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Linking groundwater-surface water exchange to food production and salmonid growth

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Abstract

Materials, energy, and organisms from groundwater serve as resource subsidies to lotic systems. These subsidies influence food production and post-emergent fish growth and condition through nutrient inputs and water temperature changes. To test whether post-emergent fish grew faster in gaining sites, we grew hatchery post-emergent salmon in enclosures, sampled periphyton, benthic invertebrates and wild salmon, and modeled fish growth across a gradient of groundwater-surface water exchange. Fish grew almost twice as fast in gaining ($2.7 \% \text{ g d}^{-1}$) than in losing sites ($1.5 \% \text{ g d}^{-1}$). Fish from transient sites grew as much as gaining sites, but their condition was significantly lower (18.3 % vs. 20.7 %). Results suggest groundwater-surface water exchange affect fish growth and energetic condition through direct and indirect pathways. Elevated nitrogen concentrations and consistently warmer water temperature in gaining sites have a strong effect on basal production with subsequent effects on invertebrate biomass, fish growth and condition. Findings highlight the importance of groundwater-surface water exchange as a subsidy to rearing salmon and may inform strategies for restoring fish rearing habitat.

Keywords: floodplain, hyporheic exchange, juvenile, post-emergent, rearing habitat, salmon, subsidy, temperature, vertical connectivity, winter

35 Introduction

36 Fluxes of materials, energy, and organisms across habitat boundaries, referred to as
37 resource subsidies, are ubiquitous ecological phenomena that link land and water (Polis et al.
38 1996, Vanni et al. 2004). Stream food webs, because of close connections to their watersheds
39 and the constant downstream movement of materials and organisms, are often strongly
40 influenced by subsidies of resources from adjacent habitats (Baxter et al. 2005, Richardson et al.
41 2009). Subsidies from terrestrial, tributary, marine, and hyporheic habitats can be important to
42 sustaining populations of stream fishes like salmonids (Wipfli and Baxter 2010, Nelson and
43 Reynolds 2015). However, the importance of subsidies created by either hyporheic flows or
44 groundwater-surface water exchange (GW-SW exchange) to fish has received less investigation.

45 An abundant body of literature indicates GW-SW exchange as a significant transport
46 process of materials and nutrients, which can enrich basal production in lotic ecosystems (Valett
47 et al. 1994, Jones et al. 1995, Wyatt et al. 2008). In this paper, we refer to the combined
48 subsurface flows (which may include, shallow hyporheic flow) as GW-SW exchange, because of
49 the complex interaction between groundwater and subsurface flows (Larned et al. 2015, Boano et
50 al. 2014). Studies of GW-SW influence on fishes have principally focused on physical habitat
51 conditions, especially as it relates to spawning habitat and egg survival (Curry and Noakes 1995,
52 Malcolm et al. 2003, Bowerman et al. 2014), but less so for its influence on the energetic
53 conditions for growth (Power et al. 1999, Whitley et al. 2006, French et al. 2014), and rarely
54 for its possible direct and indirect influences on prey resources (but see French et al. 2014).

55 Several mechanisms exist by which GW-SW exchange may directly and indirectly
56 influence the energetic conditions for fish growth and prey resources. GW-SW exchange flows
57 can affect energetic conditions for growth by stabilizing water temperature and providing

thermal refugia (Power et al. 1999, Whitley et al. 2006), increasing metabolic rates (Brown et al. 2004) and increasing primary production and invertebrate production in the absence of other limiting factors such as light and nutrients (McCullough et al. 2009). GW-SW exchange in upwelling areas that are rich in nutrients may influence prey resources. Nutrients in upwelling water can directly stimulate primary production and primary producers in these habitats may recover quickly from disturbance (Valett et al. 1994, Wyatt et al. 2008). In turn, higher primary production may influence invertebrate biomass (Pepin and Hauer 2002). Fluxes of invertebrates derived from the hyporheic zone also provide prey to stream fishes (Wissmar et al. 1997). In this light, we view materials, energy and organisms provided by GW-SW exchange flows as a resource subsidy that is both temporally and spatially dynamic in a watershed.

Locations of GW-SW exchange are often associated with unconstrained stream reaches (floodplains), and this exchange is often cited as part of the basis for the high productivity and fish use of these habitats (Stanford et al. 2005). Stream reaches with GW-SW exchange are actively selected by adult salmonids during spawning (Geist and Dauble 1998, Baxter and Hauer 2000, Hall and Wissmar 2004) and have been shown to be important sites for salmonid rearing (Sommer et al. 2001, Bellmore et al. 2013, Malison et al. 2015). Areas of GW-SW exchange may also be critical habitat for post-emergent salmonid growth and survival, though this has received less study. As post-emergent salmonids transition from endogenous to exogenous feeding, their bodies contain minimal energy reserves after yolk absorption (Armstrong and Nislow 2006). This transition occurs in Chinook salmon in late winter or early spring when input of terrestrial prey resources may be low (Baxter et al. 2005). GW-SW resource contributions delivered during critically low food periods may maintain fish growth at higher

levels than in the absence of this subsidy. However, evidence from experimental studies regarding the causal connections between GW-SW exchange and fish growth are lacking.

In this study, we investigated the influence of GW-SW exchange on post-emergent fish growth and prey resources. We considered the quantitative impacts of this subsidy along a gradient in the rates of resource input (losing, transient and gaining) and developed statistical models to examine how subsidy inputs influence higher trophic levels. In particular, we tested the overarching hypothesis that post-emergent fish grow faster in gaining sites due to the effects of a consistent water temperature regime on fish bioenergetics, and in response to nutrient and temperature influences that contribute to increased invertebrate food availability.

