

Juvenile Salmonid Use of Reconnected Tidal Freshwater Wetlands in Grays River, Lower Columbia River Basin

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Abstract.—Degraded wetland systems with impaired hydraulic connections have resulted in diminished habitat opportunity for salmonid fishes and other native flora and fauna in the Pacific Northwest. Many of these lost habitats were once intertidal freshwater marshes and swamps. Restoration of these systems is effected in part by reestablishing tidal processes that promote connectivity, with a central goal of restoring rearing habitat for juvenile Pacific salmon *Oncorhynchus* spp. In the Grays River tidal freshwater system of Washington, we measured hydrologic changes that resulted from the removal of tide gates from diked pastureland and we determined the subsequent time series of salmonid abundance and size frequency in the restoring marshes. Dike breaching caused an immediate return of full semidiurnal tidal fluctuations to the pasturelands. Juvenile Pacific salmonids quickly expanded into this newly available habitat and used prey items that were presumably produced within the marshes. Habitat use varied by species and life history stage. Fry of chum salmon *O. keta* migrated rapidly through the system, whereas populations of Chinook salmon *O. tshawytscha* and coho salmon *O. kisutch* resided from March to at least July and were composed of fry, fingerlings, and (for coho salmon) yearlings. Based on salmon size at date and the timing of hatchery releases, we concluded that most salmon sampled in restored and reference sites were the progeny of natural spawners. However, the presence of adipose-fin-clipped Chinook salmon indicated that hatchery-raised fish originating outside the Grays River system also used the restoring wetland habitat. Because of extensive mixing of stocks through hatchery practices, genetic analyses did not provide additional insight into the origins of the Chinook salmon but did reveal that out-migrating juveniles were an admixed population composed of lower Columbia River ancestry and nonindigenous Rogue River stock. Restoration of tidal wetlands in the Columbia River estuary will improve overall ecosystem connectivity and reduce habitat fragmentation and may therefore increase survival of a variety of Pacific salmon stocks during migration.

Tidal wetlands are important rearing habitat for migrating juvenile Pacific salmon *Oncorhynchus* spp. (Healey 1980; Levy and Northcote 1982; Levings et al. 1986; Bottom et al. 2005a). However, most of the historical wetlands of the lower Columbia River and its estuary have been converted to agricultural land or altered by logging practices and are disconnected from salmon migration routes (Thomas 1983). Hydrological

barriers (e.g., dikes and levees) and flood control structures (e.g., tide gates) have reduced or eliminated the opportunity for salmonids to use the once-extensive off-channel rearing habitat. Even in partially connected systems, such as those with leaking tide gates, decreased water exchange can adversely affect temperature and dissolved oxygen regimes of impounded areas (USEPA 2003; Ritter et al. 2008). In the lower Columbia River, habitat restoration is considered pivotal for increasing overall population resiliency based on varying life history strategies of threatened and endangered Pacific salmon species (Bottom et al. 2005b).

Recently, policy initiatives have enabled design and

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completion of several wetland restoration projects in the lower Columbia River (FCRPS 2008). These initiatives were designed in part to increase hydrologic connectivity of degraded habitat, with the primary goal being to recover opportunity and capacity functions that may increase juvenile salmonid growth and survival (Simenstad and Cordell 2000). The two main types of reconnection actions in the region are tide gate replacement or upgrade, which maintains flood control capability while striving to improve fish access, and dike removal or breaching, which returns wetlands to more ambient tidal and flood event conditions. Dynamic tidal forcing is a primary factor affecting wetland structure and function and is a main driver controlling water quality variation (Ritter et al. 2008), topographic evolution (Williams and Orr 2002), and vegetation community development during wetland restoration (Cornu and Sadro 2002; Thom et al. 2002). Seasonal riverine processes—particularly flood events—are also important for wetland development, especially above head of tide and for sites farther upriver where tides are attenuated. Tidal-scale variation in water elevation also determines the period in which fish can access and use wetland habitats. Juvenile salmonids in particular enter intertidal wetlands during high water to forage on emergent insects and other wetland-derived prey (Healey 1980; Levings et al. 1991).

With hydraulic reconnection, tidal forces and inundation–submersion cycles immediately begin to shape wetland drainage and vegetation patterns. While this process is assumed to generate a number of benefits to the ecosystem, virtually no research has been conducted on the restoration of tidal freshwater habitats of the lower Columbia River. Additionally, few studies have tracked the physical and biological changes that are important for verifying project success, implementing adaptive management, assessing the cumulative effects of multiple restoration projects, or aiding design of similar projects anticipated for the region.

In this study, we documented the initial hydrologic changes associated with a tide gate removal project in the Grays River, Washington, and we report on the response of juvenile salmonids at two reconnected wetlands during this period. We hypothesized that increased hydraulic connectivity would lead to increased habitat use by fish, particularly juvenile salmonids. Our main objective was thus to conduct assessments of fish community structure and salmon abundance, size, and diet in wetland and adjacent riverine habitats. During the first year of the study, we observed adipose-fin-clipped Chinook salmon *O. tshawytscha* in restoration sites, which raised the

possibility that salmon originating outside the Grays River watershed were accessing the wetlands. Therefore, a second objective was to investigate the genetic stock of origin for juvenile Chinook salmon in the system.

Study Area

The lower Columbia River is under tidal influence from the Pacific Ocean to Bonneville Dam (river kilometer [rkm] 235), and tidal influence extends to the lower reaches of most lower Columbia River tributaries. The maximum salinity intrusion, which occurs in late summer or autumn, extends only to about rkm 30, so the majority of the lower Columbia River is a tidal freshwater ecosystem. The Grays River is a tributary that joins the Columbia River at rkm 34 (Figure 1) and drains a 321-km² area in Washington (Johnson et al. 1997). Head of tide occurs at approximately rkm 10, which divides the watershed into fluvial and tidal freshwater environments. Salinity does not intrude into the Grays River. Maximum tidal amplitude is about 3.6 m, depending on spring–neap tidal cycle, river flow, distance from the river mouth, and channel topography. The upper Grays River watershed was extensively modified by clear-cut logging during 1920–1950, which resulted in a 95% loss of old-growth forests (Scott 2001). Logging activity used streams to transport timber, and the development of splash dams, log and debris jams, and sluice gates altered hydrographic patterns and impaired salmonid spawning habitat (Johnson et al. 1997). Forested wetlands in lowland floodplains were cleared and converted to pasture (Scott 2001), and dikes and tide gates that were built to contain river flow reduced or eliminated access to off-channel habitat. Thus, the Grays River watershed lost salmonid rearing areas in addition to spawning area losses. However, recent acquisitions and restoration by conservation organizations, such as the Columbia Land Trust (www.columbialandtrust.org), have provided the opportunity to monitor changes in hydrodynamic connectivity and habitat use by juvenile salmonids as a result of tidal reconnection.

We monitored two restoration projects: (1) Kandoll Farm, a 378-ha site situated between the confluence of Grays River and Seal Slough and (2) Johnson Farm, a 198-ha site located farther downstream along the Grays River (Figure 1). Both sites had been diked to produce pastureland in the early 20th century, with tide gates added as flood control measures. Restoration treatments entailed the removal of the tide gate structures. For the Johnson Farm restoration, a dike along the Grays River was breached in 2004. At Kandoll Farm, two 4.2-m-diameter culverts were installed in the dike during 2005 to reconnect Seal Slough, an arm of the

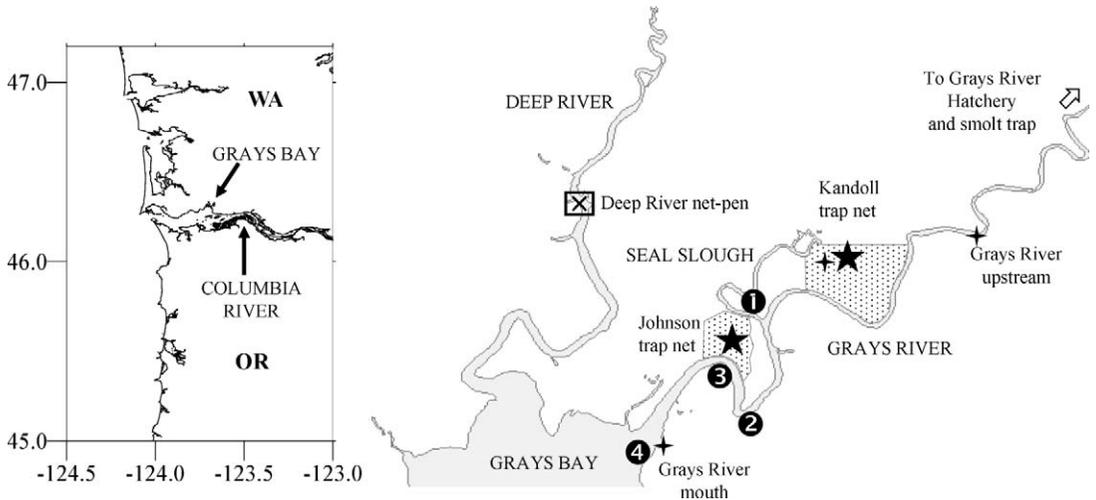


FIGURE 1.—Map of the Grays River system, Washington. Numbered circles indicate primary beach seine sites (1 = Seal Slough; 2 = Devils Elbow; 3 = Johnson Farm; 4 = Grays River mouth). Stippling indicates approximate areas of restoration sites (Kandoll Farm and Johnson Farm). Stars denote trap-net sites. Crosses show the positions of pressure-temperature sensors. Inset depicts the location of the study area in the lower Columbia River system, Washington-Oregon.

Grays River. Both treatments reestablished connections to relic channel reaches and resulted in tidal flooding on the pasture surface.

Salmon Production and Life History Traits

The Grays River system is an important spawning and juvenile rearing watershed for Chinook salmon, coho salmon *O. kisutch*, chum salmon *O. keta*, steelhead *O. mykiss*, and cutthroat trout *O. clarkii* (LCFRB 2004). Historically, annual adult returns were substantial for fall Chinook salmon (1,500–10,000 fish), coho salmon (5,000–40,000 fish), chum salmon (8,000–14,000 fish), and winter steelhead (at least 4,500 fish; LCFRB 2004). However, Grays River salmonid populations are greatly depressed from historic levels, with population viability rated “low” and extinction risks in the next 100 years estimated at 30–70% (LCFRB 2004). Along with other populations of Chinook salmon, coho salmon, and chum salmon in the lower Columbia River, the Grays River populations are listed as threatened under the U.S. Endangered Species Act (Good et al. 2005).

