Effects of subsidies from small anadromous Pacific salmon populations on stream and riparian food webs are mediated by channel gradient

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Abstract: Ecological effects of migratory animal populations on ecosystems can be significant, but these impacts may be modified by other environmental factors, especially when migratory populations are small. This study implements a before–after (BA) impact design and takes advantage of natural, reach-scale variation in channel gradient to explore how environmental context influences the response of stream and riparian ecosystems to a small, recolonizing population of anadromous Pacific salmon. After a 102-y absence, adult Pacific salmon began naturally recolonizing the Cedar River in northwest Washington, USA, following installation of a fish passage at the Landsburg Dam in 2003. For our BA analysis, we sampled water chemistry, stream biofilm, aquatic macroinvertebrates, and fish assemblages before (1999–2003) and after (2008, 2015) fish passage installation in 3 study reaches above the dam. We also conducted an above-dam reach-scale ($n = 7$) comparison in 2015, for which we sampled the same metrics, as well as riparian spider and bird assemblages, across 500-m-long sections in each study reach, spanning a total of 18 km of river habitat that varied in both adult salmon inputs and channel gradient. The BA and reach-scale analyses both indicated that salmon biomass inputs were associated with increases in aquatic macroinvertebrate taxa richness and the densities of 2 primary consumers (*Glossosoma* spp. and Chironomidae larvae). Stable isotope analysis indicated that adult salmon subsidies were also associated with dietary changes in pelagic-foraging predators (the non-anadromous resident Rainbow Trout *Oncorhynchus mykiss* Walbaum, 1792) and benthic-foraging sculpin (*Cottus* spp.). The reach-scale analysis also showed that channel gradient best explained variation in several metrics, including a negative association with adult Chinook Salmon inputs ($r = -0.70$, $p = 0.08$) and bird diversity ($r = -0.91$, $p < 0.01$). We found that channel gradient was a key driver of observed biotic variation through its effects on channel morphology and complexity, factors that influence biotic assemblages and ecosystem processes. Overall, this study provides a holistic assessment of the ecosystem impacts of a small recolonizing salmon population while accounting for spatial variation in stream geomorphology. Understanding these dynamics is important for river conservation in the Pacific Northwest as migratory barriers are increasingly removed.

Key words: salmon, freshwater, resource subsidies, geomorphology, recolonization, macroinvertebrates, birds, spiders, biofilm, Pacific Northwest

Resource subsidies deposited by migratory animals can affect the ecosystems through and to which they travel, but these ecosystem impacts are often variable and depend heavily on within-site variability (Deegan 1993, Varpe et al. 2005, Bauer and Hoye 2014, Subalusky and Post 2019). Many studies have demonstrated that the net gain of nutrients and

organic matter from the excretions, gametes, and carcasses of anadromous Pacific salmon (*Oncorhynchus* spp.) modifies energy, nutrient, and trophic dynamics in stream and adjacent riparian ecosystems (e.g., Quinn et al. 2009, Darimont et al. 2010, Collins et al. 2016, 2020). In riparian habitats, salmon-derived organic matter can benefit riverbank vegetation. For example, stable isotope studies have shown that marine-derived N from salmon carcasses can be assimilated by riparian plants (Helfield and Naiman 2001, Reimchen et al. 2003, Bartz and Naiman 2005), potentially increasing their growth rates (e.g., Helfield and Naiman 2001). Within the river itself, salmon carcasses may provide nutrients that increase the biomass and density of certain macroinvertebrates (Naiman and Latterell 2005, Morley et al. 2016). Many of those aquatic macroinvertebrates emerge from the water at maturity, providing food for and increasing the densities of terrestrial consumers such as birds (Gende and Willson 2001, Iwata et al. 2003, Obermeyer et al. 2006, Jackson and Sullivan 2015, Tonra et al. 2015). Alternately, spawning salmon also scour the riverbed and increase turbidity, which can decrease macroinvertebrate biomass in streams with fine inorganic substrata (Moore et al. 2008, Janetski et al. 2009, Holtgrieve et al. 2010, Verspoor et al. 2010).

Physical habitat characteristics can mediate the impacts of salmon resource subsidies on stream and riparian ecological processes (Montgomery 1999, Janetski et al. 2009). For example, channel gradient, or steepness, can influence sediment, organic matter, and foodweb dynamics (Montgomery and Buffington 1997, Montgomery 1999, Bellmore and Baxter 2014). Channel gradient also influences scouring and substrate mobility, and Pacific salmonid spawning distributions often track changes in gradient (Montgomery 1999). However, there is limited evidence for how gradient and other stream attributes that operate at broad spatial scales (e.g., water temperature) mediate the effects of salmon nutrient subsidies (Armstrong et al. 2010, Collins and Baxter 2014). For instance, the role of stream geomorphic conditions on the ecological effects of spawning salmon populations in natal watersheds is critically understudied (Subalusky and Post 2019, but see Holtgrieve et al. 2010).

Salmon populations have declined severely (up to 90% relative to pre-European settlement) in the Pacific Northwest (Nehlsen et al. 1991, Gresh et al. 2000). Efforts to remove artificial barriers, such as dams and culverts, or install fish passage facilities have become increasingly common, and these restoration projects are critical for restoring salmon populations and the nutrient and biomass subsidies that anadromous salmon bring to upstream food webs (Thorstad et al. 2007, Kiffney et al. 2009, 2014). However, the recovery of salmon populations is often slow, and ecological and trophic responses to these small and recovering populations may be subtle. In such cases, other variable habitat features, such as geomorphology, may strongly mediate ecosystem response. It is critical to understand how hetero-

geneous habitats interact with recolonization so we can better comprehend how the recovery of salmon populations affects aquatic and terrestrial food webs.

In this study, we took advantage of a natural experiment in the Cedar River in western Washington, USA, to investigate the effects of reintroducing salmon resource subsidies into formerly blocked aquatic and riparian habitats. Following installation of a fish passage facility at Landsburg Dam in 2003, anadromous Pacific salmon (Coho Salmon *Oncorhynchus kisutch* Walbaum, 1792 and Chinook Salmon *Oncorhynchus tshawytscha* Walbaum in Artedi, 1792) recolonized ~33 km of the river above the dam after a 102-y absence (Anderson and Quinn 2007). Prior experiments in the watershed indicate that secondary production in the Cedar River food web is limited by the availability, and possibly the concentration, of adult salmon carcasses (Cram et al. 2011, Kiffney et al. 2014, 2018a). For example, the addition of salmon carcasses (0.6 kg/m^2) to flow-through stream mesocosms increased benthic macroinvertebrate density, drift rates, and body size, as well as summer growth of juvenile Coho (Kiffney et al. 2014), with more modest impacts during autumn and winter (Cram et al. 2011, Kiffney et al. 2014).

Adult Pacific salmon are naturally enriched (i.e., higher values) in the heavier isotopes ^{13}C and ^{15}N relative to most freshwater sources (Kline et al. 1993). These differences can be used to estimate the biological assimilation by stream organisms of nutrients accrued in the Pacific Ocean and released during adult salmon reproduction and carcass decomposition (Kline et al. 1993, Chaloner et al. 2002, Kiffney et al. 2018b). Stable isotope analysis has shown increased assimilation of marine-derived C and N by macroinvertebrates and fishes in experimental streams, indicating that salmon carcasses represent a key energetic pathway for the Cedar River food web (Kiffney et al. 2014, 2018a). Thus, comparing natural abundance levels of C and N of resident fishes before and after salmon recolonization, as well as above and below a formerly blocked dam, can demonstrate whether reestablishment of anadromous salmon above a dam leads to ecosystem conditions (e.g., isotopic composition) comparable to a reference site with long-term exposure to salmon inputs (Lundberg and Moberg 2003, Soulé et al. 2003).

To understand the effect of salmon recolonization on aquatic and riparian habitats in the Cedar River, we tested the hypothesis that after restoration of fish passage at Landsburg Dam, resource inputs from spawning Pacific salmon would positively covary with biotic assimilation of marine-derived energy, population productivity, and taxonomic richness in stream and adjacent riparian habitats. Specifically regarding the assimilation of marine-derived energy, we hypothesized that 1) the tissue of resident Rainbow Trout (*Oncorhynchus mykiss* Walbaum, 1792) and sculpin (*Cottus* spp.) would be enriched in marine-derived (i.e., heavier) isotopes of C and N following salmon recolonization, and 2) resident Rainbow Trout and sculpin from below

Table 1. Environmental characteristics of study reaches above Landsburg Dam, Cedar River, Washington, USA. Water temperature is given as mean (min, max). Wood cover recorded during the fish survey is given as mean (±SD).

Reach	Distance from Landsburg Dam to reach midpoint (km)	Water temperature (°C)	Channel gradient (%)	% boulder	Wood cover (m^2) fish survey	Wood cover bird survey (no./reach)
CR1	2.5	10.5 (7.4, 13.5)	0.5	1	45.0 (103.0)	42
CR3	8.0	10.0 (7.3, 12.4)	1.2	30	3.7 (10.0)	2
CR4	9.9	11.0 (7.7, 14.0)	0.5	1	32.0 (119.0)	19
CR5	11.0	10.4 (7.0, 13.4)	0.9	23	2.5 (7.5)	1
CR6	12.4	11.0 (8.2, 13.1)	0.8	4	18.0 (42.0)	15
CR7	14.2	9.0 (5.0, 13.0)	1.1	10	10.2 (32.0)	8
CR8	17.7	12.8 (8.0, 18.0)	0.7	2	11.0 (41.0)	13

the dam would be enriched in heavier C and N isotopes compared with individuals from above the dam because anadromous salmon populations below the dam are larger and have been contributing nutrients for much longer.

