9410170)	1.733
San Diego Bay (SDB)	32° 38' 29"N, 117° 06' 33"W	171	0.037 to 1.660	San Diego Bay (9410170)	1.733
Newport Bay (NEW)	33° 38' 59"N, 117° 53' 13"W	247	−0.187 to 1.686	San Diego Bay (9410170)	1.733
Morro Bay (MOR)	35° 20' 49"N, 120° 49' 58"W	621	0.306 to 1.721	Port San Luis (9412110)	1.739
Bolinas Lagoon (BOL)	37° 55' 07"N, 122° 41' 21"W	311	0.258 to 1.663	San Francisco (9414290)	1.670
Mad River Slough (MAD)	40° 41' 20"N, 124° 12' 36"W	173	0.515 to 1.520	North Spit (9418767)	1.590
Coquille River (COQ)	43° 07' 50"N, 124° 24' 25"W	373	0.179 to 1.676	Charleston (9432780)	1.720
Coos Bay (COO)	43° 22' 36"N, 124° 10' 35"W	380	0.374 to 1.246	Charleston (9432780)	1.720
Siletz Bay (SIL)	44° 53' 41"N, 124° 00' 59"W	126	0.597 to 1.326	South Beach (9435380)	1.702
Gray's Harbor (GRA)	46° 58' 47"N, 123° 55' 60"W	271	0.308 to 1.272	Toke Point (9440910)	1.786
Skokomish River (SKO)	47° 20' 30"N, 123° 08' 24"W	128	0.165 to 1.309	Seattle (9447130)	1.514
Stillaguamish River (STI)	48° 11' 35"N, 122° 21' 55"W	210	0.137 to 1.458	Seattle (9447130)	1.514

on average (i.e., 0.16% of high tides reach this elevation; Thorne et al. 2018). Since time series of water level across many years were usually not available to determine  $z^*_{\text{upland}}$  at each site, values were estimated by compiling 10-year records (2004–2013) of daily high tides from reference NOAA stations located in different regions along the Pacific coast (Table 1). For example, the long-term high tide inundation frequency at Charleston, Oregon, was used to estimate the upper boundary of inundation at the two study sites in southern Oregon.

**Data Analysis** Descriptive and inferential statistics were used to describe plant distributions within and between sites and differences among species, and to test hypotheses about spatial variation in zonation. At each site, the cumulative frequency distributions of all vegetated marsh elevations (in  $z^*$ ) were compiled to qualitatively compare relative elevation and gradients among sites. The vertical distributions of the nine most frequently occurring species per site were examined by compiling the  $z^*$  values of all plots in which each species was present and graphically representing their distributions with violin plots (“vioplot” in R v.3.1.2). Violin plots summarize distributions simultaneously with box plots and non-parametric kernel density estimation.

To examine vertical distributions of each common species relative to intertidal elevation profiles at each site (hypothesis 1), individual species distributions were compared statistically with the distribution of all vegetated plots within the site with Kolmogorov-Smirnov tests using the function “ks.test.” Significance levels ( $P$ ) for the tests were obtained with the function “ks.boot” in package “matching” using 10,000 Monte-Carlo simulations (Sekhon 2011) because of non-independence of each pair of distributions (Feigelson and

Babu 2017). The Kolmogorov-Smirnov test statistics ( $D$ , ranging from 0 to 1) were used as relative measures of effect size to assess which species had distributions most dissimilar to overall marsh elevation distributions at their respective sites; effect sizes are generally less influenced by variation in sample size than  $P$  values.

Because the overall elevation of marshes relative to local tidal datums (and thus  $z^*$ ) varied, hypothesis 1 was also tested by evaluating whether common species consistently occurred above or below the local median elevation of the sites in which they occurred. This was tested for species present in at least eight plots at four or more sites (14 species) by computing the difference between the median marsh elevation ( $M_{\text{marsh}}$ ) and the median species distribution ( $M_{\text{species}}$ ) at each site ( $M_{\text{diff}} = M_{\text{species}} - M_{\text{marsh}}$ ). Then, using sites as replicates for each species ( $n = 4$  to  $n = 12$ , depending on species), the mean value of  $\bar{M}_{\text{diff}}$  and 95% confidence limits ( $CL_{95}$ ) for the difference were determined, where  $CL_{95} = SE \times t_{0.05[n-1]}$ , in which  $SE$  is the standard error of  $\bar{M}_{\text{diff}}$ ,  $t$  is the two-tailed  $t$ -distribution value, and  $n$  is the number of sites at which the species was present (Sokal and Rohlf 1995). Confidence intervals that did not cross zero were treated as statistically significant. We used median values because they are potentially less sensitive to outliers, although mean and median elevations were generally very similar.

The degree to which species were spread out vertically from each other within individual sites (hypothesis 2: “degree of zonation”) was assessed by comparing differences in the median elevation of the nine most common species per site using two approaches. First, the variance in median elevation was compared across the 12 sites with Levene’s test. Second, species were ordered from lowest-occurring (rank 1) to

**Table 2** Scientific name, abbreviation, and family of plant species analyzed in this study from the field data collected at 12 estuaries along the Pacific coast of North America

Species	Abbreviation	Family
<i>Agrostis stolonifera</i>	AgrSto	Poaceae
<i>Arthrocnemum subterminale</i>	ArtSub	Chenopodiaceae
<i>Atriplex prostrata</i>	AtrPro	Chenopodiaceae
<i>Batis maritima</i>	BatMar	Bataceae
<i>Bolboschoenus maritimus</i>	BolMar	Cyperaceae
<i>Carex lyngbyei</i>	CarLyn	Cyperaceae
<i>Cotula coronopifolia</i>	CotCor	Asteraceae
<i>Cuscuta pacifica</i>	CusPac	Convolvulaceae
<i>Deschampsia cespitosa</i>	DesCes	Poaceae
<i>Distichlis littoralis</i>	DisLit	Poaceae
<i>Distichlis spicata</i>	DisSpi	Poaceae
<i>Frankenia salina</i>	FraSal	Frankeniaceae
<i>Glaux maritima</i>	GlaMar	Myrsinaceae
<i>Grindelia integrifolia</i>	GriInt	Asteraceae
<i>Grindelia stricta</i>	GriStr	Asteraceae
<i>Jaumea carnosa</i>	JauCar	Asteraceae
<i>Juncus balticus</i>	JunBal	Juncaceae
<i>Lepidium draba</i>	LepDra	Brassicaceae
<i>Limonium californicum</i>	LimCal	Plumbaginaceae
<i>Oenanthe sarmentosa</i>	OenSar	Apiaceae
<i>Plantago maritima</i>	PlaMar	Plantaginaceae
<i>Potentilla anserina</i>	PotAns	Rosaceae
<i>Salicornia bigelovii</i>	SalBig	Chenopodiaceae
<i>Salicornia pacifica</i>	SalPac	Chenopodiaceae
<i>Schoenoplectus americanus</i>	SchAme	Cyperaceae
<i>Schoenoplectus pungens</i>	SchPun	Cyperaceae
<i>Spartina foliosa</i>	SpaFol	Poaceae
<i>Spergularia canadensis</i>	SpeCan	Caryophyllaceae
<i>Suaeda esteroa</i>	SuaEst	Chenopodiaceae
<i>Triglochin concinna</i>	TriCon	Juncaginaceae
<i>Triglochin maritima</i>	TriMar	Juncaginaceae
<i>Vicia gigantea</i>	VicGig	Fabaceae

