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RESEARCH ARTICLE

Changes in habitat availability for outmigrating juvenile salmon (*Oncorhynchus* spp.) following estuary restoration

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The restoration of the Nisqually River Delta (Washington, U.S.A.) represents one of the largest efforts toward reestablishing the ecosystem function and resilience of modified habitat in the Puget Sound, particularly for anadromous salmonid species. The opportunity for outmigrating salmon to access and benefit from the expansion of available tidal habitat can be quantified by several physical attributes, which are related to the ecological and physiological responses of juvenile salmon. We monitored a variety of physical parameters to measure changes in opportunity potential from historic, pre-restoration, and post-restoration habitat conditions at several sites across the delta. These parameters included channel morphology, water quality, tidal elevation, and landscape connectivity. We conducted fish catch surveys across the delta to determine if salmon was utilizing restored estuary habitat. Overall major channel area increased 42% and major channel length increased 131% from pre- to post-restoration conditions. Furthermore, the results of our tidal inundation model indicated that major channels were accessible up to 75% of the time, as opposed to 30% pre-restoration. Outmigrating salmon utilized this newly accessible habitat as quickly as 1 year post-restoration. The presence of salmon in restored tidal channels confirmed rapid post-restoration increases in opportunity potential on the delta despite habitat quality differences between restored and reference sites.

Key words: fish, Nisqually River Delta, *Oncorhynchus tshawytcha*, Puget Sound, tidal channel, tidal marsh estuary

Implications for Practice

- Increases in opportunity potential may occur rapidly following estuarine restoration, even after several decades of excluded tidal flows. This suggests that tidal marshes that have been diked for long periods of time can still recover functionality.
- Systematic monitoring has shown that changes to habitat availability following large-scale restoration can be immediate but physical and biological metrics may be slower to respond.
- The interaction between habitat connectivity, density dependence, and salmon distribution across a connectivity gradient provides valuable information for determining the suitability of restored estuarine habitats and identifying the locations for future restoration efforts.

Introduction

Estuaries are a crucial source of biodiversity at the land–sea interface, providing valuable resources to a variety of wildlife species. Urbanization, agricultural development, and resource extraction pressures have led to a worldwide decline in estuarine habitat, making these coastal ecosystems some of the most heavily used and threatened natural systems in the world (Lotze et al. 2006). Today, coastal wetlands are a fraction of their historic extent, and many are highly modified systems where channels have been severed by dikes or tidegates (Hood 2004; Greene 2012). Tidal channels link highly productive salt marshes to the nearshore marine environment, acting as vital conduits for sediment, nutrients, detritus, and aquatic organisms (Simenstad 1983; Odum 1984; Rozas et al. 1988; French & Spencer 1993). As a result, modified estuaries experience sediment starvation

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and marsh erosion due to limited hydrologic exchange with surrounding habitat and reduced tidal function (Hood 2007).

Estuaries serve as important rearing habitat for anadromous salmonids (*Oncorhynchus* spp.; hereafter referred to as "salmon"), contributing to their overall fitness and ocean survival (Healey 1980; Levy & Northcote 1982; Levings et al. 1986). The loss of 70% of Puget Sound's historic estuarine wetlands has been associated with the decline of Pacific salmon populations (Lane & Taylor 1996; White 1997; Dean et al. 2000; Simenstad et al. 2011). Consequently, their recovery has become a critical driver for habitat restoration in the Pacific Northwest, U.S.A. (Bernhardt et al. 2005).

In autumn 2009, the Nisqually National Wildlife Refuge (hereafter "Refuge") and Nisqually Indian Tribe (hereafter "Tribe"; Olympia, Washington, U.S.A.) removed the century-old Brown Farm Dike, allowing for the return of tidal processes to over 308 ha of the Nisqually River Delta. This project, along with several smaller phased restorations, represented one of the largest restoration efforts in the Pacific Northwest. One of the primary motivations for restoring this large river delta was ensuring the recovery of native salmonids such as the Nisqually fall Chinook salmon (*Oncorhynchus tshawytscha*)—one of 27 evolutionarily unique stocks in the Puget Sound that are listed as threatened under the Federal Endangered Species Act (NCRT 2001; SSDC 2007). Chinook are thought to be the most estuary-dependent of the Pacific salmon, and thus provide a basis for examining habitat development and indicators of ecosystem functioning in restored wetlands (Reimers 1973; Magnusson & Hilborn 2003). Nisqually winter chum (*Oncorhynchus keta*) also utilize the estuary for feeding and growth, and have one of the largest wild runs in Washington State (Fresh et al. 1979; Pearce et al. 1982; WDFW 2002; Ellings & Hodgson 2007). Both the Chinook and chum salmon populations are culturally and economically vital resources for the Nisqually Indian Tribe, which was guaranteed fishing rights in perpetuity as part of the Medicine Creek Treaty in 1854.

Evaluating the effect of restoration on the growth and survival of salmon is challenging because, in addition to the lag time between the development of suitable habitat and prey resources, their densities are highly variable across space and time within the landscape mosaic (Simenstad & Cordell 2000; Kondolf et al. 2008). Furthermore, salmon populations are subject to variable outmigration success and adult return rates, both of which are impacted by broad-scale climactic and environmental factors outside of restoration influence (Greene et al. 2005; David et al. 2014). Response to restoration processes may be difficult to detect using fish catch data alone as such measurements cannot effectively capture how fish take advantage of increased prey abundance and expansion in available habitat (Simenstad & Cordell 2000).

In light of these challenges, the Nisqually Monitoring Framework identifies restoration performance criteria in terms of opportunity potential (habitat accessibility), foraging capacity (conditions for prey resources and salmonid growth), and realized function (measureable foraging or growth response; Simenstad & Cordell 2000; Ellings 2011). In this study, we specifically addressed the functionality of the restored delta in terms of change in opportunity potential using metrics that are associated with the ability for juvenile salmon to access and benefit from restored habitat (Simenstad & Cordell 2000). Such metrics include surface elevation and water level, which can be used to model the frequency and duration of inundation. Other parameters include channel area, channel depth, water temperature, temporal variation in channel availability, and landscape connectivity. We examined these parameters along with accompanying fish catch surveys for natural-origin Chinook, hatchery-origin Chinook, and natural-origin chum salmon to quantify post-restoration increases in opportunity potential on the delta. The integration of physical parameters and proportional presence of salmon offered valuable insight into broad-scale changes in habitat availability resulting from the restoration of a large river delta.

Methods

Study Area

The Nisqually Glacier on Mount Rainier forms the headwaters of the Nisqually River, the largest river in the southern Puget Sound, Washington, U.S.A. The river flows to the Nisqually Delta (47.08°N, 122.70°W), which is comprised of diverse habitat types including tidally influenced forested riverine, emergent forest transition, estuary emergent marsh, delta mudflat, and nearshore habitats, all of which contribute to the survival of outmigrating salmon. Since 1996, the Tribe and Refuge have restored approximately 365 ha of estuary habitat to tidal flow through multiple dike removal projects: 4 ha in 1996 (Pilot), 13 ha in 2002 (Phase I), 41 ha in 2006 (Phase II), and 308 ha on the Refuge in 2009 (Restored Refuge). Several channels were not directly affected by the restoration because they had not previously been diked, including McAllister Creek on the west side of the Refuge, Animal Slough on the northeast side of the Refuge, and the northern branch of Red Salmon Slough on the east side of the Nisqually River (Fig. 1).