However, the salmon population in the Cedar River remains small, and densities of adult Pacific salmon above the dam are lower than levels where ecological effects are typically detected (~0.1–1.0 kg/m^2; e.g., Janetski et al. 2009, Kiffney et al. 2018a). Therefore, we expected carcass effects on local food webs to be localized and weak as well as influenced by habitat characteristics. One such characteristic is channel gradient, which partially determines stream power and influences channel morphology, stream hydrology, energy and nutrient budgets, and biotic assemblages (Halwas et al. 2005, Bellmore and Baxter 2014). We predicted that local channel gradient would mediate focal responses to salmon resource subsidies. In addition, biotic changes in the Cedar River food web following salmon recolonization could result from weather-driven changes in temperature and discharge regimes, which also act as key drivers of riverine assemblages and ecosystem processes (Poff 1997) and potential drivers of differences in stable isotope composition (Yanes et al. 2009). To account for this, we also identified patterns in summer temperature and discharge to as-

sess their potential influence on observed ecological effects following salmon recolonization.

METHODS

We used a 2-pronged approach to test our hypotheses. First, we conducted a before–after (BA) impact study above the dam to compare: 1) total N (TN) and total P (TP) in stream water, 2) benthic biofilm biomass and macroinvertebrate and fish populations, and 3) natural abundance levels of stable C and N isotope values in tissues of resident fish populations before and after salmon recolonization. Second, we conducted a field survey to compare 7 distinct geomorphic reaches of the Cedar River in July and August 2015, 12 y after recolonization. We measured the same suite of biotic metrics as in the BA study, as well as riparian spider and bird assemblages. We conducted this survey above the dam where adult Chinook Salmon inputs ranged 17.7-fold (1.4–24 kg km^{-1} y^{-1}) along with variation in other environmental attributes (Tables 1, 2).

Study area

The study area (Fig. 1) lies within the protected Cedar River Municipal Watershed, which is located 77 km southeast

Table 2. Year sampled, presence (N = no, Y = yes), duration of presence of anadromous Pacific salmon, sample location (see Fig. 1), and number and size range of fish sampled to test whether natural abundance levels of C and N isotopes in resident fish populations varied with Pacific salmon populations. In 2008, salmon had been present in CR1 for 6 y, whereas salmon below the dam were continuously present.

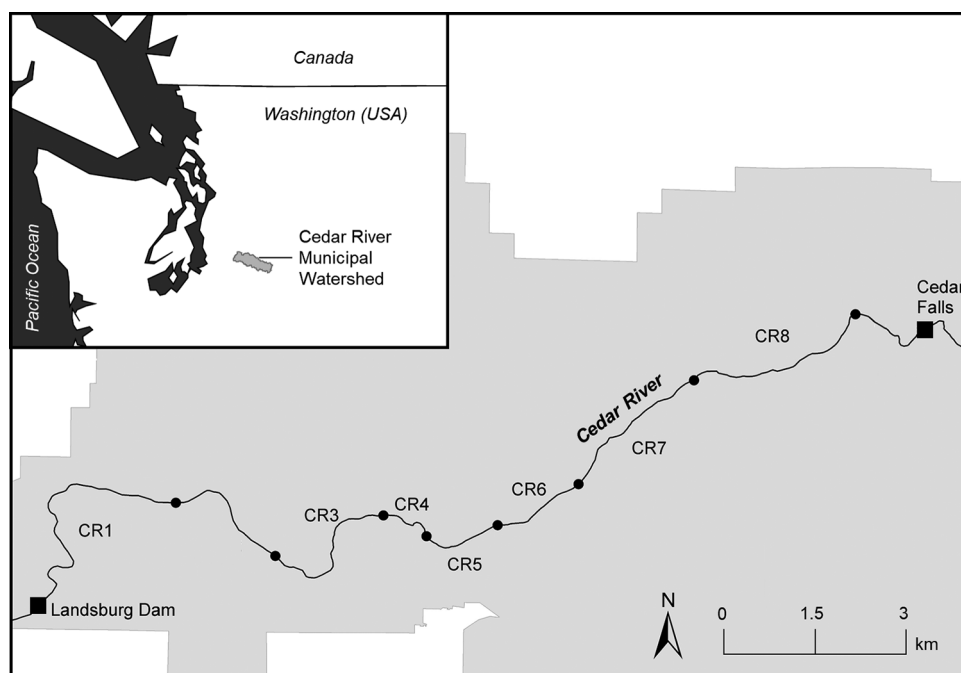| Year	Salmon	Sample site	Sculpin		Rainbow Trout	
			n	Size range (mm)	n	Size range (mm)
2000	N	CR1	5	60–65	13	94–330
2001	N	CR1	5	57–105	16	131–275
2008	Y (6 y)	CR1	4	67–130	18	152–340
2008	Y (continuous)	Below dam	4	67–124	13	125–337

Figure 1. Map of study area including 7 study reaches (CR1, CR3–CR8), defined by solid circles, and location of Landsburg Dam and Cedar Falls (natural barrier), represented by solid squares, within the Cedar River Municipal Watershed (shaded area), Washington, USA.

of Seattle, Washington, USA. The study sites are within the Western Hemlock Zone (Franklin and Dyrness 1973, City of Seattle 2000), which is dominated by mixed-age stands (~90–450 y old) of temperate coniferous forest (Kiffney et al. 2006). The mainstem Cedar River above the dam is relatively confined, 15 to 30 m wide (wetted width), sunlit, and rocky bottomed, with cool summer temperatures (Table 1) and relatively low levels of dissolved and total nutrients (Kiffney et al. 2002, 2006).

In 1901, Landsburg Diversion Dam was built on the Cedar River, blocking the upstream migration of anadromous Coho and Chinook Salmon and reducing available habitat in the catchment by about 60%. In 2003, a fish passage facility installed at the dam allowed multiple fish species access to upstream freshwater habitat (Anderson and Quinn 2007). To establish baseline conditions before recolonization by anadromous salmonids, we collected data prior to fish passage installation on nutrient (N, P) water chemistry, stream algae and macroinvertebrates (biomass, abundance, composition, isotopes), and fishes (density, composition, growth, stable isotopes) across available freshwater habitat above the dam. Here, we present data collected from 3 geomorphic reaches (CR1, CR6, and CR8), as well as directly below the dam.

Stream and riparian assemblages Stream and riparian assemblages in the study area are representative of coastal mountain river food webs of the region (Naiman and Bilby 1998). Macroinvertebrate communities are dominated by chironomid midges (Diptera:Chironomidae), mayflies (Ephemeroptera:Baetidae, Heptageniidae, Ephemerellidae), and caddisflies (Trichoptera:Limnephilidae, Glossomatidae, Hydropsychidae) that represent a range of functional feeding groups (e.g., Kiffney et al. 2014; PMK, National Marine Fisheries Service, unpublished data; Table S1). Resident salmonids above the dam primarily consist of Rainbow Trout and Coastal Cutthroat Trout (*Oncorhynchus clarkii clarkii* Richardson, 1836). Following installation of the fish passage facility, the fish assemblage above Landsburg Dam added 3 new species—anadromous Coho and Chinook Salmon and resident Mountain Whitefish (*Prosopium williamsoni* Girard, 1856; Table 2). Recent surveys indicate that juvenile Coho account for about 78% of total salmonid density above the dam in summer (PMK, unpublished data). In addition to salmonids, multiple species of sculpin, which are small benthic fishes that primarily consume benthic macroinvertebrates but will also opportunistically consume small fishes and salmon eggs (Swain et al. 2014), comprise a major component of the Cedar River fish assemblage in both abundance and biomass (Kiffney et al. 2002, Naman et al. 2014).

In the riparian zone, the most common aquatic-prey specialist spiders belong to the Tetragnathidae family. Common piscivorous birds include Belted Kingfisher (*Megaceryle alcyon* Linnaeus, 1758), Osprey (*Pandion haliaetus* Linnaeus, 1758), and Bald Eagle (*Haliaeetus leucocephalus* Linnaeus, 1766). Two of the most abundant songbirds are the American Dipper (*Cinclus mexicanus* Swainson, 1827) and

the American Robin (*Turdus migratorius* Linnaeus, 1766; Tables S1, S2).

Estimating adult salmon inputs   We estimated total annual adult salmon inputs (kg) above Landsburg Dam based on counts of adult Coho and Chinook salmon dispersing through the fish passage each year (Anderson et al. 2015, Unrein et al. 2018) and mean mass of adult Coho (2.4 kg) and Chinook (4.7 kg) salmon (Dr Thomas Quinn, University of Washington, unpublished data; Shaul et al. 2007). Estimates of reach-scale adult Chinook Salmon biomass inputs (kg km^{-1} y^{-1}) above the dam were derived from adult Chinook nests, or redds, identified by boat each autumn from 2003 to 2015 (Burton et al. 2013). Surveys primarily focused on identifying Chinook redds but also identified Coho redds for several years (Burton et al. 2013, Anderson et al. 2015). We based our reach-scale adult salmon flux rates on Chinook redds because they were collected across the entire time series, and concurrent Coho and Chinook redd surveys (2003–2008) showed the distribution of Coho redds strongly overlapped with adult Chinook redds ($r = 0.95$, $p < 0.01$, $n = 8$ y; Anderson et al. 2015). In estimating reach-scale variation in adult Chinook flux, we assumed each redd consisted of 2 individuals and there was no loss of carcasses outside the reach (e.g., Quinn et al. 2009). Because we based our flux rates on adult Chinook only, our reach-scale estimates provide a relative index of the spatial variability in adult salmon flux rather than an absolute rate.

BA study

Study design   Prior to the installation of a fish passage facility, 7 study reaches were established, spanning a total of ~18 km of the mainstem Cedar River and adjacent riparian forest (Fig. 1). Reaches (CR1, CR3, CR4, CR5, CR6, CR7, and CR8) were distinguished by natural variation in channel gradient, location of tributary junctions, valley width, and substrate composition (Kiffney et al. 2006, 2009). The BA study consisted of 2 components: 1) measurements of stream nutrients and biological assemblages before (1999–2003 for nutrients, 2002 for other metrics) and after (2013–2015 for nutrients, 2015 for other metrics) salmon recolonization from CR1, CR6, and CR8; and 2) ratios of C (^{13}C/^{12}C) and N (^{15}N/^{14}N) stable isotopes measured in tissue of trout and sculpin collected from CR1 and directly below the dam (where salmon migration had not been interrupted) before (2000 and 2001) and after (2008) recolonization.