Methods

Study area and Site Selection

The Methow River watershed in the Columbia River basin in Washington, USA has a catchment area of 4,462 km² and elevations ranging from 2,700 m in the Cascade Mountains to 240 m near the confluence with the Columbia River. The Methow River basin has a snowmelt driven hydrology with high-altitude areas on the western side of the basin receiving approximately 2000 mm in precipitation annually and areas in the lower river valley receiving 300 mm (Konrad 2006). The river has no major impoundment, and a typical snowmelt hydrograph - high flows in late spring (May –June) and early summer and low flows in late summer and winter (August-January). Discharge (Q) during the duration of the study was representative of discharge within the historic flow record. Groundwater discharge from the floodplain aquifer (comprised of alluvium and glacio-fluvial sediments) is the primary source of

base flow in the Methow and Twisp Rivers and is highest during the summer and lowest in the late winter and early spring (Konrad 2006).

The Methow River basin, with its low nutrient levels and cool water temperatures, supports among other native and non-native fish species populations of spring and summer Chinook salmon (*Oncorhynchus tshawytscha*) runs, steelhead (*Oncorhynchus mykiss*), bull trout (*Salvelinus confluentus*) and Coho salmon (*Oncorhynchus kisutch*) (Willms and Kendra 1990, Konrad et al. 2006, Bellmore et al. 2013). Despite the relatively intact, connected river-floodplain segments in the basin, native salmonid populations have decreased considerably. These declines have led to numerous restoration efforts to improve habitat for juvenile salmonids, including efforts to improve habitat of floodplain side channels, providing additional motivation for our study.

We classified and selected our study sites according to large-scale groundwater discharge and recharge areas identified by Konrad (2006) as gaining, losing and transient. To classify streams in the Methow River basin, Konrad (2006) used a mass-balance budget of inflows and outflows and attributed gains in streamflow to ground-water discharge, and losses to ground-water recharge. Transient sites were located in neutral areas. We selected six accessible sites across a gradient of GW-SW exchange; two of each classified as gaining, losing or transient, including low velocity habitats used by post-emergent salmonids such as alcoves, side channels or springs (Figure 1). The selected sites had similar instream and riparian cover, water velocity and water depth. We conducted the study for five weeks from March 1 to April 5 in 2014 and measured environmental conditions and biota at the beginning and end of the study.

Multi-trophic level responses

Growth of fish in enclosures

We conducted an enclosure experiment to compare growth rates among sites spanning the range of GW-SW exchange conditions (gaining, transient and losing exchange) encompassed by the selected sites. We built enclosures with PVC pipes of 4 m² and 0.5 m high, and mesh walls (3 mm). We added boulders or large woody debris to each enclosure to provide fish refugia and to better mimic natural conditions. The mesh allowed movement (e.g., drift) of aquatic invertebrates and insects but prevented fish from moving in or out of the enclosure. We measured dissolved oxygen at each enclosure with a handheld YSI multiprobe (Yellow Springs, Ohio, USA) at the beginning and end of experiment and monitored fish behavior every other day to ensure enclosures were not placed under anoxic conditions.

We constructed four separate enclosures at each site, into which we placed ten un-fed, recently emerged Chinook salmon fry (0.36g ±0.02g) obtained from the Winthrop National Fish Hatchery. We weighed fish at the beginning and end of the experiment and estimated specific growth rates for each site. Specific growth rate (SGR) is the difference between the natural logarithm of successive weights over a unit of time and expressed as a percentage.

$$SGR = \frac{\ln(w_f) - \ln(w_i)}{days} \times 100$$

Where w_f is the final weight and w_i is the initial weight and days is the total number of days between weight measurements. At the end of the experiment, we euthanized the fish with a buffered solution of 10mL of tricaine methane sulfonate (MS222) per liter of water. We froze fish carcasses to estimate percent dry weight (DW) to infer energetic status. We also removed and froze their stomachs to later identify their contents to the lowest practical taxon using a dissecting microscope and weight to the nearest 0.001 g. We estimated energy density (ED) by

relating ED to DW (Trudel et al. 2005). Gut contents and ED were subsequently used in the bioenergetics model. Hatchery post-emergent Chinook salmon were weighed wet (± 0.001 g) and oven dried to constant weight at 70°C. We weighed each fish and calculated the percent dry weight. One enclosure at a gaining site (G2; see Figure 1) was removed due to dewatering. We assumed the constrained movement of fry in experimental enclosures did not yield erroneous results. Although few studies of post-emergent Chinook salmon exist, we used an enclosure size based upon the range of movement observed while fish in this post-emergent life stage rear within a given habitat (e.g., 2-26 m for Atlantic salmon, Einum et al. 2011).