To monitor changes in tidal inundation and salmon densities across the delta, our primary study sites included two restored channels—2006 Restored and 2009 Restored—and two previously undisturbed salt marsh reference channels (Animal Slough, hereafter "Nisqually Reference," and Red Salmon Reference). The 2006 Restored and Nisqually Reference sites were brackish marshes with large freshwater inputs. They contained a combination of both fresh and salt marsh vegetation, whereas the Red Salmon Reference site included vegetation common to high and mid salt marshes of the Pacific Northwest (Belleveau et al. 2015). The Restored Refuge sites (including 2009 Restored) were primarily influenced by seawater and represented marine habitats. Prior to the 2009 restoration, the Restored Refuge was disconnected from tidal flow and the fallow freshwater fields became increasingly dominated by the invasive reed canary grass (*Phalaris arundinacea*). With restoration to tidal flow, much of the freshwater vegetation and invasive reed canary grass died back, and as of 2015, most

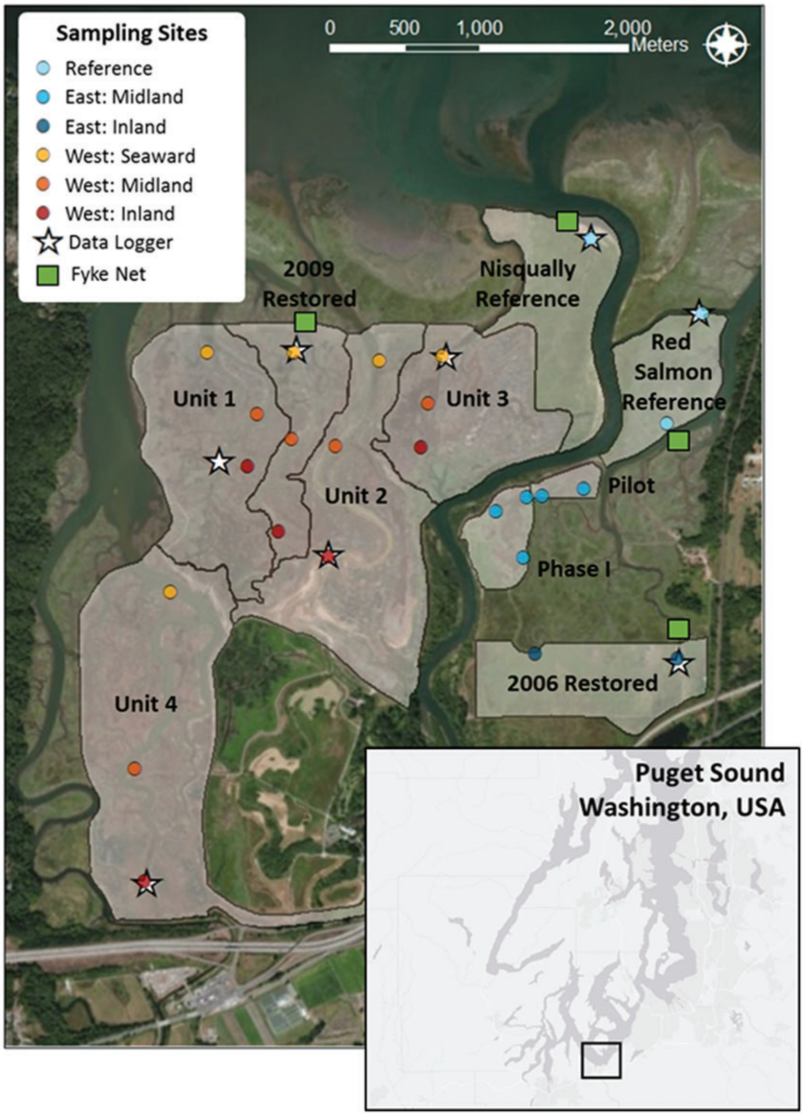

Figure 1. Map of all sampling locations including sampling units, data loggers, channel cross sections, and fyke netting sites on the Nisqually River Delta. Data logger locations are marked with a star. Channel cross section locations are marked with circles color coded by distance from the delta. Fyke netting locations are marked with green squares.

restored sites on the Refuge were surrounded by mudflats and newly colonizing salt marsh vegetation.

Data Collection

Channel Morphology. To document historic channel morphology, we used a georeferenced, 1878 Puget Sound River T-sheet. We examined pre- and post-restoration conditions with false color infrared aerial photographs flown in summer 2005 and 2011 at mid day low tide (<0 m) during cloud-free days (Bergman Photographic Services Inc., Portland, OR, U.S.A.). We hand-digitized channel morphology on resulting georeferenced imagery with ArcGIS software (ESRI Inc., Redlands, CA, U.S.A.). We digitized channels with a width ≥15 m estimated at bank-full (using vegetation guidelines) as polygon features, whereas channels less than 15 m were digitized as polyline features at a scale between 1:400 and 1:1,000. We also digitized fine channels as linear features as far as image resolution would allow. We used LiDAR imagery flown in winter 2011 (Watershed Sciences Inc., Portland, OR, U.S.A.) to help distinguish channel features without vegetation. All digitized channels within the subsided Restored Refuge were classified separately to characterize the remnant network, and to delineate areas subject to ponding water during low tide.

To supplement channel digitization, we surveyed channel cross sections at sites on the east and west sides of the Nisqually River annually from 2009 to 2014 (Fig. 1). Eastern sites included at least two measurements each at Pilot, Phase I, 2006 Restored, and Red Salmon Reference. We chose sampling locations at these sites such that one cross section was always closer to the delta (seaward), whereas the other was further inland. For western sites, we sampled six channels including a north (seaward), middle (midland), and south (inland) site for each channel. We measured cross section elevations at 0.5 m intervals along established transects using a real-time kinematic global positioning system (RTK GPS; Leica Viva SmartRover, Leica Geosystems, Heerbrugg, Switzerland) with an estimated accuracy of ±3 cm.

Water Quality. We installed Solinst LTC data loggers (Solinst, Georgetown, Ontario, Canada) at eight locations (Fig. 1) to monitor water quality across the delta. We deployed data loggers at fixed locations, with each sensor suspended approximately 15 cm above the sediment surface. Data loggers measured water level (m), temperature (°C), and specific conductance (μS/cm) at pre-programmed 6 or 15 minutes intervals.

Tidal Inundation and Habitat Connectivity. We modeled landscape connectivity and inundation for pre- and post-restoration conditions using a combination of bathymetry, topographic (LiDAR) and water level data. Due to the lack of comparable pre-restoration elevation and water level datasets, we characterized pre-restoration inundation and connectivity conditions in the estuary using post-restoration data clipped at the boundaries of levees that prevented circulation prior to restoration in 1996 and 2006.

We conducted bathymetric surveys in winter 2009 and 2011 using a boat-mounted 234 kHz phase-differencing interferometer (swath sonar) across large portions of the estuary, Nisqually River and McAllister Creek channels, and tidal flats. In 2009, 2010, and 2012, we collected 200/50 kHz single-beam sonar data in Phase I tidal channels and areas lacking coverage following swath sonar and LiDAR surveys. These sonar datasets range in vertical certainty between 0.1 and 0.2 m. Airborne topographic LiDAR data were collected during low tide (<0 m) on 3 January 2011 at an altitude of 1,500 m above ground level (Watershed Sciences Inc., Portland, OR, U.S.A.). We validated LiDAR data to ± 3 cm within vegetated tidal marsh sites with an RTK-GPS unit in summer 2010 and 2012.