Nutrients and biological assemblage data   To examine changes in nutrient water chemistry, we used data from a long-term monitoring program in which water samples were collected bi-monthly to monthly between July and September before (1999–2003) and after (2013–2015) salmon recolonization from a station within CR1 (Moya Joubert, Seattle

Public Utilities, unpublished data). Water samples were analyzed for TN and TP (µg/L) using field and laboratory methods as described in Kiffney et al. (2006, 2014).

To estimate stream biofilm biomass as ash-free dry mass (AFDM, g/m^2) and macroinvertebrate density and richness (Kiffney et al. 2006) before (2002) and after (2015) salmon recolonization, we placed 3 sets of unglazed terracotta tiles, consisting of 5 tiles (10 × 10 cm) attached to chicken wire, in riffles of each reach in late June and early July. We used tiles because of their reproducibility compared with that of natural inorganic substrata and because of evidence indicating that tiles support algal and macroinvertebrate assemblages comparable to natural substrata (Lamberti and Resh 1983). We submerged tiles in riffles and anchored them to the riverbed with rocks stacked on excess chicken wire. We collected tiles weekly over 6 wk by gently removing them from the chicken wire while holding a net behind the tile to collect any escaping macroinvertebrates. To collect biofilm and attached macroinvertebrates, we rinsed tiles with distilled water, scrubbed them with a toothbrush, then re-rinsed while holding the tile over a bucket covered with a 250-µm sieve (Kiffney et al. 2003). The rinse water was filtered, dried, weighed, ashed, and reweighed to determine biofilm AFDM (Kiffney et al. 2003). We preserved all macroinvertebrates collected on the sieve in 95% ethanol and identified individuals to family using a dissecting microscope and established taxonomic keys (e.g., Merritt and Cummins 1996), focusing on Ephemeroptera, Plecoptera, and Trichoptera (EPT). We analyzed data from samples collected during the 3rd wk because biofilm biomass and macroinvertebrate density and richness generally peaked at that time. We repeated the same procedure in 2002 and 2015.

Dicosmoecus spp., which is primarily a grazer of stream biofilm, is a highly abundant and conspicuous (~20–30-mm case length) caddisfly above the dam (PMK, unpublished data) and can be surveyed visually. We collected 10 or more *Dicosmoecus* individuals from reaches CR1, CR6, and CR8. For this portion of the study, we estimated *Dicosmoecus* growth rate using change in total body length (mm/d) instead of mass because only length measurements were taken in both sampling periods (2002 and 2015). Caddisflies were measured with a ruler after removing them from their cases.

Total salmonid density (no./m^2) was estimated by snorkeling 500-m sections of each study reach according to established methods (Thurow 1994). We identified salmonids to species, counted them, and classified them into different size categories, which was done by 4 to 5 trained snorkelers who spanned the channel and moved upstream in tandem relaying data to a recorder on the bank (Kiffney et al. 2018b). We analyzed only 2 size categories of stream salmonid (Coho, trout, and Mountain Whitefish; no juvenile Chinook were detected in 2015): class 1 (age 0+), corresponding to individuals ≤90 mm total length; and class 2

(age 1+ and older), corresponding to individuals >90 mm total length.

To analyze changes in stream water nutrient (N, P) chemistry and biological assemblages (biofilm biomass and macroinvertebrate density and richness on tiles, *Dicosmoecus* growth, and total salmonid density), we contrasted values aggregated across sample events (n = 2–20 depending on metric) and reaches (CR1, CR6, and CR8) before salmon (1999–2003 for nutrients, 2002 for other metrics) with the same responses in the same locations after salmon recolonization (2013–2015 for nutrients, 2015 for other metrics). Because data were not normalized with transformations, we used the non-parametric Wilcoxon signed-rank test (Chi square approximation, χ^2) on the JMP® (version 10; SAS Institute, Inc., Cary, North Carolina) platform to evaluate differences in most response metrics before and after salmon recolonization. The only exception was EPT richness on tiles, where we used a *t*-test to assess differences in mean richness before and after salmon recolonization. To address our question about the potential role of climatic variation in affecting observed ecological responses, we compared summer (June–August) water temperature and discharge patterns during the pre-recolonization (1999–2003) sample period with post-recolonization sample years (2008, 2015; USGS 2018) by calculating descriptive statistics, plotting temperature and discharge over time, and visually assessing patterns.

Stable isotope data   To test our hypothesis that the tissues of resident fishes would be enriched in marine-derived isotopes following salmon recolonization and that these same fishes would be more enriched in heavier isotopes below than above the dam, we assessed natural abundance levels of C ($^{13}C/^{12}C$) and N ($^{15}N/^{14}N$) stable isotopes (defined by δ values, units in ‰; Fry 2006) measured in muscle or fin tissue of resident trout and sculpin collected from CR1 before (2000 and 2001) and after (2008) recolonization, as well as from trout collected below the dam (2008) (Table 3; Kiffney et al. 2002, 2018b). We used 2 analytical approaches to test whether $\delta^{13}C$ and $\delta^{15}N$ values of resident trout and sculpin increased after salmon recolonization and were greater below the dam (which experienced continuous inputs from anadromous salmonids) than above. First, we used a Bayesian approach to quantify the distributions of standard ellipse areas corrected for small sample sizes (SEAc; Jackson et al. 2011) of Rainbow Trout from CR1 before (average of 2000 and 2001) and after (2008) recolonization. The SEAc describes the width of a species' isotopic niche by accounting for variation in the C and N dimensions simultaneously and is, thus, analogous to the standard deviation of univariate data (Jackson et al. 2011). Second, we compared the SEAc of Rainbow Trout from CR1 with Rainbow Trout from below the dam, both collected in 2008. We used the package *SIBER* (version 2.1.4; Jackson et al. 2019) in R (version 3.50; R Project for Statistical Computing, Vienna, Austria) to calculate SEAc. This approach was not appropriate to use with sculpin because of smaller sample sizes, so we used the Kruskal–Wallis test followed by Dunn's multiple comparisons in JMP to assess if sculpin $\delta^{13}C$ and $\delta^{15}N$ values varied with exposure to salmon subsidies.

Table 3. Mean (±SD) and % change for total N and P, biofilm ash-free dry mass (AFDM), macroinvertebrate densities and richness on colonization tiles, *Dicosmoecus* growth rate, density of trout ≤90 and >90 mm in fork length, and total salmonids (sum of trout, Coho Salmon, and Mountain Whitefish) above Landsburg Dam, Cedar River, Washington, USA, before and after salmon recolonization. EPT = Ephemeroptera, Plecoptera, and Trichoptera. All test statistics are Wilcoxon signed rank test's *W* except EPT richness, which is a *t* statistic (* = $p \leq 0.1$).

Response	Before salmon	After salmon	Test statistic	% change[a]
Total N (µg/L)	187 (61)	160 (14)	−2.0*	−14.4
Total P (µg/L)	5.7 (1.9)	6.7 (2.0)	−1.7	17.5
Tile AFDM (g/m^2)	0.16 (0.09)	0.05 (0.04)	3.4*	−69
Chironomidae density (no./m^2)	310 (500)	1430 (1700)	3.0*	361
EPT density (no./m^2)	70 (60)	300 (210)	2.7*	328
EPT richness	0.7 (0.6)	1.1 (0.8)	1.5	57
Total macroinvertebrate family richness	1.6 (1.2)	3.0 (1.2)	2.2*	88
Dicosmoecus growth (mm/d)	0.04 (0.02)	0.06 (0.003)	−1.1	50
Trout ≤90 mm (no./m^2)	0.03 (0.04)	0.02 (0.03)	−1.8	−33
Trout >90 mm (no./m^2)	0.01 (0.02)	0.006 (0.01)	−3.7*	−40
Total salmonids (no./m^2)	0.04 (0.05)	0.43 (0.6)	4.7*	1250

[a] % change ($[(x_{after} − x_{before}) / x_{before}] \times 100$) represents the relative difference in value from before salmon (1999–2003 for nutrients, 2002 for other metrics) to after salmon (2013–2015 for nutrients, 2015 for other metrics).

Reach-scale comparison
Study design   To examine the potential for long-term, cumulative effects of salmon subsidies on stream and riparian biota above Landsburg Dam, we conducted a comprehensive field survey in July and August 2015, 12 y after salmon recolonization. The field survey spanned a range of adult Chinook inputs in addition to other environmental attributes, including channel gradient. Within each of the 7 established study reaches above the dam, we designated a 500-m-long study section that was chosen to be representative of the corresponding reach as a whole. We divided each 500-m section into 5 consecutive 100-m transects within which we conducted surveys, and we collected data in summer to best capture potential long-term effects. Although primary producers, macroinvertebrates, and freshwater salmonids may be enriched in marine-derived N and C released by adult salmon immediately after they spawn in autumn/winter, with decreasing levels over the following several months (e.g., Bilby et al. 1996, Claeson et al. 2006), there is evidence that the overall foodweb and population effects of salmon inputs can carry into summer (Verspoor et al. 2010, Rinella et al. 2013, Collins et al. 2016; see Fig. S1 for timing of adult salmon inputs).

Data collection
   Biofilm and macroinvertebrates on tiles.   We deployed and measured biofilm and macroinvertebrates on tiles as previously described for the BA study.

   Caddisflies.   We used a mask and snorkel to estimate density (no./m^2) of *Dicosmoecus* spp. and *Glossosoma* spp. larvae using a 0.5-m^2 PVC frame. Caddisfly surveys were limited to ~30 to 60 cm water depth and riffle or run habitat. We conducted 4 quadrat samples/500-m section, 2 in downstream transects and 2 in upstream transects. We also collected *Dicosmoecus* larvae from each section in early July ($n = 216$) and early August ($n = 112$) to calculate an average section-scale growth rate (mg/d) for the summer months. For this metric, we measured changes in the size (length and width) of individuals collected at random to calculate an average reach-scale value in 2 time points. Because we did not collect data on individually marked caddisflies, we could not estimate the section-scale variability (i.e., SD) in *Dicosmoecus* growth rate. We removed cases and dried individuals for 24 h at 60°C and weighed them using a balance (model 361F; Sartorius, Göttingen, Germany).

