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Total ecosystem carbon stocks at the marine-terrestrial interface: Blue carbon of the Pacific Northwest Coast, United States

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Abstract

The coastal ecosystems of temperate North America provide a variety of ecosystem services including high rates of carbon sequestration. Yet, little data exist for the carbon stocks of major tidal wetland types in the Pacific Northwest, United States. We quantified the total ecosystem carbon stocks (TECS) in seagrass, emergent marshes, and forested tidal wetlands, occurring along increasing elevation and decreasing salinity gradients. The TECS included the total aboveground carbon stocks and the entire soil profile (to as deep as 3 m). TECS significantly increased along the elevation and salinity gradients: 217 ± 60 Mg C/ha for seagrass (low elevation/high salinity), 417 ± 70 Mg C/ha for low marsh, 551 ± 47 Mg C/ha for high marsh, and 1,064 ± 38 Mg C/ha for tidal forest (high elevation/low salinity). Soil carbon stocks accounted for >98% of TECS in the seagrass and marsh communities and 78% in the tidal forest. Soils in the 0–100 cm portion of the profile accounted for only 48%–53% of the TECS in seagrasses and marshes and 34% of the TECS in tidal forests. Thus, the commonly applied limit defining TECS to a 100 cm depth would greatly underestimate both carbon stocks and potential greenhouse gas emissions from land-use conversion. The large carbon stocks coupled with other ecosystem services suggest value in the conservation and restoration of temperate zone tidal wetlands through climate change mitigation strategies. However, the findings suggest that long-term sea-level rise effects such as tidal inundation and increased porewater salinity will likely decrease ecosystem carbon stocks in the absence of upslope wetland migration buffer zones.

KEYWORDS

blue carbon, carbon stocks, climate change mitigation, coastal wetlands, salt marsh, seagrass, tidal forest

1 | INTRODUCTION

Coastal blue carbon ecosystems such as tidal marshes, seagrass beds, and tidal forests are exceptional carbon sinks (Mcleod et al., 2011). These ecosystems occupy the intertidal margins of shorelines, estuaries, and bays worldwide. The presence of vascular plants distinguishes them from the phytoplankton-dominated oceanic blue carbon ecosystems, which tend to support relatively low rates of primary production and carbon burial (Megonigal et al., 2016). Although these blue carbon ecosystems occupy a relatively

small area globally, they also provide a wide variety of other well-known ecosystem services such as pollutant sinks and habitats for economically important fisheries and wildlife (Luisetti et al., 2014). Furthermore, the role of mangroves and marshes in the protection of shorelines and infrastructure from tsunamis and storms has been convincingly demonstrated (Barbier, 2013; Pearce, 2014; Shepard, Crain, & Beck, 2011).

The carbon sequestration and co-benefits of conservation and restoration of coastal blue carbon ecosystems are of interest because of their potential inclusion in regional, national, and global climate change adaptation and mitigation strategies (CEC, 2016; IPCC, 2014). This is related to: (a) their large carbon stocks, (b) their greenhouse gas emissions when anthropogenically disturbed, and (c) the areal extent of their loss. Greenhouse gas emissions from the conversion of coastal wetlands (e.g., mangroves) to pasture and aquaculture have been reported to be as high as 1,067–3,003 Mg CO_2e/ha (Kauffman et al., 2017). The global area of coastal blue carbon ecosystems continues to decrease at a rate of 0.7%–7% annually (Mcleod et al., 2011). Brophy et al. (2019) reported that about 85% of vegetated tidal wetlands have been lost from land use in West Coast US estuaries.

Emerging greenhouse gas offset methods for crediting conservation and restoration projects in blue carbon ecosystems such as tidal wetlands, forested wetlands, and seagrasses have the potential to stimulate the protection of blue carbon ecosystems through carbon finance markets (VCS, 2015a, 2015b). However, implementation is only possible in locations where carbon stocks data and information are sufficient to predict outcomes, and there is a dearth of available data and models.

Increasing numbers of studies are estimating the total ecosystem carbon stocks (TECS) of coastal wetlands of temperate North America (CEC, 2016) and the United States (Holmquist et al., 2018; Nahlik & Fennessy, 2016). However, the wetlands of the Pacific Northwest (PNW; Northern California to the US—Canada border) are poorly represented (Canuel, Cammer, McIntosh, & Pondell, 2012; Windham-Myers et al., 2018). In contrast, the high productivity of forested upland ecosystems in the PNW is widely known (Gray & Whittier, 2014). The understudied coniferous forested tidal wetlands of the PNW, the marshes occurring along saline to tidal freshwater gradients, and the widespread seagrass beds provide expansive opportunities for blue carbon sinks in the region (Callaway et al., 2012). Our goals were to determine the range and variability of carbon stocks of relatively undisturbed examples of these PNW blue carbon ecosystems through uniform approaches to sampling, similar to methods used to quantify ecosystem blue carbon stocks elsewhere (Kauffman et al., 2020).

In a meta-analysis of coastal ecosystems of the continental United States (CONUS), Holmquist et al. (2018) reported that carbon density was well constrained with little effect exerted by vegetation type. They reported the mean carbon stock of tidal wetlands to a 100 cm depth was 270 Mg C/ha. This is quite similar to the Intergovernmental Panel on Climate Change (IPCC) tier 1 default value of 255 Mg C/ha (IPCC, 2014). Alternatively, we hypothesized that there would be increases in TECS along the gradient of coastal wetland ecosystems common in the PNW: seagrass, low marshes, high marshes, and tidal forests. We predicted that these differences would arise corresponding to changes in the soil profile depth, soil carbon density, elevation, salinity, and aboveground carbon pools along the aquatic-terrestrial gradient between community types. The development of a permanent plot network (inventory) in a synoptic study of carbon stocks and environmental factors will provide ecologically meaningful information from which to value these ecosystems and to base future studies of greenhouse gas emissions.

2 | STUDY AREAS

We conducted a synoptic study of tidal ecosystems across the PNW coast from Humboldt Bay, California (latitude: 40.7172; longitude: −122.1502), to Padilla Bay, Washington (latitude: 48.51032; longitude: −124.3327; Figure 1; Table 1). We sampled common coastal

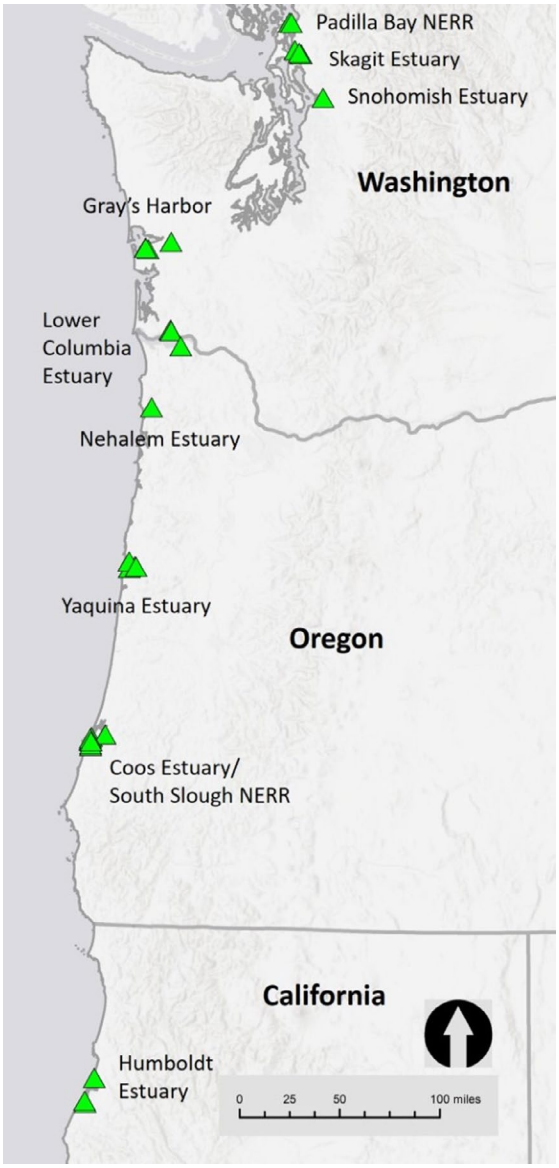

FIGURE 1 Location of the study sites from Humboldt Bay, California to Padilla Bay, Washington