highest-occurring (rank 9) at each site based on their median elevation. Then, differences between the median elevation of species with neighboring ranks were determined (e.g.,  $M_{\text{species}(k+1)} - M_{\text{species}(k)}$ ), yielding eight distances between pairs of adjoining species per site. These distances were tested among sites with one-factor ANOVA, followed by a Tukey HSD a posteriori mean test. Levene's test suggested that variances were not highly heteroscedastic ( $F_{11,84} = 1.3, P = 0.23$ ). Species ranks within individual sites were also used to examine whether species ordering from low to high marsh was consistent relative to co-occurring (hypothesis 3) species by averaging the rank values of a species for all sites at which it was among the nine most abundant species.

Variation in the vertical distribution ( $z^*$ ) of common species among sites (hypothesis 4) was tested with Kruskal-Wallis tests, where significant differences indicate differences in distribution shape and/or central tendency. This was tested for the 14 species present in at least eight plots across at least four sites. For significant Kruskal-Wallis test results, pair-wise differences among sites were examined with Conover's test after applying the Bonferroni correction as implemented in R package "PMCMR" (v.4.1).

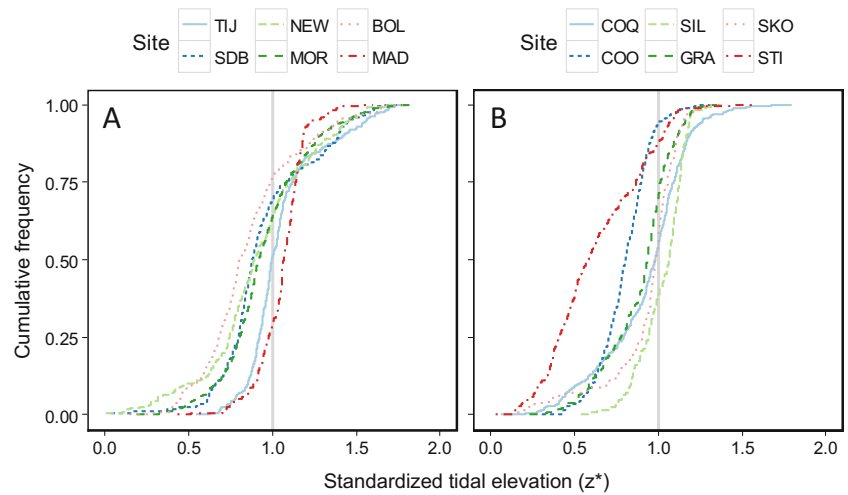
The interquartile range ( $IQR_{z^*}$ , where  $IQR = z^*_{.75\% \text{ quartile}} - z^*_{.25\% \text{ quartile}}$ ) of each species' distribution was used to assess whether vertical niche breadth varied among the 14 common species analyzed (hypothesis 5).  $IQR_{z^*}$  was computed at each site at which a species was present (in at least eight plots), and then, differences in elevation range among species were compared with one-factor ANOVA (treating sites as replicates) followed by a Tukey HSD a posteriori test. Differences in niche size were also evaluated using absolute elevation values in meters ( $IQR_m$ ). Levene's test suggested that the variances among species were not markedly heteroscedastic for either test ( $F_{13,75} < 0.8, P > 0.6$ ). Finally, variation in median elevation and niche breadth by latitude (hypothesis 6) was tested with linear regression using the three most wide-spread Pacific coast species in the data set (*S. pacifica*, *Jaumea carnosa*, and *Distichlis spicata*).