Salmon Distribution. We used coarse- and fine-scale fish sampling to measure juvenile salmon distribution throughout the estuary. To conduct coarse-scale fish sampling, we used a standard Puget Sound beach seine measuring 37 × 2 m with a 2.4 m bag of 6 mm mesh, set by boat and hauled to shore by hand. We sampled 30 sites between mid to high tide, encompassing freshwater, forested riverine tidal, emergent forested transition, estuary emergent marsh, delta mudflat, and near shore habitat types. Pre-restoration beach seine sampling events occurred twice monthly throughout the delta from February through October 2003–2006. Post-restoration sampling events occurred monthly February through October 2010–2012.

For fine-scale fish sampling, we used fyke nets measuring 280 cm deep with 3 mm mesh and a live trap in the center of the net. We set fyke traps across the channel at a falling high tide on a neap tide series, removing the net after 4 hours or once the channel drained (whichever came first). Tidal channels within restored and reference marshes were typically trapped once or twice a month from April to July and occasionally in March and August for pre-restoration (2003–2006) and post restoration (2010–2012) sampling. We did not sample restoration sites until hydrologic connectivity was reestablished.

We processed all captured fish following standard procedures (Ellings & Hodgson 2007). We enumerated the total catch and measured fork length to the nearest millimeter for 10 individuals of each species. Chinook salmon released by Nisqually hatcheries are marked with and adipose fin clip and/or an implanted coded wire tag. The average mark/tag rate for Nisqually hatchery Chinook is around 95% (RMIS 2003–2012); thus all unmarked and untagged Chinook were presumed to be offspring of naturally spawning parents (natural origin) though a small portion of them may have been unmarked hatchery fish.

Data Analysis

Channel Morphology. We calculated channel area, length, and perimeter metrics for each slough and for the entire delta (Calculate Geometry tool, ArcGIS). We defined channel sinuosity (K) as the ratio of the sinuous length of the channel segment divided by the straight line length, where values closer to 1 approximate a straight channel, and larger values represent a more meandering channel. Due to differences in resolution between the historic 1878 T-sheet and the 2005 and 2011 aerial photographs, only major channels (≥3rd order or ≥15 m in width) were compared between pre- and post-restoration channel metrics. We performed a paired t test to compare pre- and post-restoration measurements of major and minor channel area, length, perimeter, and sinuosity as response variables. All statistical analyses were conducted using R version 3.2.0 (R Core Development Team 2014).

We conducted a linear regression analysis with channel elevation (i.e. mean channel depth), yearly rate of elevation change, and entrenchment ratio as our response variables (Appendix S1). Entrenchment represents a measurement of the depth of a channel in relation to its uppermost banks, with greater entrenchment ratios representing more disconnect from adjacent floodplains (Rosgen & Silvey 1996). The entrenchment ratio was defined as:

$$\frac{E_{mean} - E_{min}}{E_{max} - E_{min}}$$

where E_{mean} is the mean channel elevation, E_{min} is the minimum channel elevation, and E_{max} is the maximum channel elevation. We used year (2009–2014), location (east, west), site (units 1–4, 2009 Restored, Nisqually Reference, Pilot, Phase I, 2006 Restored, Red Salmon Reference), and offshore distance (inland, midland, seaward, reference) as predictor variables. We separated sites on the east and west sides of the river for analysis because they had different elevations and restoration histories, and we ran a separate linear regression analysis for restored and reference sites.

Table 1. Channel metrics derived from ArcGIS digitization of historical (approximately 1878), pre-restoration (2005), and post-restoration (2011) conditions. Delta-wide measurements were obtained via channel digitization data for the entire Nisqually River Delta. Restored sites represent channel metrics for study areas only (units 1–4, 2009 Restored, Nisqually Reference, 2006 Restored, and Red Salmon Reference).

Habitat and Channel Metric	*Historic (Approximately 1878)*	*Pre-Restoration (2005)*	*Post-Restoration (2011)*
Delta-wide			
Major (>3rd order) channel area (m^2)	1,624,176	1,599,070	2,272,798
Major (>3rd order) channel length (m)	33,998	37,091	85,655
Major (>3rd order) channel edge length (m)	70,579	76,570	173,285
Major (>3rd order) mean channel sinuosity	1.62	2.71	4.2
Minor (<3rd order) channel area (m^2)	N/A	31,018	97,373
Minor (<3rd order) channel length (m)	N/A	31,018	97,373
Minor (<3rd order) channel edge length (m)	N/A	62,036	194,746
Minor (<3rd order) mean channel sinuosity (K)	N/A	1.99	2.09
Restored sites			
Major (>3rd order) channel area (m^2)	427,259	77,710	528,908
Major (>3rd order) channel length (m)	16,970	5,708	38,698
Major (>3rd order) channel edge length (m)	35,102	13,759	81,148
Major (>3rd order) mean channel sinuosity	1.5	2.77	2.79
Minor (<3rd order) channel area (m^2)	N/A	9,040	57,391
Minor (<3rd order) channel length (m)	N/A	9,040	57,391
Minor (<3rd order) channel edge length (m)	N/A	18,080	114,782
Minor (<3rd order) mean channel sinuosity (K)	N/A	2.08	2.22

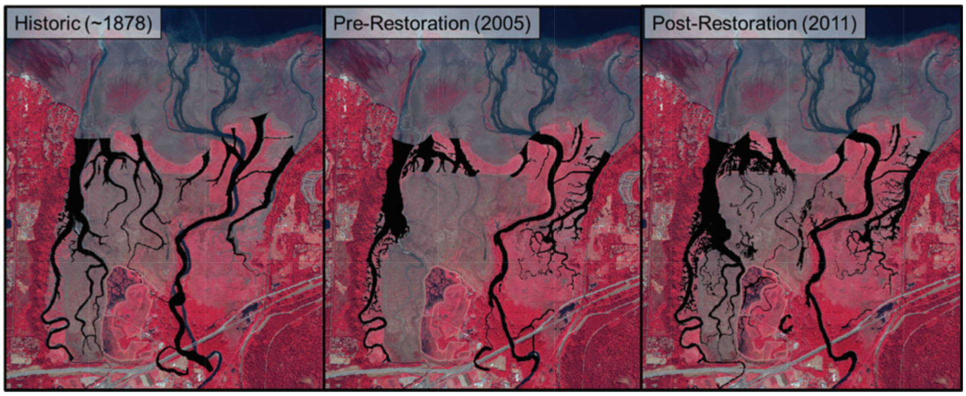

Figure 2. Digitized major channel morphology for historic (approximately 1878), pre-restoration (2005), and post-restoration (2011) tidal channels on the Nisqually River Delta. We performed digitization using ArcGIS 10.2.2 software (ESRI Inc.). Bergman Photographic Services Inc. flew base map imagery in July 2014.

Water Quality. We downloaded water level, temperature, and salinity data seasonally, and quality checked each logger annually to safeguard against error. We examined each dataset to ensure all values were within a biologically realistic range (i.e. $-15°C < T < 50°C$ for temperature and $0\ \mu S/cm < SPC < 50{,}000\ \mu S/cm$ for specific conductance), and any outlying values were excluded from analysis. We calculated salinity from specific conductance based on methods in UNESCO (1983).