TABLE 1 Salinity, pH, soil depth, elevation (m), and the geographic coordinates of the sampled sites. Numbers are the means ± *SE* for salinity, pH, and soil depth

Site	Estuary	Dominant species	Salinity (PSU)	pH	Soil depth (cm)	NAVD88G12A (m)	Local MHHW (m)	Standard tidal elevation (z*)	Latitude	Longitude
Seagrass										
Barview	Coos	*Zostera marina*	36.8 ± 0.6	7.6 ± 0.0	176.3 ± 7.0	−0.287	−2.177	−1.299	43.3457	−124.3186
Humboldt Eelgrass	Humboldt	*Z. marina*	41.5 ± 0.8	7.4 ± 0.1	300.0 ± 0.0	−0.285	−2.670	−1.650	40.7172	−124.2265
Lower Eel	Padilla	*Zostera japonica*	27.3 ± 0.4	8.7 ± 0.0	111.2 ± 3.8	−0.203	−2.515	−1.244	48.5492	−122.5323
Sallie's Bend	Yaquina	*Z. marina*	34.0 ± 0.0	7.3 ± 0.0	300.0 ± 0.0	0.241	−2.147	−1.130	44.6254	−124.0212
Upper Eel	Padilla	*Z. marina*	27.7 ± 0.6	9.1 ± 0.1	136.2 ± 3.6	0.274	−1.883	−0.929	48.5102	−122.4909
Valino Island	Coos	*Z. marina*	34.2 ± 1.5	7.5 ± 0.0	288.7 ± 7.3	−0.287	−2.177	−1.299	43.3137	−124.3191
Mean			33.6 ± 2.2	7.9 ± 0.3	218.7 ± 35.7					
Low marsh										
Delta Island	Skagit	*Sarcocornia perennis–Eleocharis palustris*	10.0 ± 1.2	6.7 ± 0.1	188.7 ± 0.0	1.961	−0.823	0.417	48.3528	−122.4638
Hidden Creek	Coos	*Jaumea carnosa–S. perennis*	28.5 ± 0.5	6.8 ± 0.0	300.0 ± 15.8	1.760	−0.388	0.594	43.2932	−124.3235
Humboldt Low	Humboldt	*S. perennis*	46.3 ± 2.5	7.7 ± 0.1	300.0 ± 0.0	1.844	−0.051	0.947	40.7042	−124.2161
Metcalf Low	Coos	*Distchilis spicata–S. perennis*	28.8 ± 1.7	6.4 ± 0.1	300.0 ± 0.0	2.038	−0.143	0.867	43.3350	−124.3279
Poole Slough	Yaquina	*S. perennis–D. spicata*	37.5 ± 1.4	7.0 ± 0.1	300.0 ± 0.0	2.102	−0.238	0.801	44.5782	−124.0142
Secret River	Columbia	*Eleocharis palustris*	nd	6.3 ± 0.0	100.2 ± 7.0	1.287	−1.326	−0.073	46.3055	−123.6951
Mad River	Humboldt	*D. spicata–S. perennis*	47.5 ± 2.6	6.8 ± 0.1	300.0 ± 0.0	1.996	−0.026	0.975	40.8861	−124.1406
Mean			33.1 ± 5.7	6.8 ± 0.2	255.5 ± 30.3					
High marsh										
Criterser's High	Yaquina	*Grindelia integrifolia–S. perennis–Juncus balticus*	22.0 ± 1.1	6.9 ± 0.2	300.0 ± 0.0	2.506	0.062	1.050	44.5898	−123.9470
Fir Island	Skagit	*Schoenoplectus lacustris–Schoenoplectus pungens*	12.5 ± 1.6	6.8 ± 0.1	227.5 ± 9.3	2.422	−0.371	0.739	48.3322	−122.4174
Hampel Marsh	Coos	*Carex lyngbyei–Agrostis stolonifera*	14.2 ± 2.9	6.9 ± 0.1	296.0 ± 4.0	2.116	−0.064	0.940	43.3194	−124.3319
John's River	Grays Harbor	*J. balticus–Potentilla anserina–Deschampsia cespitosa*	15.5 ± 1.1	6.0 ± 0.2	300.0 ± 0.0	2.674	0.173	1.134	46.8912	−123.9872

(Continues)

TABLE 1 (Continued)

Site	Estuary	Dominant species	Salinity (PSU)	pH	Soil depth (cm)	NAVD88G12A (m)	Local MHHW (m)	Standard tidal elevation (z*)	Latitude	Longitude
Metcalf High	Coos	*C. lyngbyei–Triglochin maritimum*	7.2 ± 1.1	6.5 ± 0.2	178.7 ± 0.0	2.130	−0.051	0.953	43.3355	−124.3283
Millicoma	Coos	*A. stolonifera–C. lyngbyei*	18.2 ± 1.9	6.5 ± 0.1	270.2 ± 9.6	2.164	−0.126	0.896	43.3687	−124.1849
Skagit Wildlife	Skagit	*Typha latifolia–S. lacustris*	7.0 ± 0.8	6.3 ± 0.1	283.5 ± 12.1	2.430	−0.365	0.743	47.4963	−122.6929
Secret River	Columbia	*C. lyngbyei*	nd	6.2 ± 0.1	215.3 ± 3.9	2.057	−0.555	0.550	46.3052	−123.6924
Danger Point	Coos	*C. lyngbyei–A. stolonifera*	17.2 ± 6.1	7.0 ± 0.2	300.0 ± 31.2	2.068	−0.084	0.913	43.2832	−124.3233
Mean			14.2 ± 1.7	6.6 ± 0.1	263.5 ± 15.1					
Tidal forest										
Chehalis Surge Plain	Grays Harbor	*Picea sitchensis*	5.0 ± 0.5	6.3 ± 0.1	300.0 ± 0.0	2.728	0.057	1.038	46.9415	−123.7212
Coal Creek	Nehalem	*P. sitchensis*	4.8 ± 1.9	6.2 ± 0.1	293.3 ± 6.7	2.794	0.253	1.206	45.7441	−123.8572
John's River Swamp	Grays Harbor	*P. sitchensis*	7.7 ± 1.1	7.2 ± 0.0	275.0 ± 25.0	2.842	0.338	1.261	46.8809	−123.9586
Otter Island	Snohomish	*P. sitchensis*	12.7 ± 2.0	6.4 ± 0.1	300.0 ± 0.0	2.531	−0.232	0.834	48.0134	−122.1502
Secret River	Columbia	*P. sitchensis*	nd	6.2 ± 0.1	229.5 ± 9.8	2.962	0.349	1.282	46.3067	−123.6900
Blind Slough	Columbia	*P. sitchensis*	nd	nd	244.2 ± 12.8	2.680	−0.020	0.984	46.1922	−123.5798
Mean			7.5 ± 1.8	6.5 ± 0.2	273.7 ± 15.2					

Abbreviations: MHHW, mean higher high water; nd, no data available.