Observation of wild fish

We complemented our experimental approach with field surveys (Power et al. 1998) of wild post-emergent salmon during the five-week experiment. We dip netted, snorkeled and electrofished wild post-emergent Chinook salmon to obtain lengths and weights, and record evidence of yolk sac for the first 30 wild post-emergent Chinook salmon collected at each site. We did not keep wild fish for stomach analysis as spring Chinook salmon are protected under the Endangered Species Act. We continued fish surveys until recently emerged fry were observed at all sites, except for sites Losing Site 2 (L2) and Gaining Site 1 (G1) where no fish were observed. We conducted extensive electrofishing at G1 in March and April, after which, we deemed reasonable to assume fry did not emerge from the gravel. At least one recently-built spawning nest (redd) had been previously identified in G1 near where sampling took place. At L2, we snorkeled and dip netted multiple occasions; the closest redds identified near this site were approximately nine kilometers upstream and 0.6 kilometers downstream. Because of the difference in emergence dates among redds, we only used weights from the first set of surveys to compare among sites, as incorporation of new sibling groups made discerning growth patterns

difficult. Lastly, we drew inferences about the fish growth trajectories by comparing their length-weight distributions among the sites we were able to sample.

Benthic invertebrates, gross primary production and periphyton biomass

We sampled benthic invertebrate biomass, gross primary production (GPP) and periphyton biomass to examine food availability for post-emergent Chinook salmon, more specifically, whether gaining sites produced more food. We sampled benthic substrates for invertebrates at each site at the beginning and end of the experiment. On each sampling date, we collected two benthic samples using a standard Hess sampler (sample area of 0.086 m², 250-um mesh, Wildlife Supply Company, Yulee, Florida) at the most downstream area of the sampling site, near the enclosures. One person held the sampler in place, while disturbing substrate to a depth of 10 cm. Our sampling technique would only have reached invertebrates inhabiting the shallow hyporheic zone, or perhaps those in motion from deeper areas. We sorted samples and identified invertebrates to family. We counted all invertebrates, then combined and dried at 60°C for 24 hours, and weighed them to 0.001 g. Because Chironomidae was the most common family of prey item in spring Chinook salmon stomachs, the first 30 Chironomidae of each sample were measured. Chironomid weights were based on published length weight relationships (Benke et al. 1999).

We measured gross primary production (GPP) to determine whether increased primary production in gaining sites might drive a “bottom-up” increase in food availability responsible for any response observed in post-emergent fish growth. We measured GPP and ER via the open channel, single-station, diel O₂ method by recording dissolved oxygen (DO) concentrations and water temperatures in each site every 10 minutes for at least a week with an YSI sonde (Yellow Springs, Ohio, USA) outfitted with an optical oxygen probe. We used the BAYesian Single-

station Estimation (BASE) program (Grace et al. 2015) to generate estimates of metabolism from the diel DO curves. We used the average of the daily GPP estimates for the statistical analysis.

The open channel method provided an estimate of GPP, integrated over a scale larger than that of enclosures (likely 10s of meters versus a few meters). Thus, we used standing periphyton biomass collected at the enclosure scale in our predictive models of fish growth. We collected periphyton to measure the standing biomass available to invertebrates by scrubbing the surface of three randomly selected rocks near enclosures at the beginning and end of the experiment. From the slurry of each rock, we collected two replicate samples. We then traced the top surface of sampled substrate to determine planar surface area (Bergey and Getty 2006). We sent samples to the University of Idaho, Analytical Science Laboratory (Moscow, Idaho) where they followed standard APHA methods to determine chlorophyll-*a* (Chl-*a*) content. Chl-*a* biomass is the measurement most commonly used as a proxy for primary production, as it is a measure of the photosynthetically active biomass (Steinman et al. 2006).

Groundwater-surface water exchange

We used piezometric measurements of vertical hydraulic gradient (VHG, cm cm^{-1}) and specific vertical discharge (Q_s , $\text{cm}^3 \text{cm}^2 \text{s}^{-1}$) as a proxy for groundwater discharge. VHG is a dimensionless ratio that estimates pressure differentials between hyporheic and surface waters (Baxter et al. 2003). VHG is positive in areas of hyporheic discharge and negative in areas of hyporheic recharge. Q_s is the vertical component of water flux in the streambed and K_s is the hydraulic conductivity (cm s^{-1}). To measure VHG and Q_s and K_s at each site, we drove four PVC pipe piezometers (38.1mm diameter) with a sledgehammer approximately 30-35 cm deep during the fall preceding the experiment; this was done after salmon spawning occurred, to minimize disturbance to redds.

216 **Environmental variables**

217 We measured a suite of environmental variables known to be influenced by groundwater-
218 surface water exchange, and/or may influence invertebrate prey or the feeding and growth of
219 salmonid fishes. We measured water depth (cm) inside the enclosures at each site at the
220 beginning and end of the experiment. Water velocity (m s^{-1}) was measured in front of each
221 enclosure at the beginning and end of experiment. We also measured substrate size at each site
222 before enclosures were placed by randomly selecting one hundred rocks and determining each
223 rock diameter using a gravelometer (Wolman 1954). We estimated the median grain size (D_{50} ;
224 mm) at each enclosure location.

225 Because GW-SW exchange is known to positively influence primary production via
226 delivery of available forms of nutrients (Valett 1994, Jones et al. 1995), we collected samples of
227 surface and hyporheic water at each site at the beginning and end of the experiment for chemistry
228 analysis. For the hyporheic samples, water was drawn from piezometers with a peristaltic pump
229 (Pegasus Athena, Mississauga, Ontario, Canada), the first 500 ml were discarded, and then water
230 was directly pumped and filtered into the sample bottles. Water samples intended for
231 ammonium nitrogen ($\text{NH}_4\text{-N}$), nitrate nitrogen ($\text{NO}_3\text{-N}$), nitrite nitrogen ($\text{NO}_2\text{-N}$) and soluble
232 reactive phosphorus (SRP) analyses were frozen immediately after collection, while dissolved
233 organic carbon, (DOC) was kept refrigerated and later sent for analysis to the IEH Aquatic
234 Research Laboratory and Consulting Services (Seattle, Washington, USA).