## Results

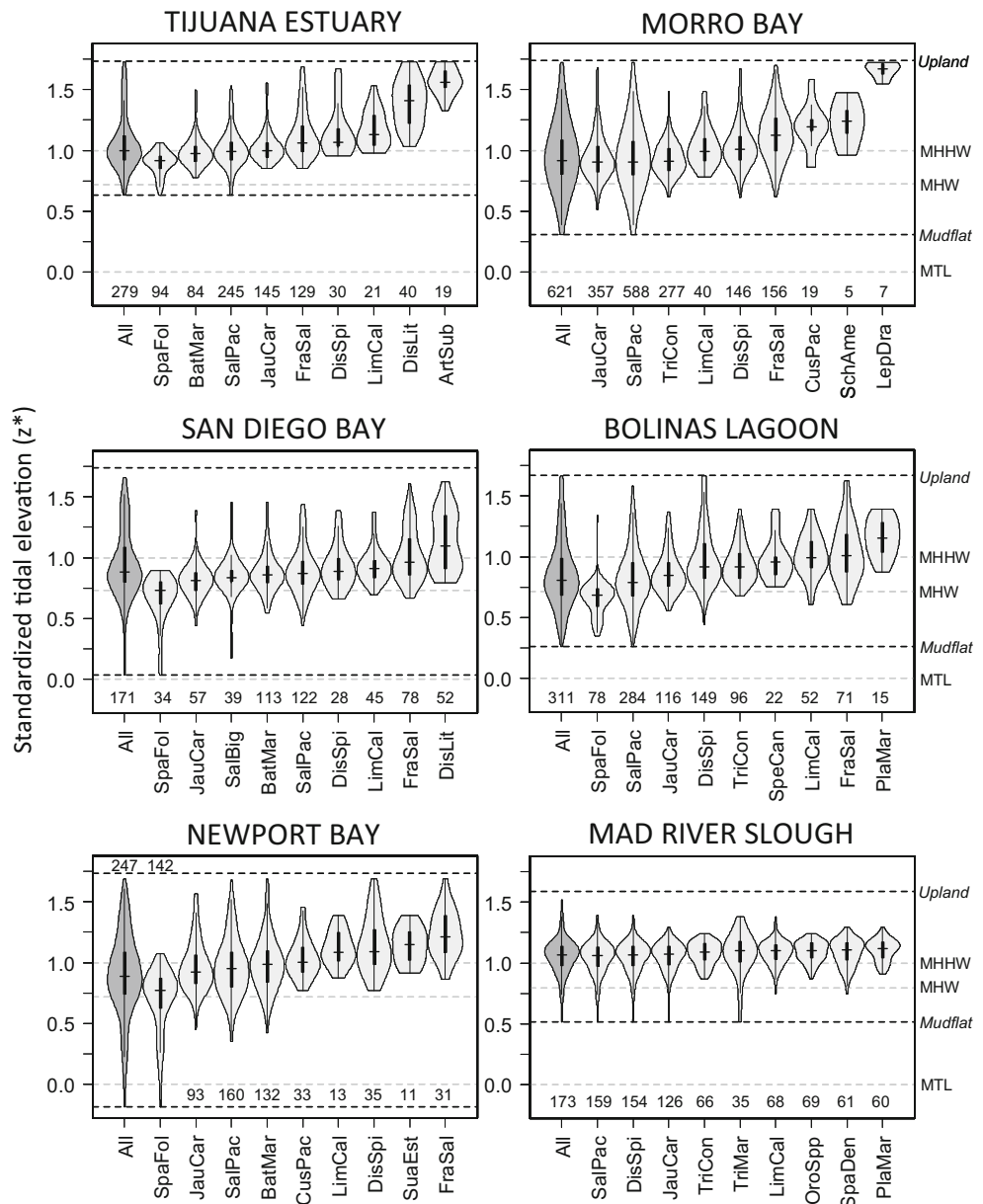
**Marsh Elevations and Species Distributions Within Individual Sites** Marsh sites varied in their elevation profiles (Fig. 2). Mad River, Tijuana, Siletz, Skokomish, and Coquille tended to be higher in elevation with a greater proportion of marsh area occurring above local MHHW. Relatively low-elevation sites included Bolinas, Stillaguamish, and Coos. Bolinas and Stillaguamish had more gradually sloping profiles, while Mad River, Skokomish, and Siletz consisted of relatively flat marsh benches. Common species at sites in California (Fig. 3) and the Pacific Northwest (Fig. 4) occurred across a range of tidal elevations from below MHW to above MHHW. In California, lower-elevation species included *Spartina foliosa* and *J. carnosa*. Higher-elevation species included *Limonium californicum*, *Distichlis littoralis*, *Arthrocnemum subterminale*, and *Frankenia salina*. Depending on site, *S. pacifica* and *D. spicata* tended to have either broad distributions, or they occupied variable parts of the intertidal zone among sites. In the Oregon and Washington sites, lower-elevation species included *Carex lyngbyei*, *Triglochin maritima*, and *S. pacifica*. Higher-marsh species included *Juncus balticus* and *Potentilla anserina*.

At most sites, the intertidal distribution of the majority of common species differed significantly from overall marsh elevation profiles, indicating that species had specific vertical

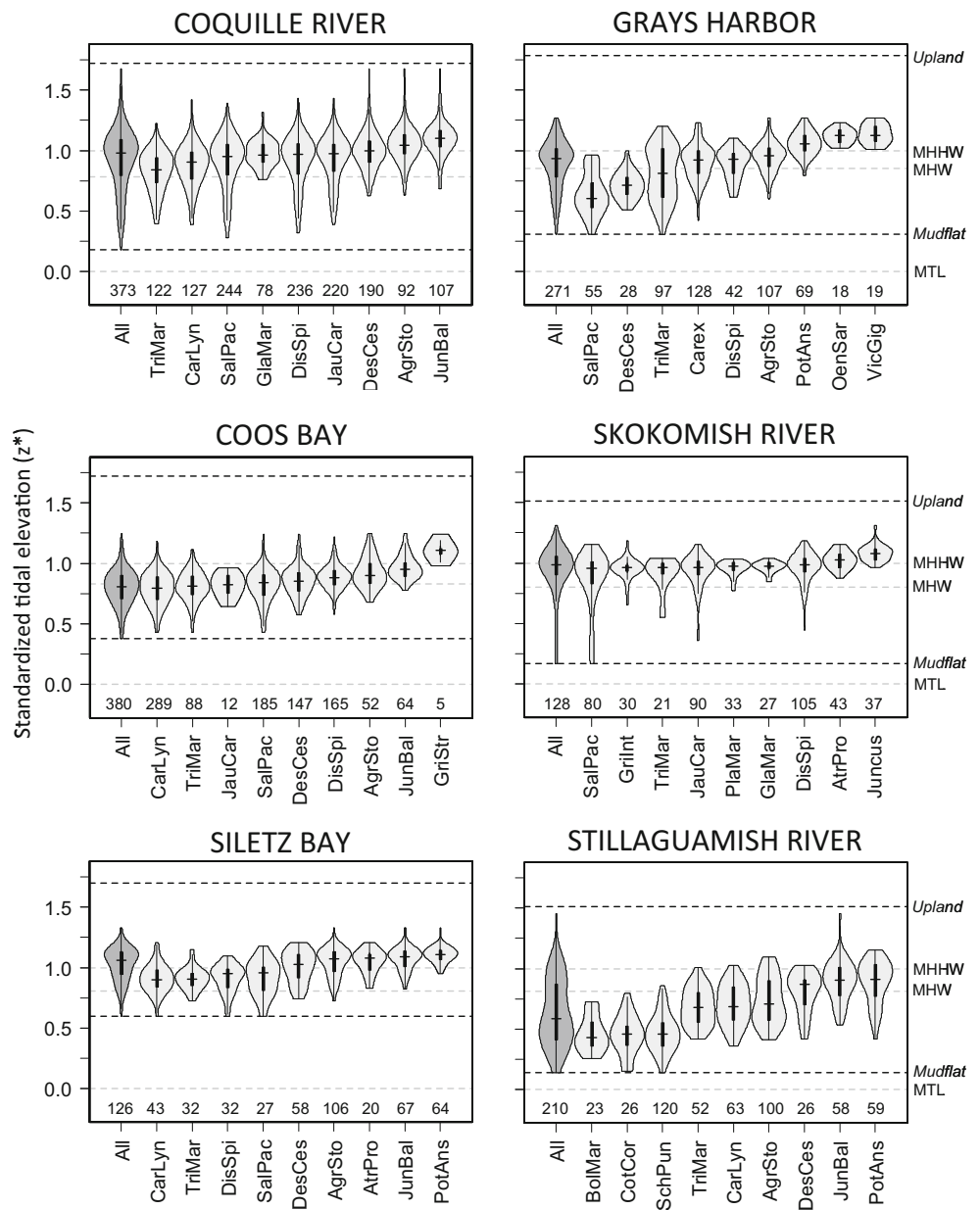
**Fig. 2** Cumulative frequency distribution of vegetated marsh plots in **a** California and **b** Oregon and Washington, with elevations at each site standardized by local tidal datums ( $z^*$ ). The vertical gray line at  $z^* = 1.0$  is MHHW