In recent years, salmon abundance in the Grays River has been highly variable and includes both naturally produced and hatchery-produced fish. A recent assessment of salmon stocks and hatchery practices in the Grays River was compiled by the Lower Columbia Fish Recovery Board (LCFRB 2004), and we calculated average escapement values from data collated by the Washington Department of Fish and Wildlife (WDFW; wdfw.wa.gov/hat/escape). Dur-

ing 1995–2006, fall Chinook salmon annual returns averaged 243 ± 210 fish (mean \pm SD), with a range of 14–745 fish. Hatchery production of fall Chinook salmon (from a variety of genetic stocks) occurred from 1947 to 1997 and was then discontinued with the goal that the Grays River could provide a natural fish refuge (LCFRB 2004). The Grays River Hatchery presently rears spring Chinook salmon juveniles produced at hatcheries in other lower Columbia River tributaries (such as the Cowlitz and Lewis rivers); these fish are transferred to Deep River net-pens for further grow out before release (Figure 1). The Grays River Hatchery also produces coho salmon, with recent hatchery releases of about 150,000 yearling fish, all of which are adipose-fin-clipped. Adult returns of coho salmon during 1998 to 2007 were variable and averaged $3,113 \pm 4,089$ fish (range = 72–12,842 fish), with hatchery production thought to account for most of the returns. Approximately 130,000–260,000 hatchery chum salmon fry were released into the Grays River each year during 2005–2007, and estimated adult returns based on spawning surveys indicate a relatively robust return of 3,832–14,377 fish from 2004 to 2007 (T. Hillson, WDFW, personal communication). Therefore, the Grays River is one of the few remaining locations that support natural spawning of chum salmon in the Columbia River basin (Johnson et al. 1997; McElhany et al. 2007). Estimated adult returns of winter steelhead during 2003 to 2007 based on escapement averaged 313 ± 308 fish (range = 100–818 fish). Cutthroat trout production has not been estimated.

These salmonid stocks have different juvenile life history traits that are important for designing effective habitat restoration practices (LCFRB 2004). Grays River fall Chinook salmon are subyearling migrants that rear in riverine and tidal freshwater areas for up to several months before migrating to the estuary in late spring or early summer. Coho salmon have a mainly yearling juvenile life history type, with residency in riverine, tidal freshwater, and estuarine environments before ocean entry, and their life history may also include a subyearling migrant component (e.g., Koski 2009). Chum salmon have a fry migrant life history, with emergence occurring in early spring and a rapid migration to the estuary and ocean. Winter steelhead rear in riverine habitat for 1 to 3 years and migrate to the sea as smolts during April–May, with a peak in early May. Cutthroat trout exhibit both resident and anadromous life histories, with sea-run individuals usually migrating to the ocean after 2 to 3 years of freshwater rearing.

Methods

Hydrography.—Changes in water level were used to demonstrate levels of connectivity before and after tide gate removal at Kandoll Farm. We monitored hydrography with a network of pressure–temperature sensors (HOBO Model U20-001-04, Onset Computer Corp.) established at stations within Kandoll Farm and along the Grays River system (Figure 1). At each station, instruments were secured subtidally to vertical poles or on bottom weights. Pressure readings were corrected for barometric pressure and site topography to yield water level relative to the North American Vertical Datum of 1988 (Roegner et al. 2009). Measurements were logged at 0.5-h intervals. To demonstrate hydrological reconnection, we highlight before–after time series of water level inside and outside Kandoll Farm. Connectivity was evaluated with exposure–depth curves computed for 24-d periods before and after tide gate removal. Further details of Grays River system hydrology are available from Johnson and Diefenderfer (2009).

Temperature time series were used to evaluate periods of suitable water quality conditions for rearing salmonids. We calculated the 7-d average maximum daily (7-DAM) temperature, and we refer to a critical threshold of 16°C as the upper criterion for optimum thermal conditions (USEPA 2003; Richter and Kolmes 2005). We compared temperature time series from inside Kandoll Farm and from locations on the Grays River upstream and downstream from the restoration sites (Figure 1).

Fish community composition.—At Kandoll Farm, fish communities were sampled before (2005) and after

(2006 and 2007) tide gate removal as well as at several reference sites not directly affected by the restoration activity (Seal Slough and the Grays River; Figure 1). At Johnson Farm, fish populations were monitored after the tide gate removal (2005–2007), which occurred in summer 2004.

Sampling within the preresoration Kandoll Farm site was limited to three seine hauls conducted in May 2005 with a small pull seine (7 × 2 m) as fish habitat was found to be marginal (previously the site was primarily a cow pasture). Postrestoration sampling inside Kandoll Farm (2006–2007) and Johnson Farm (2005–2007) was accomplished by deploying a trap net (fyke net) in developing intertidal channels. The trap net consisted of two 15.0- × 2.4-m net leads connected to a 0.75-m² throat and a 1.8-m-long cod end. The trap net was set at high water and fished for 4–5 h during the outgoing (ebb) tide to catch fish moving toward the river as water within the restoration site drained. Both pre- and postrestoration (2005–2007) reference sites in Seal Slough were sampled with a 50- × 3-m beach seine. In 2007, we seined three additional reference sites in the Grays River within 2 d of the trap-net sampling dates (stations 2–4 in Figure 1). These sites, located downstream from the Seal Slough reference site out to the Grays River mouth, were used to evaluate variation in salmon migration timing in the Grays River main stem. Time series data were collected at bimonthly to monthly frequencies. Since determining the presence–absence of salmonids was a goal, we concentrated fishing effort from winter to early summer (January–July), the usual timing of salmon out-migration in the lower Columbia River (e.g., Bottom et al. 2008; Roegner et al. 2008).

All captured fish were identified to species, enumerated, and measured to the nearest millimeter (fork length [FL]). Salmonids were anesthetized with a 50-mg/L solution of tricaine methanesulfonate (MS-222) before measurement. Stomach contents of suitably sized juvenile coho salmon and Chinook salmon were sampled by gastric lavage to determine prey composition (Seaburg 1957). This is a nonlethal sampling method that uses filtered water to evacuate fish stomachs. Stomach content samples were fixed with 10% formalin. We did not monitor gut contents of chum salmon because individuals were too small for gastric lavage. We closely examined all salmon for adipose fin clips or other external marks indicating hatchery origin. However, because only a proportion of all hatchery fish are marked, we could not unambiguously distinguish whether unmarked individuals were naturally spawned or produced in a hatchery. After noting the presence of adipose-fin-clipped Chinook salmon in 2005 and 2006, we conducted genetic

surveys in 2007 and 2008 by collecting nonlethal samples of fin tissue (analytical methods are detailed in the genetic analysis section). Fish were allowed to recover before being released downstream of the trap net.

Fish community analysis.—A single gear type or method cannot be used to sample the spatial complexity of wetland habitats. The areas sampled by seines and trap nets were dissimilar, and the numerical catch data were gear dependent and not readily standardized by density. However, both techniques were effective at capturing the fish present in the areas where these gear types were used. Therefore, we used fish species abundance data measured as catch per unit effort (CPUE) to describe general patterns of community structure among reconnected marshes and tidal freshwater habitats. We pooled abundance data from all seine or trap-net samples between restoration and reference habitats for each site and year. Community structure was evaluated by means of two standard measures: (1) number of species (S) and (2) Shannon–Wiener species diversity index ($H' = \sum [-P_i \times \log_e P_i]$, where P_i is the proportion of species in the sample). Values of H' closer to zero indicate a less-diverse fish assemblage. Comparisons of CPUE, S , and H' are properly confined to each gear type.

Salmon life history, habitat use, and migration.—Salmon life history stage was estimated based on fish size and date of capture. For the period January–July, salmon up to 60 mm were considered to be fry, and we used the following equation to distinguish fingerlings from yearlings (data modeled from Dawley et al. 1985): $FL \text{ (mm)} = 0.5 \times (\text{day of year}) + 50$. We used size-frequency distributions of Chinook salmon, chum salmon, and coho salmon to quantify the proportions of life history types present at restoration trap-net sites and the Seal Slough reference site. To compare the timing of salmon habitat use among years and sites, we calculated time series of relative annual abundance as $N_R \text{ (\%)} = 100 \times (N_t/N)$, where N_t is the CPUE at sample time t and N is the total annual catch. We also generalized temporal trends in the abundance data with scatter plots of salmon CPUE by day of year. The migration timing of salmon in the Grays River during 2007 was evaluated with time series of CPUE at the four seine sites shown in Figure 1.

Salmon size and hatchery production.—The presence of adipose-fin-clipped fish indicates possible migration from outside the Grays River system. However, fin-clipped individuals could have been unintended hatchery releases. Therefore, we plotted the annualized distribution of salmon in relation to the size and timing of hatchery releases. We examined size variation as functions of time (day of year) and capture

location (trap-net sites, Grays River seine sites, and Grays River mouth). The latter site was highlighted because salmon captured there could be out-migrants from the Grays River system or fish moving down the Columbia River main stem. On the plots, we also distinguished between (1) adipose-fin-clipped and unclipped individuals and (2) yearling and subyearling fish.

Salmon distribution and temperature.—We compared salmon abundance by 7-DAM temperature regime to ascertain possible thermal constraints on salmon habitat use.

Diet analysis.—Salmon diets were measured as an indicator of habitat use. Stomach contents were wet-weighted and then sorted and identified to the lowest possible taxonomic level (depending on the extent of digestion and taxonomic authority) under a dissection microscope. For analysis, we grouped the data into major taxonomic categories to emphasize dominant prey groups by count and weight. Diet data metrics were recorded as percent numerical and gravimetric prey composition, which were used to calculate an index of relative importance (IRI). The IRI is defined as $\%O \times (\%N + \%W)$, where $\%O$ is the percent frequency of occurrence, $\%N$ is the percent contribution by number, and $\%W$ is the percent contribution by weight (Pinkas et al. 1971). The $\%IRI$ for both Chinook salmon and coho salmon and for each sample location was computed as $IRI/\sum IRI$. This index indicates the relative level at which the prey categories were consumed by juvenile salmon.

Genetic analysis.—We used genetic stock identification (GSI) techniques (see Manel et al. 2005) to investigate whether juvenile Chinook salmon originating from outside the Grays River were using the tidal freshwater sites in our study. Our approach was to estimate the stock composition of juveniles with a regional microsatellite DNA data set (Seeb et al. 2007). We included baseline data for spawning populations from throughout the Columbia River basin that potentially contribute to the juvenile population using the Grays River wetland habitats. Although the Seeb et al. (2007) data set includes data for lower Columbia River spawning populations, it does not include data for Chinook salmon produced in the Grays River. Therefore, we genotyped individuals sampled in the upper Grays River in 2008 with the goal of supplementing the baseline for our analysis.

In 2007, fin tissues were sampled from fry and fingerling Chinook salmon collected at Grays River tidal freshwater sites. Fish were sampled at Kandoll Farm ($n = 3$), the mouth of Grays River ($n = 6$), two seine sites on Grays River ($n = 6$), and the Seal Slough seine site ($n = 22$). Genetic sampling was conducted

during February through May. However, because Chinook salmon abundance was very low, all but the Kandoll Farm fish were captured in May and June during peak migration. In 2008, fin tissues for baseline analysis were sampled from migrating juveniles captured in an upper Grays River smolt trap operated by personnel from WDFW. Fish were sampled from 17 May to 5 August ($n = 129$) to represent the peak out-migration period of subyearling fall Chinook salmon. Tissues were preserved in nondenatured ethanol for subsequent genetic analysis.