235 Water temperature ($^{\circ}\text{C}$) and light intensity (Lux) data were recorded at each site on an
236 hourly basis throughout the study using Onset HOBO data loggers (Pocasset, Massachusetts,
237 USA). Water temperature data were used to verify areas of groundwater discharge, as an input

to bioenergetics simulations, and in the multivariate analysis to investigate which factors were most important for predicting growth of post-emergent Chinook salmon.

Bioenergetics simulations

After empirically estimating daily growth of post-emergent Chinook salmon, we simulated the effects of water temperature and diet on the Chinook salmon growth trajectory under the different site conditions (Stewart and Ibarra 1991). Bioenergetic models can be used to estimate rates of consumption using data on observed growth and physiological parameters. This approach requires site-specific data on initial and final fish weights, diet composition, energy density (ED) of predator and prey and thermal distribution (Table 1). Energy density (ED) is not only a measure of fish condition that integrates the history of the fish feeding environment (Fergusson et al. 2010), but is also necessary to provide an accurate estimate of consumption. EDs for prey items were obtained from the literature (Cummins and Wuycheck, 1971). We used several bioenergetic model output variables, including proportion of maximum consumption (P , 0 to 1), specific consumption rates (C , $\text{g g}^{-1} \text{d}^{-1}$) and percent gross conversion efficiencies (GCE) to examine fish consumption and how fish growth trajectories differed under different sets of diet and temperature regimes.

Statistical analyses

GW-SW exchange associations

To evaluate the direct effect of GW-SW exchange on each trophic level, we used repeated measures mixed-effects models in R (R Development Core Team 2013) using lme4 (Bates et al. 2013) package for the log and squared root transformed data (Chl-a, GPP, total invertebrate and chironomid biomass, SGR and percent fish dry weight). The models included

random intercept terms (grouped by site and cage) to account for non-independence of repeated measurements. The random effects structure for the models was selected by using the restricted maximum likelihood approach (REML). Throughout the paper, we refer to these models as treatment-effects models. We tested normality with the Shapiro–Wilk test and deemed results significant if $p < 0.05$ and marginally significant if p was between 0.05 and 0.1 but of potential ecological importance, given the low sample size and statistical power of our study. We used this graded approach because p -values are a continuous measure of evidence and are influenced by small sample size (Gelman 2013). P -values were generated using the lmerTest package (Kusnetzova et al. 2015) based on Satterthwaite's approximations. $R^2_{\text{GLMM}(m)}$, marginal R^2 for fixed factors and $R^2_{\text{GLMM}(c)}$ conditional R^2 for both fixed and random factors $R^2_{\text{GLMM}(m)}$ were estimated with the R function 'r.squaredGLMM' from the package 'MuMIn' (Bartoń 2015).

Comparisons among GW- SW exchange categories were also carried out for each of the environmental variables using linear mixed models, with the exception of nutrient chemistry measures. All of these models included a random intercept term grouped by site to account for non-independence of repeated measurements. For nutrients, we used the nonparametric method for non-detects in the NADA package (Lopaka 2013) to test for treatment effects because measurements of stream water ammonia and SRP contained many values at or below method detection limits (0.001 mg L^{-1} for SRP and 0.01 mg L^{-1} for ammonia). In addition, we also carried out Kruskal-Wallis test using substitution of one-half of reporting limit. Both analyses yielded similar results. Thus, we decide to use substitution of one-half of reporting limit for subsequent multivariate analysis. Additionally, surface water and hyporheic stream water samples were not significantly different, so they were grouped and their mean values used for further multivariate analysis.

Direct and indirect associations across trophic levels

To investigate direct and indirect associations between specific fish growth rates and water temperature and food availability, we developed complementary linear mixed models based on a priori causal hypotheses (Benjamin et al. 2013). We fit a multivariate model of periphyton as a function of light, temperature, SRP, N, and water velocity, which are all factors known to mechanistically influence streambed periphyton (Larned 2010). Similarly, we fit a multivariate model of invertebrate biomass as a function of water temperature, Chl-*a* biomass and D₅₀ because these are factors that have been identified to affect invertebrate biomass, particularly grazers (Lamberti et al. 2006). Lastly, specific fish growth rate was estimated as a function of water temperature and invertebrate biomass (Sommer et al. 2001). We also included D₅₀, water velocity and water depth in the multivariate fish model to account for potential energetic costs associated with habitat characteristics because post-emergent fish seek out shallow, slow habitats (Power et al. 1999, Etnum et al. 2011). When detecting and quantifying indirect effects in a study, researchers traditionally use statistical methods such as path analysis or structural equation modelling. However, as described by Benjamin et al. (2013), small number of replicates and potential confounding influences of covariates make these statistical approaches impracticable. We tested models for collinearity using the function vif (variance inflation factor) from the car package (Fox and Weisberg 2011). Variables were considered collinear if vif values were greater than three and they were subsequently removed from the model. Finally, we estimated for each trophic level the percent increase or decrease attributed to each explanatory variable in the multivariate models after combining the influence of the treatment effect models.