**Fig. 3** Violin plots showing the tidal elevation distribution of all vegetated plots (leftmost violin in each panel, labeled “All”) and the nine most-common marsh species per site in six California tidal marshes. The wider portions of each violin indicate the elevations at which a species is relatively more abundant, based on all occurrences of the species (> 0% cover). Box plots superimposed on the violin plots show the median elevation (black horizontal bar) and 25 and 75% quantiles (black vertical bar) for each species. Numbers next to each violin show the sample size for each species. See Table 2 for species codes



**Fig. 4** Violin plots showing the tidal elevation distribution of all vegetated plots (leftmost violin in each panel) and the nine most-common marsh species per site in six tidal marshes in Oregon and Washington. See Table 2 for species codes

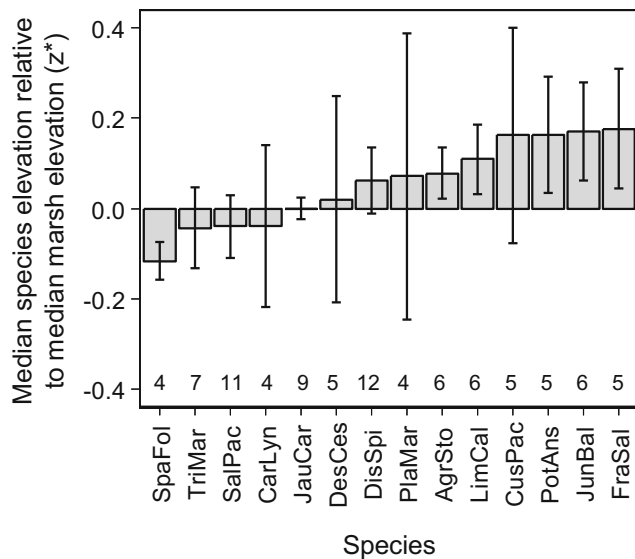


niches (Supplementary Tables 2 and 3). Exceptions to this pattern included species that were very common locally such as *S. pacifica* at all California sites, *C. lyngbyei* at Coos Bay, and *D. spicata* at Skokomish; these species were found across almost all marsh elevations. Strong differences between species distributions and overall marsh elevation profiles ( $D > 0.5$ ) tended to occur for species with a pronounced affinity for either low or high tidal elevations such as *S. foliosa* at San Diego Bay, *D. littoralis* at Tijuana, *Lepidium draba* at Morro, and *Grindelia stricta* at Coos.

Of the 14 common species examined, six had median distributions significantly above or below the median elevation of the marshes in which they occurred (Fig. 5). For example, *S. foliosa* (present at four California sites) occurred on average

$z^* = -0.12$  below each site’s median elevation. In California marshes, *L. californicum* and *F. salina* had median distributions 0.11 and 0.18  $z^*$  units above the local median marsh elevation. In the Pacific Northwest, the median occurrence of *Agrostis stolonifera*, *P. anserina*, and *J. balticus* averaged 0.08, 0.16, and 0.17 standard tidal units above the median marsh elevation. However, more than half of the common species had median elevations similar to the median elevation of the marshes in which they occurred, including the most geographically widespread and locally common species (e.g., *S. pacifica*, *J. balticus*, and *D. spicata*).

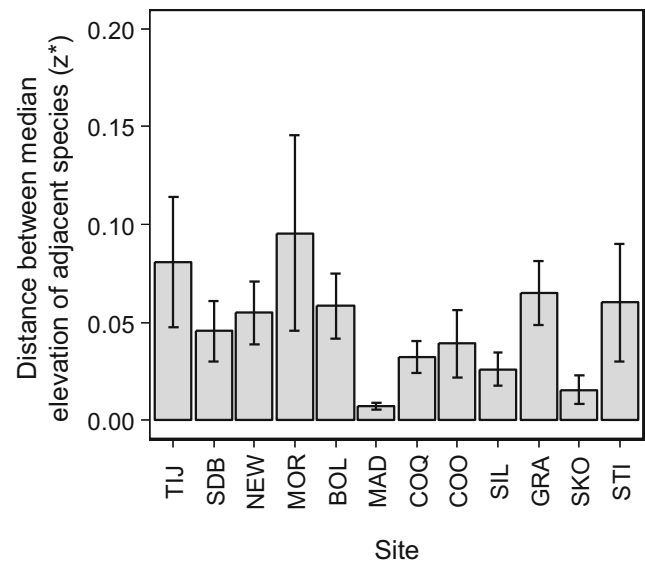
**Degree of Zonation Within Sites** Variance in the median elevation of common species differed among sites (Levene’s test;



**Fig. 5** Median elevation of 14 common Pacific coast marsh species relative to local median marsh elevation. Bars show the mean ( $\pm 95\%$  confidence limits) of median species distribution minus median marsh elevation for all sites at which a species occurred. Error bars which do not cross the  $x$  axis are significantly different from zero. Numbers above the  $x$  axis indicate the number of sites used to compute each mean

$F_{11,96} = 2.2$ ,  $P = 0.02$ ), suggesting that species were more spread out vertically across the intertidal at some sites than at others. Within some sites such as Mad and Skokomish, there was little difference in the median elevation among common species (Figs. 3 and 4), illustrating vertical clumping of species. At Skokomish, seven of the nine dominant species had nearly identical median distributions (each occurring just below local MHHW). Species were separated to greater degrees from each other along the elevation gradient at other sites such as Tijuana, Morro, and Grays. However, when we attempted to quantify whether species were more vertically clumped at some sites than others by comparing the vertical distance between the median elevation of neighboring species, we did not find a statistically significant difference ( $F_{11,84} = 1.3$ ,  $P = 0.23$ ; Fig. 6).