To determine post-restoration changes in water quality variables, we conducted a linear regression analysis with temperature and salinity aggregated by week as response variables and year, channel, and offshore distance as predictor variables (Appendix S1). We used season as a covariate to account for harmonic, temporal variation in temperature and salinity, and data gaps that occurred when instruments malfunctioned or were lost. We ran a separate linear regression analysis to compare temperature and salinity values for restored sites to reference sites, although due to differences in factors such as vegetation type and location on the delta, reference sites could not be used as ideal controls for a paired study.

Tidal Inundation and Habitat Connectivity. To quantify habitat accessibility for juvenile salmon, we modeled tidal inundation across the delta with measured water levels, derived tidal datums, and a detailed digital elevation model. We modeled tidal connectivity pathways and inundation frequencies for pre- and post-restoration conditions with a connectivity analysis algorithm in ArcGIS that classified surface elevation for regions that were hydrologically connected. Inundation was calculated for every 1-cm interval of the tidal range with connectivity to five tidal datums; mean lower low water (MLLW), mean low water

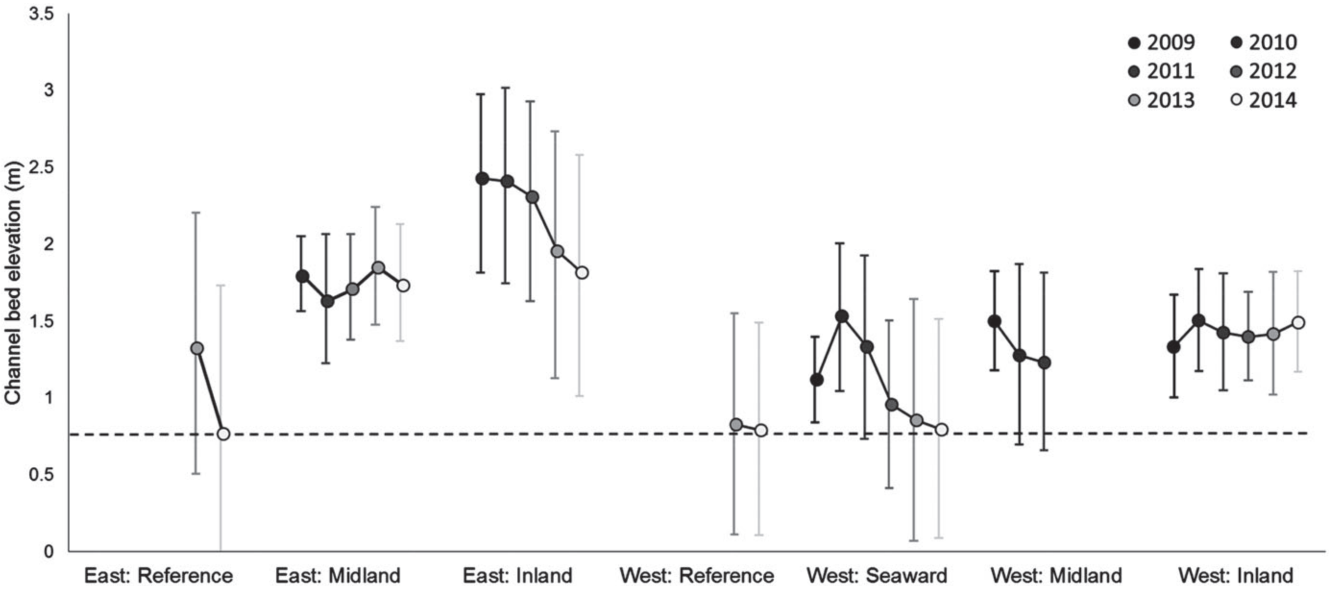

Figure 3. Mean channel elevations through time (2009–2014 left to right) by distance from the Nisqually River Delta (i.e. seaward, midland, inland, and reference). Due to their differing restoration histories, channel cross sectional data were split up into east and west sites. Delta sites on the Refuge and 2006 Restored on the east side of the river are approaching reference channel elevations through time, whereas inland site elevations appear to hold constant ($p < 0.001$). Error bars represent standard deviation in channel elevation. The dashed line shows the mean reference site channel elevation.

(MLW), mean tide level (MTL), mean high water (MHW), and mean higher high water (MHHW).

When connected areas exceeded a threshold water depth of 0.4 m, we recorded them as available juvenile Chinook migratory paths based on a passive integrated transponder (PIT) tag study that found that 94% of total detections of juvenile Chinook occurred when water depth was ≥0.4 m (Hering et al. 2010). We mapped the connected pathways between the Nisqually River and six study sites throughout the delta (reference sites: Red Salmon Reference, Nisqually Reference, and McAllister Creek; restored sites: Phase I, 2006 Restored, and 2009 Restored), and tabulated distances for pre- and post-restoration conditions for each tidal datum. To characterize connectivity, we also calculated tortuosity as the ratio derived from the straight-line distance between the river and our study sites divided by the connectivity pathway length to each site for each tidal datum and pre- versus post-restoration conditions.

Salmon Distribution. To measure natural and hatchery-origin Chinook and chum salmon channel use throughout the rearing season, we calculated a site-specific index of fish presence for each year. This index (proportional presence) was defined for a given year as:

$$\frac{p}{s-a}$$

where p is the number of months in the year in which a species was documented as present at a fyke trap site, s is the total number of months sampled at the site in that year, and a is the number of months in which the species was absent both at the fyke trap site and in estuary-wide beach seining. Proportional presence values of 1 represent a high degree of site use when fish are present in the delta, whereas values close to 0 indicate low site use. We summarized beach seine catch data as the catch per set (CPS), averaged by month across all sites. We did not adjust site-specific catch data for trap efficiency, area trapped, or distance from the mouth of the river.

Results

Channel Morphology

In restored areas, major and minor channel area, length, and edge differed between pre-restoration and post-restoration conditions, whereas sinuosity remained the same (Table 1; Fig. 2). As of 2011, major channel area increased 42% delta-wide and 580% in restored areas from 2005 pre-restoration conditions ($df = 7$, $t = -2.650$, $p = 0.033$). Major channel length increased 131% delta-wide and 579% in restored areas ($df = 7$, $t = -4.081$, $p = 0.005$), and major channel edge increased 126% delta-wide and 490% in restored areas ($df = 7$, $t = -3.763$, $p = 0.007$). Minor channel area, length, and edge increased 214% delta-wide and 534% in restored areas from pre-restoration conditions ($df = 7$, $t = -3.542$, $p = 0.009$). There was no statistically significant change detected in major or minor channel sinuosity ($df = 7$, $t = -1.225$, $p = 0.345$; $df = 7$, $t = -1.863$, $p = 0.203$). Historical and post-restoration channel areas did not differ; however, measured major channel lengths and edges were greater post-restoration due to better photographic resolution ($df = 7$, $t = -4.714$, $p < 0.002$).