Results

GW-SW exchange and associated environmental variables

We chose sites to control variation in environmental variables other than GW-SW exchange. As a result, water velocity ($F_{2,5,6}=0.766$, $p=0.5082$), median substrate (D_{50} , $F_{2,6}=0.668$, $p=0.547$) and light intensity ($F_{2,2443}=1.622$, $p=0.198$) did not differ significantly among GW-SW exchange categories. On average losing sites tended to be deeper (25.6 cm) than gaining and transient sites (17.2 and 15.2), though this difference was marginally significant ($F_{2,6}=3.92$, $p=0.083$).

Local field measurements of vertical hydraulic gradient (VHG) and specific vertical discharge (Q_s) matched groundwater discharge and recharge segments per Konrad's (2006) classifications. The mean values for both VHG ($F_{2,23}=20.22$, $p<0.0001$, Figure 2) and Q_s ($F_{2,16}=3.47$, $p=0.056$) were significantly lower for losing sites and transient sites, than for gaining sites, but there were no differences between losing sites and transient sites.

Measurements of water temperature and nutrients showed variation across sites and GW-SW classes (Figures 3, 4a, and 4b). As expected, mean water temperature was highest (6.3 °C) in the gaining sites, lowest in the losing sites (4.3 °C) and transient sites had intermediate values, 5.2 °C ($F_{2,6}=6.00$, $p<0.038$; Figure 3). Mean inorganic nitrogen was also approximately twice as high in transient, 0.120 mg L⁻¹ and gaining sites, 0.112 mg L⁻¹ as in losing sites, 0.058 mg L⁻¹ ($H=19.6$, $p<0.0001$; Figure 4b). In contrast to our expectations, the point estimate of the mean SRP was not significantly different due to the high variation in samples ($H=2.9$, $p=0.229$; Figure 4a).

Responses of trophic levels to GW-SW exchange

For each GW-SW category, we estimated average specific fish growth and percent fish dry biomass, benthic invertebrate biomass, chironomid biomass, chlorophyll *a* biomass and GPP (Figure 5a-f). We found that for each trophic level, the biomass or growth, was generally higher in the gaining sites (G1, G2) and/or transient sites (T1, T2) than in losing sites (L1, L2) (Figure 5a-f). Post-emergent Chinook salmon in the enclosures ate mostly chironomids (77% to 98% biomass of gut contents). Fish stomachs also contained stoneflies, mayflies and caddisflies but in much lower proportions (Table 1) and there were no empty stomachs. Enclosed fish in gaining sites gained mass almost twice as fast as fish in losing sites, with a specific growth rate of 2.7 percent d^{-1} compared to 1.5 percent d^{-1} (Figures 5a, $F_{2,6}= 6.42$, $p= 0.032$). Percent dry weight and energy density (as estimated from percent dry weight) were also greater in gaining sites than in losing sites and transient sites, 20.7%, 18.8% and 18.3%, respectively (Figure 5b, $F_{2,6}= 9.31$, $p= 0.014$). Although fish in T2 grew as much as those in G1 and G2, their average percent dry weight was considerably lower than those of the gaining sites, 18.6%.

Invertebrate biomass in gaining sites and transient sites was approximately 7 and 10 times higher than in losing sites, respectively, but variability was high across sites of the same exchange category, thus differences were not significant at the 0.05 level (Figure 5c, $F_{2,6}= 4.16$, $p= 0.067$). Specifically, chironomid biomass, the most important prey item for post-emergent Chinook salmon, was also six and 11 times higher in the gaining and transient sites than in losing sites, but due to the high variability among sites, these differences were not significant (Figure 5d, $F_{2,6}= 1.199$, $p= 0.361$).

GPP in gaining sites was approximately seven times higher than that of losing sites and two times higher than that of transient sites (Figure 5e, $F_{2,6}= 4.81$, $p= 0.055$). Chl-*a* biomass was also

seven times greater in gaining sites than losing sites and two times greater than in transient sites (Figure 5f, $F_{2,6} = 6.50$, $p = 0.032$).

Bioenergetics model simulations revealed that fish ate at a relatively moderate proportion (0.63 to 0.76) of maximum consumption regardless of the GW-SW exchange category. Post-emergent fish grew steadily in the gaining sites. In contrast, fish in the losing and transient sites lost weight at the beginning of the experiment when temperatures were colder, their growth generally fluctuated more, and as water temperature rose fish grew faster (Figures 6a and 6b). Percent gross conversion efficiencies (GCEs) associated with these growth trajectories also increased with rising temperatures as expected; median GCE values ranged from 7.1% in the losing sites to 14.6% in the transient sites. Overall, GCE variance was much higher for losing sites (60% and 128%) and transient sites (16% and 86%) than for gaining sites (8.7% and 13.4%) as a result of the rapid temperature increases in the losing and transient sites.

Similar to the observed weights of the enclosed fish, length-specific weights from wild post-emergent Chinook salmon in G2, a gaining site, were higher (0.563 g) than mean weights from T2, a transient site, and L1, a losing site, (0.384g and 0.375g, respectively). This is despite our having sampled and recorded G2 wild fish weights at least a week earlier than fish from T2 and L1 (Figure 7). However, we acknowledge that these differences may be within the error margin of our measurements.

Direct and indirect relationships across trophic levels

The linear mixed models used to examine potential mechanisms determining post-emergent fish growth were consistent with our hypothesis that higher growth rates in gaining areas were due to elevated water temperatures and increased food production (Table 2). First, the model for fish growth revealed that water temperature was the most important variable

explaining fish growth, followed by invertebrate biomass (Table 2). Second, the model for invertebrate biomass showed that Chl-*a* biomass explained most of the variability in invertebrate biomass (Table 2). Third, the model for Chl-*a* biomass indicated that water temperature, SRP and N were all significant variables explaining Chl-*a* biomass (Table 2).