   Fish.   We quantified salmonid populations (no./m^2) in each 500-m section by snorkeling according to established methods as described in the BA study.

   Spiders.   To quantify riparian spider density (no./m^2) and Shannon–Wiener diversity, we created 10-m transects along the riverbank in 2 to 4 subsections (depending on accessibility) of each survey section in which we identified and counted all web-building spiders. Each transect extended 2 m high and 1 m into the riparian zone (Burdon and Harding 2008). We also identified and counted empty but intact webs to account for spiders that may not have been active during daylight hours because we did not have nighttime access to the watershed (e.g., Collier et al. 2002, Burdon and Harding 2008). We also counted individuals within the Phalangioidea superfamily (non-web-building spiders) that were often observed near webs of other spiders. We identified all spiders to family. When a web contained no spiders, we identified it to family based on its shape, structure, and orientation using a field guide (Adams 2014) and personal observations. For intact webs with absent spiders, we assumed 1 spider/web because spiders are usually solitary and territorial (e.g., Wise 2006).

   Birds.   We conducted riparian bird surveys along the 5 consecutive 100-m sections to estimate a relative index of abundance, approximated by density (no./100 m), and Shannon–Wiener diversity. Every section was surveyed 3-fold on different days between 1000 h and 1400 h by 2 surveyors walking or wading along the bank. Birds detected in or directly adjacent (within 30 m) to the 100-m section were identified by appearance or song.

Reach-scale comparison statistical analysis   To explore the relationships between salmon subsidies and channel gradient with aquatic and terrestrial organisms, we used correlation and linear regression, with study section as the sample unit. We used Pearson's correlation coefficient to examine whether a biotic response covaried with adult Chinook inputs and other environmental covariates. We used linear regression and an information-theoretic model comparison approach to examine the strength of evidence supporting the effects of adult Chinook subsidies and channel gradient on the following biotic responses: biofilm and macroinvertebrates on tiles (biofilm AFDM, chironomid density, EPT density and richness, and total taxa richness), caddisflies (*Glossosoma* and *Dicosmoecus* density, *Dicosmoecus* growth rate [mg/d]), fishes (class 1 and 2 trout density), spiders (Tetragnathidae and total spider density and Shannon–Wiener diversity), and birds (American Dipper and total bird density and Shannon–Wiener diversity). We focused on Tetragnathidae and American Dippers because they were the most abundant spiders and birds observed, respectively. For response data that displayed a non-normal distribution, we transformed data by log(x+1). We used residual plots to assess whether observed error was consistent with random error. We assessed the relative support of a model using outputs of Akaike's Information Criteria corrected for small sample sizes (AICc). ΔAICc is the difference between each candidate model and the model with

the lowest AICc value. Model Akaike weights (w_i) indicate the probability a given model is best within a set of models (Burnham and Anderson 2002). Coefficients of determination (adjusted R^2) inform model fit. Because our sample size was small ($n = 7$), we did not test an interaction term to avoid model overfitting, but we evaluated the relative support for the combined effects of adult Chinook input and gradient (2-variable model), two 1-variable models (channel gradient or adult salmon inputs), and an intercept-only model. We conducted model selection using the *MuMIn* package (version 1.40.4; Barton 2020) in R. There was little to no support (ΔAICc > ~7) for the 2-variable model; therefore, we limit our inference to the remaining models. Because there was little support for the 2-variable model, and because channel gradient and salmon inputs were correlated ($r = -0.70$, $p = 0.08$; Fig. S2), we used partial correlation analysis to examine the relative importance of each variable, after controlling for the other, on the biotic response of interest.

Our field-survey study design introduces the possibility of spatial structure in the biotic response that could result from the dam's effect on upstream fish migration and natural longitudinal environmental and ecological change (Vannote et al. 1980). Therefore, we used correlation to explore the role of spatial structure, defined by distance from the dam to the study reach midpoint, in environmental data. This analysis showed a negative correlation between adult salmon inputs and distance from the dam (km; $r = -0.77$, $p = 0.05$), which was largely driven by high inputs at CR1. This relatively long reach is closest to presumed source populations below the dam and contains an abundance of suitable adult Chinook and Coho spawning (Burton et al. 2013) and juvenile-rearing habitat (Anderson et al. 2008, Kiffney et al. 2009). Furthermore, evidence for gradual longitudinal change in environmental data was either weak or counterintuitive. For example, instead of a gradual downstream increase in the mean and range of water temperature values as predicted by the river continuum concept (Vannote et al. 1980), we observed the warmest and most variable temperature values in upstream reaches (CR7 and CR8). Graphical assessment of other correlations ($r > |0.4|$) with distance from the dam (Fig. S2) showed they were largely driven by CR1 in conjunction with CR8 (the study reach farthest from the dam). Therefore, because support for spatial structure was ambiguous and we sought to minimize model overfitting, a variable for spatial structure was not included in either the correlation or linear regression analyses.

RESULTS
Adult salmon

Between 2003 and 2015, total adult salmon (Coho and Chinook) inputs above Landsburg Dam increased at a rate

of 407 kg/y (Fig. 2A; adjusted $R^2 = 0.54$ for the relationship between adult salmon inputs and time since fish passage). Meanwhile, the spatial distribution of adult Chinook inputs declined in the upstream direction with an annual flux rate at CR1 ~5-fold higher than CR8, the farthest upstream reach (Fig. 2B).

BA study

The majority (64%) of metrics measured above Landsburg Dam (CR1, CR6, and CR8) increased following salmon recolonization (2015) relative to before recolonization (2002;
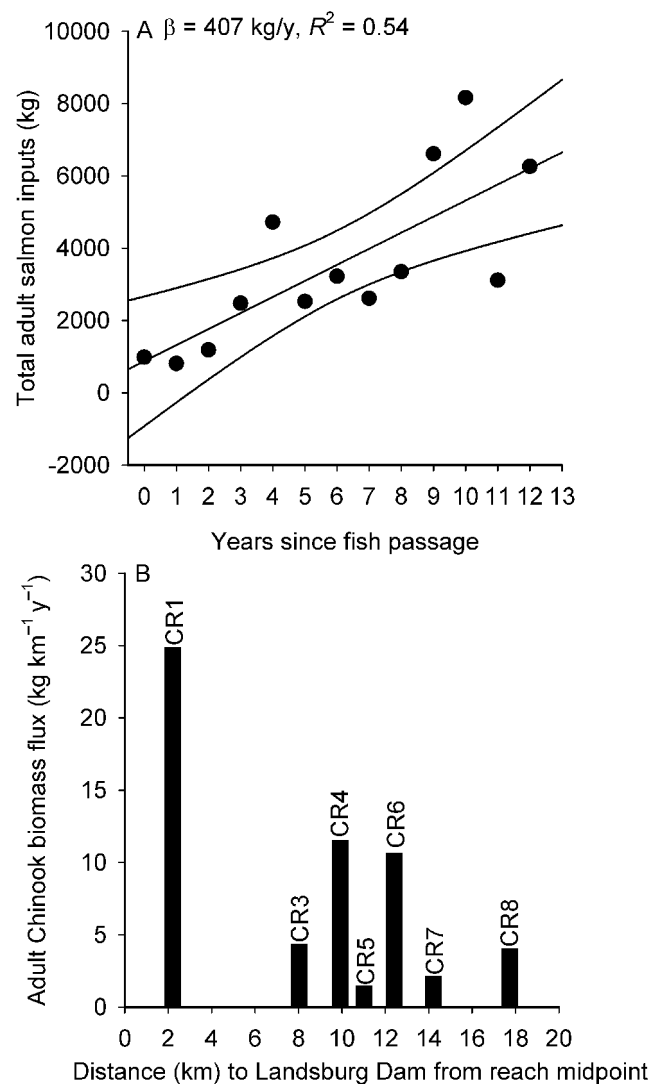

Figure 2. Scatterplot, best-fit line with 95% confidence interval, and estimated annual flux rate (ß, kg/y, adjusted R^2) describing the relationship between adult salmon inputs (kg) above Landsburg Dam, Cedar River, Washington, USA, and time since restoration of fish passage at the dam (2003–2015, y 0–13) (A). Annual reach-scale estimates of adult Chinook Salmon flux (kg km^{-1} y^{-1}) as a function of distance (km) from Landsburg Dam to each reach midpoint (CR1, CR3–CR7) (B).

Table 3). These effects occurred at various trophic and biological organization levels. At the individual level, *Dicosmoecus* growth rate was 50% higher post-recolonization. At the population level, Chironomidae larvae density (361%), EPT density (328%), and total macroinvertebrate density (31%) on tiles were higher after salmon recolonization. At the assemblage level, EPT richness (57%) and total taxa richness (88%) were higher post-recolonization. Total salmonid density increased ~1250% after (0.54 fish/m^2) salmon recolonization relative to before (0.04 fish/m^2) largely because of increases in juvenile Coho populations, whereas densities of small and large trout were about 33 and 40% lower, respectively. Mean streamwater TP concentration at CR1 was 18% higher after salmon recolonization, whereas TN was 14% lower.

All stable isotope metrics were higher above the dam after recolonization (Fig. 3A–C) and higher below the dam than above, supporting our hypothesis. Sculpin δ^{15}N (5%, $\chi^2 = 0.38$, $p = 0.5$; Fig. 3A) and δ^{13}C (6%, $\chi^2 = 0.2$, $p = 0.6$; Fig. 3B) values above the Landsburg Dam were higher 6 y after salmon recolonization relative to before, however, these differences were small relative to isotopic differences between sites above and below the dam. The Kruskal–Wallis test indicated group differences in median values for both isotopes, with below-dam sculpin more enriched in the heavier isotope than above. Specifically, sculpin below the dam had δ^{15}N ($\chi^2 = 5.3$, $p = 0.02$) and δ^{13}C ($\chi^2 = 4.1$, $p = 0.04$) values that were 93 and 14% higher, respectively, than sculpin above the dam. Salmon recolonization above the dam was also strongly associated with changes in the isotopic niche width of the resident trout population. Median SEAc values of trout from CR1 in 2008 were 394% higher than before the fish passage installation (2000–2001). Despite this pronounced increase above the dam, the below-dam trout SEAc value was 131% higher than above-dam trout, indicating a wider isotopic niche where anadromy has been uninterrupted since the last glacial recession, over 10,000 y ago (Fig. 3C).