**Consistency of Species Ordering With Elevation** Common species varied in their average rank order (1–9) from low to high marsh across the sites in the study (Table 3). *S. foliosa* was consistently the lowest occurring species at the four sites in which it was present (rank = 1.0). Other species with lower ranks included *C. lyngbyei* (2.3) and *S. pacifica* (2.6). In the Pacific Northwest, *J. balticus* and *P. anserina* (8.3) were usually the highest or second highest-occurring species. Species with more variable ranks included *Deschampsia cespitosa* (second lowest at Grays to seventh lowest at Coquille and Stillaguamish), *D. spicata* (second lowest at Mad to seventh lowest at Newport and Skokomish), and *J. carnosa* (first lowest at Morro to sixth lowest at Coquille).



**Fig. 6** Average distance (in  $z^*$ ) between the median elevation of “neighboring” species at each site. Larger values indicate that species medians are more spread out across the intertidal

**Differences in Species Median Elevation by Site** The 14 common species tested all varied significantly in their vertical distribution among sites (all  $P < 0.0001$ ; Table 4 and Supplementary Fig. 2). There were many significant pairwise site differences among marshes, including pairs of sites in close geographic proximity. For example, median elevations of *D. spicata*, *F. salina*, *L. californicum*, *S. pacifica*, and *S. foliosa* differed between Tijuana and San Diego Bay. Similarly, *A. stolonifera*, *C. lyngbyei*, *D. cespitosa*, *J. carnosa*, *J. balticus*, and *S. pacifica* differed between Coquille and Coos.

**Species Niche Breadth** Species varied more than twofold in their niche breadth, ranging from  $IQR_{z^*} = 0.13$  in *P. anserina*, *J. balticus*, and *Cuscuta pacifica* to  $IQR_{z^*} = 0.28$  in *F. salina* ( $F_{13,75} = 2.1$ ,  $P = 0.02$ ; Fig. 7). In pairwise comparisons of differences among species, the high- to mid-marsh species *P. anserina*, *J. balticus*, and *C. pacifica* differed significantly from the high-marsh species *F. salina*, but all other species comparisons were not significantly different. There was a trend towards differences in vertical range among species when absolute values of elevation were considered ( $IQR_m$ ), but differences were not statistically significant ( $F_{13,75} = 1.8$ ,  $P = 0.055$ ).

**Distribution Trends With Latitude** *Distichlis spicata*, *J. carnosa*, and *S. pacifica* were present in at least eight plots at 9–12 sites, enabling comparison of species distributions with latitude across the study area. There was no relationship between median elevation of occurrence and latitude for each species (all  $R^2_{adj} \leq 0.07$ , all  $P \geq 0.20$ ; Fig. 8). The standardized vertical niche widths ( $z^*_{IQR}$ ) of all three species were



**Table 3** Summary of ranks of the median elevation of common Pacific coast tidal marsh plant species

Species	No. of sites	Mean rank	Species common in	Typical zone
<i>Spartina foliosa</i>	4	1.0	California	Low marsh
<i>Carex lyngbyei</i>	4	2.3	Oregon, Washington	
<i>Salicornia pacifica</i>	11	2.6	Whole West Coast	
<i>Triglochin maritima</i>	7	2.9	Whole West Coast	
<i>Jaumea carnosa</i>	9	3.1	Whole West Coast	Mid marsh
<i>Batis maritima</i>	3	3.3	California	
<i>Triglochin concinna</i>	3	4.0	California	
<i>Distichlis spicata</i>	11	5.1	Whole West Coast	
<i>Deschampsia cespitosa</i>	5	5.2	Oregon, Washington	High marsh
<i>Limonium californicum</i>	6	6.2	California	
<i>Agrostis stolonifera</i>	5	6.6	Oregon, Washington	
<i>Frankenia salina</i>	5	7.2	California	
<i>Plantago maritima</i>	3	7.7	Whole West Coast	
<i>Juncus balticus</i>	4	8.3	Oregon, Washington	
<i>Potentilla anserina</i>	3	8.3	Oregon, Washington	

Species were first ranked from low (1) to high (9) elevation within individual sites, and then, ranks were averaged across all sites at which the species was common

unrelated to latitude ( $R^2_{adj} \leq 0.16$ ,  $P \geq 0.11$ ), but absolute vertical range (IQR in meters) significantly increased with increasing latitude for *S. pacifica* ( $R^2_{adj} = 0.45$ ,  $P = 0.01$ ).

### Discussion

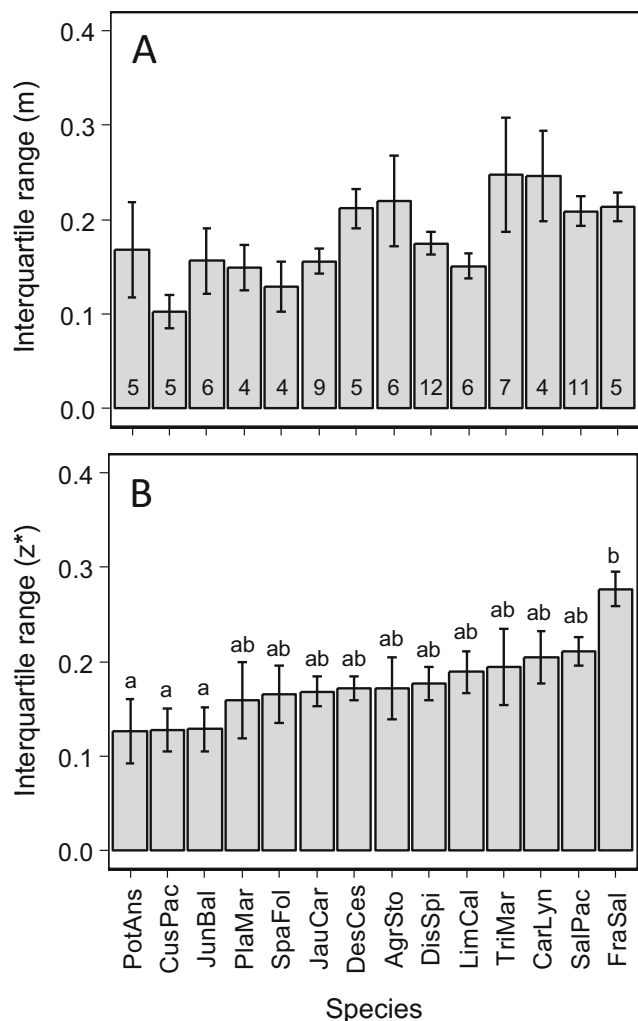
Zonation of vascular plants is a well-documented phenomenon in tidal marshes (Bertness 1991b); however, variation in the vertical distribution of these foundation species across a range of spatial scales or over larger geographic areas has only been examined in a handful of studies (e.g., Chapman 1940;