Genomic DNA was extracted from tissues by means of Wizard genomic DNA purification kits (Promega Corp.). Isolated genomic DNA was used in polymerase chain reactions (PCRs) to amplify 13 standardized microsatellite DNA loci (Seeb et al. 2007). The PCR products were electrophoresed with an Applied Biosystems 3100 genetic analyzer, and the GeneScan and Genotyper software programs (Applied Biosystems) were used to determine genotypes. Genotypic data were tested for deviation from Hardy–Weinberg equilibrium with the Markov-chain Monte Carlo algorithm implemented in GENEPOP version 3.3 (Raymond and Rousset 1995). The GSI analysis was conducted with a baseline of genotype data retrieved from a coastwide data set (Seeb et al. 2007). We used data for the 30 Columbia River basin baseline populations described by Teel et al. (2009). Our baseline also included data for Chinook salmon sampled in the Rogue River on the Oregon coast (Seeb et al. 2007), the source population used for a fall Chinook salmon hatchery program in the lower Columbia River (North et al. 2006). The overall proportional stock composition of Grays River samples was estimated with the GSI computer program ONCOR (Kalinowski et al. 2007), which implemented the likelihood model of Rannala and Mountain (1997).

Allocations to individual baseline populations were summed to estimate contributions of 10 regional genetic stock groups (Seeb et al. 2007; Teel et al. 2009). Confidence intervals of the stock composition estimates were derived by bootstrapping baseline and mixture data 100 times (Kalinowski et al. 2007). We evaluated the ancestry of individual Chinook salmon sampled in the Grays River with the admixture clustering model implemented in the program STRUCTURE version 2.2 (Pritchard et al. 2000). We used genotypic data from nine populations in the standardized baseline as individuals of known origin in the clustering analysis. These data were from eight lower Columbia River fall- and spring-run Chinook salmon populations and from the Rogue River fall-run population. After a burn-in period of 30,000 iterations, a maximization period of 50,000 iterations was then

used to estimate the proportion of Rogue River ancestry in each Grays River fish. Estimates for the eight lower Columbia River populations were summed to estimate the proportion of Columbia River ancestry in each fish.

Results

Hydrology

Tide gate removal had an immediate effect on water level fluctuations within the Kandoll Farm site (Figure 2a). Prebreach water level fluctuations changed from a weak tidal signal to a fully semidiurnal tidal pattern. Exposure–height curves indicated that maximum amplitudes increased from about 2.0 to 3.0 m, although preconnection water levels were less than 1.0 m for 85% of the time period evaluated (Figure 2b), and mean water level increased from 0.6 to 1.5 m in the 2-week period around the tide gate removal.

Fish Community Composition

In the Grays River system, we collected 45 seine samples from 2005 to 2007, sampled 15 tides by trap net at the Kandoll Farm restoration site in 2006 and 2007, and sampled 25 tides at the Johnson Farm restoration site from 2005 to 2007 (Table 1). Nearly 52,000 individual fish were identified (see Table 1 for a list of species collected). Threespine sticklebacks dominated most samples (93.6% of total). The next most abundant species was chum salmon (2.1%) followed by the introduced banded killifish (1.6%), coho salmon (0.9%), prickly sculpin (0.5%), Chinook salmon (0.5%), and peamouth (0.5%). Other species were caught incidentally and together comprised less than 0.3% of the total. Overall, H' was negatively related to threespine stickleback abundance ($r^2 = -0.92$, $P < 0.001$). When threespine sticklebacks were excluded, Chinook salmon constituted 8.3% of the remaining total catch, chum salmon contributed 32.7%, and coho salmon constituted 13.4%, and the overall H' increased from 0.35 to 1.78 (Table 1).

Before the Kandoll Farm tide gate removal, no fish other than threespine sticklebacks were found inside the tide gate controlled area (Table 1); in contrast, we captured seven species, including coho salmon, at the Seal Slough reference site ($N = 418$ fish, all species combined; $H' = 0.92$). After the dike breach at Johnson Farm in 2005, we caught 10 species, with relatively high numbers of chum salmon, coho salmon, and Chinook salmon ($N = 5,977$ fish; $H' = 0.41$). In 2006, after tide gate removal at Kandoll Farm, trap-net samples yielded nine species, three of which were salmonids ($N = 19,575$ fish; $H' = 0.07$). At Johnson Farm in 2006, we caught 11 species, including four salmonids ($N = 14,783$ fish; $H' = 0.27$). Diversity

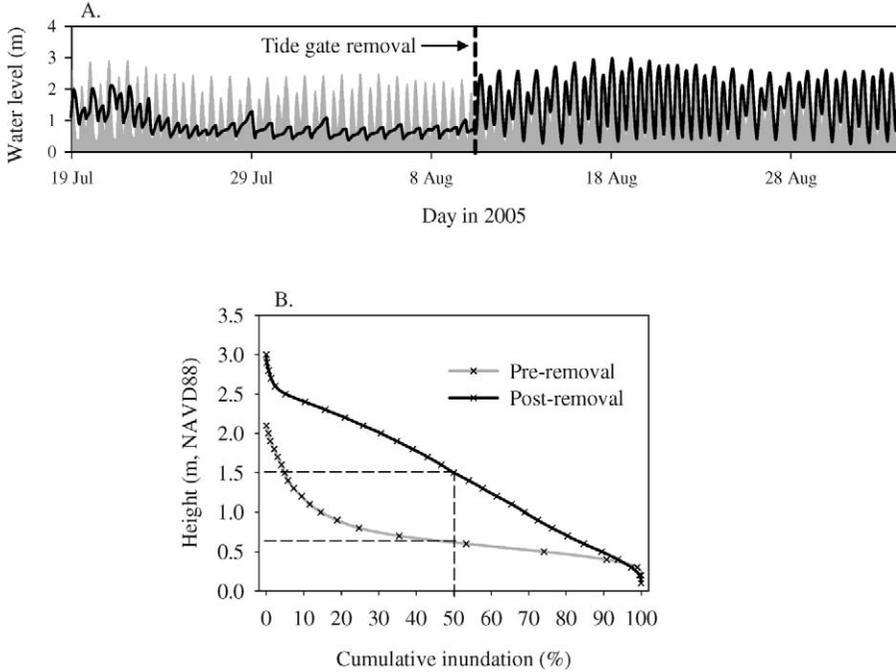


FIGURE 2.—Hydrology of the Kandoll Farm, Washington, restoration project: (A) time series of water level at reference (gray fill) and restoration (black line) sites during the period surrounding the tide gate removal in August 2005; and (B) exposure–height curves comparing inundation levels before and after tidal reconnection (NAVD88 = North American Vertical Datum of 1988). The 50% inundation levels for the curves are denoted by dashed lines.

TABLE 1.—Fish abundance and diversity indices for restoration and reference sites in the Grays River system, Washington, 2005–2007: Kandoll Farm before restoration (K-B), Kandoll Farm trap-net site after restoration (KTN), Johnson Farm trap-net site after restoration (JTN), and Seal Slough reference seine site (SS). Samples were sorted by overall abundance. Numbers in parentheses designate number of samples (N = abundance; S = number of species; H' = Shannon–Weiner diversity index).

Species	2005			2006			2007			Total
	K-B (3)	JTN (6)	SS (14)	KTN (6)	JTN (10)	SS (21)	KTN (9)	JTN (9)	SS (7)	
Threespine stickleback <i>Gasterosteus aculeatus</i>	82	5,460	312	19,389	14,021	2,620	883	4,388	1,472	48,627
Chum salmon	0	277	0	70	63	22	556	54	45	1,087
Banded killifish <i>Fundulus diaphanus</i>	0	76	5	44	477	114	5	80	21	822
Coho salmon	0	35	6	51	133	66	37	87	30	445
Prickly sculpin <i>Cottus asper</i>	0	1	28	1	18	85	2	141	41	317
Chinook salmon	0	108	0	15	34	52	6	9	53	277
Peamouth <i>Mylocheilus caurinus</i>	0	15	49	3	27	49	0	7	81	231
Starry flounder <i>Platichthys stellatus</i>	0	0	14	1	1	90	0	0	1	107
Largescale sucker <i>Catostomus macrocheilus</i>	0	1	0	1	6	5	0	0	1	14
Cutthroat trout	0	0	0	0	0	0	0	0	9	9
Smallmouth bass <i>Micropterus dolomieu</i>	0	0	4	0	0	0	0	0	0	4
Northern pikeminnow <i>Ptychocheilus oregonensis</i>	0	3	0	0	0	0	0	0	0	3
Steelhead	0	1	0	0	2	0	0	0	0	3
American shad <i>Alosa sapidissima</i>	0	0	0	0	0	2	0	0	0	2
Centrarchid	0	0	0	0	1	0	0	0	1	2
N	82	5,977	418	19,575	14,783	3,105	1,330	4,766	1,755	51,950
S	1	10	7	9	11	10	6	7	11	15
H'	0	0.41	0.92	0.07	0.27	0.73	0.72	0.39	0.70	0.35
N without threespine sticklebacks	0	517	106	186	762	485	606	378	283	3,323
H' without threespine sticklebacks		1.29	1.41	1.42	1.22	1.91	0.35	1.40	1.32	1.78