Summer stream discharge and water temperature varied among sample years (Fig. 4A, B). Mean daily flow was ~1.8-fold higher and 4.1-fold more variable in 2002 relative to 2015, whereas mean daily water temperature was cooler by ~1.7°C in 2002. Mean daily flow in 2008 was ~1.8-fold higher and more variable (SD = 12.99) than in 2000 and 2001 (~12.18 m^3/s, SD = 4.4). On average, water temperature in 2000 and 2001 was ~1°C cooler than in 2008.

Reach-scale comparison

Stream surveys   In addition to variable adult Chinook inputs, we observed considerable variation in stream channel gradients across reaches, which ranged 2.4-fold from 0.5 to 1.2% (Table 1). Steeper channels were generally associated with more boulders (>256-mm diameter), less instream riparian wood cover, and smaller adult Chinook inputs.
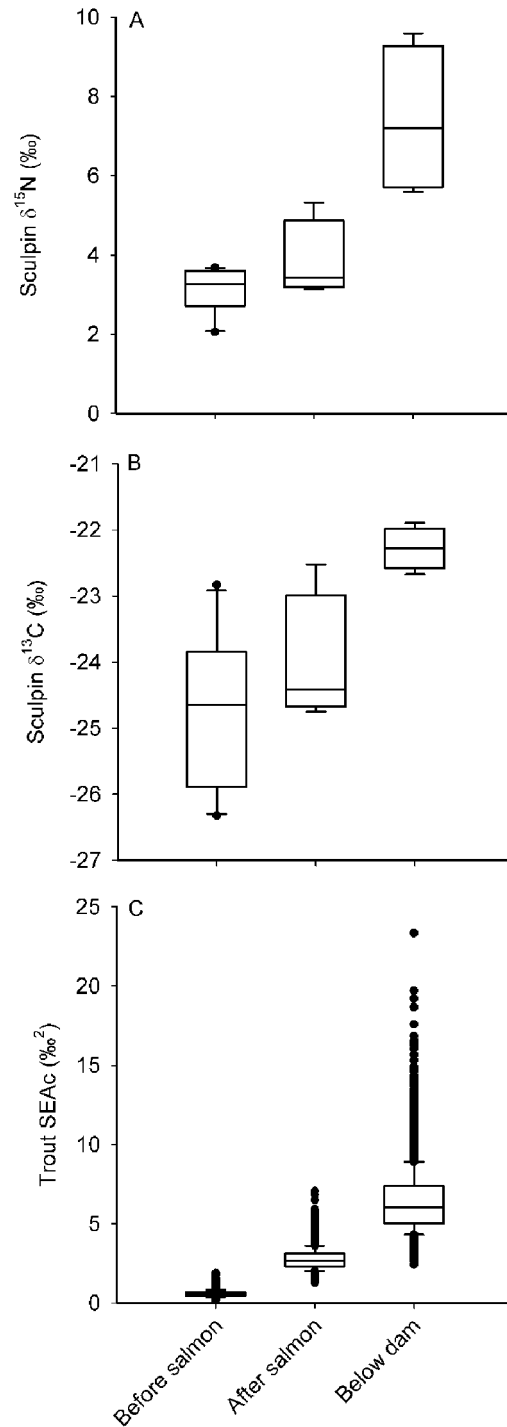

Figure 3. Isotopes of sculpin δ^{15}N (A), sculpin δ^{13}C (B), and standard ellipse areas corrected for small sample sizes (SEAc; ‰^{2}) of Rainbow Trout (C) collected from the Cedar River, Washington, USA. Samples were taken from study reach CR1 (above Landsburg Dam) before (average of 2000 and 2001) and after (2008) salmon recolonization and from below Landsburg Dam (2008). Boxplots describe the interquartile range (the box), median (horizontal line in box), the 10th and 90th percentiles (whiskers), and values outside the 10th and 90th percentiles (outlier points).
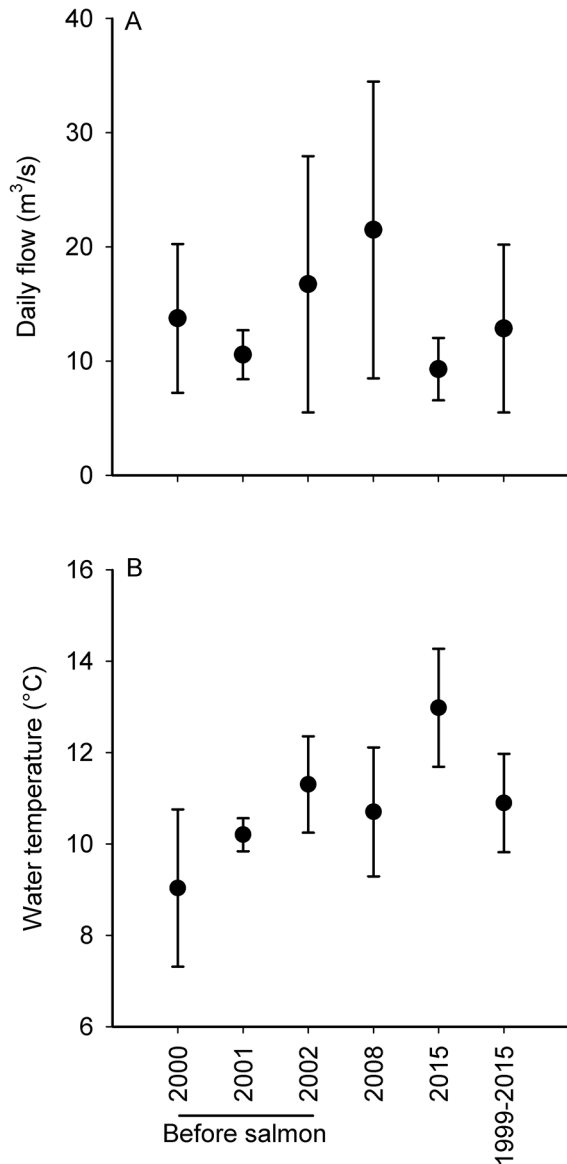
Figure 4. Mean (±SD) daily flow (m³/s) (A) and water temperature (°C) (B) measured near Landsburg Dam, Cedar River, Washington, USA, during summer (1 June–30 August) of each sample y and average conditions over the course of the study period (1999–2015).

Mean maximum daily water temperature was relatively stable and cool across all study sections (~13°C), except in CR8 where maximum temperature was 5°C higher (18°C) than the overall reach average.

Consistent with our hypothesis, some benthic responses positively covaried with the spatial gradient of adult Chinook inputs; however, the direction and strength of these associations were highly variable (Fig. 5A–F). For example, there was no clear pattern in biofilm AFDM or *Dicosmoecus* growth rate with adult Chinook flux, but there was consid-

erable reach-scale variation in mean values for both: reach-scale biofilm AFDM ranged 4.5-fold and *Dicosmoecus* growth ranged 3-fold. It should be noted that we sampled only 216 individuals in July and 112 individuals in August, which may have limited our inference with regards to reach-scale variation in *Dicosmoecus* growth rates. *Dicosmoecus* density was weakly negatively correlated ($r = -0.40$, $p = 0.5$) with adult Chinook inputs, peaking in CR7 (~60 no./m²). Supporting our hypothesis, the density of *Glossosoma* ($r = 0.87$, $p = 0.01$) and Chironomidae ($r = 0.84$, $p = 0.02$) larvae strongly positively covaried with adult Chinook inputs. For example, *Glossosoma* and Chironomidae densities in CR1, where adult Chinook inputs peaked, were 2.3- and 2.6-fold higher, respectively, than the overall reach average (110.9 no./m² for *Glossosoma*, 1273 no./m² for Chironomidae). Macroinvertebrate taxa richness increased with adult Chinook inputs ($r = 0.58$, $p = 0.2$), which also supports our hypothesis.

Riparian surveys   Similar to aquatic indicators, riparian indicators displayed a variety of spatial patterns, with some supporting our hypothesis that population productivity and taxonomic richness would positively covary with increased salmon subsidies. Surprisingly, spider diversity strongly negatively covaried with adult Chinook inputs ($r = -0.81$, $p = 0.03$; Fig. 6C). Total riparian bird relative density ($r = 0.46$, $p = 0.3$; Fig. 6D) and diversity ($r = 0.82$, $p = 0.02$; Fig. 6F) positively covaried with Chinook Salmon inputs. Other relationships showed some evidence of correlation with salmon inputs but these associations were weak and would require a larger sample size to detect potential relationships. Specifically, total spider density weakly but positively correlated with adult Chinook inputs ($r = 0.23$, $p = 0.6$; Fig. 6A), whereas Tetragnathidae density displayed a somewhat stronger ($r = 0.59$, $p = 0.2$) association (Fig. 6B). In contrast, American Dipper density was weakly negatively correlated ($r = -0.20$, $p = 0.7$) with Chinook inputs (Fig. 6E).

Model comparisons   Although we observed several moderate-to-strong associations between biotic indicators and reach-scale variation in adult Chinook inputs ($|r| > 0.5$), there was also strong evidence that channel gradient is an important predictor of a variety of abiotic and biotic indicators. For example, wood abundance ($r = -0.77$, $p = 0.04$), adult Chinook inputs ($r = -0.70$, $p = 0.08$), macroinvertebrate taxa richness ($r = -0.85$, $p = 0.01$), and bird diversity ($r = -0.91$, $p < 0.01$) declined with channel gradient (Fig. 7A–D). In contrast, *Dicosmoecus* density appears to be weakly positively correlated with channel gradient ($r = 0.44$, $p = 0.3$; Fig. S2).