McKee and Patrick 1988; Silvestri et al. 2005). Scale-dependent variability in the vertical distribution of intertidal plants may be due to the large number of factors that potentially affect zonation including inundation and salinity stress, climate conditions, marsh geomorphology, differences in species composition, and species interactions. In this study, we assessed local and regional patterns of zonation in the northeast Pacific to gain insight into the degree of variability in species distributions within and between sites and potential factors structuring zonation. We found that the degree of zonation varied among sites with species spread more widely along the elevation gradient in some marshes. We also found

**Table 4** Results of Kruskal-Wallis tests of differences in elevation distribution of 14 common species across sites

Species	df	$\chi^2$	Pair-wise site comparisons
<i>Agrostis stolonifera</i>	5	173.3	COQ <sup>a</sup> COO <sup>b</sup> SIL <sup>a</sup> GRA <sup>b</sup> SKO <sup>a</sup> STI <sup>c</sup>
<i>Carex lyngbyei</i>	3	71.9	COQ <sup>a</sup> COO <sup>b</sup> SIL <sup>a</sup> STI <sup>c</sup>
<i>Cuscuta pacifica</i>	4	44.7	SDB <sup>a</sup> NEW <sup>b</sup> MOR <sup>c</sup> BOL <sup>c</sup> COQ <sup>b</sup>
<i>Deschampsia cespitosa</i>	4	139.9	COQ <sup>a</sup> COO <sup>b</sup> SIL <sup>a</sup> GRA <sup>c</sup> STI <sup>b</sup>
<i>Distichlis spicata</i>	11	209.4	TIJ <sup>a</sup> SDB <sup>bc</sup> NEW <sup>a</sup> MOR <sup>ad</sup> BOL <sup>b</sup> MAD <sup>a</sup> COQ <sup>b</sup> COO <sup>c</sup> SIL <sup>bc</sup> GRA <sup>bc</sup> SKO <sup>bd</sup> STI <sup>bcd</sup>
<i>Frankenia salina</i>	4	42.3	TIJ <sup>a</sup> SDB <sup>b</sup> NEW <sup>a</sup> MOR <sup>a</sup> BOL <sup>b</sup>
<i>Jaumea carnosa</i>	8	197.7	TIJ <sup>a</sup> SDB <sup>b</sup> NEW <sup>cd</sup> MOR <sup>cd</sup> BOL <sup>b</sup> MAD <sup>a</sup> COQ <sup>d</sup> COO <sup>bc</sup> SKO <sup>d</sup>
<i>Juncus balticus</i>	5	107.0	MAD <sup>a</sup> COQ <sup>a</sup> COO <sup>b</sup> SIL <sup>a</sup> GRA <sup>a</sup> STI <sup>b</sup>
<i>Limonium californicum</i>	5	55.5	TIJ <sup>a</sup> SDB <sup>b</sup> NEW <sup>ac</sup> MOR <sup>c</sup> BOL <sup>c</sup> MAD <sup>a</sup>
<i>Plantago maritima</i>	3	50.0	BOL <sup>a</sup> MAD <sup>a</sup> COQ <sup>b</sup> SKO <sup>b</sup>
<i>Potentilla anserina</i>	4	97.1	COQ <sup>a</sup> SIL <sup>a</sup> GRA <sup>b</sup> SKO <sup>ab</sup> STI <sup>c</sup>
<i>Salicornia pacifica</i>	10	349.4	TIJ <sup>ab</sup> SDB <sup>cd</sup> NEW <sup>c</sup> MOR <sup>c</sup> BOL <sup>de</sup> MAD <sup>a</sup> COQ <sup>c</sup> COO <sup>c</sup> SIL <sup>bcd</sup> GRA <sup>f</sup> SKO <sup>c</sup>
<i>Spartina foliosa</i>	3	118.6	TIJ <sup>a</sup> SDB <sup>bc</sup> NEW <sup>b</sup> BOL <sup>c</sup>
<i>Triglochin maritima</i>	6	101.6	MAD <sup>a</sup> COQ <sup>bc</sup> COO <sup>c</sup> SIL <sup>b</sup> GRA <sup>bc</sup> SKO <sup>ab</sup> STI <sup>d</sup>

For each species, degrees of freedom and  $\chi^2$  statistics are shown for tests of individual species across sites ( $P < 0.0001$  for all  $\chi^2$  values). Sites sharing the same letter were not significantly different in pair-wise a posteriori comparisons



**Fig. 7** Variation in vertical niche width (interquartile range) of common species in Pacific tidal marshes (mean  $\pm$  SE) measured as **a** absolute elevation range in meters and **b** standardized tidal range ( $z^*$ ). Numbers at the base of the bars indicate the number of sites from which interquartile ranges were determined. Pairs of means that share the same letter are not significantly different at a family-wise  $\alpha = 0.05$

that common species varied in their median elevation among sites, in their average vertical niche breadth, and (in some cases) their rank order of median occurrence along the tidal gradient relative to other common species.

**Spatial Variability in Zonation** At the site scale, unique elevation profiles of individual marshes appeared to play a major role in affecting the location and spread of species distributions. At sites with relatively flat marsh plains (e.g., Mad, Siletz, and Skokomish), the median occurrences of common species tended to be very similar, with broad overlap in distributions (e.g., Figs. 3 and 4; Zedler 1977). In contrast, San Diego Bay, Newport, Morro, Bolinas, Grays, and Stillaguamish had more gradually sloping elevation profiles and zonation was more evident. Nearby marshes in the San Diego area had different overall elevation profiles resulting in