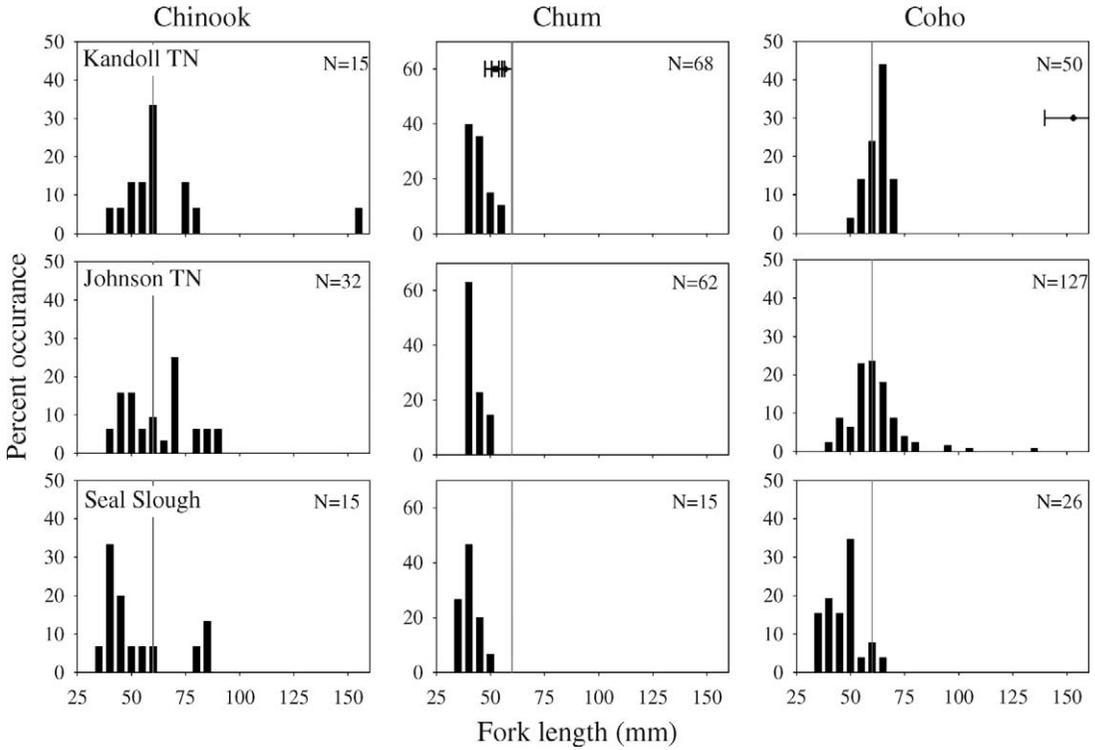


FIGURE 3.—Size-frequency histograms of Chinook salmon, chum salmon, and coho salmon at restoration and reference sites in the Grays River system, Washington, 2006 (TN = trap-net site). Horizontal bars indicate fork length (FL) at 5-mm intervals. Symbols show mean (\pm SD) FL of hatchery chum salmon and coho salmon at release. There were multiple chum salmon release dates and a single coho salmon release date. Vertical line at 60 mm delineates fry from fingerling-sized individuals. Numbers (*N*) indicate the quantity of fish used to determine the frequency distribution.

remained low due to the high numbers of threespine sticklebacks. Species counts and total numbers of individuals decreased at trap-net sites in 2007 with the loss of incidental species and decline in the number of threespine sticklebacks (Kandoll Farm: $N = 1,330$ fish, $S = 6$, $H' = 0.72$; Johnson Farm: $N = 4,766$ fish, $S = 7$, $H' = 0.39$). In comparison, the mean values of S and H' from beach seine samples at lower Columbia River main-stem freshwater sites from 2002 to 2008 were 13.1 and 0.55, respectively (G. C. Roegner, unpublished data). However, overall salmonid abundance remained relatively high in restoration sites. Only three winter steelhead and nine cutthroat trout were observed in our samples; all of the steelhead and none of the cutthroat trout were captured in restoration sites.

Salmon Size-Frequency Patterns

Based on composite size-frequency histograms, the salmon species exhibited variation in life history stages among reconnected wetland and reference sites (Figures 3, 4) (not all captured salmon were measured). In 2006, Chinook salmon populations were dominated by

fry, with some fingerlings and one yearling captured. Sizes ranged from 30 to 157 mm FL. Size-frequency distributions at restoration and reference sites were very similar. In 2007, only six Chinook salmon were captured at the Kandoll Farm site (40–75 mm) and nine Chinook salmon were captured at the Johnson Farm site (45–95 mm), whereas 53 fish were captured at the Seal Slough reference site (30–90 mm). Each of these samples indicated the presence of both newly emerged fish and fingerling-sized fish. The chum salmon population was composed almost entirely of fry at all sites in both 2006 and 2007, and the size structure was similar at restored and reference habitats. Coho salmon size distributions exhibited the most variation both among sites and between years. In 2006, coho salmon ranged from 40 to 80 mm FL at wetland sites (plus a few yearlings) and from 30 to 65 mm FL at the Seal Slough reference site; both fry and fingerlings were present. In 2007, a similar size range of subyearlings was found at all three sites, but groups of yearling fish were also present at Kandoll Farm and Seal Slough and ranged from about 110 to 130 mm FL. Thus, the chum

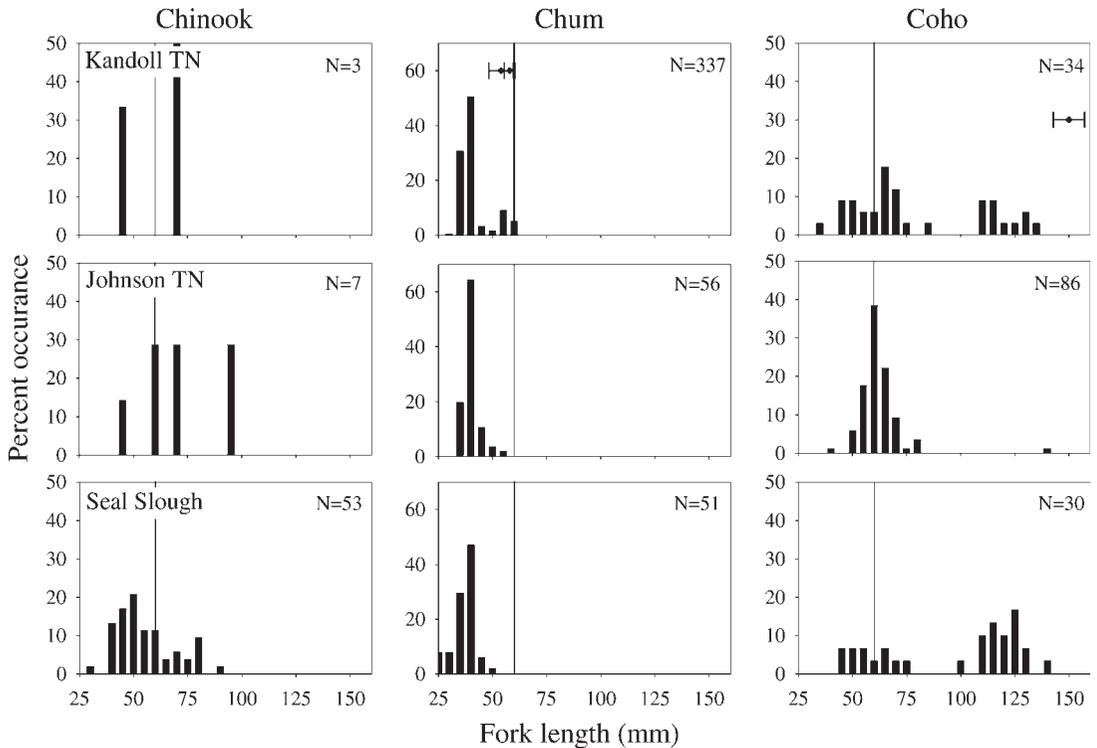


FIGURE 4.—Size-frequency histograms of Chinook salmon, chum salmon, and coho salmon at restoration and reference sites in the Grays River system, Washington, 2007 (TN = trap-net site). Horizontal bars indicate fork length (FL) at 5-mm intervals. Symbols show mean (\pm SD) FL of hatchery chum salmon and coho salmon at release. There were multiple chum salmon release dates and a single coho salmon release date. Vertical line at 60 mm delineates fry from fingerling-sized individuals. Numbers (N) indicate the quantity of fish used to determine the frequency distribution.

salmon were all fry migrants, Chinook salmon were composed predominately of fry- and fingerling-sized subyearlings, and the coho salmon population consisted of fry, fingerlings, and yearlings.

Salmon Temporal Patterns

We calculated N_R to standardize the timing of fish habitat use between years (Figure 5). Each year, time series of N_R in restoration and reference sites indicated that salmonid presence tended to be pulsed: 60–80% of the annual catch was often acquired during a single sample date, and the temporal distribution of salmon was typically limited to two or three consecutive biweekly samples. Among reconnected wetland and reference sites, species presence was broadly coincident within years, whereas peak timing was variable among years. We plotted salmon CPUE by day of year to generalize the temporal trends (Figure 6). Chinook salmon were present from March to July, with a variable annual peak in March through May; however, overall presence of Chinook salmon in restoration sites was very low in 2006 and 2007 (Table 1). Chum

salmon tended to be present for 2 to 3 weeks in March–April, and numbers declined sharply by 1 May. Subyearling coho salmon presence was more variable, extending from March to June (and occasionally into August), with peak abundance in April or May. Yearling coho salmon abundance peaked in April. The temporal pattern of coho salmon at Johnson Farm was remarkably consistent among years. Samples at Johnson Farm were collected into the autumn in 2005 and 2006; no salmonids were captured after 9 August in 2005 or after 18 July in 2006 (sampling ended on 21 June in 2007).

In 2007, the spatiotemporal distributions of salmon at the four Grays River reference sites varied by species (Figure 7). Chum salmon were especially episodic and exhibited a coincident pulse at three of four stations around 1 April and lower abundances outside this date. This suggested the occurrence of a rapid migration within the 2-week sampling interval. Chinook salmon and coho salmon had more irregular distributions and exhibited a longer period of residence in the Grays River system. In no case was there an obvious

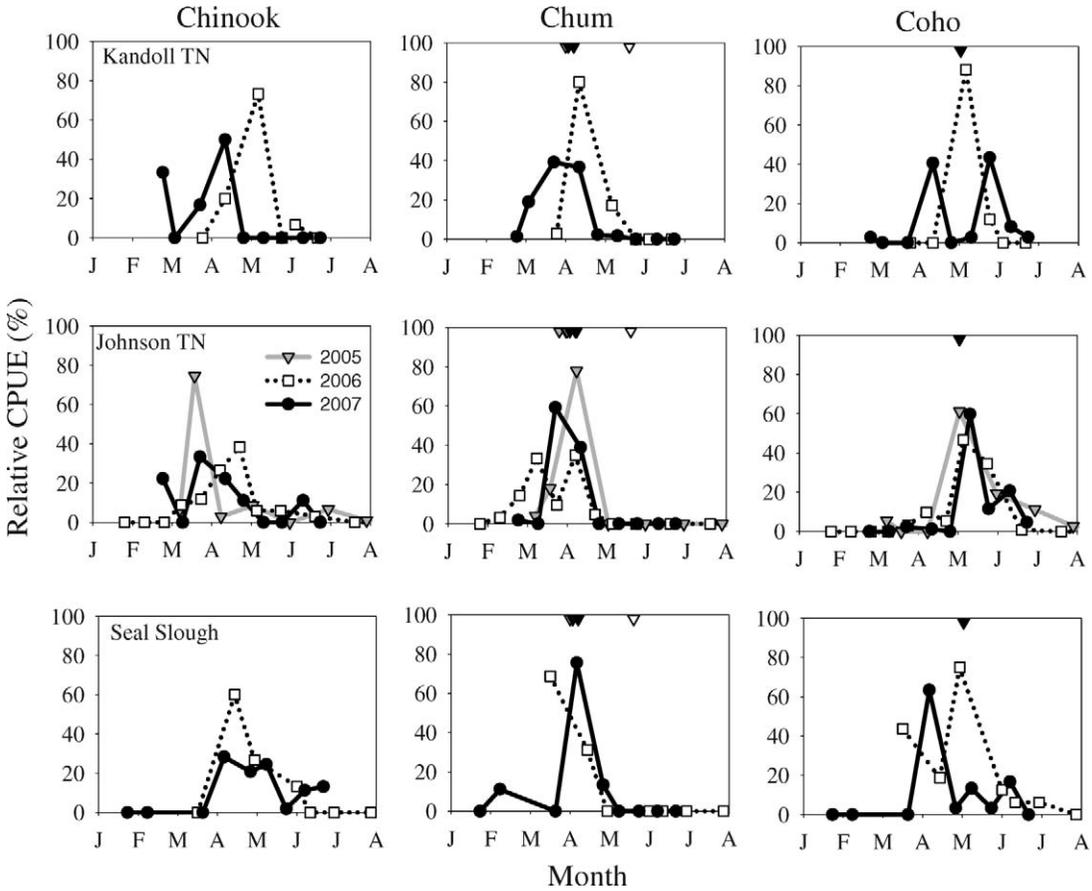


FIGURE 5.—Salmonid relative catch per unit effort (CPUE; percent of annual total) at restoration and reference sites in the Grays River system, Washington (top row: Kandoll Farm trap-net [TN] site, 2006 and 2007; middle row: Johnson Farm TN site, 2005–2007; bottom row: Seal Slough seine site, 2006 and 2007). Triangles at the top of each panel denote hatchery release dates (chum salmon: shaded = 2005, open = 2006, solid = 2007; coho salmon: 1 May for all years).

migration signal (e.g., abundance peaks staggered by distance). Overall, the Seal Slough reference site, located at the slough’s confluence with the Grays River, exhibited high abundance for all species.