The AICc model comparison indicated that, individually, adult Chinook Salmon inputs and channel gradient were important predictors of stream and riparian metrics (Table 4). The top model predicting variation in Chironomidae density
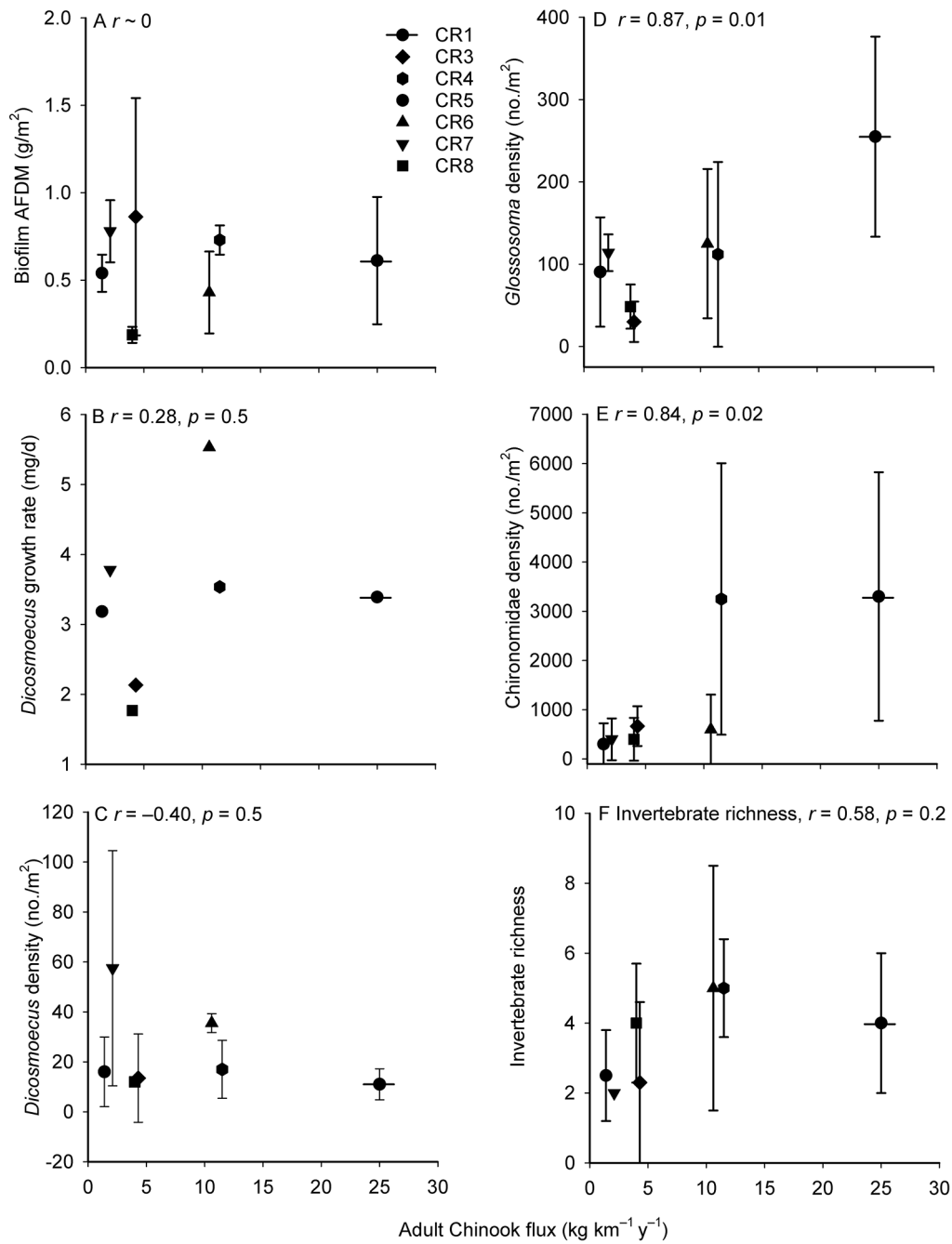
Figure 5. Mean (±SD, except for Panel B) reach-scale tile biofilm ash-free dry mass (AFDM, g/m^2) (A), *Dicosmoecus* growth rate (mg/d) (B), *Dicosmoecus* density (no./m^2) (C), *Glossosoma* density (no./m^2) (D), Chironomidae density (no./m^2) (E), and macroinvertebrate family richness (F) above Landsburg Dam, Cedar River, Washington, USA, ordered from lowest to highest annual adult Chinook biomass flux (kg km^{-1} y^{-1}). Pearson's correlation coefficients testing the strength of the association between reach-scale Chinook flux and biotic response are included in each panel.

included Chinook inputs (adjusted R^2 = 0.63). Based on w_i, this model was almost twice as likely as the 2nd-ranked model (null). However, because the ΔAICc for the null model was <2, the evidence supporting the role of salmon subsidies on Chironomidae density is equivocal. There was relatively

strong support that reach-scale variation in Chinook Salmon inputs predicted variation in *Glossosoma* density (adjusted R^2 = 0.71). Based on w_i, this model was 4.4-fold more likely than the 2nd-ranked model. In contrast to expectations, salmon inputs had a negative association with spider diversity
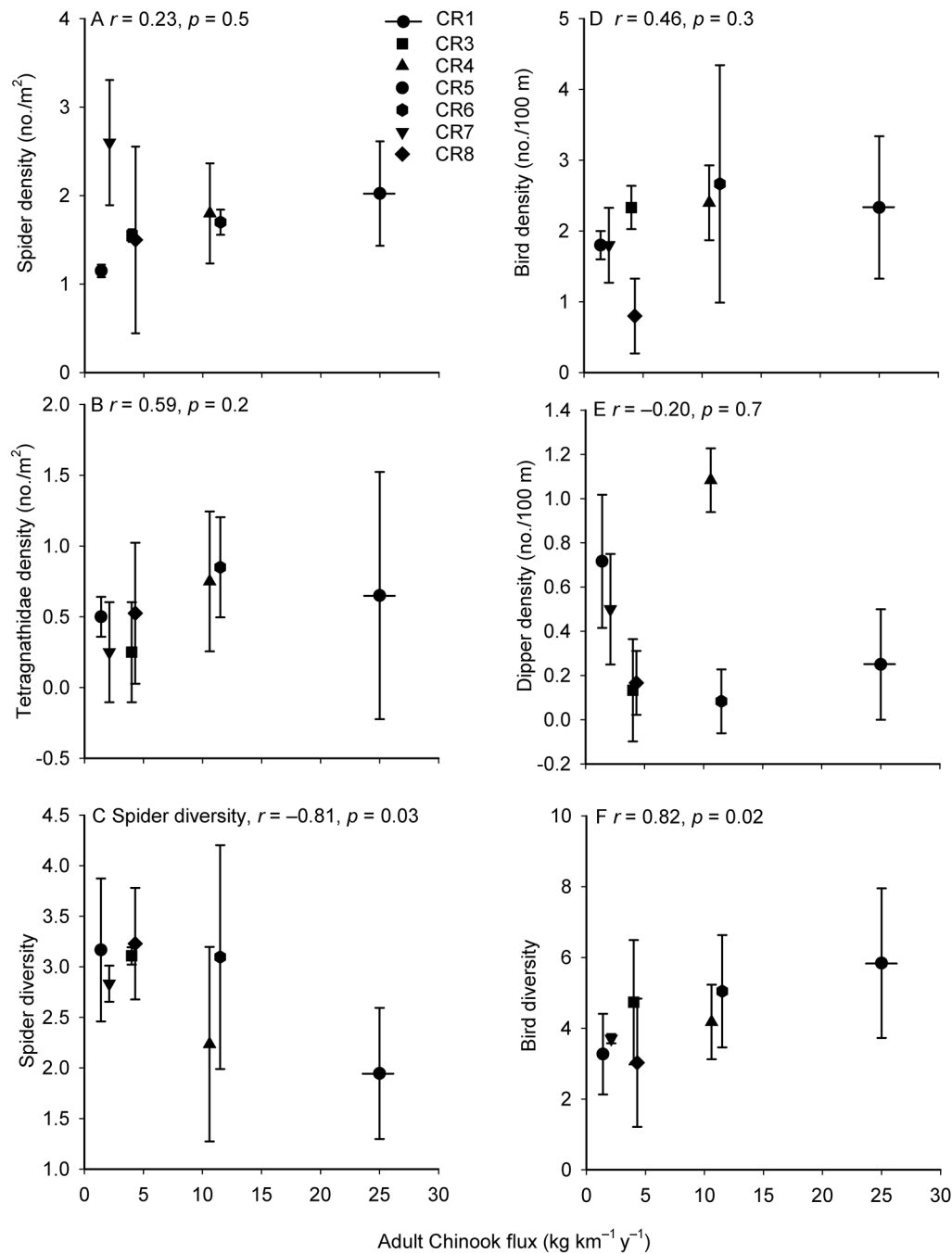
Figure 6. Mean (±SD) reach-scale total spider density (no./m^2) (A), Tetragnathidae density (no./m^2) (B), Shannon–Weiner spider diversity (C), total bird density (no./100 m) (D), American Dipper density (no./100 m) (E), and Shannon–Weiner bird diversity (F) above Landsburg Dam, Cedar River, Washington, USA, ordered from lowest to highest adult Chinook biomass flux (kg km^{-1} y^{-1}). Pearson's correlation coefficients testing the strength of the association between reach-scale Chinook flux and biotic response are included in each panel.

(top model, adjusted R^2 = 0.58), yet this model was virtually indistinguishable from the 2nd-ranked or null model.