communities that occur along broad gradients of elevation, salinity and tidal influences in the intertidal zone: seagrass, low marsh, high marsh, and tidal forest (Callaway et al., 2012). The seagrass meadows sampled ($n = 6$) were largely dominated by *Zostera marina*. The low marshes ($n = 7$) were largely dominated by *Distichlis spicata* and *Sarcocornia perennis*. The high marshes ($n = 9$) were often dominated by *Carex lyngbyei*, *Deschampsia cespitosa*, *Agrostis stolonifera* and other emergent marsh species. Low marshes were separated from high marshes on the basis of elevation (Table 1) as well as by geomorphic differences and species composition. Finally, the tidal forests ($n = 6$) were dominated by a conifer overstory (*Picea sitchensis*) with a prominent midstory of deciduous broadleaved shrubs and trees, and an understory with large quantities of downed wood and a dense cover of woody and herbaceous plants. The sampled estuaries included Humboldt Bay, Coos Bay, Yaquina Bay, Nehalem Bay, the Columbia River Estuary, Grays Harbor Estuary (Chehalis River), the Snohomish Estuary, the Skagit River Estuary, and Padilla Bay (Figure 1). Sites were selected across this broad region of the northwestern CONUS through examination and interpretation of aerial imagery, field data for vegetation and elevation previously collected by the investigators, LiDAR (where available), and historical maps; communications with local land managers; and new field reconnaissance. Our objectives were to sample sites that encompassed the broad range in salinity, climate, soil and hydrologic/tidal conditions on intertidal ecosystems of the US Pacific Coast.

3 | METHODS

Within each site, we measured ecosystem carbon stocks (above- and belowground) following methods outlined by Kauffman and Donato (2012) and Fourqurean et al. (2014; Figure S1). We randomly selected the initial plot location at each site and established six 10 m fixed radius plots 20 m apart along a 100 m transect that bisected the sampled community. We determined the coordinates of plots with hand-held GPS. At each plot, we collected data necessary to calculate total carbon stocks derived from both aboveground biomass and the soil profile. Laboratory analyses were conducted at Florida International University, Oregon State University, and the PNW National Laboratory.

3.1 | Aboveground biomass and carbon pools of tidal forests

For all sites, we followed the recommendations to sample the five dominant carbon pools of forest ecosystems (IPCC, 2006): aboveground biomass, belowground biomass, litter and organic horizons, dead wood, and soil organic carbon.

3.2 | Trees and shrubs

Woody biomass can be a long-term (i.e., decadal- or century-scale) carbon sink (Megonigal et al., 2016). Trees were stratified based on the diameter of all trees at 1.3 m height. Following Kauffman and Donato (2012) and Fourqurean et al. (2014), trees >5 cm in diameter were measured in larger circular plots with a 10 m radius. Trees <5 cm diameter were measured in six subplots with a 2 m radius. All trees with >50% of their rooted base located within the plot were included. Field measurements included species identification of all measured individuals. We determined the density and basal area of the live trees from these measurements (Table S5; Kauffman & Donato, 2012). Biomass of trees and shrubs were determined by applying species-specific allometric equations from BIOPAK (Means, Hansen, Koerper, Alaback, & Klopsch, 1994) and Chojnacky, Heath, and Jenkins (2014; Table S1).

Dead individuals accounted for about 7% of all trees. We partitioned standing dead trees into three classes based on their degree of decay and calculated the biomass of each decay class differently. Class 1 dead trees were those that had recently died with fine branches still attached. Biomass was calculated by subtracting the predicted mass of live foliage from the predicted total mass. For Class 2 dead trees, where only the main stem and large branches were present (but the main stem had not yet been broken), we subtracted the predicted mass of both foliage and fine branches. Class 3 dead trees (including stumps) were those with broken or fragmented trunks, where only part of the main stem remained. Biomass of this class was determined by multiplying the trunk volume (basal area times remaining trunk height) by dead wood specific gravity (0.37, Table S2). The density and basal area of dead trees were also determined from these measurements. Total tree mass, density, and basal area were calculated as the sum of both the live and dead trees. Root mass of the trees in tidal forests was calculated using an equation developed by Cairns, Brown, Helmer, and Baumgardner (1997). Tree carbon was calculated by multiplying biomass by a factor of 0.48 for aboveground and 0.39 for belowground biomass (Kauffman & Donato, 2012).

3.3 | Downed wood

We determined the mass and carbon pool comprised of dead and downed wood using the planar intersect technique (Kauffman & Donato, 2012) parameterized for tidal forests. At the center of each plot, we established four, 14 m transects with the first established in a direction that was offset 45° from the azimuth of the main transect. The other three were established 90° clockwise from the first transect (Figure S1). At each transect, we measured the diameter of any downed, dead woody material (fallen/detached twigs, branches, or main stems of trees and shrubs) intersecting the transect. Along the last 5 m of the transect, we measured downed wood ≥2.5 cm but <7.5 cm in diameter at the point of intersection. We measured downed wood ≥7.5 cm in diameter at the point of intersection from the second meter to the end of the transect (12 m in total). Large downed wood was separated into two decay categories: sound and rotten. Large downed wood was considered rotten if it visually appeared decomposed and broke apart when kicked. In order to determine mass, it was

necessary to determine the mean wood density of the wood particles (Table S2). Thirty to 50 randomly collected samples of each size class were measured to determine the wood particle density. The carbon mass of downed wood was determined by multiplying wood mass by carbon concentration (a factor of 0.50; Kauffman & Donato, 2012).

3.4 | Aboveground herbaceous biomass and carbon pools of marsh and seagrass communities

We quantified the herbaceous component of all sampled sites through harvest of all aboveground materials within two 25 × 25 cm (0.0625 m^2) quadrats in each of six plots at each sampled wetland ($n = 12$ quadrats/sampled site). The samples were transported to the laboratory and oven-dried to a constant weight at 45°C to determine mass. Carbon concentrations of aboveground and belowground biomass were determined in the laboratory with a CN analyzer (induction furnace method) as described for soils below.

3.5 | Soil carbon

At each of the six subplots at every sampling site, we collected soil samples to determine bulk density and carbon content (Figure S1). This was accomplished by extracting soil cores with an open-faced auger consisting of a semi-cylindrical chamber with an 18–23 cm^2 cross-sectional area. This auger was efficient for collecting relatively undisturbed soil cores with minimal compaction (Donato et al., 2011; Kauffman & Donato, 2012). The soil core was systematically divided into depth intervals of 0–15, 15–30, 30–50, 50–100 and >100 cm (if indurated soil horizons or layers were not encountered before 100 cm in depth). A 5 cm long sample of known volume was then collected from the central portion of each depth interval. At each sampling plot, we determined soil depth by inserting a graduated aluminum probe until refusal (indicating indurated soil horizons, or layers such as bedrock or marine sands). Depth was measured at three locations near the center of each plot. The probe length was ≈3 m, which is the inference limit of this study when soil depth exceeded 3 m (Figure S1). We determined soil carbon stocks of the entire profile depth as well as the soil carbon limited to a 1 m depth. This facilitated understanding the proportion that the top meter of soils comprised of both the total belowground carbon stock and the TECS.

Following soil extraction, all samples were transported to laboratories, dried to constant mass at ≤65°C, and then weighed to determine bulk density. In the laboratory, we determined organic carbon concentrations for all soil samples using the dry combustion method (induction furnace). Prior to carbon analysis, we removed identifiable roots from the soils to be sampled (root biomass was calculated as described in Section 3.2).

We tested for the presence of soil carbonates by taking a random sample of 150 samples (of about 840 total samples) and testing for both organic and inorganic carbon following the methods outlined in Fourqurean et al. (2014). The mean organic concentration of the total soil carbon fraction of these samples was 99.6%; therefore, we assumed the total carbon was essentially organic carbon content. Bulk density and carbon concentration were then combined with plot-specific soil depth measurements to determine the carbon density and soil carbon stocks.