By combining the multivariate model results with the treatment-effect models that accounted solely for GW-SW exchange effects, we examined how GW-SW exchange interacted with the environmental variables considered important predictors of post-emergent fish growth, invertebrate biomass and Chl-*a* biomass (Table 2). We calculated that water temperature increased fish growth by 64.1 % in gaining sites compared to losing sites. Invertebrate biomass increased fish growth by 10.8 % in gaining sites compared to losing sites. In contrast, variables deemed to correlate with energetic costs, substrate size (D_{50}), water velocity and water depth decreased post-emergent fish growth marginally (0.4% to 5.7%, Table 2). We also calculated that Chl-*a* biomass increased invertebrate biomass by 80.6% in gaining sites compared to losing sites. Moreover, although effects of water temperature and D_{50} on invertebrate biomass were not significant, they both increased invertebrate biomass by about 10%, on average, in gaining sites compared to losing sites. Lastly, water temperature increased Chl-*a* biomass the most, by 42.9% in gaining sites compared to losing sites, followed by N (26.7%). In contrast to our expectations, we observed a negative association between SRP and Chl-*a* biomass (49.8%), likely owing to high phosphorus uptake in the gaining sites. Light and water velocity had marginal effects on Chl-*a* biomass (0.9% to 3.1%).

Discussion

The findings of our study demonstrate that groundwater inputs can positively influence growth of post-emergent salmon fry, and point to direct and indirect pathways by which these inputs may affect their growth and energetic condition. This illustrates how groundwater-surface water exchange of materials, energy, and organisms may serve as another cross-boundary subsidy of potential importance to stream fishes. Although our experiment did not explicitly determine causal mechanisms, we showed that the elevated nitrogen concentrations and consistently warmer water temperature associated with sites gaining groundwater have a strong effect on basal production, which has subsequent effects on invertebrate biomass and growth of post-emergent salmonids and their energetic status. Our use of a manipulative field experiment and replicated enclosures helped distinguish effects of groundwater-surface water exchange character from other sources of environmental variation. The experiment also aided in separating direct and indirect effects associated with post-emergent salmon growth. Moreover, results of concurrent sampling of wild fish confirmed the patterns we observed in the experimental setting, while the growth trajectories from bioenergetics simulations informed interpretation of the consumption patterns in reaches that were gaining, losing, or transient with respect to groundwater exchange.

Prior studies have shown that nutrient contributions from groundwater inputs can positively impact biomass of algae and invertebrates (Valett et al. 1994, Pepin and Hauer 2002, Wyatt et al. 2008), but they have not directly shown an effect on fish. Here, we demonstrated that in gaining sites, exchange can affect the energetic conditions for post-emergent salmonid growth directly through increased temperature and increased prey availability, and indirectly through increased nitrogen concentrations and temperature, that then stimulated prey biomass. Because we aimed to control conditions that affected energetic costs to the fish, as expected

factors associated with energetic costs such as water velocity and substrate size did not explain the variation we observed among sites with variable groundwater-surface water exchange characteristics. We determined that stable, higher winter water temperatures and increased invertebrate prey availability in gaining sites had a direct GW-SW exchange effect on post-emergent Chinook salmon growth and energetic condition.

Our bioenergetics model results showed that fish growth was steady and consistent in gaining sites, whereas it fluctuated widely at the transient and losing sites. The highest estimated growth rates also occurred towards the end of the experiment at the losing and transient sites where fish had initially been starving, which suggests that these fish exhibited compensatory feeding. Kennedy et al. (2008) determined that juvenile Atlantic salmon exhibited compensatory feeding, as sites with the highest late-season consumption were the sites that had the lowest mid-season consumption and a majority of starving individuals in the early season. Low temperatures, feeding from yolk sack remains and poor swimming ability may have decreased feeding in the early part of the experiment. As a result, energetic status paralleled growth except for fish in one transient site (T2) where compensatory growth and consumption were highest. The occurrence of compensatory growth, the accelerated growth after a period of resource limitation, may reduce energy reserves, survival probability, delay maturation, and reduce physical performance and cognitive function (Ab Ghani et al. 2014). We reason that as water temperatures continue to rise at all sites, fish in the losing and transient streams are likely to experience higher growth rates than fish in the gaining sites as experienced in T2. However, we cannot speculate as to whether or not fish condition in losing and transient sites would be the same as in gaining sites. This would likely depend on whether the temperature fluctuations experienced in these areas are outside their energetic optimum or preference (Jobling 1997).