Channel gradient received the most support predicting reach-scale variation in tile macroinvertebrate family richness (adjusted R^2 = 0.71); this model was 3.3-fold more likely than the 2nd-ranked model (null). Furthermore, channel gra-

dient explained $>^2/_3$ of the variation in bird density (adjusted R^2 = 0.71) and diversity (adjusted R^2 = 0.80), and a model with channel gradient only was 4.6- and 14-fold more likely than the 2nd-ranked models (null). Based on Akaike weights (w_i > 0.70), the null was the top model predicting variation in biofilm AFDM, EPT density and richness, *Dicosmoecus*
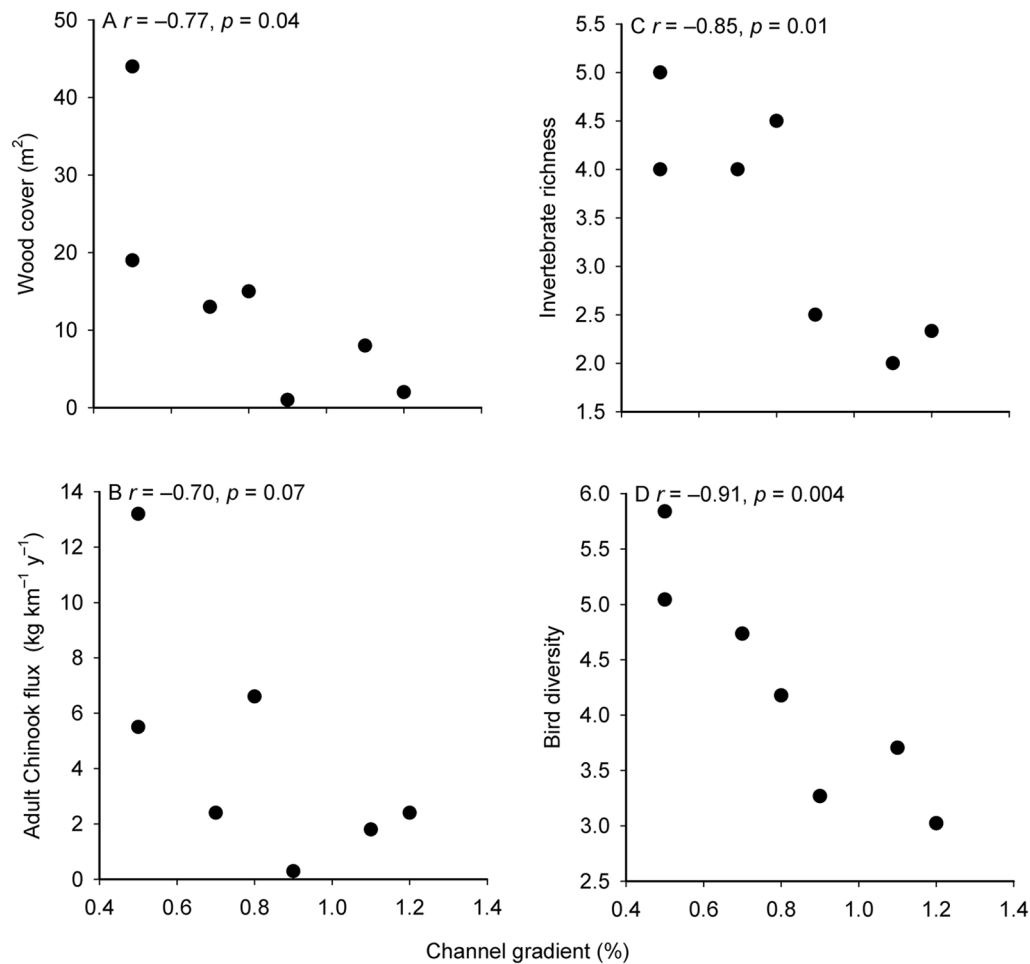
Figure 7. Scatterplots describing the relationship between reach-scale channel gradient (%) and instream wood cover (m^2) (A), adult Chinook flux (kg km^{-1} y^{-1}) (B), invertebrate richness (C), and Shannon–Wiener bird diversity (D).

growth, trout density, and total spider and Tetragnathidae density, indicating that neither channel gradient nor adult Chinook inputs explained spatial variation in these responses (results not presented).

Partial correlation showed that 73% of all responses exhibited either a negative relationship with channel gradient or a positive relationship with adult Chinook inputs after controlling for the other variable (Table 5), displaying trends consistent with the linear model comparison. For example, *Glossosoma* density remained positively correlated with salmon inputs (partial $r = 0.79$, $p = 0.08$) after controlling for channel gradient, and macroinvertebrate taxa richness was negatively correlated with channel gradient (partial $r = -0.78$, $p = 0.08$) after controlling for salmon inputs.

DISCUSSION

In this study, we tested the hypothesis that resources from spawning Pacific salmon in the Cedar River above Landsburg Dam positively covary with biotic assimilation of marine-derived energy, population productivity, and biotic richness in stream and associated riparian habitat. Despite relatively small adult salmon returns, results from the 2 related field studies (BA salmon recolonization, reach-scale comparison) provide some support for this hypothesis. However, as we expected, channel gradient is also important in predicting the distribution and abundance of riparian and stream organisms above the dam, including spatial variation in adult Chinook flux rate. Additional experimental and observational studies conducted at a variety of spatial and temporal scales are necessary to address the importance of resource subsidies from spawning salmon populations, especially addressing the ecological influence of environmental heterogeneity on these subsidies (Armstrong et al. 2010, Collins and Baxter 2014).

Bottom-up and top-down effects

Organic and nutrient inputs from reproducing adults, adult salmon carcasses, and possibly juvenile salmon can

Table 4. Model comparison and direction of effect for the relationships between channel gradient (%) and adult salmon inputs (kg km^{-1} y^{-1}) and select responses measured in summer 2015 above Landsburg Dam, Cedar River, Washington, USA.

Response	Model	k[a]	ΔAIC_c[b]	w_i[c]	Adjusted R^2	Direction of effect
Chironomidae density (no./m^2)	Salmon	3	0	0.54	0.63	+
	Null	2	1.3	0.28		
	Gradient	3	2.2	0.18	0.50	−
Tile macroinvertebrate family richness	Gradient	3	0	0.76	0.75	−
	Null	2	2.4	0.23		
Glossosoma density (no./m^2)	Salmon	3	0	0.79	0.71	+
	Null	2	3.0	0.18		
Dicosmoecus density (no./m^2)	Null	2	0	0.51		
	Gradient	3	0.19	0.46	0.50	+
Shannon–Wiener spider diversity	Salmon	3	0	0.53	0.58	−
	Null	2	0.4	0.44		
Bird relative density (no./100 m)	Gradient	3	0	0.82	0.71	−
	Null	2	3.1	0.18		
Shannon–Wiener bird diversity	Gradient	3	0	0.89	0.80	−
	Null	3	5.5	0.05		

[a] Number of parameters (k).
[b] Corrected Akaike Information Criterion (AICc) differences, $\Delta AIC_c = AIC_i - AIC_{min}$; lower value indicates more support for that model.
[c] Akaike weights (w_i) with a higher number indicate more support for that model relative to other models.

exert bottom-up effects on aquatic ecosystems. Our results showed that salmon biomass inputs were positively associated with a variety of ecosystem responses, including increased water P concentrations, macroinvertebrate density and richness, increased isotopic niche of resident trout, and higher densities of river-rearing salmonids. The stream macroinvertebrate groups that responded most to salmon biomass inputs in the BA study, including Chironomidae and EPT taxa, may have, thus, benefited indirectly from increased river productivity (Wipfli et al. 1998, Kiffney et al. 2014). Although adult salmon inputs may cause bottom-up effects on local food webs, increased macroinvertebrate productivity may lead to concurrent top-down effects through herbivory on biofilm (Power 1990). Several studies have observed aquatic macroinvertebrates exerting top-down control on biofilm in response to nutrient subsidies (Lamberti and Resh 1983, Poff and Ward 1995, Biggs 1996, Cram et al. 2011), and, indeed, biofilm AFDM in our study was 69% lower after salmon recolonization, potentially because of grazing pressure by increased macroinvertebrate populations. Furthermore, field studies, especially in streams with high densities of adult salmon (e.g., Holtgrieve et al. 2010), have shown that the bioturbation effects of spawning salmon can decrease macroinvertebrate and periphyton biomass (Moore et al. 2008, Janetski et al. 2009, Verspoor et al. 2010). For example, Verspoor et al. (2010) found that although salmon-derived N was taken up and retained by periphyton communities for several years, overall periphyton biomass was negatively affected by salmon spawning because of bioturbation. Al-

though this finding is another potential explanation for the negative AFDM response post-recolonization observed in this study, we suspect adult spawner densities were not high enough to have a significant bioturbation effect that carried over into summer months. However, further study is needed to separate out the disturbance vs fertilization effects of spawning anadromous fishes.

The reach-scale comparison component of this study also indicated bottom-up response to salmon subsidies. Specifically, both *Glossosoma* and Chironomidae larvae density positively covaried with adult Chinook inputs. However, the response of higher-order consumers (fishes, spiders, birds) to salmon recolonization varied widely. Composition of the fish community changed as overall salmonid density increased 1250%, largely from increased juvenile Coho densities. These numerical increases were a direct result of recolonization, population growth, and spatial spread above the dam by Coho Salmon (Kiffney et al. 2009, Pess et al. 2011, Burton et al. 2013, Anderson et al. 2015), a species more productive than resident salmonids (Quinn 2005). Concomitantly, we observed lower trout densities in 2015 after recolonization by anadromous salmonids. Thus, competition for limiting resources may play a role in decreased numbers of resident fishes following salmon recolonization (Grossman and Simon 2019). However, based on our long-term fish monitoring program, this difference falls within the natural range of annual variability in trout density and, thus, may not reflect changes due to salmon recolonization, possibly because salmon populations are small or because of

Table 5. Partial correlation coefficients (Pearson's r) testing the strength of the relationships between select responses measured in summer 2015 above Landsburg Dam, Cedar River, Washington, USA, and reach-scale variation in channel gradient after controlling for adult Chinook Salmon inputs, and adult Chinook Salmon inputs after controlling for channel gradient (* = $p \geq 0.1$). EPT = Ephemeroptera, Plecoptera, and Trichoptera.

Response	Gradient (%)	Chinook inputs (kg km^{-1} y^{-1})
Chironomidae density (no./m^2)	−0.45	0.65*
EPT density (no./m^2)	−0.39	0.40
EPT richness	−0.32	0.22
Total macroinvertebrate richness	−0.78*	−0.07
Dicosmoecus density (no./m^2)	0.78*	0.36
Glossosoma density (no./m^2)	0.06	0.79*
Shannon–Wiener spider diversity	0.34	−0.78*
Bird relative abundance (no./100 m)	−0.87*	−0.43
Shannon–Wiener bird diversity	−0.82*	0.61

survey methods used (Buehrens et al. 2014; PMK, unpublished data).