Interstitial salinity and pH were measured from porewater samples directly extracted from the core holes using portable handheld refractometers and pH meters following methods described in Kauffman and Bhomia (2017). Porewater was sampled at each soil sampling plot ($n = 6$ in each sampled stand).

At each of the six plot centers at each site, we measured wetland surface elevation with real-time kinematic GPS using Eos and Trimble rovers and connection to a single base station or state-wide RTK base station network (e.g., ORGN in Oregon) or by optical leveling from an RTK-GPS-measured reference point at the site. We obtained geodetic elevations in the North American Vertical Datum of 1988 (NAVD88) using the geoid12A model and estimated NAVD88 values for local mean tide level (MTL) and mean higher high water (MHHW) using NOAA's VDATUM v3.6.1 model. We then converted measured geodetic elevations at each coring location into a unitless measure of elevation, z^*, that scales elevation to local half tide range, where $z^* = (z - \text{MTL})/(\text{MHHW} - \text{MTL}$; Swanson et al., 2014).

3.6 | Statistical analysis

The TECS were defined as the mass of all organic carbon in both aboveground and belowground pools to a maximum depth of 300 cm.

TECS can be expressed as:

$$\text{TECS} = \sum C_{AB} + C_{BB} + C_{DW} + C_{SOC} + C_L,$$

where C_{AB} is aboveground plant biomass C pool; C_{BB} is belowground biomass C pool; C_{DW} is in dead wood C pool; C_{SOC} is soil organic C pool; C_L is litter, surface litter C pools.

We hypothesized that there would be significant differences in TECS between wetland types and in how carbon is partitioned between soil and biomass pools. We tested for possible differences among TECS and carbon pool components (i.e., soils, trees, downed wood, etc.) using one-way analysis of variance (ANOVA). When we interpreted a significant difference with the ANOVA, a Fisher's Least Significant Difference test was employed to determine where differences among wetland types existed. We also examined differences among sites within the plant communities using ANOVA and Least Significant Difference tests.

4 | RESULTS

Along the intertidal gradient from seagrass through the marsh types to the tidal forests, there was a decrease in mean soil salinity, with a

concomitant increase in elevation (Table 1). Comparing all sampled sites, the soil porewater salinity ranged from 0 to 46. PSU. There was a 3.2 m range in wetland surface elevation. Mean soil porewater salinity was highest in the seagrass and low marsh community types (mean > 33 PSU) and declined to a mean of 14.2 PSU in the high marsh and 7.5 PSU in the tidal forest. The ranges in salinity were quite high among the sampled stands within communities. Although not measured during this study, the porewater salinity approached 0 PSU in prior measures at the Secret River tidal forest by the authors, which is consistent with local models (Chawla, Jay, Baptista, Wilkin, & Seaton, 2008), suggesting an overall range of 0–12.5 PSU for tidal forests. In the marshes, salinity ranged from 10 to 48 PSU in the low marsh, and from 7 to 22 in the high marsh. Similarly, soil pH decreased along this gradient with a mean of 7.9 in the seagrass communities and 6.5 in the tidal forest.

The mean soil depth was 210 cm for the seagrass community, and >255 cm for all other community types. However, these numbers are somewhat conservative as 43% of the sampled sites had soil profiles exceeding our sample depth limit of 300 cm. Only four sites (14%) had mean soil profile depth <2 m (Table 1). No site was ≤100 cm in depth.

4.1 | Aboveground biomass

The mean aboveground C stocks of the *Z. marina* that dominated most of the seagrass sites was 0.8 ± 0.2 Mg C/ha (range 0.25–1.23 Mg C/ha). The aboveground C stocks of the low marshes dominated by halophytic species such as *S. perennis* and *D. spicata* averaged 5.3 ± 1.2 Mg C/ha (range 1.78–9.15 Mg C/ha). In contrast, the high marshes tended to be dominated by a variety of more mesophytic species that varied by the sampled estuary (Table 1). The aboveground C stocks (herbaceous mass) of the high marshes were significantly larger than seagrass meadows and low marshes with a mean 8.2 ± 1.0 Mg C/ha (range 5.2–14.6 Mg C/ha; Table 2). The largest aboveground C stocks in the high marshes were found in those sites dominated by tall species (>2 m height) such as *Schoenoplectus lacustris* and *Typha latifolia* in the Skagit River Delta.

The mean aboveground C stocks of the seagrass and marsh communities (<8.2 Mg C/ha) were quite minor compared to those of the tidal forests (mean 220.1 Mg C/ha). The total aboveground C stock in the tidal forests ranged from 74 to 395 Mg C/ha (Figure 2). Standing trees comprised 51% of the total aboveground C stocks. The other dominant component comprising the total aboveground C stocks of tidal forests was dead and downed wood, comprising 43% of the total. The total aboveground C stock of the Secret River tidal forest was 395 Mg C/ha; this was significantly greater ($p < .05$) than four of the other sampled tidal forests (Figure 2; Table S4). The three forested sites with the lowest aboveground C stocks (≤170 Mg C/ha) had evidence of past logging, indicated by the presence of stumps as well as lower amounts of downed wood and standing trees relative to other sites. For example, the total downed wood C mass of the Otter Island, Coal Creek, and John's River tidal forests was <42 Mg C/ha. In contrast, downed wood in the other tidal forest sites with little or no indication of past logging had a C mass >153 Mg C/ha ($p \leq .05$; Table S3). The downed wood comprised 8%–28% of the total aboveground C pool at the sites with presumed past disturbance, but 41%–65% of the aboveground C pool at the three undisturbed sites (Figure 2). The herbaceous/litter layer accounted for a mean of 3% of the aboveground C stock (6.2 Mg C/ha). The mean tree roots C mass was estimated at 21 Mg C/ha.

4.2 | Soil carbon stocks

Comparing the sampled coastal plant communities revealed their distinctive soil characteristics (Table 3). Soil C concentration tended to increase along the elevation/salinity gradient from the seagrass to the tidal forest (Table 3). For example, at the surface elevation (0–15 cm), C concentration was 0.69% in seagrass communities, >8.4% in the marshes and 11.2% in the tidal forests. This trend of increasing soil C concentration was apparent at all depths in the soil profile. While concentration increased along this community gradient, the soil bulk density decreased. Carbon density and C mass significantly increased from seagrass through low and high marshes to tidal swamp (Table 2).

TABLE 2 Total ecosystem carbon (TECS), aboveground C (TAGC), and belowground C (TBGC) stocks of sampled blue carbon ecosystems of the Pacific Northwest, United States. Numbers are mean (Mg C/ha) ± 1 *SE*. Different superscripted letters denote significant difference ($p \leq .10$) when testing for difference between the plant communities

Component	Seagrass	Low marsh	High marsh	Tidal forest
TECS	217.1 ± 60.3^{a}	416.4 ± 70.0^{b}	551.4 ± 47.0^{c}	1,063.7 ± 37.5^{d}
TAGC	0.8 ± 0.2^{a}	5.3 ± 1.2^{a}	8.2 ± 1.0^{a}	220.1 ± 45.1^{b}
herb. mass	0.8 ± 0.2^{a}	5.3 ± 1.2^{b}	8.2 ± 1.0^{c}	6.2 ± 0.7^{bc}
TBGC	216.3 ± 60.4^{a}	411.1 ± 69.7^{b}	543.2 ± 46.9^{c}	843.6 ± 38.4^{d*}
0–15 cm	12.4 ± 1.8^{a}	46.0 ± 7.0^{b}	50.9 ± 6.0^{b}	59.3 ± 7.5^{b}
15–30 cm	11.23 ±0.1.8^{a}	34.4 ± 2.9^{b}	44.6 ± 3.7^{c}	46.7 ± 3.8^{c}
30–50 cm	16.48 ± 2.8^{a}	37.8 ± 3.2^{b}	49.3 ± 4.3^{c}	64.3 ± 6.4^{d}
50–100 cm	39.9 ± 6.2^{a}	72.4 ± 7.4^{a}	117.0 ± 14.3^{b}	189.3 ± 11.4^{c}
>100 cm	136.4 ± 51.6^{a}	220.5 ± 55.3^{ab}	281.4 ± 36.9^{b}	463.0 ± 42.9^{c}

*In addition to soil carbon, the TBGC includes a tree root mass estimate of 21.0 Mg C/ha.