Salmon Size and Hatchery Production

Salmon size by date (day of year) was used to distinguish yearling from subyearling Chinook salmon and coho salmon, to detect the influence of hatchery

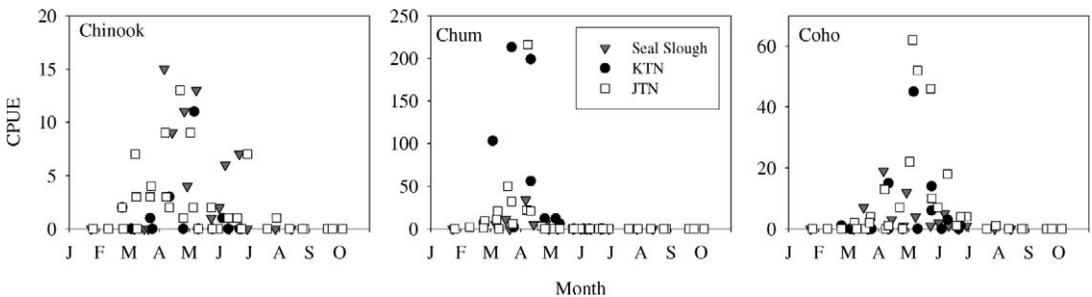


FIGURE 6.—Temporal distribution of Chinook, chum, and coho salmon catch per unit effort (CPUE) by sampling location in the Grays River system, Washington, 2005–2007 (KTN = Kandoll Farm trap-net site; JTN = Johnson Farm trap-net site).

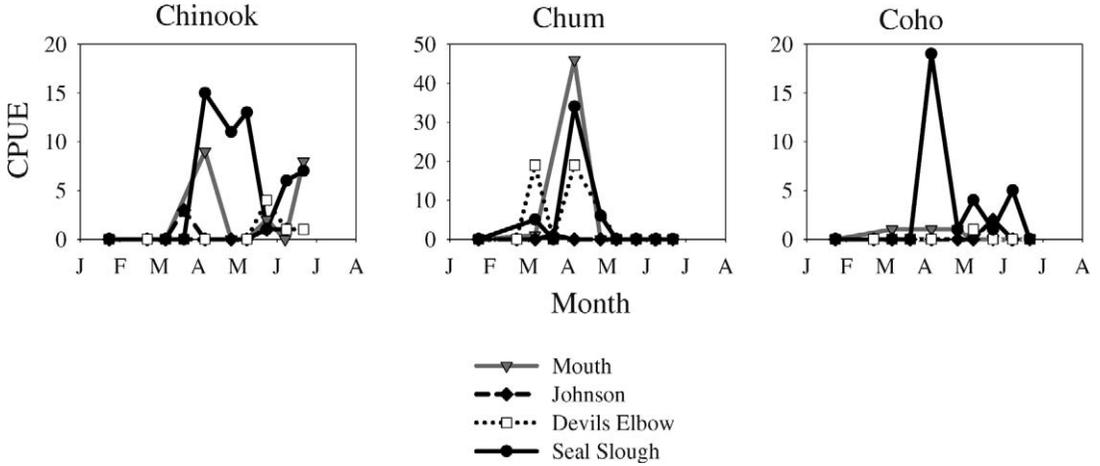


FIGURE 7.—Salmonid catch per unit effort (CPUE) at Grays River beach seine stations during the 2007 migration period (mouth = station 4; Johnson = station 3; Devils Elbow = station 2; and Seal Slough = station 1; see Figure 1).

releases of chum salmon and coho salmon on abundance patterns, and to identify the sizes of adipose-fin-clipped Chinook salmon and coho salmon (Figure 8). Between 2005 and 2007, 34 of 269 (12.6%) Chinook salmon could be identified as hatchery fish because their adipose fins had been clipped. Of the subyearlings, five were captured at the mouth of the Grays River, six were sampled from stations in the Grays River, one was from the Kandoll Farm restoration site, and 19 were from the Johnson Farm restoration site. We caught five yearling Chinook salmon, three of which were adipose-fin-clipped. One fin-clipped yearling was caught in a Kandoll Farm trap net, and the other two were captured at the Grays River mouth. Unclipped yearling fish were sampled from the Johnson Farm trap-net site and the Seal Slough site. Scatter plots of salmon size by day of year for 2005–

2007 show that adipose-fin-clipped fish were generally larger than unclipped fish at a given time (Figure 8). Most adipose-fin-clipped fish were present from mid-March to the first week in May, while unclipped subyearling fish could be found from March to June. Yearling fish were present from February to the beginning of May. Spring Chinook salmon were raised in the Grays River Hatchery during 2005 to 2007 but were released from net-pens located in the nearby Deep River (Figure 1). To our knowledge, no adipose-fin-clipped Chinook salmon were purposely released into the Grays River system in 2005–2007; therefore, the fin-clipped fish we observed were migrants from outside the basin.

Four of the 457 (0.8%) coho salmon sampled were identified as hatchery fish, with two caught on 5 April 2007 at Seal Slough and a third caught on 24 April

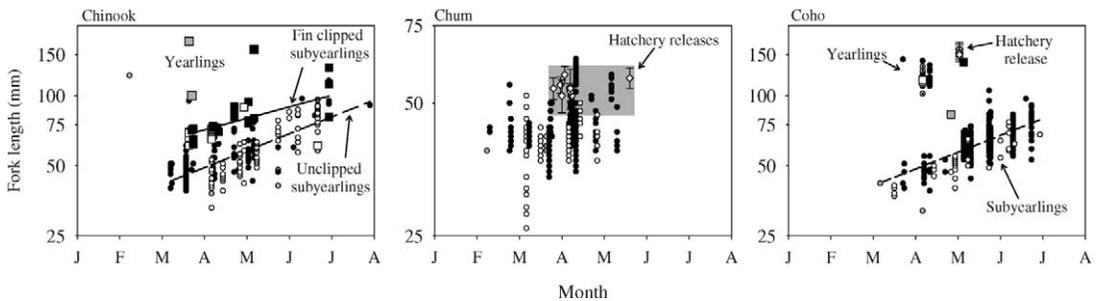


FIGURE 8.—Fork lengths (FLs; log₁₀ scale) of Chinook salmon, chum salmon, and coho salmon by month in the Grays River system, Washington, 2005–2007. Life history is denoted by symbol type (squares = yearlings; circles = subyearlings). Hatchery status is denoted by symbol size (large symbols = adipose-fin-clipped fish; small symbols = unclipped fish). Sample location is denoted by color (white = Grays River seine stations 1–3; gray = Grays River mouth; black = Kandoll Farm and Johnson Farm trap-net sites). Diamonds indicate the mean (±SD) FL of hatchery releases. Ordinate scale varies between plots.

2007 at the mouth of the Grays River. This latter fish was anomalously small, and its origin is uncertain. It is unknown whether these clipped fish were escapees from Grays River Hatchery. The final clipped fish was caught in the Johnson Farm wetland on 4 May 2006 immediately after a hatchery release and probably was of hatchery origin (Figure 8). Schools of yearling coho salmon were detected in the Kandoll Farm trap net and at Seal Slough in April 2007; these fish averaged 117.1 ± 2.5 mm FL (mean \pm SD) and were caught 26 d before the hatchery-raised fish were released (Figure 8). It is likely that these coho salmon were naturally spawned fish.

In contrast to the coho salmon data, chum salmon hatchery releases occurred around the peak migration period and we detected chum salmon of the appropriate size and timing to indicate that some hatchery-reared stock were using the restoration sites (Figure 8). However, based on size and date, the majority appeared to be naturally spawned stock.

Temperature Effects

The 7-DAM temperature time series during the January–July period of high salmonid abundance exhibited similar temporal trends within and across the years from 2005 to 2007 but varied in magnitude among stations (Figure 9a). Temperatures at the upstream station diverged in spring and remained 3–5°C lower than temperatures downstream at the Grays River mouth and Kandoll Farm stations throughout summer (Figure 9b); the lower-river locations had more similar temperatures. Each year, 7-DAM temperature exceeded the 16°C criterion earlier at the lower-river stations (May versus June) and remained above 16°C for a longer period (usually through September) than at the upstream station. Maximum daily temperature regularly exceeded 20°C at the Grays River mouth and within the restoration site but did so only occasionally at the upstream station.

We plotted salmon CPUE by 7-DAM temperature to investigate salmon distribution based on thermal regime (Figure 10). Chinook salmon abundance was greatest at 7-DAM temperatures between 11°C and 15°C, but an individual fish was found at 23°C. Chum salmon peaked at temperatures between 9°C and 12°C and were not found at 7-DAM temperatures above 16°C. Coho salmon abundance peaked between 16°C and 18°C, but individuals were also found in water with temperatures up to 23°C.

Salmon Diets

The gut contents of 56 subyearling Chinook salmon collected in 2006 and 2007 were analyzed; 13 samples were from the Johnson Farm site, and the remaining

stomach content samples were from Grays River reference seine sites (Figure 11). Chinook salmon fed on a variety of prey items, and relative diversity and %IRI varied by location. At the mouth of Grays River, the dominant prey taxa consisted of insects and amphipods *Corophium* spp., with the occasional annelid (which scored high in %W). Chinook salmon caught at the Grays River and Seal Slough seine sites fed almost entirely on insects. Chinook salmon at the Johnson Farm restoration site in 2006 had the most diverse diets and were feeding on mysids, amphipods, insects, and annelids. Calculations of %IRI indicated that insects were the most important prey type except at the Grays River mouth, where amphipods were dominant.