Spider communities showed a decrease in diversity in reaches with higher salmon inputs. Other studies have demonstrated that nutrient inputs provided by adult spawning populations of Pacific salmon were associated with reductions in plant diversity and a shift in composition to fast-growing species (Hocking and Reynolds 2011). A similar process may be operating in our study, where only a few spider species exploited emergent aquatic insects that fed on salmon carcass material, leading to a reduction in overall spider diversity. A recent study of salmon carcass addition in the North Fork Boise River in Idaho, USA, found that Pacific salmon subsidies increased fish predation and altered aquatic insect emergence patterns, leading to fewer aquatic invertebrates in the riparian zone and lower Tetragnathidae populations (Collins et al. 2020). In contrast to that study, we observed a possible positive correlation between adult Chinook flux and Tetragnathidae density ($r = 0.59$, $p = 0.2$); however, this relationship appears potentially spurious or indirect, because mean reach-scale values in Tetragnathidae density strongly overlapped, and adult Chinook flux was not included in the model set predicting variation in Tetragnathidae density. We speculate some aspect of physical habitat complexity, such as riparian and instream wood abundance in addition to prey delivery, are important predictors of Cedar River riparian spider populations. For example, post-hoc analysis of our reach-scale survey showed that Tetragnathidae density strongly and positively covaried with EPT density ($r = 0.89$, $p = 0.007$) and richness ($r = 0.91$, $p = 0.005$). More research is needed to identify and quantify the different energetic pathways between anadromous fish and riparian assemblages, including the effects of local habitat structure and productivity.

Bird assemblages demonstrated several positive correlations between bird diversity and macroinvertebrate populations (Fig. S2), which may also have been a response to bottom-up-driven food availability. Benthic macroinvertebrates eventually mature, emerge, and often serve as prey for some riparian birds. River geomorphic conditions, such as channel gradient, modify macroinvertebrate abundances and, therefore, modify prey sources. Although small sample size and the observational nature of our study preclude sweeping conclusions, our results are consistent with available literature (Iwata et al. 2003, Sullivan et al. 2007). Additional research should more fully examine direct and indirect ecological linkages between streams and terrestrial consumers such as birds.

Marine-derived nutrient enrichment

We hypothesized that Pacific salmon recolonization would lead to biotic assimilation of salmon-derived energy, and the changes we observed in the isotopic composition of resident fishes are consistent with that hypothesis. Specifically, the isotopic niche of resident Rainbow Trout as defined by SEAc value was almost 5-fold higher 6 y after salmon recolonization, possibly resulting from the addition of energy and nutrients provided by migrating adult Pacific salmon and their offspring. Similarly, sculpin tissue showed small increases in δ^{13}C and δ^{15}N values where carcasses were abundant, although effects did not statistically differ. Our results were consistent with field studies that have demonstrated enrichment in marine-derived C and N in a variety of organisms living in or adjacent to freshwater systems where anadromous fishes spawn (e.g., Kline et al. 1993). These results were somewhat surprising because in previous mesocosm experiments, we found that the 1st pronounced change in the mesocosm food web occurred at 0.1 kg/m^2, which was >7-fold higher than adult Chinook biomass inputs into CR1 (~0.014 kg/m^2; Kiffney et al. 2018b). However, the reach-scale loading rate used in our study does not capture the within-reach variability in adult biomass deposition, with some sections of CR1 likely experiencing loading rates

higher than the reach average. Although increases in sculpin C and N stable isotope values and Rainbow Trout isotopic niche are consistent with a marine-derived energy source from spawning Pacific salmon, these increases were not large enough to match values below the dam where salmon inputs have been continuous since the last glacial recession (Whitlock 1992). Therefore, these latter results indicate the functional role of salmon above the dam has yet to achieve that observed below the dam.

Habitat factors that mediate ecosystem response to subsidies

Precipitation and temperature   Inter-annual variation in environmental conditions, such as precipitation, which influences discharge and temperature, could lead to differing responses to increased nutrient subsidies. For example, in the BA salmon recolonization comparison, mean daily water temperature was 13% higher and mean daily flow 53% lower in the summer of 2015 relative to 2002. Therefore, we cannot discount the influence of natural climatic inter-annual differences on response metrics, including changes in the stable isotope composition of organisms. For example, a prior study showed the range in oxygen and C stable isotopic values of land snail shells was greater in drier, hotter areas, possibly related to water stress (Yanes et al. 2009). However, our stable isotope data does reveal that marine-derived subsidies from migrating salmon have made their way into the Cedar River food web, which is consistent with a recent study in the Elwha River (Washington, USA) that found American Dippers to be enriched in the heavier isotopes of N and C after dam removal and salmon recolonization (Tonra et al. 2015).

Channel gradient   Prior studies have shown that geomorphic conditions, such as channel gradient, are associated with high-transport velocities that modify substrate composition and accumulation of organic matter (e.g., Montgomery and Buffington 1997). These conditions, in turn, contribute to the distribution, abundance, and composition of aquatic and riparian assemblages (Hicks and Hall 2003, Sullivan et al. 2007). For example, high flow velocities associated with high-gradient stream channels can reduce biofilm accrual and aquatic macroinvertebrate assemblages (Biggs and Close 1989, Biggs 1996, Lamberti and Steinman 1997, Bellmore and Baxter 2014). Similarly, we identified channel gradient as a key variable influencing a variety of stream and riparian responses. For example, channel gradient was negatively associated with wood cover, adult salmon inputs, and 7 of 9 macroinvertebrate responses. Negative responses may occur because it is challenging for small-bodied macroinvertebrates like mayflies and chironomids to settle on tiles in high-velocity areas. The only macroinvertebrate group that showed

a positive relationship with channel gradient was the large caddisfly *Dicosmoecus*. We suspect that because the Cedar River's hydrology is regulated (Gendaszek et al. 2012), high-gradient reaches may not experience high enough flows to dislodge the relatively large stone-cased *Dicosmoecus* (Wootton et al. 1996). Additionally, high-gradient reaches may attract *Dicosmoecus* because water velocity reduces competition from small-bodied macroinvertebrate grazers and stimulates nutrient uptake and algal photosynthesis (Horner et al. 1990).

Geomorphic conditions are also fundamental in determining the distribution, abundance, and community structure of salmonids and other higher trophic levels (Montgomery 1999, Hicks and Hall 2003, Sullivan et al. 2007). In coastal Oregon streams, juvenile Coho Salmon were more abundant in low-gradient reaches, reflecting their physiologic preference for low-velocity habitats (Hicks and Hall 2003). A similar pattern is observed in our study, as well as in several other systems (e.g., Moir et al. 2004) where channel gradient was negatively associated with adult Chinook Salmon inputs. We speculate that low transport velocities in low-gradient channels increase accumulation of woody debris as well as preferred substrate for spawning salmon (e.g., Cederholm and Peterson 1985). Besides providing cover from predators, woody debris in streams retains salmon organic matter, which is an energy-rich source that can stimulate secondary production (Verspoor et al. 2010, Rinella et al. 2013, Collins et al. 2016). In our study, channel gradient may be the strongest driver of the spatial variation in adult salmon subsidies, thereby affecting the spatial heterogeneity of bottom-up effects of salmon on local food webs.

Channel gradient may also influence the distribution and abundance of riparian consumers by altering environmental features, such as the availability of nest sites and food, but studies on linkages between stream geomorphology and riparian species are rare (see Iwata et al. 2003). A study in Vermont streams found Belted Kingfisher abundance was negatively associated with geomorphic characteristics (including maximum depth, width, meander pattern, and bed-sediment diameter) but positively related to fish abundance and biomass, suggesting that abiotic and biotic factors simultaneously influenced riparian bird populations (Sullivan et al. 2007). Similarly, we surmise that multiple factors contribute to variation in reach-scale bird assemblages in the Cedar River. Bird density and diversity may have been lower in high-gradient reaches because of a lack of physical habitat features like woody debris. We documented several bird species (Belted Kingfisher, American Robin, Cedar Waxwing [*Bombycilla cedrorum* Vieillot, 1808], and Pacific Wren [*Troglodytes pacificus* S. F. Baird, 1864]) using instream woody debris as perches or foraging substrates, especially where this wood was most abundant in low-gradient reaches. The importance of instream wood for Cedar River riparian bird assemblages is supported by

positive correlations between its surface area and bird density ($r = 0.58$, $p = 0.2$) and diversity ($r = 0.92$, $p < 0.01$).

A number of studies have demonstrated that spawning adult anadromous salmon modify both aquatic and riparian ecosystems (e.g., Helfield and Naiman 2001, Gende et al. 2002, Hocking and Reimchen 2009, Quinn et al. 2009), but few have investigated salmon effects within the context of other sources of natural variation, such as differences in local geomorphology (but see Holtgrieve et al. 2010). In an Idaho river system, arthropod communities responded to the addition of salmon carcasses in vegetated and unvegetated riparian areas, with stronger salmon effects in vegetated habitats (Collins and Baxter 2014). In southwestern Alaska, mean summer water temperature regulated the growth of juvenile Coho Salmon, which in turn determined whether the fish were large enough to consume egg subsidies from spawning Sockeye Salmon (*Oncorhynchus nerka* Walbaum in Artedi, 1792; Armstrong et al. 2010). These studies illustrate the influence of spatial variation in habitat conditions on responses of consumers receiving resource subsidies. Our research highlights channel gradient as a spatially variable environmental factor that mediates the effects of salmon subsidies, potentially by influencing where salmon spawn.

Understanding the ecosystem effects of salmon subsidies in the context of environmental variables such as climate inputs and channel gradient is especially important in river systems with small salmon populations. As dams are removed across the Pacific Northwest and more salmon populations are restored (Bellmore et al. 2016), small recolonizing populations like the one in the Cedar River will likely become more common. The unique interaction of small populations with stream geomorphology and other ecosystem features will be an increasingly important component of river conservation in years to come. Additional research including experiments and field studies with more reaches or that span multiple river systems would enhance our understanding of small populations and how their ecosystem effects vary with landscape and geomorphic conditions.

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