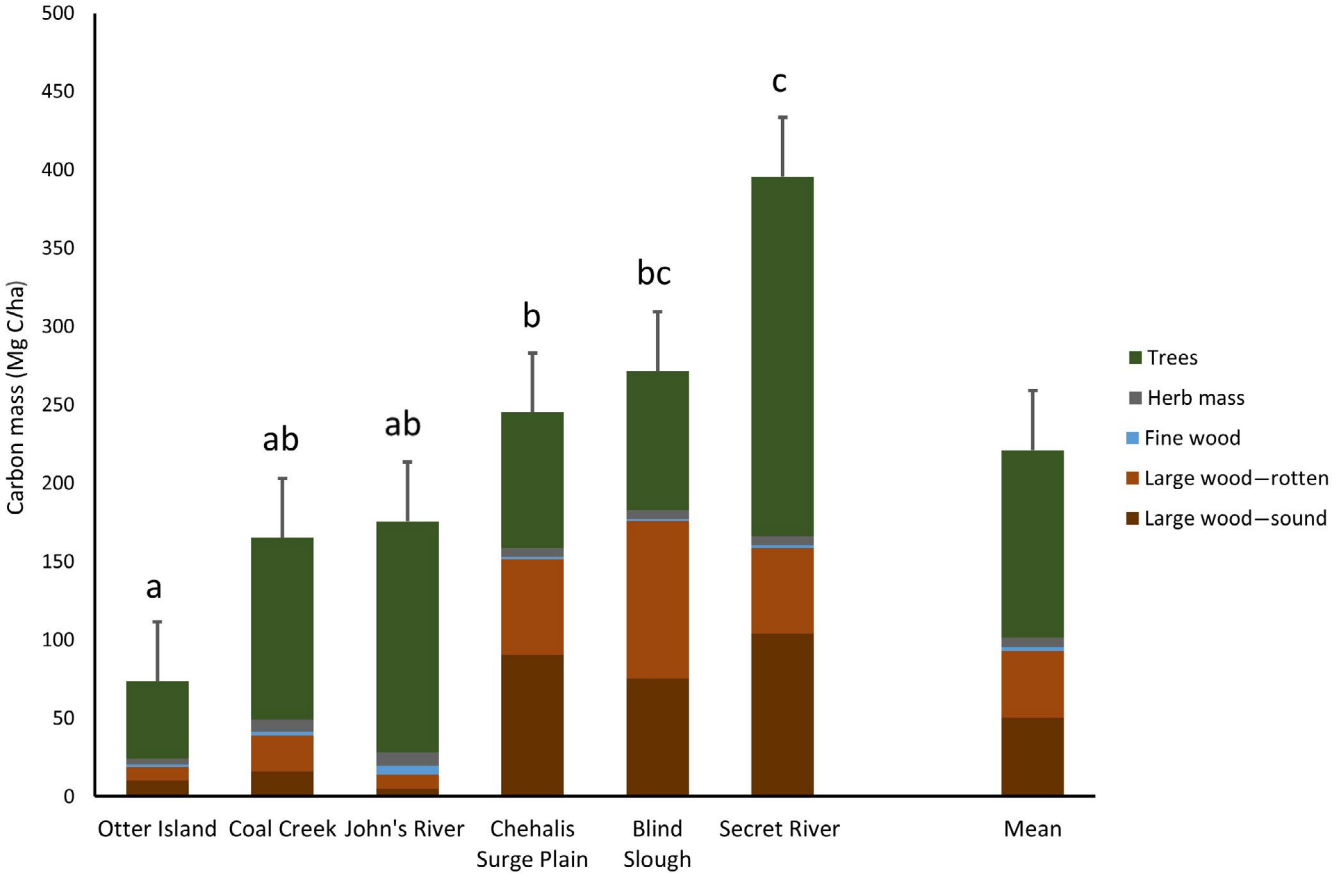

FIGURE 2 The total aboveground carbon stocks (Mg C/ha) of the tidal forests in the Pacific Northwest. Different letters above the bars note a significant difference ($p < .10$) in the total aboveground carbon stocks among sites

Comparing the different soil depths, there was a trend of decreasing soil C concentration and an increase in bulk density moving from the shallow to deepest soil layers (Table 3). Thus, differences in C density were not as great as differences in soil C concentration.

The fixed volume soil samples collected following this methodology were used to estimate soil C across depth intervals of different sizes (i.e., a size of 20 cm for the 30–50 cm depth interval vs. 50 cm for the 50–100 cm depth interval). Yet an analysis of the variation in C and bulk density values for soil samples from different depth intervals did not suggest undersampling at deeper depths. There was no systematic increase in the coefficient of variation of the soil samples when comparing shallow to deeper soil layers, suggesting that the dispersion of C and bulk density values was not greater for samples collected from larger depth intervals (Table 3).

Of all wetland types sampled, total soil C mass was highest in the tidal forest (822 ± 95 Mg C/ha; Table 3). In the high and low marshes, the total soil C mass was 543 ± 47 and 411 ± 70 Mg C/ha, respectively. Soil C mass was lowest in the seagrass community (216 ± 60 Mg C/ha). Each community was significantly different from the others ($p \leq .05$).

Similar to the total soil C pool, there was wide disparity between wetland types in the C mass of soils considering the top 100 cm alone. Soil C mass from the 0–100 depth interval ranged from 80 ± 12 Mg C/ha in seagrass to 360 ± 17 Mg C/ha in tidal forest. The upper 100 cm mass for the low and high marshes was 190 ± 16 and 262 ± 23 Mg C/ha, respectively (Table 2). The 0–100 cm soil C mass was significantly different between each community type. On average, soils 0–100 cm depth comprised about 50% of the total soil C pool in the seagrass and marsh communities, and about 40% of the total soil C pool in tidal forest (Table 2; Table S5). However, there was a large range in the proportion of the total soil C pool comprised by the first 100 cm, especially in the seagrass and marsh communities. For example, soils 0–100 cm accounted for 21%–88% of the total soil C pool in seagrass communities and from 34% to 90% in low marsh communities. Soils of the top 100 cm comprised a smaller proportion of the total soil C stock when the soil profile in sampled stands was deep (e.g., ≥300 cm).

4.3 | Total ecosystem carbon stocks

The TECS was significantly different between each of the community types (Figure 3; Table 3). The TECS of the tidal forests (1,064 Mg C/ha) were almost twice that of marshes (416 and 551 Mg C/ha) and fivefold greater than seagrass communities (217 Mg C/ha).