We analyzed gut contents from 107 subyearling and 6 yearling coho salmon collected in 2006 and 2007 (Figure 12). All but 14 of these coho salmon were captured within restoration sites. For subyearlings at all sites, insects were the primary prey (numerical abundance and %IRI). Coho salmon within restoration sites ate a variety of additional organisms, including annelids, cladocerans, amphipods, and larval fish. Coho salmon captured at Grays River seine sites ate primarily insects but also fed on arachnids, amphipods, and mysids. Six yearling coho salmon were caught together at the Kandoll Farm restoration site. They had a more balanced diet (%IRI) consisting of annelids, insects, amphipods, and fish (including chum salmon).

Genetic Analysis

In total, 166 Chinook salmon sampled in 2007 and 2008 from tidal freshwater sites and upper Grays River riverine sites were genotyped at 13 microsatellite DNA loci. Tests for deviations from Hardy–Weinberg equilibrium were significant at 6 of 13 loci in fish collected at tidal freshwater sites and at 11 of 13 loci in the sample of juveniles from the upper Grays River. These results indicate that neither set of samples represented a randomly mating population. As a consequence, the data were not suitable to include in the baseline data set used to analyze the tidal freshwater samples (see Rannala and Mountain 1997). Instead, we conducted mixture analyses on both the upper-river and wetland samples using existing baseline data (Table 2). About 33% of the tidal freshwater sample and 64% of the upper Grays River sample were estimated to be of Rogue River origin; the Rogue River stock consists of fish raised in hatcheries on the Oregon side of the Columbia River. The West Cascade Tributary fall stock group also constituted substantial proportions of both sets of samples (41% and 26% from tidal freshwater and upper Grays River sites, respectively). Genetic cluster

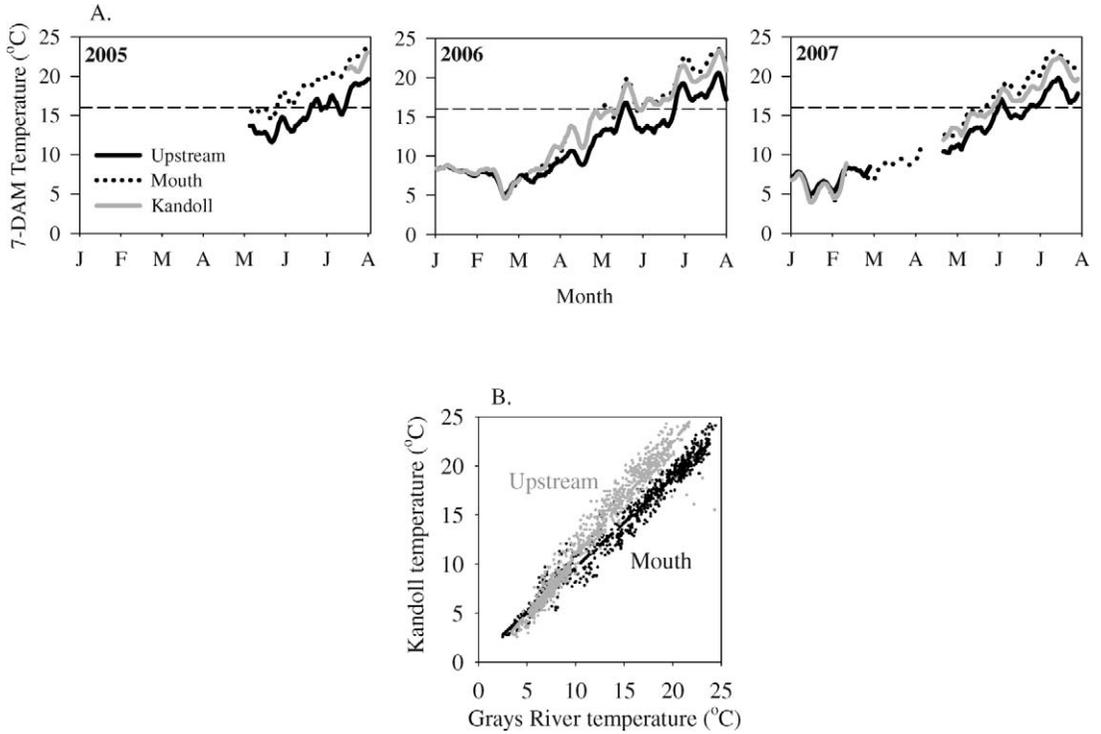


FIGURE 9.—(A) The 7-d average maximum daily (7-DAM) temperature at the Kandoll Farm restoration site and Grays River reference stations, Washington, during January–July 2005–2007; and (B) scatter plot of 7-DAM temperatures contrasting Kandoll Farm with Grays River upstream and mouth stations.

analysis revealed that while most individuals were largely of either Rogue River or Columbia River ancestry, some individuals appeared to trace ancestry to genetic sources from both rivers (Figure 13). These genetic patterns spanned all sizes of fish sampled.

Discussion

Hydraulic reconnection of diked pastureland to tidal inundation in the Grays River system dramatically increased the habitat opportunities of juvenile salmo-

nids. Tide gate removal resulted in complete reestablishment of semidiurnal tidal patterns within the former pastureland (Figure 2). Higher water levels and longer inundation times resulted in an increased surface area of wetland available to Pacific salmon, although the natural hydrology is still affected by the remaining dikes. The restoration trajectory after tidal reconnection, which includes tidal channel development and floral community response, is an ongoing and dynamic process (Cornu and Sadro 2002; Williams and Orr

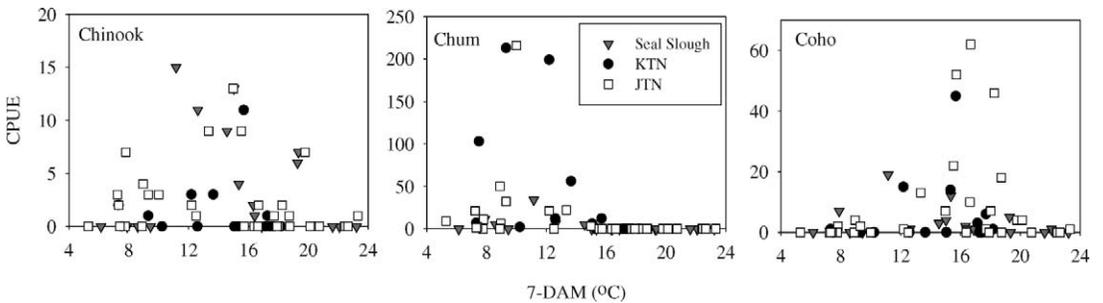


FIGURE 10.—Chinook salmon, chum salmon, and coho salmon abundance (catch per unit effort [CPUE]) plotted in relation to 7-d average maximum daily (7-DAM) temperatures in the Grays River system, Washington, 2005–2007.

Subyearling Chinook

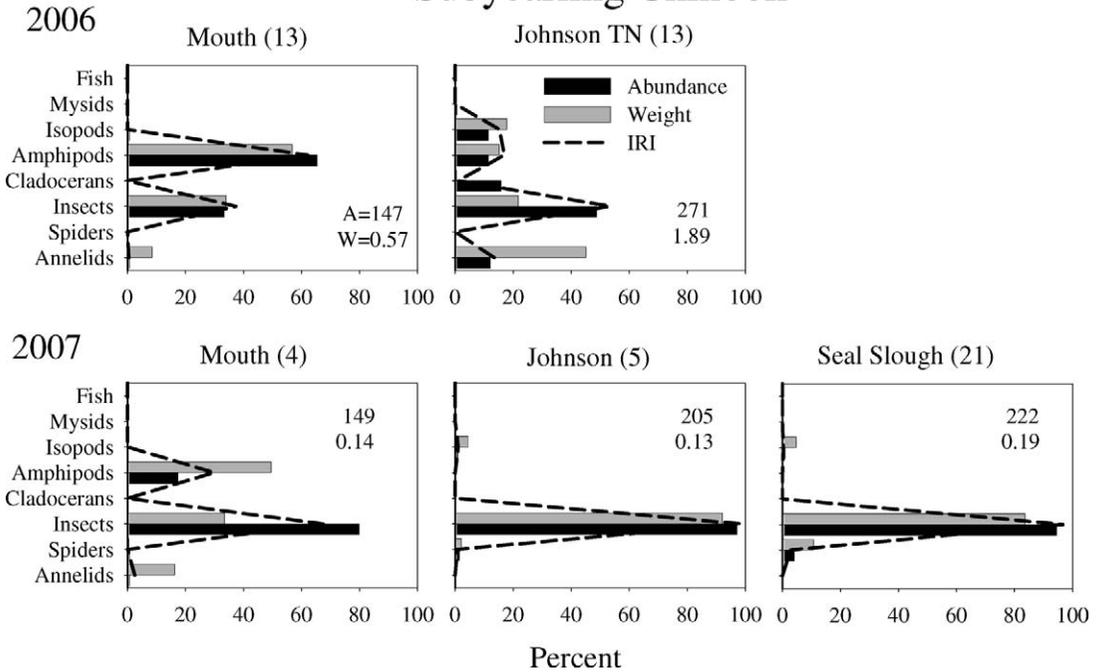


FIGURE 11.—Diet of subyearling Chinook salmon (*N* in parentheses) at Grays River, Washington, monitoring sites in 2006–2007 (*A* = number of prey items; *W* = wet weight of prey items; IRI = index of relative importance; mouth = seine station 4; Johnson = seine station 3; Seal Slough = seine station 1; and Johnson TN = Johnson Farm trap-net site).

2002), especially for sites in the Grays River floodplain that historically were forested swamps (Scott 2001; Diefenderfer and Montgomery 2008). Despite this, Chinook salmon, chum salmon, and coho salmon responded to the increased access to the Kandoll Farm and Johnson Farm restoration sites in the first migration year after tidal reconnection. Steelhead were incidental visitors to restoring wetlands. These results demonstrate that multiple salmonid species were using—and presumably benefiting from—the restoring tidal freshwater wetlands in this tributary to the lower Columbia River.