Cross section data showed that restored channels across the delta grew deeper through time (means ± SE: -6.4 ± 0.5 cm/year), while reference sites remained relatively stable (1.2 ± 0.7 cm/year; $p < 0.001$). When

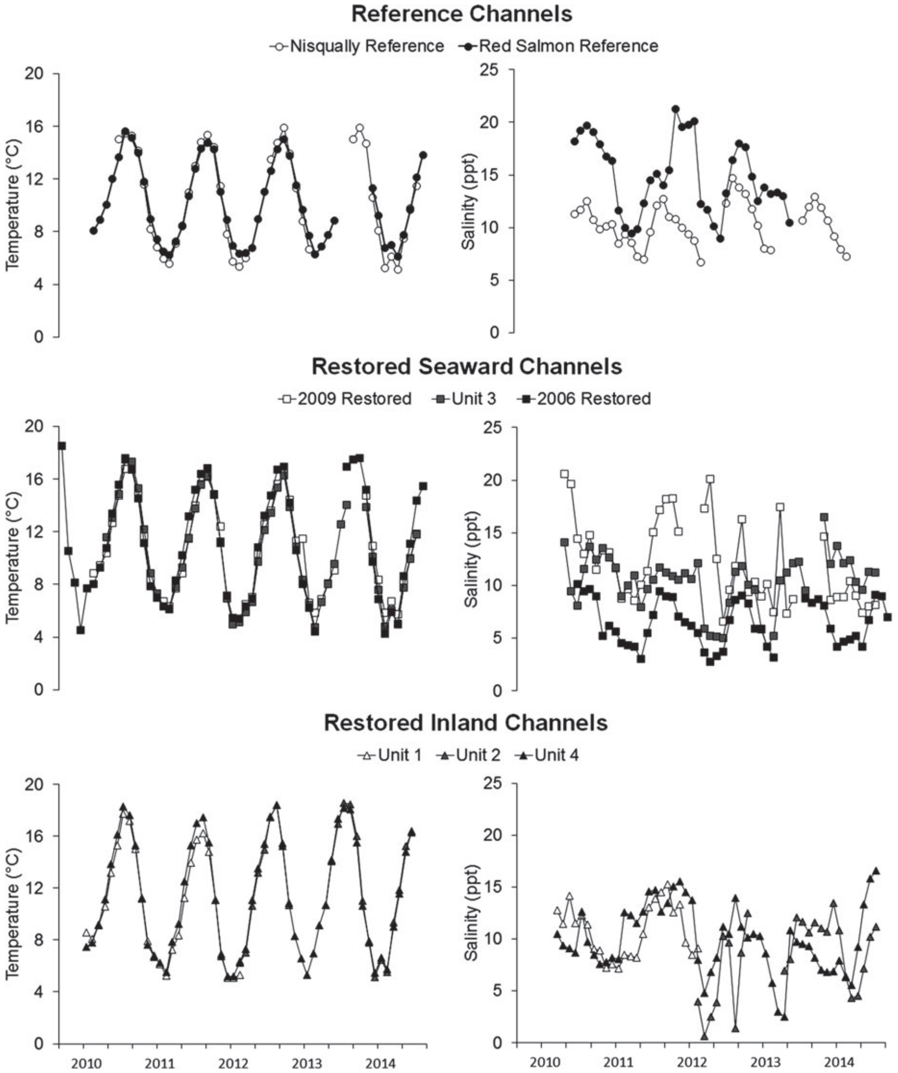

Figure 4. Monthly mean water temperatures and salinities by channel. Plots are split up by distance from the Nisqually River Delta to demonstrate how seasonal variability in temperature and salinity differs between reference and restored sites. Months for which only partial data exist are excluded.

we compared channels on either side of the river, we found that channels to the east were higher in elevation (east = 1.8 ± 0.8 m, west = 1.2 ± 0.6 m; $p < 0.001$) and experienced less change through time (east = -1.6 ± 0.5 cm/year, west = -7.4 ± 0.6 cm/year; $p < 0.001$) than channels on the west side. Channel depth remained fairly constant, except at the 2006 Restored site where the channel was 25% deeper ($p < 0.001$; Fig. 3) and 26% more entrenched ($p = 0.008$). For western sites, cross sections near the channel outlets (seaward) and mid-channel (midland) grew deeper, while upstream (inland) channels appeared to be relatively stable, especially for lower-elevation channels such as unit 1 and unit 4 Sloughs ($p < 0.001$; Fig. 3).

Water Quality

Water temperatures decreased roughly 0.2°C/year across the delta post-restoration from 2009 to 2014 ($p < 0.001$), and changes in temperature were site-specific. In general, restored sites that were seaward (such as 2009 Restored, unit 3, and 2006 Restored) experienced the greatest decreases in temperature, while reference sites (Nisqually and Red Salmon Reference) maintained a relatively constant temperature ($p < 0.001$; Fig. 4). Inland restored sites (unit 1, unit 2, and unit 4) were warmer on average and experienced greater temperature fluctuations throughout the year (means ± SD: reference = 10.3 ± 4.2°C, seaward = 10.5 ± 4.8°C, inland = 11.6 ± 5.5°C; $p < 0.001$; Fig. 4).

Changes in salinity occurred on the delta through time, and were also site-specific ($p < 0.001$; Fig. 4). Overall, salinity decreased at a rate of 0.1 ppt/year ($p < 0.001$). These decreases were least notable for restored inland sites (unit 1, unit 2, and unit 4), which also had the lowest salinity levels (means ± SD: reference = 12.3 ± 8.0 ppt, seaward = 11.2 ± 6.9 ppt, inland = 8.7 ± 5.8 ppt; $p < 0.001$). Reference sites had salinity levels 3 ppt greater than the restored sites,