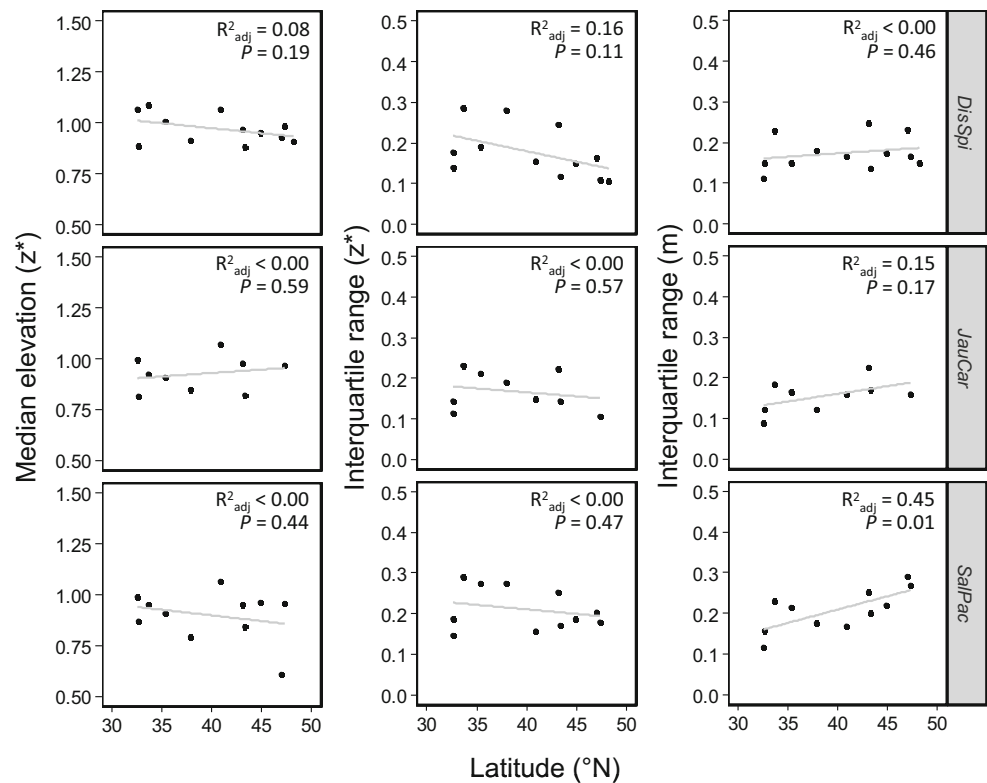
lower median elevation of individual species at San Diego Bay than at Tijuana. Rank order of common taxa was similar, and two very common species, *S. pacifica* and *J. carnosa*, had median elevations that closely matched site elevations. The two sites also differ hydrologically, with Tijuana Estuary closing intermittently while San Diego Bay was continuously open to full tidal influence. Site geomorphic history including age and accretion rates, as well as hydrologic differences among sites, may be important factors in imprinting local variation on species zonation.

The variety of zonation patterns we observed within our study region has been documented in other global studies focused on one or a few sites. For example, Costa et al. (2003) found considerable overlap in the distribution of three dominant species in a microtidal marsh in Brazil, and Watson and Byrne (2009) note overlap in species distributions in the San Francisco Bay-Delta Estuary. In contrast, there was relatively strong vertical separation of species in marshes in the North Atlantic, Southern California, and Chile (Bertness 1991b; Pennings and Callaway 1992; Fariña et al. 2009). Other marshes show intermediate scenarios, where some species are well separated along the elevation gradient, while others co-occur within very similar elevation zones, including in Southern California (Zedler 1977), Spain (Sanchez et al. 1996), and Alaska (Vince and Snow 1984). Collectively, these studies show that a variety of marsh zonation patterns are present at a global scale, variation which could be due to ocean basin-scale differences in species composition, tide range, and climate, or site-to-site differences in dominant mechanisms affecting zonation.

Our work indicates that such site-to-site variability is also present within a single coastal region. Few other studies on wetland plant zonation have been conducted at multiple sites within a region. Within the Venice Lagoon Silvestri et al. (2005) found similar rank order of common halophyte species along the elevation gradient among sites, but differences in average elevation for a given species depending in the elevation profile of specific marshes. Environmental gradients within an estuary, such as salinity regime (Eleuterius and Eleuterius 1979), or elevation profiles (Silvestri et al. 2005) may affect position or degree of elevation overlap among dominant species. In contrast, Sanchez et al. (1996) found no difference in species distribution with elevation in marshes in two nearby river valleys in Spain.

At regional to continental scales, a different suite of factors may affect zonation within and between sites, including species composition and climate gradients (McKee and Patrick 1988). Our sites comprised large differences in dominant species composition between California and the Pacific Northwest. Variability in species assemblages among sites may lead to differences in the strength and types of species interactions present that could ultimately affect emergent patterns of zonation. Contrary to expectations, however, we found little

**Fig. 8** Variation in median occurrence and interquartile range with latitude for three widely distributed species in Pacific coast marshes. *SalPac* *Salicornia pacifica*, *JauCar* *Jaumea carnosa*, *DisSpi* *Distichlis spicata*



evidence that latitude (a proxy for climate differences in the northeast Pacific) was correlated with the location or spread of several common species that span the region (Fig. 8).

**Intra-Specific Variation in Species Distributions** Species-level differences also appear to play a role in zonation patterns at regional scales. Intra-specific differences were manifest as both vertical niche size among species and variation in rank position along the tidal gradient. By standardizing species ranges with local tidal range to better approximate inundation conditions, we observed greater than twofold differences in species niche width. Chapman (1940) noted a nearly eightfold variability in the vertical range of New England tidal marsh plants. A few high-marsh species at our West Coast sites (*J. balticus*, *P. anserina*) had smaller vertical ranges than other common species (Fig. 7b), suggesting that physiological intolerance or competition may limit their presence to more marginal intertidal wetland areas. Species with more limited distributions within the intertidal may be more vulnerable to the impacts of invasive species or climate-change related stressors.

In contrast, species with larger vertical niches may have broader tolerance to the range of salinity, inundation, and redox conditions that occur across intertidal marshes and greater resilience to disturbance or ecosystem change. Globally, one such eurytopic plant group may be cordgrasses (*Spartina* spp.). Chapman (1940) found that *Spartina alterniflora* had the greatest vertical niche of the species he investigated, and

Sanchez et al. (1996, and references therein) found that *Spartina* spp. tended to have relatively large elevation ranges, potentially due to lack of competition with other species in the low marsh. In California, we did not find a particularly large vertical niche for the native *S. foliosa*, which is also a low marsh species, but competition with other species like *S. pacifica* may limit its distribution to lower elevations. *Salicornia pacifica* was among the most broadly occurring species along the tidal gradient (Hinde 1954) and was common at most sites in our study. This species appears tolerant of a wide range of hydrologic and climate conditions, even though it may have optimal growth in the high marsh (Janousek et al. 2016), or near well-drained channels (Schile et al. 2011).