TABLE 3 Carbon and nitrogen concentration (%), bulk density and C and N density (g/cm^3) and C and N mass (Mg/ha) for soils of blue carbon ecosystems of the Pacific Northwest, United States. Numbers are the mean, standard deviation (*SD*), and the coefficient of variation (CV)

	Carbon concentration (%)			Bulk density (g/cm^3)			Carbon density (g/cm^3)			Carbon mass (Mg/ha)		
Depth	Mean	*SD*	CV (%)	Mean	*SD*	CV (%)	Mean	*SD*	CV (%)	Mean	*SD*	CV (%)
Seagrass (*N* = 6)												
0–15	0.69	0.28	41.35	1.26	0.16	12.68	0.008	0.003	34.91	12.38	4.32	34.91
15–30	0.58	0.25	43.07	1.34	0.21	15.92	0.007	0.003	39.24	11.23	4.41	39.24
30–50	0.66	0.30	44.71	1.30	0.16	12.55	0.008	0.003	41.73	16.48	6.88	41.73
50–100	0.61	0.26	43.29	1.36	0.13	9.85	0.008	0.003	37.87	39.86	15.09	37.87
>100	0.71	0.39	54.62	1.35	0.13	9.45	0.009	0.004	48.22	136.37	126.30	92.62
Total										216.31	147.83	68.34
Low marsh (*N* = 7)												
0–15	8.47	4.97	58.64	0.47	0.20	42.07	0.031	0.012	40.31	46.04	18.56	40.31
15–30	5.16	2.29	44.46	0.54	0.23	43.29	0.023	0.005	22.09	34.36	7.59	22.09
30–50	3.56	1.47	41.28	0.66	0.27	41.03	0.019	0.004	22.69	37.80	8.58	22.69
50–100	1.96	1.08	55.04	0.98	0.34	34.44	0.015	0.004	26.53	72.40	19.47	26.89
>100	1.54	1.28	83.33	1.02	0.34	32.80	0.013	0.005	38.44	220.48	146.25	66.34
Total										411.08	184.50	44.88
High marsh (*N* = 9)												
0–15	10.18	4.43	43.50	0.42	0.11	25.25	0.034	0.012	35.55	50.93	18.10	35.55
15–30	6.80	2.22	32.61	0.55	0.15	27.12	0.030	0.007	25.01	44.59	11.15	25.01
30–50	5.35	2.70	50.51	0.61	0.19	30.91	0.025	0.006	26.23	49.30	12.93	26.23
50–100	3.95	2.22	56.18	0.74	0.21	28.50	0.023	0.009	36.68	116.99	42.92	36.68
>100	1.99	0.70	35.45	0.98	0.21	21.85	0.017	0.005	26.35	281.40	110.71	39.34
Total										543.20	140.84	25.93
Tidal forest (*N* = 6)												
0–15	11.07	4.74	42.80	0.41	0.09	20.84	0.040	0.012	30.73	59.28	18.22	30.73
15–30	7.06	3.13	44.33	0.52	0.12	22.75	0.031	0.006	19.87	46.66	9.27	19.87
30–50	6.90	3.27	47.29	0.56	0.13	22.53	0.032	0.008	24.33	64.30	15.64	24.33
50–100	7.81	1.97	25.21	0.58	0.10	17.61	0.038	0.006	14.81	189.26	28.03	14.81
>100	5.40	2.00	37.00	0.60	0.11	18.97	0.028	0.005	18.31	462.96	105.16	22.71
Total										822.47	103.74	12.61

There was no significant difference in the TECS between the sampled tidal forests ranging from 925 to 1,164 Mg C/ha. In contrast, there was a wider and significant ($p < .05$) range in variation in the TECS within the marshes and within the seagrass communities (Figure 3). There was a twofold difference in the TECS of high marshes (359–742 Mg C/ha) and a fourfold difference in TECS in low marshes (154–627 Mg C/ha). There was over an eightfold difference in the TECS across individual seagrass sites ranging from 46 to 389 Mg C/ha (Table S6).

The overwhelming majority of the TECS in the sampled intertidal ecosystems of the PNW was comprised of the soil component. The aboveground C pool was a minor component of the TECS in the marshes (0.3%) and seagrass communities (<1.4%; Table 2). In contrast, the aboveground C pool in the tidal forests comprised 22% of the TECS. Standing trees comprised 11% of the TECS and downed wood accounted for 9% of the TECS in tidal forest (Table 2; Figure 3). In the tidal forest, the surface soils (0–100 cm) only comprised 34% of the TECS.

5 | DISCUSSION

While the ecological, economic, and social values of blue carbon ecosystems have been recognized, accurate information on the TECS for most regions remains limited due to a paucity of data, especially for belowground carbon stocks. The wide range in TECS suggests caution when using default values (e.g., IPCC, 2014) which assume uniformity in carbon stocks across ecosystems and landscapes for these blue carbon ecosystems. While many studies report soil carbon in tidal wetlands to 50 cm, few have examined carbon stocks beyond 100 cm in depth (CEC, 2016). In their global meta-analysis of

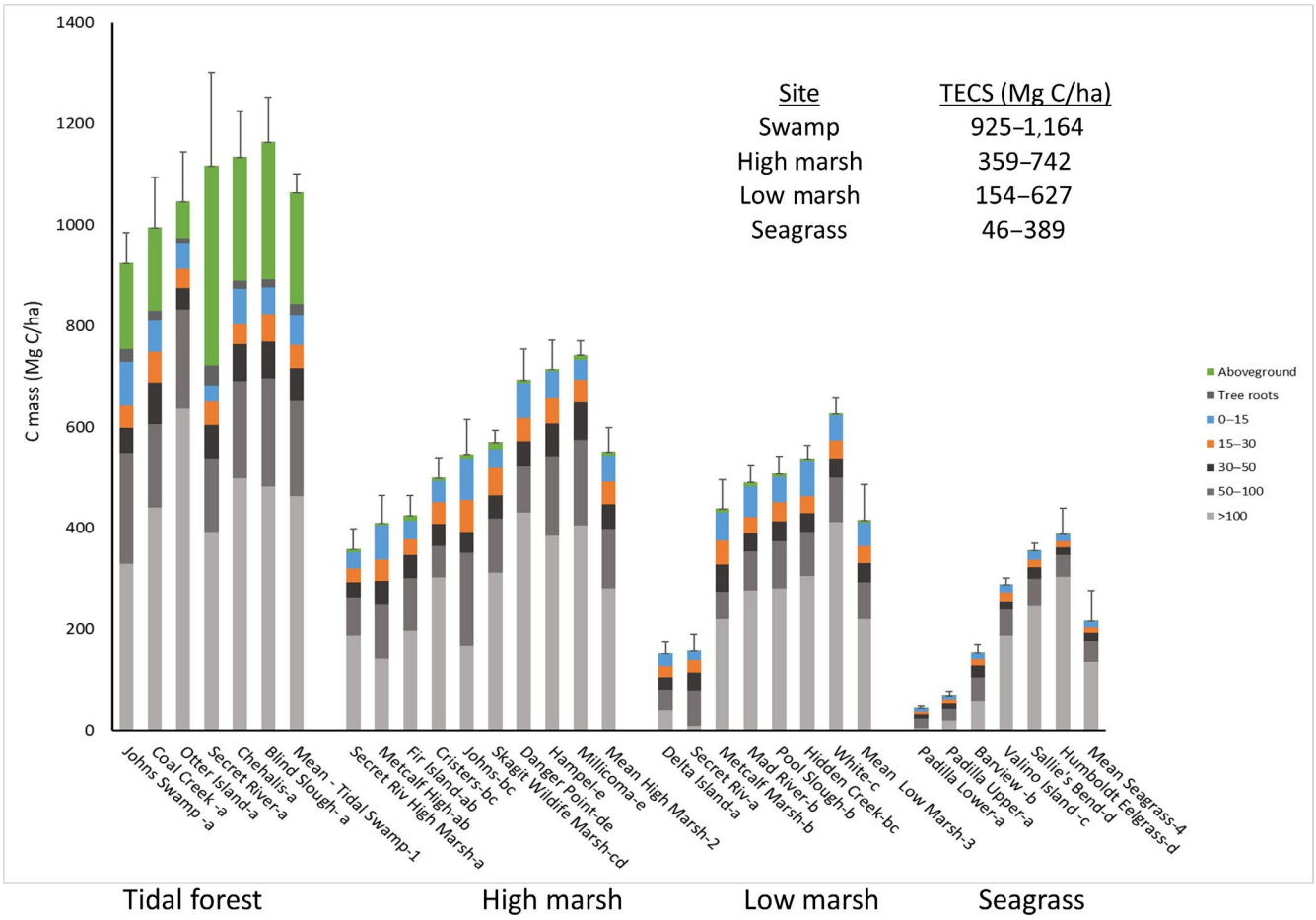

FIGURE 3 Total ecosystem carbon stocks in major tidal wetland ecosystems of the Pacific Northwest, United States (Mg C/ha). Small vertical bars represent one standard error. Different letters following the community names note a significant difference when testing between sites within each community type. Different numbers following the means of each community type denote significant difference between community types