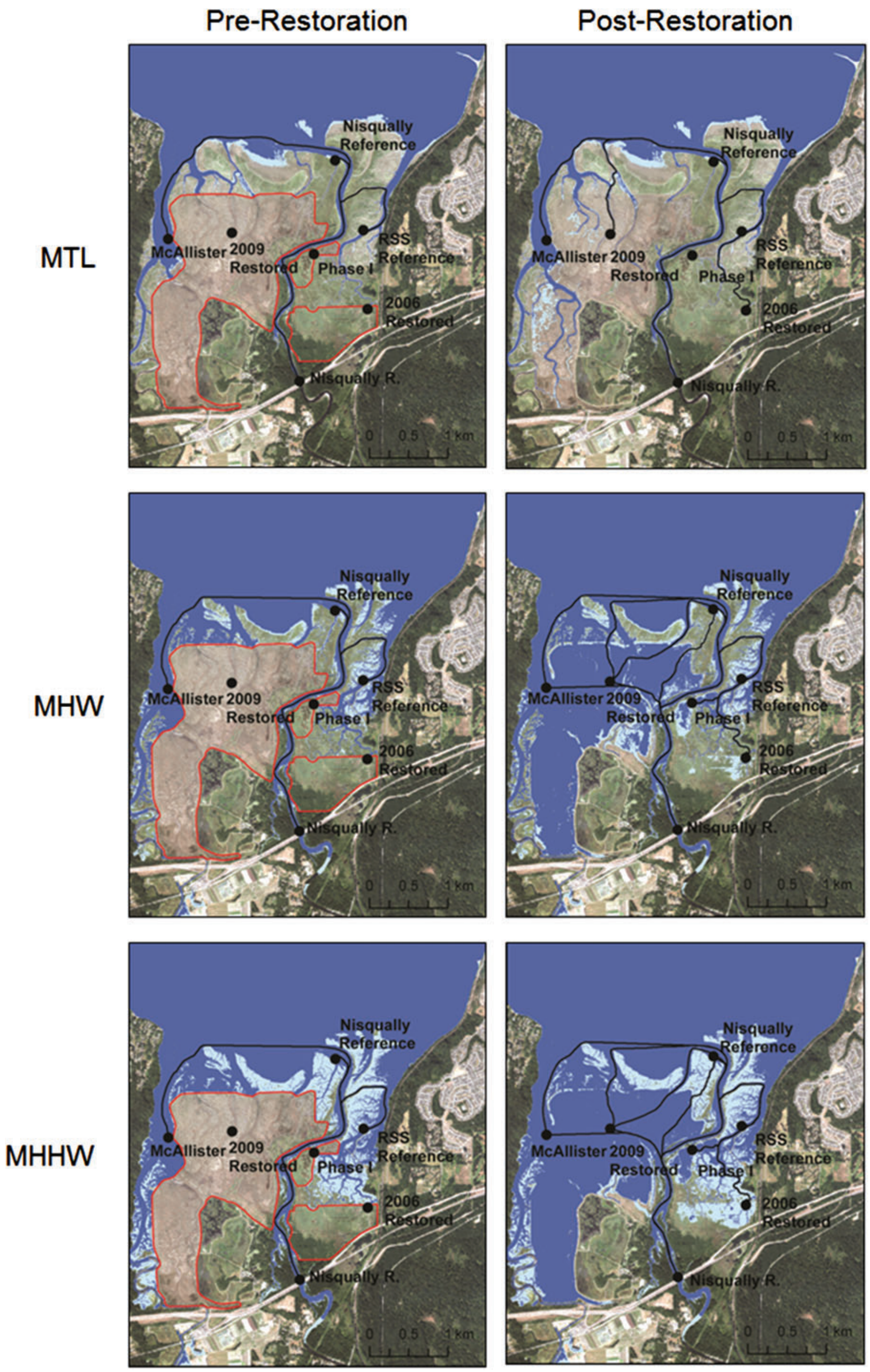

Figure 5. Inundation and habitat connectivity model by tidal datum for pre- and post-restoration conditions. The map shows connected paths (≥0.4 m depth) for reference (Nisqually Reference, Red Salmon Reference, and McAllister Creek) and restored (2006 Restored, 2009 Restored, and Phase I) sites.

and experienced broader fluctuations in salinity ($p < 0.001$; Fig. 4), even though there was no significant yearly change in salinity at reference sites when season was adjusted for.

Tidal Inundation and Habitat Connectivity

Landscape connectivity increased throughout the delta with dike removal (Fig. 5). Following restoration, the percent of time the estuary supported access and provided suitable habitat for juvenile Chinook during the outmigration season increased from approximately 30 to approximately 75%. McAllister Creek was the only reference site that maintained connectivity at all tidal levels both pre- and post-restoration, with access by juvenile Chinook available 100% of the time throughout the outmigration season. Following restoration, tortuosity ratios increased

Table 2. Number of connected channels (No.), fish path tortuosity (TR), and site inundation frequency (%) for pre- and post-restoration time periods during MLLW, MLW, MTL, MHW, and MHHW. McAllister Creek, Red Salmon Reference, and Nisually Reference represent reference sites. Phase I, 2006 Restored, and 2009 Restored represent restored sites.

	MLLW				*MLW*				*MTL*				*MHW*				*MHHW*				*Inundation*	
	Pre		*Post*		*Pre*		*Post*		*Pre*		*Post*		*Pre*		*Post*		*Pre*		*Post*		*Pre*	*Post*
Site	*No.*	*TR*	*No.*	*TR*	*No.*	*TR*	*No.*	*TR*	*No.*	*TR*	*No.*	*TR*	*No.*	*TR*	*No.*	*TR*	*No.*	*TR*	*No.*	*TR*	*%*	*%*
2009 Restored (Madrone)	0	0	0	0	0	0	0	0	0	0	1	0.31	0	0	3	0.82	0	0	3	0.84	0	0.55
2006 Restored (Phase II)	0	0	0	0	0	0	0	0	0	0	1	0.21	0	0	1	0.21	0	0	1	0.21	0	0.52
Phase I	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0.32	0	0	1	0.32	0	0.41
Nisqually Reference	0	0	0	0	0	0	0	0	1	0.65	1	0.65	1	0.66	2	0.66	1	0.66	2	0.66	0.42	0.67
Red Salmon Reference	0	0	0	0	0	0	0	0	1	0.50	1	0.50	1	0.56	2	0.61	1	0.56	2	0.63	NA	0.47
McAllister Creek	1	0.3	1	0.25	1	0.3	1	0.28	1	0.35	1	0.35	1	0.36	2	0.74	1	0.36	2	0.74	0.78	0.78

from 0.25 to 0.36 with the incoming tide as the distance from the river to our sampling sites decreased. Post-restoration connectivity to the McAllister Creek study site also increased with two additional pathways at higher tides. The tortuosity ratio increased to 0.78 during MHHW.

The Nisqually Reference site was directly connected to the main stem of the river. Although the slough was only accessible to juvenile salmon at or above MTL during both pre- and post-restoration, it was accessible 65% of the time during the outmigration season. Tortuosity ratios were the highest at this site both pre- and post-restoration (0.66 at MTL, MHW, and MHHW). Restoration also increased the number of pathways to Nisqually Reference, with a second connection accessible through the upper reaches of the slough at MHHW.

The Red Salmon Reference site, accessible from the river via a distributary channel to Red Salmon Slough, was not accessible below MTL. The number of paths to the slough did not increase with increasing tidal height or restoration, nor did the tortuosity ratio (Table 2).

Connectivity to the river at or above MTL was expected to increase at all three restoration sites (Fig. 5). Similar to the Red Salmon Reference site, only one new pathway linked the river to the 2006 Restored site at MTL and to Phase I at MHW. Tortuosity ratios to these restoration sties were low, ranging 0.32 for Phase I, and 0.21 for 2006 Restored. In contrast, the number of pathways from the river to 2009 Restored increased from one channel at MTL to three at MHHW. Tortuosity ratios also increased from 0.31 to 0.84 with increasing tidal height.

Salmon Distribution

Fyke net sampling indicated that natural-origin Chinook, hatchery-origin Chinook, and natural-origin chum were all captured in restored channels during the first sampling season following restoration. The average post-restoration (2010–2012) proportional presence of natural-origin Chinook was highest at the Nisqually Reference site at 93% (Fig. 6). Proportional presence for natural-origin Chinook was 62% at Red Salmon Reference, 80% at 2009 Restoration, and 47% at 2006 Restoration (Fig. 6). The average post-restoration proportional presence of hatchery-origin Chinook was highest at the Nisqually Reference and 2009 Restoration sites (89% at both). Proportional presence of hatchery-origin Chinook was 67% at Red Salmon Reference and 32% at the 2006 Restoration site (Fig. 6).

For natural-origin chum, the average proportional presence was higher at Nisqually and Red Salmon reference sites (87 and 68%) than at the 2006 and 2009 Restoration sites (50 and 42%, respectively; Fig. 6). Chum salmon use of the 2006 Restoration site was not consistent, with proportional presence ranging from 0 to 75% depending on the year (Fig. 6). The consistently high proportional presence of Chinook and chum salmon at the Nisqually reference site (Fig. 7) is an indication of its direct connectivity with the main stem Nisqually River (Fig. 5) as expressed through a combination of relatively high inundation frequency and tortuosity ratios (Table 2).