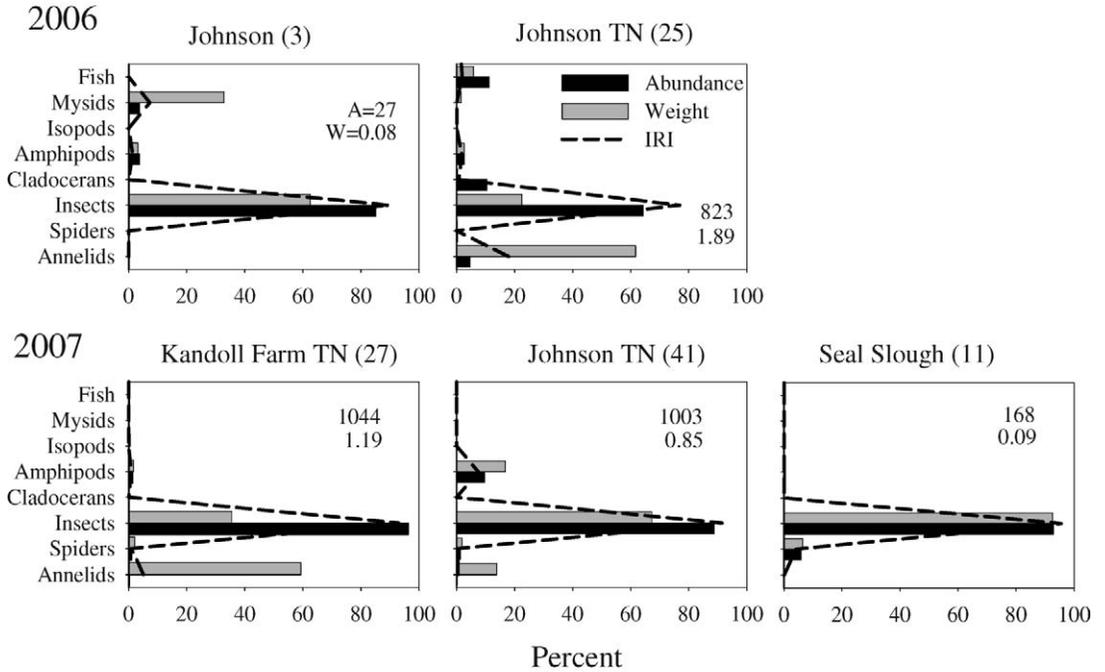
Importance of Tidal Freshwater Habitat

Salmonids have long been known to use tidal wetland habitat in the Pacific Northwest, but reports of the extent and duration of wetland use by various salmonid species and life histories continue to emerge (Shreffler et al. 1990, 1992; Miller and Simenstad 1997; Miller and Sadro 2003; Bottom et al. 2005a; Baker 2008; Teel et al. 2009). Most studies have focused on estuarine (brackish) wetlands and have demonstrated the relevance of estuaries as sites of feeding (Levings et al. 1991), refuge from high-velocity flow (Macdonald et al. 1987), and locations to facilitate physiological

adaptation to seawater (Levy and Northcote 1982). Several studies in the region have investigated salmonid opportunity and habitat use in estuarine wetland restoration projects. Shreffler et al. (1990, 1992) and Miller and Simenstad (1997) demonstrated that salmon residence and diets were similar between constructed and natural sloughs in Washington. Gray et al. (2002) and Bottom et al. (2005a) examined Chinook salmon use of natural and reconnected freshwater and estuarine marshes in the Salmon River estuary, Oregon. They observed differential use by juvenile Chinook salmon in marshes at varying stages (age) of restoration. Miller and Sadro (2003) demonstrated life history variation in habitat use and migration timing of coho salmon in South Slough, Oregon. Their analysis showed subyearling and yearling coho salmon migration patterns that included upstream migration and overwintering by subyearlings in freshwater tributary environments and limited residence in lower-estuary saline areas. Other recent studies have shown the importance of seasonally available floodplain habitat in nontidal riverine reaches (Sommer et al. 2001, 2005; Henning et al. 2006; Baker 2008).

In contrast, fewer investigations have examined habitat use in restoring tidal freshwater wetlands.

Subyearling Coho



Yearling Coho

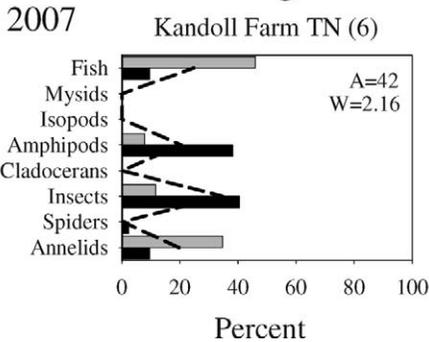


FIGURE 12.—Diet of subyearling and yearling coho salmon (*N* in parentheses) at Grays River, Washington, monitoring sites in 2006–2007 (Kandoll Farm TN = Kandoll Farm trap-net site; see Figure 11 for other abbreviations).

Tanner et al. (2002) found six species of salmonids in the newly reconnected tidal freshwater habitat near the head of salinity intrusion at Spencer Island, Washington. Baker (2008) reported the presence of Chinook salmon and coho salmon in several tidal freshwater wetlands in the Columbia River. Teel et al. (2009) found that spring and fall Chinook salmon subyearlings were present in the floodplain of the Willamette River, Oregon. Our study documents the presence of Chinook

salmon, chum salmon, and coho salmon and the incidental occurrence of steelhead in wetland habitat undergoing restoration. In the Cathlamet Bay portion of the Columbia River, Bottom et al. (2008) and Roegner et al. (2008) documented extensive Chinook salmon use of tidal freshwater emergent, forested, and scrub-shrub habitats. It is clear that migrating salmon use the full spectrum of wetland types, which range from nontidal river floodplains and tidal freshwater

TABLE 2.—Genetic estimates of the proportional stock composition and 95% confidence intervals (CIs) for 37 juvenile Chinook salmon sampled at Grays River, Washington, tidal freshwater sites in 2007 and 129 migrating juveniles sampled in the upper Grays River in 2008. Because six stock groups from the interior Columbia River basin and Willamette River were in low abundance, their estimates were combined. Confidence intervals were from 100 bootstrap resamplings of the baseline and mixture genotypes.

Stock group	Tidal freshwater		Upper Grays River	
	Proportion	CI	Proportion	CI
Rogue River	0.326	0.140–0.491	0.635	0.492–0.696
West Cascade Tributary, fall	0.412	0.127–0.508	0.256	0.140–0.354
West Cascade Tributary, spring	0.155	0.038–0.330	0.083	0.031–0.164
Spring Creek group, Tule, fall	0.108	0.000–0.199	0.008	0.000–0.050
Interior Columbia River basin and Willamette River	0.000	0.000–0.177	0.019	0.004–0.121

habitat of varying floral composition to estuarine marsh systems. Of these, tidal freshwater wetland habitats were once extensive in the lower Columbia River and appear to offer great promise as targets for restoration (www.lcrep.org/restoration-inventory).

Salmon Abundance and Life History Diversity

In the Grays River system, we found that habitat use varied by species and life history stage. Only three steelhead and nine cutthroat trout were captured during the study period (Table 1), and all were large (>150 mm FL) age-1 and older fish. Overall, Chinook salmon were less abundant than either chum salmon or coho salmon, and their presence in reconnected wetlands declined to low levels after 2005 (Table 1). This may be a consequence of the reduced numbers of spawning adults in the system at present (LCRCB 2004). Chinook salmon had a broad temporal distribution (February– July), with a variable peak in abundance during March through early May (Figures 5, 6). Of all Chinook salmon sampled in 2006–2007, 68% were fry-sized fish, 31% were fingerling-sized subyearlings, and one fish was a yearling (Figures 3, 4). In contrast, the size frequency of Chinook salmon sampled by beach seine in shallow-water locations in the Columbia River main stem had a pronounced peak between 70 and 90 mm FL in saline areas and a wider peak distribution between 45 and 70 mm FL in tidal freshwater sites (Roegner et al. 2008).

In contrast, chum salmon dominated the salmonid catch numerically, but their presence in the system was concentrated to a 2- to 3-week period, with a peak in March or April (Figure 6). Although all chum salmon were less than 65 mm, 80% were recently emerged fish smaller than 45 mm FL (Figures 3, 4). Based on timing and the comparatively large size of hatchery fish, most chum salmon we sampled were probably of natural origin (Figure 8). The mean size of chum salmon released from the Grays River Hatchery ranged from 52 to 58 mm FL; these sizes are larger than 91% of the chum salmon captured in either restored or reference sites. In 2005, hatchery releases of chum salmon in late April coincided with catches at the Johnson Farm site. In 2006, chum salmon releases in late March and early April coincided with peak abundance of chum salmon at the Kandoll Farm site but not at the Johnson Farm

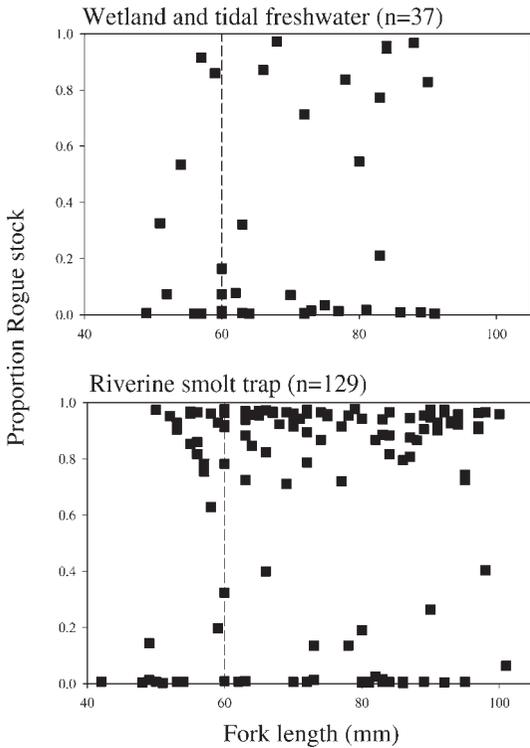


FIGURE 13.—Estimated proportion of Rogue River stock ancestry in Chinook salmon sampled in the Grays River system, Washington, 2007 and 2008. Columbia River ancestry is 1.0 minus the Rogue River ancestry proportion. Individuals were ordered by size, with the dashed line at 60 mm fork length delineating fry from fingerlings.

site or Seal Slough site (Figures 5, 8). A later release of hatchery chum salmon in April 2006 was not observed in our samples. In 2007, peak chum salmon presence preceded hatchery releases in both restoration sites, while catches in Seal Slough coincided with hatchery releases. Punctuated abundance during the 2007 migration in the Grays River (Figure 7) and little to no increase in size with time (Figure 8) indicated rapid migration of chum salmon to the Columbia River estuary. It appeared that hatchery releases generally coincided with the peak migrations of wild stocks, all of which used the Grays River system for a few weeks at most before exiting to the estuary. Similarly, in both Duncan Creek, Washington, and the Pierce–Ives Island complex below Bonneville Dam (the other major chum salmon spawning areas in the Columbia River), 90% of chum salmon fry migrated over an approximately 25-d period ranging from March to April (Hillson 2004, 2009; Tomaro et al. 2007). The size-frequency distribution of chum salmon captured in shallow-water locations in the Columbia River main stem ranged from 35 to 80 mm FL, with peaks at around 40 mm, and chum salmon could be found during February through the end of May (Roegner et al. 2008). These data suggest that although the majority of chum salmon in the Columbia River system migrate to the ocean as fry, some individuals grow to fingerling size before emigrating to the sea. The trap-net data show that significant numbers of naturally produced chum salmon were using reconnected tidal wetlands in the Grays River system during the migration period (Figure 6).