seagrass TECS, Fourqurean et al. (2012) could find information from only 41 cores that contained data as deep as 1 m. In this study, we provided data from 36 cores extending to depths of 111–300 cm. Similarly, in a meta-analysis of coastal ecosystems in the CONUS (Holmquist et al., 2018), the mean soil core length was only 55 cm. This limitation is significant as soils 0–50 cm only accounted for 16% of the TECS in seagrass, 18% in tidal forests, and <28% in the marshes (Table 3). Measurement of soil profile depth and determination of its entire carbon density enable a more complete accounting of soil carbon stocks that informs both greenhouse gas emissions avoided from wetland conservation as well as potential emissions increase from wetland loss.

Comparing the TECS measured in this study with those of other United States and global studies suggests that the stocks of PNW coastal wetlands exceed mean estimates reported elsewhere. Global estimates of seagrass carbon stocks (IPCC, 2014) were 65% of mean ecosystem carbon stocks in our PNW seagrass sites (Figure 4a). Similarly, mean ecosystem carbon stocks of the high marshes of this study (551 Mg C/ha) were about double those reported for global marshes (255 Mg C/ha; IPCC, 2014) and for the CONUS (270 and 307 Mg C/ha; Holmquist et al., 2018; Nahlik & Fennessy, 2016). While the higher PNW stock values are likely more related to inclusion of the entire soil profile and aboveground carbon stocks in our study, this is not the case when comparing Mexican emergent marshes (258 Mg C/ha; Adame et al., 2013) or those of the Brazilian Amazon (177 Mg C/ha; Kauffman et al., 2018). Those studies also included the carbon mass of the entire profile following methods similar to this study.

In terms of TECS, the *P. sitchensis* dominated tidal forests of the PNW are a temperate equivalent of the mangrove forests of the tropics (Figure 4a; Kauffman et al., 2020). These tidal forests represent among the largest ecosystem carbon stocks per unit area of any blue carbon ecosystem measured to date globally. Using the same sampling approaches in the temperate zone and the tropics, the mean TECS of PNW tidal forests (1,064 Mg C/ha) exceeds the mean global mangrove TECS estimate of 824 Mg C/ha provided by Kauffman et al. (2020; Figure 4a). Nahlik and Fennessy (2016) reported the mean soil carbon stock of estuarine woody-dominated plant communities in the United States was 359 Mg C/ha. Our high values for tidal forests are perhaps unsurprising given the uniquely high productivity of PNW forests (Smithwick, Harmon, Remillard, Acker, & Franklin, 2002), but carbon stocks in these rare wetland forests have not previously been quantified. The high organic carbon stock values of tidal forests, along with

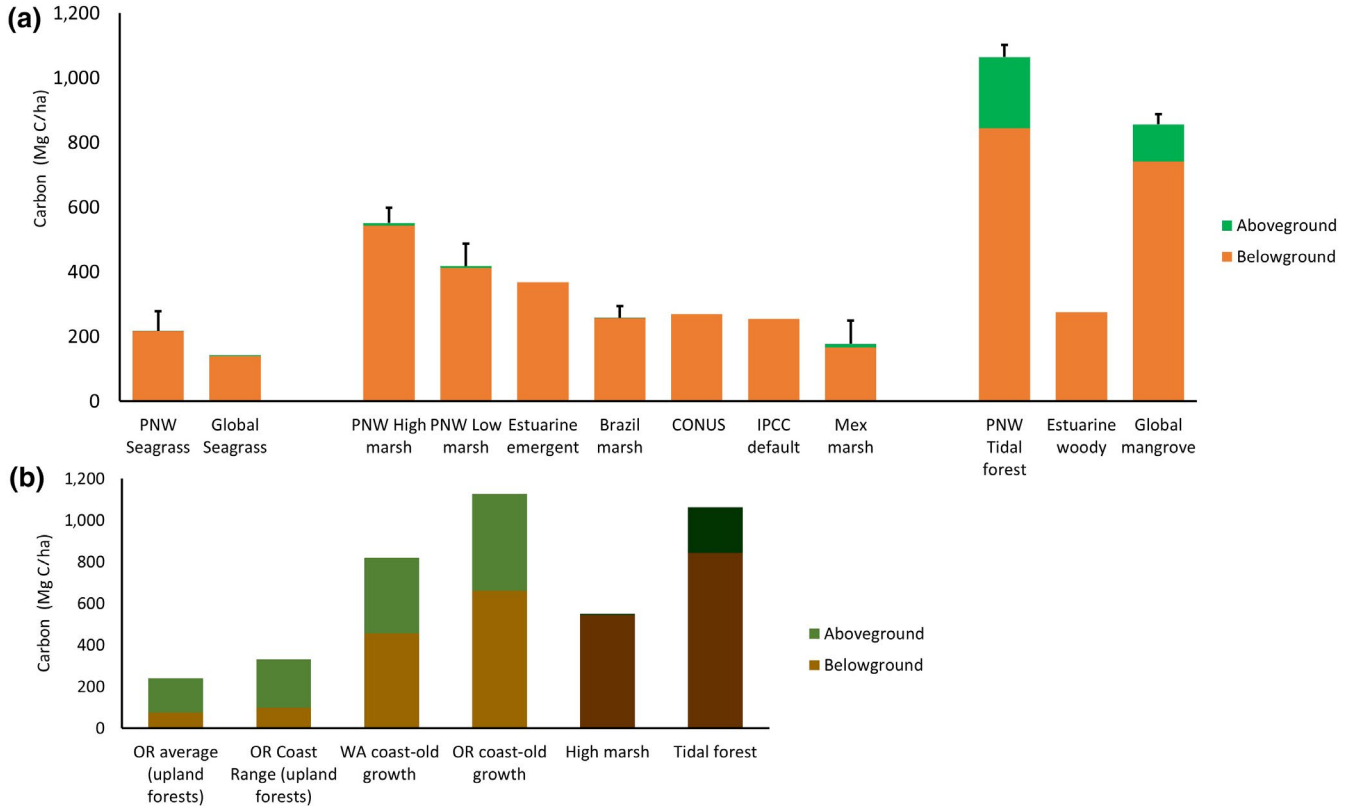

FIGURE 4 (a) A comparison of carbon stocks (Mg C/ha) of the blue carbon ecosystems of this study (the Pacific Northwest—PNW) to continental and global reviews as well as tropical studies that employed the same methods. All the PNW sites are from this study whereas global seagrass data are from Fourqurean et al. (2012). Data from Brazil marshes are from Kauffman et al. (2018) and data from Mexican marshes are from Adame et al. (2013). The estuarine emergent and estuarine woody are estimates for US tidal wetlands from Nahlik and Fennessy (2016). The IPCC default values for marshes are from IPCC (2014). The CONUS are mean estimates of ecosystem carbon stocks of USA tidal ecosystems from Holmquist et al. (2018). Global mangrove data are from Kauffman et al. (2020). (b) A comparison of the carbon stocks (Mg C/ha) of marshes and tidal forests of this study (darker greens and browns) with upland forests of the Pacific Northwest (lighter green and brown). Data on Oregon (OR) state-wide and coast range averages are from Law et al. (2018) and data from Washington (WA) and Oregon coast range old growth forest are from Smithwick et al. (2002)

their other coastal ecosystem services, suggest they should be a high conservation and restoration priority in PNW estuaries.