Discussion

Applying a combination of aerial imagery, elevation data, physical monitoring, and tidal inundation modeling, we measured distinct, post-restoration increases in opportunity potential and habitat availability for outmigrating juvenile salmon on the Nisqually River Delta. We observed rapid and substantial increase (roughly 45%) in the availability of major and minor sloughs across the delta. An analysis of channel morphology showed that major channels increased in overall area 42% and minor channel area more than tripled post-restoration. Increases in channel area were accompanied by an augmentation of existing major channel length into the restoration zone by up to 500%. Most metrics for post-restoration major channel morphology also showed significant increases from historic to post-restoration conditions; however, these differences were more likely due to the lower resolution of the 1878T-sheet used to digitize historic channels. The more notable increase in channel edge (i.e. perimeter) as opposed to overall channel area supported this assumption, as did a visual assessment of the digitized maps themselves.

In addition to a considerable growth in overall channel area, major channel depth increased at all restoration sites from 2009 to 2014. Channels grew deeper at restored sites on the Refuge at a rate of roughly 6 cm/year, with channel erosion occurring more quickly in the years immediately post-restoration (i.e. 2010 and 2011). Channel erosion was most notable at seaward delta sites, with some sites exhibiting increases in depth greater than 1 m.

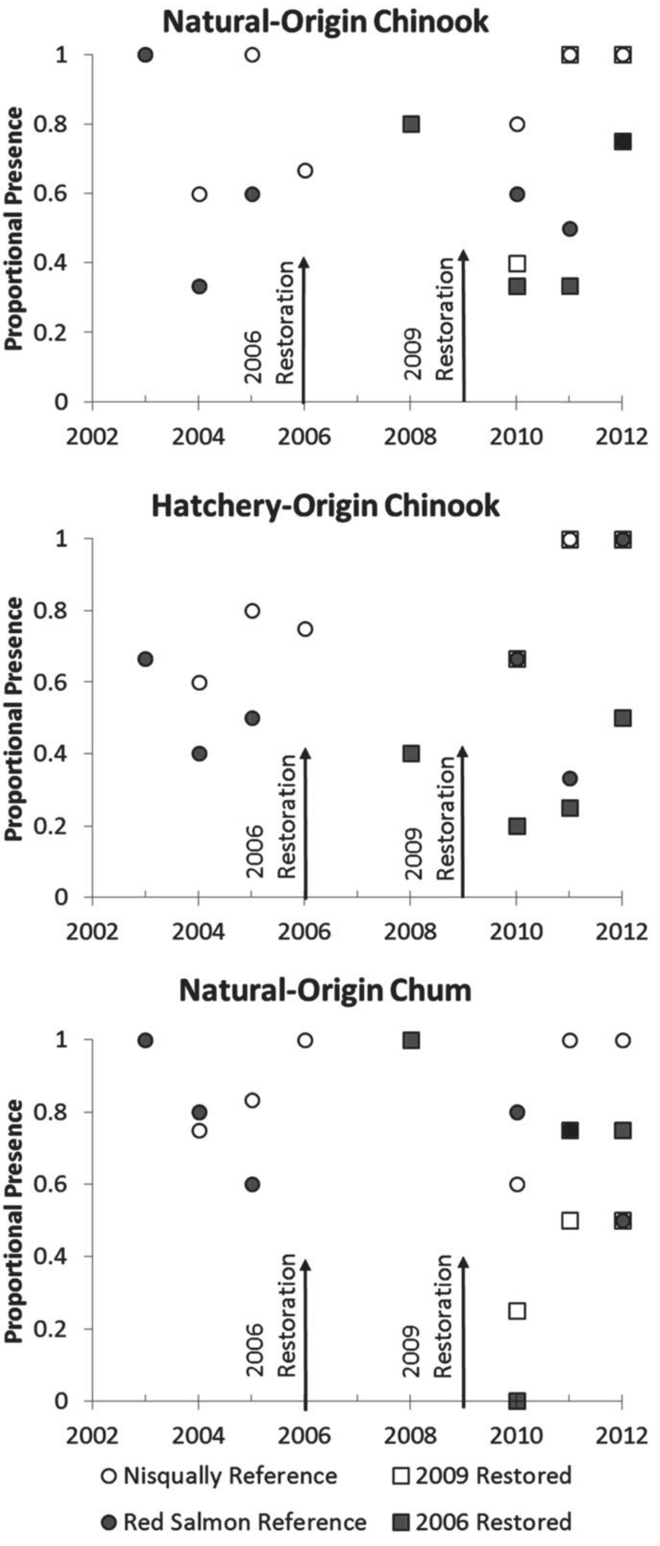

Figure 6. Proportional salmon presence (i.e. the number of months when juvenile salmon were caught in fyke traps divided by the number of months that the channel was sampled, excluding months when neither estuary-wide beach seining nor fyke trapping at the site indicated that a species was present in the estuary) for all sampling periods between 2003 and 2012.

The differences we observed with channel incision near the seaward marsh edge and channel aggradation farther inland were likely due to early sediment redistribution within the restored area. This sediment redistribution promoted accretion at higher elevations in channels that experienced lower current velocities, and erosion of lower elevation channels that experienced higher ebb current velocities associated with the renewed tidal prism, particularly near the former outer dike where flow was constrained. We expect that channel morphology will continue to change as sediment is redistributed across the restored delta and as additional sediment is delivered from the river and nearby tidal flats. At restored sites on the Refuge, sediment deposition is occurring on the adjacent inland mudflats at a rate of roughly 2.5 cm/year (2010–2014; USGS unpublished data), but the timing and rate at which channels will reach an equilibrium with the new tidal prism and sediment supply remain uncertain.

The restoration not only reconnected tidal channels but also brought about shifts in water quality, including temperature and salinity, both of which heavily influence salmon bioenergetics (Brett et al. 1969; Clarke et al. 1981; Morgan & Iwama 1991; David et al. 2014). Outmigrating juvenile salmon have an optimal temperature range of 12–15°C dependent upon salinity (Clarke & Shelbourn 1985), highlighting the importance of monitoring temperature fluctuations in restored tidal channels. Overall, water temperatures at restored sites decreased roughly 0.154°C annually across the delta from 2009 to 2014, whereas reference site water temperatures remained relatively stable. The decrease in water temperature at restored sites was most likely due to the gradual erosion of the restoration channels, because deeper channels tend to have lower water temperatures, although colder freshwater from adjacent Nisqually River and McAllister Creek may have also contributed to this decrease. Temperatures remained up to 1°C higher at inland sites than at seaward or reference sites as a result of their shallower depth and lack of emergent marsh vegetation. As vegetative colonizes across the delta and channels continue to incise, water temperatures are expected to approach levels similar to reference sites, though this may not be the case at inland channels where sediment deposition is occurring (Rutherford et al. 1997; Johnson 2004).

Likewise, salinity levels, which decreased at a mean rate of 0.086 ppt/year post-restoration, are expected to approach values similar to those at reference sites as channel depth increases and tidal inundation becomes a more dominant force compared to river outflow (Vaz et al. 2005; Vaz & Dias 2008). As of 2014, salinities at seaward sites were roughly 1 ppt lower than at reference sites, and salinities at inland sites were roughly 4 ppt lower than at reference sites. Inland sites may also become less saline as sediment deposition occurs and inland tidal channels become less prone to tidal inundation; however, given the associated decreases in habitat accessibility inland, water quality parameters at these locations may be less crucial to salmonid opportunity potential than at the more easily accessible delta sites.