Factors affecting either the fundamental or realized niche along the tidal gradient could lead to differences in vertical range among species. For example, physiological intolerance of high inundation or salinity stress could constrain a species' vertical range and limit its downslope distribution. These species may be particularly vulnerable to ecosystem changes that increase flooding or wetland salinity. The tolerance limits of many US West Coast marsh species are still poorly known (but see Mahall and Park 1976; Janousek et al. 2016; Schile et al. 2017), and further experimental data may improve understanding of how such abiotic drivers influence niche size. Competition or facilitation could alter the realized niche of a species, with competitive dominants or species benefiting from facilitation having larger vertical ranges than other

species. For example, *S. pacifica* is a good competitor (Noto and Shurin 2017) that can gradually crowd out other species in a marsh assemblage (Bonin and Zedler 2008). As one moves from individual sites to larger spatial scales, changes in species composition could impact the nature of interactions a given species has with neighboring species (Elmendorf and Moore 2007), affecting realized niche size. For instance, local absence of strongly interacting species could constrain the niche of a species dependent on facultative amelioration of harsh conditions (Bertness and Hacker 1994), or increase the realized vertical niche of a competing species. In cases where species interactions strongly affect vertical distributions, shifting species composition with climate change or species invasions could have large effects on the zonation of native species. However, many of the potential species-species interactions among common Pacific coast marsh taxa have not been experimentally evaluated, so it is difficult to assess the relative importance of these interactions to niche size or variation in zonation.

We also noted both consistency and differences in rank order of species from low to high marsh. Many common species tended to retain a similar relative position from low to high marsh with respect to other common taxa despite variability in their absolute median elevation among sites. For instance, *S. foliosa* was always the lowest-occurring species in the sites in this study in which it occurred (see also Hinde 1954). Species typical of high marsh elevations included *D. littoralis*, *F. salina*, and *A. subterminale* in Southern California (Page et al. 2003), *Plantago maritima* in central and Northern California, and *J. balticus* and *P. anserina* in the Pacific Northwest. Strong biotic interactions or limiting abiotic factors could be particularly important to the relative position of these species in the intertidal. Future shifts in species composition or changing environmental gradients may therefore particularly impact the future abundance of such species. In a detailed study of rocky intertidal invertebrate and algal assemblages along geographic and intertidal gradients in the northwest Mediterranean, Chappuis et al. (2014) found relatively consistent distributions of common and indicator species with elevation across 1100 km of coastline.

However, we also found examples where common species varied in rank order among sites. For instance, *D. cespitosa* (typically a mid-marsh species in the Pacific Northwest) occurred quite low in the marsh at Grays Harbor. *Jaumea carnosa*, *D. spicata*, and *P. maritima* were also fairly variable in their intertidal position among sites. One possible explanation of this variability is that these species may generally have broad fundamental niches in the intertidal, but local species composition affects their relative location at any given site. Disturbance, founder effects, successional processes, or sensitivity to edaphic conditions could also play a role in site-to-site variation in the distribution of some species (Costa et al.

2003; White and Madsen 2016). For instance, White and Madsen (2016) observed that freshwater groundwater flow from a forested watershed enabled a typical high-marsh species (*Juncus roemarianus*) to occur lower than expected at one part of their site because of reductions in soil salinity.

**Implications for Wetland Management** Our results provide important distribution data on tidal marsh foundation species relevant to wetland management including modeling relative SLR effects and wetland restoration. We found that many common Pacific coast species occurred across a broad range of elevations, suggesting potential persistence of vegetated marsh habitat under more modest rates of future SLR (Thorne et al. 2018). Some species may be more vulnerable to relative SLR either because they have smaller vertical niches or because of they have a more fixed position in the intertidal. For example, the species *J. balticus* and *P. anserina* tended to have more restricted vertical ranges and occurred mainly in high marshes, which may make them more sensitive to modest increases in inundation. Additionally, although species with wider vertical niches may persist under smaller levels of relative SLR, our analyses herein are based only on species occurrences which may underestimate sensitivity of a species to changes in inundation. Optimum productivity (e.g., Janousek et al. 2016), recruitment, or fecundity may only occur under a more narrow range of elevations than species occurrence.

For management of coastal climate change impacts and wetland restoration, our study suggests that local-scale site variability, especially the underlying elevation profile of a given marsh, is an important factor for species distributions. Climate gradients manifest at larger regional scales may be important indirectly, in so far as they correspond with changes in species composition at increasingly larger spatial scales. Our findings also help identify common Pacific coast marsh species which may be more suitable for planting in specific restoration projects based on elevation occurrence or niche size. For instance, more flooding-tolerant species could be planted in restoration projects to ensure some level of marsh function at sites that are lower in elevation than desired because of soil compaction or subsidence. When planting species into a restoration site however, reference site data may only provide a rough guideline of potential future plant zonation at a new site because of variability in plant distributions with local tidal datums (even in nearby sites). Practitioners may therefore wish to plant in restored marshes across a broader vertical range than suggested by reference site data to ensure eventual establishment of target species. The use of elevation data referenced to local tidal datums (e.g.,  $z^*$  or elevation relative to MHHW) is particularly valuable in restoration work since it is more directly related to differences in inundation regimes than geodetic datums.

**Conclusions** Patterns of zonation among tidal marsh plants vary by site and species in marshes along the Pacific coast of the USA. Factors affecting the location and spread of species along the intertidal elevation gradient may differ by spatial scale, but potentially include local marsh elevation profiles, vertical and horizontal gradients of abiotic stress, and changes in species composition at larger scales. Additionally, species-specific traits may impact patterns of zonation, with some species likely more vulnerable to processes that diminish available intertidal habitat area such as relative sea-level rise. Additional ecophysiological data on individual species, analyses of species distributions at biogeographic scales, and experimental tests of controlling factors may shed further light on the complex patterns of plant zonation in coastal wetland ecosystems and their sensitivity to coastal change.

**Acknowledgements** We thank K. Powelson, K. Lovett, K. Buffington, L. Curry, C. Freeman, L. Bellevue, M. Holt, and H. Robinson who conducted the extensive vegetation and elevation sampling in the field. We also thank C. Freeman (USGS) for producing Fig. 1. and Supplementary Fig. 1 and J. Callaway, J. Crooks, and two anonymous reviewers for their helpful comments on the manuscript. The Northwest and Southwest Climate Adaptation Science Centers of the US Department of the Interior funded this study, with additional support from NOAA grant NA15NOS4780171. We thank the following agencies and individuals for site access: US Fish and Wildlife Service (A. Yuen, SDB; E. Nelson, MAD; D. Ledig, COQ; R. Lowe, SIL; G. Nakai, GRA), NOAA's National Estuarine Research Reserve System (J. Crooks, TIJ; C. Cornu, COO), California State Parks (A. Kitajima, MOR), Marin County Parks (W. Carmen, BOL), California Department of Fish and Wildlife and Orange County Parks (C. Navarro, NEW), Skokomish Indian Tribe (S. Kirby, SKO), and the Nature Conservancy (J. Boyd, STI). Most raw data generated for this study are available as USGS data releases. Any use of trade, product, or firm names in this publication is for descriptive purposes only and does not imply endorsement by the US government. The US government is authorized to reproduce and distribute reprints of this article for governmental purposes.

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