Because of relatively high carbon stocks, the value of blue carbon ecosystems for inclusion in regional and global climate change mitigation strategies has long been recognized (Donato et al., 2011; Duarte, Losada, Hendriks, Mazarrasa, & Marbà, 2013; Mcleod et al., 2011). Our TECS values for coastal ecosystems of the PNW are comparable to, or exceed, values for upland temperate forests in the region (Figure 4b). Law et al. (2018) found that the mean TECS of all forests in Oregon was 241 Mg C/ha with TECS and those of the Coast Range forests were 330 Mg C/ha. These numbers would include both second growth and old growth forests of varying ages. The mean carbon stock of old growth (late successional) forests of the PNW has been reported to be 820 Mg C/ha for the Washington Coast Range and 1,127 Mg C/ha for the Oregon Coast Range (Smithwick et al., 2002). The TECS of the tidal forests of this study (1,064 Mg C/ha) are similar to that of old growth forests of the PNW even though the sampled tidal forests were of mix of old growth and second growth forests. The TECS of coastal high marshes also greatly exceeded the mean TECS of Coast Range upland forests (Figure 4b).

Differences in how carbon is partitioned among pools in upland forests as compared to tidal forests are apparent (Figure 4b). The aboveground:belowground stocks ratio was 2.1–2.3 for all upland forests and 0.70–0.79 for old growth upland forests. In contrast, it was 0.26 for the tidal forests showing the high proportion of carbon storage occurring in soils.

The TECS of upland forests in Figure 4b only include soils to 1 m depth. However, it could be argued that this is a relevant ecosystem comparison because the vast majority of soil carbon in upland forests is in the surface 1 m (e.g., Donato, Kauffman, Mackenzie, Ainsworth, & Pfleeger, 2012). As such, these are comparisons of the carbon stocks vulnerable to land use in wetlands and uplands.

Many studies have reported relatively weak relationships between carbon stocks and environmental features such as salinity and species composition (e.g., Holmquist et al., 2018; Kauffman et al., 2020). However, marsh soil organic carbon stocks 0–100 cm have been significantly correlated with salinity on the Elbe River estuary in Germany (Hansen et al., 2017) and Van de Broek, Temmerman, Merck, and Govers (2016) found a strong relationship

of increasing soil carbon stocks along salinity/compositional/elevation gradients in the Scheldt River estuary. Recently, a mechanistic analysis of soil organic carbon in tidal marshes to 60 cm depth showed that autochthonous carbon is more efficiently preserved in tidal freshwater (Van de Broek et al., 2018). Consistent with these findings, we found a trend of significantly increasing ecosystem carbon stocks along gradients of increasing elevation, decreasing salinity, and different species composition when the means of replicated sites along these gradients were examined (Figure 3; Table 2). While individual sites will vary, there exists a general trend of increasing TECS along landward gradients from seagrass to salt marshes to tidal forests. Similar relationships have been found for the top 0–30 cm of soil in Georgia marshes and a review of 61 sites in the coterminous United States, which showed lower bulk density and higher percent organic carbon in tidal freshwater and brackish marshes than salt marshes (Craft, 2007).

Perhaps the most significant factor affecting estimates of carbon stocks is the arbitrary decision on where to limit soil depth in carbon sampling. This decision clearly affects the carbon stock estimates at the site scale and is compounded when scaling to continental or global scales. Assuming a 27 kg C/m^3 average carbon mass, Holmquist et al. (2018) estimated US tidal wetlands store 0.72 (Pg) of C for the top 1 m of soil. Including soils to a depth of 120 cm depth, Nahlik and Fennessy (2016) estimated that saline wetlands in the CONUS sequestered 0.76–0.87 Pg C. The mean soil profile depths of the four sampled tidal communities in this study ranged from 219 cm in seagrass to 274 cm in tidal forest (Table 1). The fact that soils 0–100 cm in depth accounted for half or less of the TECS (Figure 3) clearly suggests that nationwide estimates of ecosystem carbon stocks limited to 1 m depth are vast underestimates of the carbon stored in these coastal landscapes. Van de Broek et al. (2016) also found that most existing studies underestimated total carbon stocks because of shallow soil sampling, which also influenced reported patterns of carbon storage along estuarine gradients. Including aboveground stocks for forested tidal wetlands and the entire soil profile for all blue carbon ecosystems would likely double the estimate of total carbon stored in coastal wetlands of North America. This is important because carbon stocks at depths below 100 cm are lost via land conversion for human uses (Arifanti, Kauffman, Hadriyanto, Murdiyarso, & Diana, 2019; Kauffman et al., 2018; Nahlik & Fennessy, 2016). The IPCC (2006) recommendations for measuring ecosystem carbon stocks include vegetation, downed wood, surface layers, and soils. Limiting the definition of ecosystem carbon stocks in tidal wetlands to 0–100 cm is tantamount to a population census where entire neighborhoods are ignored and uncounted because they are deemed insignificant or too difficult to sample.

Wetlands in the PNW have survived within the shifting intertidal zone for millennia of rising sea levels (Peterson, Gates, Minor, & Baker, 2013). This was accomplished through biophysical processes that led to the accumulation of mineral and organic matter, thereby increasing soil volume and surface elevation (Morris et al., 2016). Along the generalized gradients of increasing elevation and decreasing salinity from seagrass, through salt marshes, and ending with tidal forest communities, we found a significant increase in TECS (Figure 3; Table 3). Like the coastal Atlantic and Gulf of Mexico (Van de Broek et al., 2016; Więski, Guo, Craft, & Pennings, 2010), this suggests that with sea-level rise in the US PNW, there may be a positive feedback of losses in the capacity of the coastal communities to sequester carbon. While the marshes may keep up with sea-level rise for some time given sufficient mineral deposition and organic matter accretion (Morris et al., 2016), increasing porewater salinity due to pulses associated with storm surges and high tides will likely result in landward expansion of low marshes into sites formerly occupied by high marshes, which would likely decrease TECS. Significant pulses of carbon emissions could result following the degradation of tidal forests and their eventual replacement by high marsh due to increasing salinity. The ultimate fate of tidal wetlands will be influenced by the capacity for landward migration of wetlands which can be limited by natural steep rises in topography and human development.

The carbon stocks of tropical and temperate coastal ecosystems coupled with the other critical ecosystem services they provide for humanity suggest that conservation and restoration efforts are warranted. However, the inherent variability in the TECS will require intensive inventories to ensure accurate measurements of the carbon dynamics of these ecosystems.

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AUTHOR CONTRIBUTION

All authors contributed to project conceptualization and experimental design. C.C., J.A., C.J., H.D. and J.B.K. led site selection; C.C. and C.J. measured surface elevation; J.B.K., L.G., J.K., N.D., and A.B. led the fieldwork; J.B.K., N.D., L.G., and A.B. conducted much of the lab work; J.B.K. led the data analysis and initial writing of the manuscript; all authors contributed to writing the manuscript.

DATA AVAILABILITY STATEMENT

Much of the data that support the findings of this study are available in the supplementary material of this article. In addition, the data that support the findings of this study will be openly available in the Coastal Carbon Research Coordination Network https://serc.si.edu/coastalcarbon.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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