441 We determined that higher N concentrations and warmer water temperatures in transient
442 and gaining sites stimulated chlorophyll-*a* biomass and primary production. Upwelling
443 groundwater is often enriched in labile forms of inorganic nitrogen (Dent et al. 2001), and we
444 found that in gaining and transient sites this appeared to indirectly affect invertebrates by
445 subsidizing periphyton production, which, in turn, increased prey availability for post-emergent
446 Chinook salmon. Although we initially expected higher SRP concentrations in gaining sites, we
447 did not observe this. Instead, a large proportion of SRP samples were under the detection limit,
448 and the negative associations we found between SRP and our periphyton model suggested high
449 phosphorus demand. Lower SRP concentrations in gaining sites may have been attributable to
450 higher uptake rates in upwelling areas due to high availability of labile carbon, high microbial
451 demand in the hyporheic zone and warmer temperatures at this time of year typical of upwelling
452 areas (D'Angelo et al. 1991, Mulholland et al. 1997). High concentrations of SRP in T2, a
453 transient site that had been newly restored, may be the result of rewetting of previously isolated
454 sediments in the floodplain (Valett et al. 2005, Schönbrunner et al. 2012). Whereas a bottom-up,
455 benthic mechanism appears most consistent with our findings, it is also possible, and even likely,
456 that some component of the invertebrate prey subsidy to post-emergent salmon was at least
457 indirectly derived from the hyporheic zone itself, particularly because the chironomid prey we
458 found to be most prevalent in their stomachs are well known to utilize hyporheic habitats for
459 portions of their life cycle (Stanford and Gaufin 1974, Brunke and Gonser 1999, Reynolds and
460 Benke 2012). In addition, top-down processes may have influenced our results as well. For
461 instance, in one gaining site (G2) we observed relatively low invertebrate biomass that may have
462 been due to high prey demand by wild post-emergent Chinook salmon that were abundant at this

site. In sum, our findings point to a variety of pathways by which groundwater-derived resources may be incorporated into the food web that sustains rearing salmonid fishes.

Areas of GW-SW exchange introduce heterogeneity in stream water temperature, energy resources, and organisms into surface river environments. Understanding how this patchiness in productivity originates from the heterogeneity caused by the GW-SW exchange is important to effective conservation and restoration of habitat complexity, as this spatial complexity can promote community stability and the maintenance of biodiversity (Bellmore et al. 2015). Our findings are consistent with the hyporheic corridor and the shifting habitat mosaic concepts (Stanford and Ward 1993, Stanford et al. 2005) that the convergence of surface and groundwater in areas of active exchange (i.e., floodplains) is important to determining biological production by responding to spatially and temporally dynamic vertical and lateral processes rather than longitudinal processes (Stanford et al. 1993, Poole 2002). However, our study was limited to one study area and the strength of our inferences may be limited by the geomorphic, hydrologic and land use context that mediate the influence of GW-SW interactions on the ecology of streams (e.g., Wright et al. 2005).

For post-emergent fish rearing in active GW-SW exchange areas like floodplains, the strength and duration of groundwater-derived subsidies may not be as important as the timing of their delivery. During critically low food periods in winter and early spring, even subsidies of small magnitude may maintain growth and abundance of animal populations (e.g., Nakano and Murakami 2001). Nevertheless, the consequences of these subsidies for growth at the post-emergence life stage of Chinook salmon may or may not translate into consequences at the scale of populations or overall fitness. Because the weeks following emergence may be a critical period for survival, larger early emerging juveniles may have an advantage competing for

available territories (Skoglund et al. 2012). Alternatively, post-emergent salmonids may be subject to strong maternal effects that can conceal the connection between habitat and growth and survival (Kennedy et al. 2008). As juveniles rear in the stream in late spring and summer, losing or transient sites that exhibit higher water temperatures than juvenile Chinook salmon optimum temperatures may pose energetic bottlenecks that potentially limit their growth as a result of food limitation increased with fish size due to temperature-induced metabolic cost (Myrvold and Kennedy 2015). Moreover, any benefits realized at these early life stages of Pacific salmon may be overshadowed by limiting factors that manifest at later stages and in other habitats; in this case, processes that occur in the mainstem Columbia River, its estuary, or the marine environments used by these fish (impacts of dams, reservoirs, predators, ocean conditions, etc.).

Rivers are interacting, hierarchical mosaics of habitat heterogeneity, and in such a context understanding differences between losing and gaining areas in floodplains has important implications for planning conservation and restoration efforts to enhance rearing habitat for salmonids. At the watershed scale, the cumulative thermal and flow regimes of a stream and nutrient contributions are influenced by the arrangement and size of groundwater inputs in gaining and losing floodplain segments (Jones et al. 1995, Baxter and Hauer 2000, Dent et al. 2001). This is most clearly seen in winter, when gaining areas have less ice cover because of groundwater influence.

Anthropogenic disturbances lead to habitat simplification and loss of habitat heterogeneity (Tockner et al. 2010, Peipoch et al. 2015). This habitat simplification can decrease vertical connectivity directly by reducing in-channel and planform complexity through channel modifications such as straightening, dredging, and floodplain disconnection and indirectly

through land use changes where increased sedimentation disconnects surface water-groundwater exchange (Hester and Gooseff 2011). Traditionally, a goal of floodplain restoration has been to re-establish lateral connectivity (Roni et al. 2008). However, as evidenced in this study, restoring the dynamic processes that create and maintain GW-SW connectivity can be an equally important goal (Kondolf et al. 2006, Boulton et al. 2010). Restoration of river-floodplain connectivity (especially focused on side-channels) is being conducted along the Methow River and elsewhere in the Columbia Basin and Pacific Northwest with the aim of improving habitat for rearing salmon and steelhead. Though, it is uncertain whether these conditions limit populations, and mechanisms assumed to underpin population responses to such restoration and mitigation activities remain largely untested (Bellmore et al. 2013, Collins et al. 2015). Our findings suggest restoration or construction of a floodplain side-channel in the context of a losing or transient reach would likely result in a habitat with markedly different conditions for salmonid rearing than if either were conducted within a gaining reach. Yet, this context is rarely accounted for in planning or prioritization of such projects. Thus, our findings highlight the need for understanding groundwater-surface water exchange as a key component to context-based conservation and restoration, particularly for rearing salmon.