Coho salmon were mainly present in the Grays River system during April to June, with peak abundance around 1 May (Figure 7). Coho salmon had the most variable life history pattern, with both subyearlings and yearlings present in the system. Of the subyearlings, 59% were fry and 33% were fingerling-sized fish (Figures 3, 4). Eight percent of coho salmon were yearlings, and these were most abundant in April, whereas hatchery releases occurred on 1 May of each year (Figure 8). In 2007, the mean size at release for hatchery coho salmon ranged from 150 to 153 mm FL, which was larger than all of the yearling fish we sampled (110–140 mm FL). Only four coho salmon were adipose-fin-clipped, and only one had temporal synchrony with a hatchery release (Figure 8). Therefore, most coho salmon we sampled were probably of natural origin, with both subyearling and yearling life history stages using the restoration sites.

Temperature Regime and Salmon Abundance

One potential benefit of hydrological reconnection is to improve water quality conditions of degraded

systems. While oxygen concentrations did not appear to be limiting in the Grays River system during January–July (data not shown), the 7-DAM temperature at the Kandoll Farm restoration site did exceed the critical threshold of 16°C in May or June (Figure 9). The temperature time series at Kandoll Farm closely tracked that at the Grays River mouth, suggesting a tidal hydrological connection with the Columbia River. In contrast, temperature of water entering the floodplain from upstream (and higher elevation) was 3–5°C cooler than that at the Grays River mouth from March through summer. The majority of chum salmon were found during a 7-DAM temperature regime between 9°C and 12°C (Figure 10), and they exited the system at 7-DAM temperatures less than 16°C. Chinook salmon individuals were broadly distributed with temperature, but the majority were present at 7-DAM temperatures of 11–15°C. However, several individuals were captured in June, when the 7-DAM temperature was 19°C, and one fish was captured at 23°C. Yearling coho salmon in 2007 were only found in April (7-DAM temperatures of 10–12°C). Subyearling coho salmon were also widely distributed, with peak abundance occurring when 7-DAM temperatures were between 16°C and 18°C, but individual coho salmon were also found at temperatures up to 23°C. These higher temperatures can be stressful to salmonids (McCullough 1999). Increasing water temperature influences juvenile salmonid migration by stimulating movement downstream to the estuary and ocean (Sauter et al. 2001) as well as upstream to thermal refugia (Miller and Sadro 2003). Welsh et al. (2001) only found coho salmon in streams with mean weekly maximum temperatures less than 18.1°C. Henning et al. (2006) concluded that high temperature and low oxygen levels influenced emigration of salmonids from seasonally flooded areas, and Baker (2008) found that temperature, water level, barometric pressure, and lunar phase best explained juvenile salmon movements in seasonally inundated wetlands during winter and spring. Reconnected wetlands in the Grays River system, as in other wetlands that have been investigated, appear to support juvenile Pacific salmon during a seasonal window, probably based in part on salmon temperature tolerance.

Salmon Diets

Juvenile salmon are opportunistic feeders that exploit a variety of neustonic, planktonic, and epibenthic prey (e.g., Healey 1980; Levings 1994; Gray et al. 2002). However, insects produced in wetlands are clearly a dominant prey type for salmon foraging in many habitats, including fluvial, tidal freshwater, and estuarine environments. In our study,

we found diet differences between sample locations (based on the assumption that fish diets reflect prey availability at the location of capture). For Chinook salmon and coho salmon, insects—primarily dipterans—were important prey items at all sites (Figures 11, 12). At least 40 insect family taxa were identified, and 49% of individual insect prey items were chironomid larvae, pupae, or adults. Previous work indicates that insects are also the primary prey of chum salmon fry (Shreffler et al. 1992; Tanner et al. 2002). Salmon in the Grays River fed almost entirely on insects; the exception was that salmon caught at the Grays River mouth also ate epibenthic amphipods. However, Chinook salmon and yearling coho salmon caught in reconnected wetlands had consumed a wider diversity of prey than did fish sampled from the Grays River. Fish at wetland sites ate more annelids and fish, and although the abundance of these prey items in stomachs was relatively low, the prey items were large and probably of high total caloric value (Ciancio et al. 2007). While insects are an energy-rich resource, larger prey items may be of higher value to predators than more numerous smaller prey, which require increased foraging time. Sommer et al. (2001) found that juvenile Chinook salmon had higher consumption and faster growth in floodplain habitat than in river channel habitat, with dipterans being their main prey. Miller and Sadro (2003) reported that the condition factor was higher for coho salmon that fed in estuarine marshes than for those that fed in adjacent channel habitat in South Slough, Oregon. Tanner et al. (2002) noted high insect production in newly reconnected marshes in the Snohomish River, Washington. As an interesting species interaction, yearling coho salmon caught at the Kandoll Farm sampling site in March 2007 were feeding on chum salmon, which indicates that wetlands do not necessarily provide a predator refuge function for all species. These previous studies and our data indicate that restoring wetland habitats can benefit salmonids by providing a greater variety of food items than adjacent aquatic systems.

Chinook Salmon Origins

The restoration of wetland habitats in the Grays River potentially benefits not only locally produced salmonids but also juvenile emigrants from other Columbia River basin sources. Previous reports have shown that juvenile Chinook salmon do inhabit nonnatal streams and wetlands during migration (Murray and Rosenau 1989; Scrivener et al. 1994; Bradford et al. 2001; Teel et al. 2009). We examined juvenile Chinook salmon sampled in wetland sites for the presence of hatchery marks to learn whether juvenile salmon from outside the basin were using

the intertidal and channel habitats undergoing restoration. Overall, 12.6% of the Chinook salmon sampled were adipose-fin-clipped, and the majority were found in reconnected marshes (Figure 8). Releases of hatchery Chinook salmon into the Grays River ceased in 1998; this suggests that the marked fish were migrants from outside the Grays River system. However, despite this compelling evidence, the Grays River Hatchery continues to rear spring Chinook salmon for release in other basins, and therefore we cannot rule out the possibility that some of these marked hatchery fish (which were not identified genetically) had escaped from the Grays River Hatchery. Because we did not detect coded wire tags or passive integrated transponder tags in the sampled fish, we could not distinguish possible migrants from unintentional hatchery releases.

Genetic data can also be used to detect migrants that enter juvenile rearing areas. For example, a recent microsatellite DNA study documented the migration of juvenile Chinook salmon into Willamette River wetland floodplain habitats from areas outside of the river (Teel et al. 2009). Our approach in the present study was to incorporate genotypic data from individuals known to be of Grays River origin (i.e., collected from the smolt trap) into the Columbia River basinwide baseline data set to identify the stocks captured at wetland restoration sites. Genetic analysis of the wetland samples using the existing regional DNA baseline showed that individuals were from diverse genetic sources. However, analysis of the smolt trap samples (progeny of naturally spawning salmon) revealed that the Grays River population is itself a mixed stock derived from those same genetic sources; because the population is not in genetic equilibrium, it could not be used as baseline data (see Rannala and Mountain 1997). The GSI analysis therefore did not provide additional evidence that juvenile migrants from outside the Grays River system were using the tidal wetland habitats.

On the other hand, the genetic analysis of naturally produced juveniles sampled in the upper watershed does provide new information relevant to salmon recovery planning for the Grays River. This system has been identified as a lower Columbia River natural refuge area for fall-run Chinook salmon (LCFRB 2004). We found that the Grays River fall-run population is mainly an admixture of fish descended from either Columbia River or Rogue River stock and includes individuals with ancestry that is traceable to both stocks (Figure 13). The Columbia River component was estimated to be largely from the West Cascade Tributary fall-run stock group. It is not known whether this represents the native genetic signature for

the Grays River or reflects previous releases of hatchery fish in the Grays River. For several decades beginning in the 1950s, numerous out-of-basin Chinook salmon stocks were out-planted in the Grays River (Myers et al. 2006). The hatchery releases were primarily from lower Columbia River fall-run sources, including stock derived from the Cowlitz, Kalama, and Lewis rivers, which are tributaries in the western Cascade Range (Myers et al. 2006). However, we estimated very little contribution to our samples from the Spring Creek group Tule fall stock, which was derived from fish in Columbia River gorge tributaries. This lack of genetic affinity is surprising because of the extensive transfers of fall Chinook salmon to the Grays River from Spring Creek National Fish Hatchery and genetically similar stock from Bonneville, Abernathy, and Elochoman hatcheries (Myers et al. 2006). The predominance of the Rogue River component in the Grays River is noteworthy since the origin of these fish is the south Oregon coast, and their present distribution reflects recent hatchery effects. Our finding that few fish are of intermediate ancestries (Figure 13) is consistent with predictions of displacement rather than introgression as the outcome of colonization by an anadromous salmonid of a lineage distinct from the indigenous population (Utter 2001). Although Rogue River fish were never purposefully introduced into the Grays River system, Rogue River fall Chinook salmon eggs were transferred from the Oregon coast to Big Creek Hatchery in 1982 to initiate a project that would provide fishing opportunities in off-channel areas of the Columbia River (North et al. 2006). Straying of adult fish used in this program almost certainly explains the substantial Rogue River component now found in Chinook salmon that are naturally produced in the Grays River. Because of excessive straying of the program's adults into tributaries of the lower Columbia River, propagation of the Rogue River stock was moved downriver into the Klaskanine River, Oregon, beginning with the 1996 brood (North et al. 2006). Currently, juveniles of the Rogue River stock are released from net-pens in Youngs Bay near Astoria, Oregon (North et al. 2006), and in recent years some adult fish from those releases have been observed in spawning areas of the Grays River (T. Hillson, WDFW, personal communication). Additional studies of the origins of spawners in the Grays River and the population's genetic structure are clearly warranted. Successful recovery of Chinook salmon will require long-term opportunity for the population to become genetically adapted to the local habitats (NRC 1996), including habitats in wetlands that are restored to support juvenile rearing and migration.

Benefit of Restoration Activities

Full restoration of sites like Kandoll Farm and Johnson Farm from cattle pastures to tidal swamps will take decades at a minimum. However, reconnection of these sites to tidal inundation allowed an immediate increase in the opportunity for juvenile salmonids of several species and life history types to access productive wetland habitat. In the Grays River system, this includes rearing habitat for highly threatened Columbia River chum salmon. Importantly, evidence from adipose-fin-clipped Chinook salmon suggests that nonnatal fish are also using newly available ecosystems. This potentially broadens the contribution of restoration sites to the wider salmon population. While we cannot at present ascertain the relative performance of these fish or the potential survival benefits accrued in restoring wetlands, results from these initial few years are compelling and warrant continued study. Further, tidally influenced wetland systems function as both sources and sinks of materials, and they produce and export material, such as insect prey, to the wider ecosystem. This material flux is an important component for the cumulative effects of individual restoration projects on the overall system (Thom et al. 2008). Reversing the habitat fragmentation and hydraulic isolation that now exist in most tidal freshwater reaches of the lower Columbia River and its tributaries will probably benefit a variety of salmon stocks during juvenile migration.

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