The overall growth in major and minor tidal channel area across the Nisqually River Delta cannot be considered an increase in opportunity potential without addressing its accessibility to outmigrating juvenile salmon. Our tidal inundation

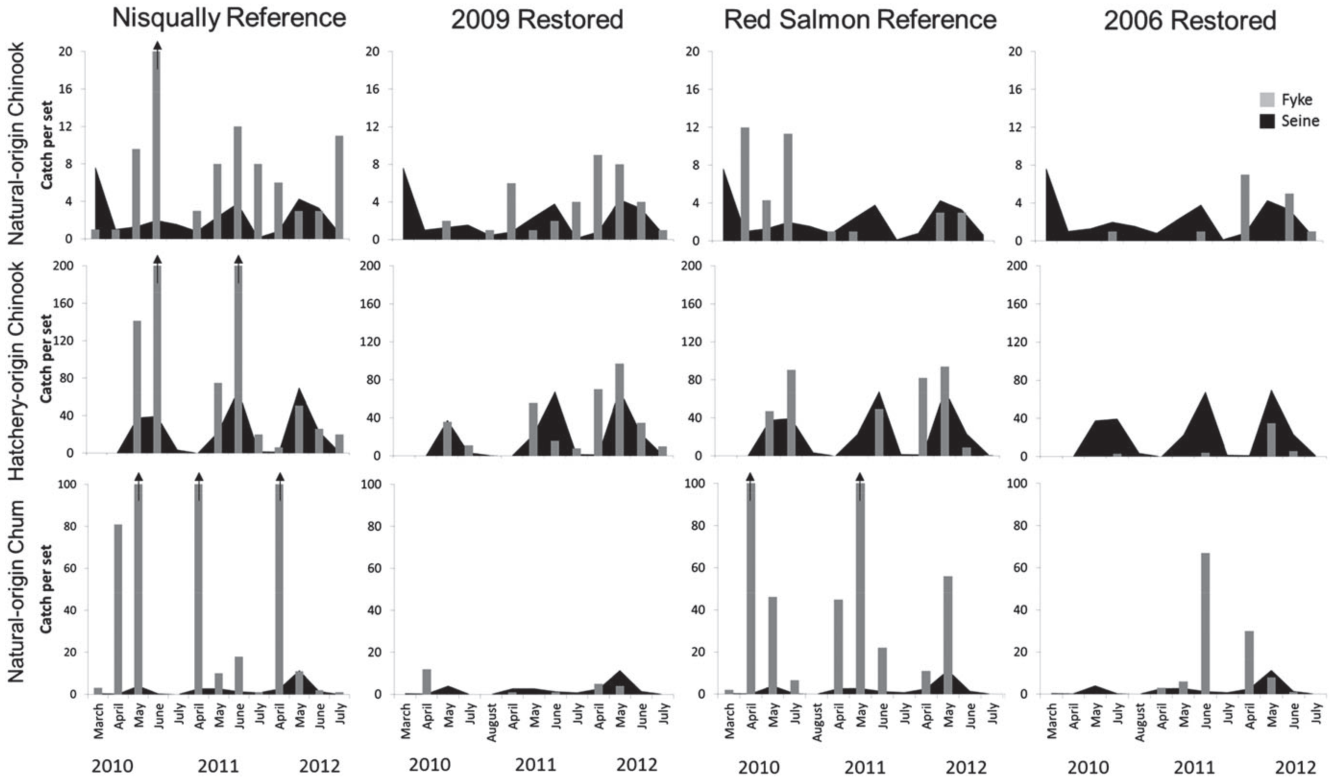

Figure 7. Post-restoration 2010–2012 monthly average Chinook and chum CPS for each fyke trap (gray bars) overlaid on average beach seine CPS across all estuary sites (shaded area). Months shown are those in which both types of sampling occurred. Arrows indicate observed abundances exceeding axis limits. Catches have not been adjusted for trap efficiencies, area trapped, or distance from the mouth of the Nisqually River.

model estimated that the amount of time tidal channels were accessible to salmon increased from 30 to 75% post-restoration. All the restoration sites for which habitat connectivity was analyzed experienced an increase in the number of available paths and tortuosity ratios pre- versus post-restoration, but none of the restored sites were accessible below MTL. Our 2009 Restored site was the most readily accessible out of any of the restored sites, with three paths available at MHW and a tortuosity ratio of 0.82. Phase I, which is the oldest restoration site, was the least accessible to outmigrating juvenile salmon. This site was only accessible above MHW with a single pathway and a low tortuosity ratio of 0.32. None of the reference sites had large increases in accessibility, although an additional pathway opened up for all three sites above MHW. Restoration doubled the tortuosity ratio for McAllister Creek (the farthest reference site from the mouth of the river), and slightly increased the tortuosity ratio for our Red Salmon Reference site at MHW and MHHW.

Salmon catch indicated that smolts were using this newly accessible habitat as early as 1 year post-restoration. Such immediate evidence of habitat use has been observed in previous restoration efforts in North America (Burdick et al. 1996). Natural-origin Chinook, the species most dependent on estuarine rearing habitat, were broadly distributed across the delta in space and time. Studies have demonstrated that natural-origin Chinook exhibit prolonged residencies in the delta (Lind-Null et al. 2008), suggesting that these individuals are more likely to take advantage of increased rearing opportunities following restoration. As natural populations recover and increase in density, their geographic distribution should expand across a connectivity gradient to more fully utilize available habitat. The importance of site connectivity was demonstrated by the consistent use of the Nisqually Reference site by all three types of salmon. The interaction between habitat capacity, density dependence, and salmon distribution across a connectivity gradient is a priority for future juvenile salmon research in restored estuaries.

Although certain opportunity metrics at restored sites such as channel depth, entrenchment, and water quality are not yet comparable to reference sites, the rapid and broad-scale increase in overall available habitat along with its improved accessibility have contributed to significant growth in opportunity potential of the restored delta to support salmon populations. Our results suggest that channel mouths on the seaward side of the marsh will benefit juvenile salmon in years to come, but inland channel sites that are filling with sediment and are less connected to the river may become decreasingly suitable for salmon unless several historical distributary channels are reconnected to the river. Our analyses indicate that access through the historic distributaries would improve connectivity and likely help maintain several of the metrics examined here, including channel depth, temperature, and salinity. We expect that within the next few decades, the amount of estuary emergent marsh and the quality of restored tidal channels will approach that of the previously unaltered reference channels, particularly at higher elevation sites. Ongoing monitoring efforts incorporating post-restoration biophysical data and climate change forecasting will aid in determining the ultimate outcome of the restored Nisqually landscape.

The success of the Nisqually River Delta restoration with respect to increased opportunity potential demonstrates that this estuary and others that have been diked for agricultural uses can rebound rapidly in terms of usable habitat, even after long-term separation from tidal influence. Habitat connectivity and accessibility are best evaluated with a full suite of monitoring data and analytical methods including connectivity modeling, long-term hydrology data, and physical measurements, all of which can be used in tandem to paint a full picture of a restored estuary's function. Although opportunity potential is a key measure of restoration success, habitat accessibility is only one metric with which managers can measure the viability of large-scale restoration projects. Other performance metrics, including the capacity of the site to support foraging for upper tropic levels (such as salmon), and the realized function of the site in terms of growth and bioenergetics, are equally as crucial. Each of these indicators should be evaluated to determine the success of estuary or wetland restoration projects.

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Supporting Information

The following information may be found in the online version of this article:

Appendix S1. Model parameters and model selection criteria for channel cross section and water quality data analyses.

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