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Figure legends

Fig.1. Map of the Methow River basin. The six sites, main tributaries and Columbia River are identified by name. The inset indicates the location of the Methow River in Washington state, USA

Fig. 2. Vertical hydraulic gradient (VHG) for each site versus segment scale surface water-groundwater exchange (two losing sites, two transient sites and two gaining sites) in the Methow River basin, Washington, USA. VHG data was measured at bed topography breaks. VHG readings from losing and transient sites were significantly lower than VHG readings from gaining sites. Surface water-groundwater exchange categories were based on the surface water-groundwater exchange analysis in Konrad (2006).

Fig. 3. Probability density distributions of surface water temperature recorded during fish growth experiment from March 1, 2014 to April 4, 2014 at all six sites (losing mean temperature of 4.27 ± 2.74 , transient mean temperature of 5.24 ± 2.06 , and gaining mean temperature of 6.33 ± 1.27 . Surface water-groundwater exchange categories were based on the surface water-groundwater exchange analysis in Konrad (2006).

Fig. 4. (a) Nitrate and nitrite and (b) soluble reactive phosphorus (SRP) concentrations (mg L^{-1}) from surface and hyporheic water samples for each segment scale surface-groundwater exchange. Reporting limits are 0.001 mg L^{-1} for SRP and 0.01 mg L^{-1} for ammonia, nitrate and nitrite. All ammonia samples were below the reporting limit.

Fig. 5. For each SW-GW category: estimated specific fish growth rate (a), percent fish dry weight (b), invertebrate benthic biomass (c), chironomid biomass (d), gross primary production (e), and chlorophyll-a biomass (f). Each figure shows associated p-value.

Fig. 6. Daily growth simulations (a) and simulated weight accrued over the course of the experiment (b) for post-emergent fish growth under the six site conditions observed in the field. G1 and G2 are gaining sites, T1 and T2 are transient sites and L1 and L2 are losing sites.

Fig. 7. Wild post-emergent Chinook salmon length-weight relationships obtained for four of the six sites included in the study. Wild fish were not captured at G1 and L2 even after extensive sampling.

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Table 1. Parameters used in the Bioenergetics model. We estimated diet composition from stomach contents and used prey energy density values from Cummins and Wuycheck (1971) and Beauchamp et al. (2004). We estimated predator energy density (ED) using study's percent dry weight data and an energy density equation that relates energy density and percent dry weight for juvenile Chinook Trudel et al. (2005). Chironomid pupae have considerably larger energy density than chironomid larvae ($3,400 \text{ J g}^{-1}$ vs $2,478 \text{ J g}^{-1}$) thus percentage consumed per chironomid life stages were entered separately in the model.

Site	Exchange	Fish weight		Percent diet composition				Chinook salmon
				Chironomid	Chironomid			energy density
		Initial	Final	larvae	pupae	EPT	Other	(kJ g ⁻¹)
		(g)	(g)	(2,478 J g ⁻¹)	(3,400 J g ⁻¹)	(4,700 J g ⁻¹)	(4,000 J g ⁻¹)	
L1	Losing	0.364	0.642	0.0	82.0	13.3	4.7	3,705
L2	Losing	0.359	0.553	0.4	76.7	21.8	1.1	3,249
T1	Transient	0.355	0.633	3.7	93.7	1.1	1.4	3,255
T2	Transient	0.354	0.913	5.7	77.6	15.3	1.4	3,462
G1	Gaining	0.369	0.900	65.0	26.4	6.6	2.0	4,059
G2	Gaining	0.360	0.874	2.8	94.8	1.6	0.8	4,353

Table 2. Effect size (coefficient estimates), standard errors, percent of the explained variance for fixed effects (R^2_m) and random and fixed effects combined (R^2_c) for a priori hypotheses driven models. Percentage increase or decrease for each trophic level when comparing losing sites to gaining sites. * degrees of freedom based on Satterthwaite approximation (Kuznetzova et. al. 2015).

Model	Percent increase or decrease from losing to gaining	Estimate	SE	df*	t	p	R^2_m	R^2_c
<i>Fish growth</i>							0.89	0.93
Water temperature	64.1	0.0053	0.0008	2.6	6.991	0.009		
Invertebrate biomass	10.8	0.0011	0.0004	11.4	2.501	0.029		
D50	-1.8	0.0005	0.0004	13.9	1.151	0.269		
Water velocity	-0.4	-0.0183	0.0147	13.6	-1.246	0.234		
Water depth	-5.7	0.0002	0.0001	13.2	1.480	0.162		
<i>Invertebrate biomass</i>							0.50	0.50
Water temperature	11.1	0.1010	0.3373	17.0	0.299	0.768		
Chl- <i>a</i> biomass	80.6	0.7689	0.3019	17.0	2.546	0.021		
D50	10.4	-0.2540	0.2164	17.0	-1.173	0.257		
<i>Chl-a biomass</i>							0.75	0.75
Water temperature	42.9	0.6034	0.16780	18.0	3.596	0.0020		
SRP	-49.8	2.1977	0.47220	18.0	4.654	0.0002		
N	26.7	1.2391	0.47150	18.0	2.628	0.017		
Light	3.1	-0.4216	1.11730	18.0	-0.377	0.710		
Water velocity	0.9	3.9230	4.65100	18.0	0.843	0.410