Response of ecosystem metabolism to low densities of spawning Chinook Salmon

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Abstract: Marine derived nutrients delivered by large runs of returning salmon are thought to subsidize the in situ food resources that support juvenile salmon. In the Pacific Northwest, USA, salmon have declined to <10% of their historical abundance, with subsequent declines of marine derived nutrients once provided by large salmon runs. We explored whether low densities (<0.001 spawners/m^2) of naturally spawning Chinook Salmon (*Oncorhynchus tshawytscha*) can affect ecosystem metabolism. We measured gross primary production (GPP) and ecosystem respiration (ER) continuously before, during, and after salmon spawning. We compared downstream reaches with low densities of spawning salmon to upstream reaches with fewer or no spawners in 3 mid-sized (4^{th}-order) rivers in northern Washington. In addition, we measured chemical, physical, and biological factors that may be important in controlling rates of GPP and ER. We observed that low densities of spawning salmon can increase GPP by 46% during spawning, but values quickly return to those observed before spawning. No difference in ER was observed between up- and downstream reaches. Based on our results, salmon density, temperature, and the proximity to salmon redds were the most important factors controlling rates of GPP, whereas temperature was most important for ER. These results suggest that even at low spawning densities, salmon can stimulate basal resources that may propagate up the food web. Understanding how recipient ecosystems respond to low levels of marine derived nutrients may inform nutrient augmentation studies aimed at enhancing fish populations.

Key words: gross primary production, ecosystem respiration, marine derived nutrients, Pacific salmon, Columbia River, subsidy

Nutrient subsidies are often transferred in pulses from areas of high productivity to areas of low productivity (Yang et al. 2008), which can create bottom-up effects in the recipient ecosystem that propagate through the food web (Polis et al. 2004). The movement or migration of organisms that have accrued nutrients and biomass in other environments can be an important vector of the subsidy. For example, biomass of grass on islands tripled when a nutrient subsidy provided by seabird droppings increased (Maron et al. 2006), and primary production in lakes increased with nutrients delivered via excretion by fish (Vanni et al. 2006). Moreover, modeling efforts suggest that the response of recipient ecosystems to subsidies should increase as the amount of subsidies delivered increases (Huxel and McCann 1998, Ostfeld and Keesing 2000, Leroux and Loreau 2008). Thus, the abundance of organisms acting as vectors may influence the magnitude of the subsidy and the corresponding effect on the recipient ecosystem. However, the response to subsidies can depend on the quality of the subsidy and the condition of the recipient ecosystem (Marczak et al. 2007, Marcarelli et al. 2011). If, for instance, recipient ecosystems are nutrient limited, even seemingly small amounts of high-quality nutrient subsidies could have a disproportionate effect on the basal productivity of the system.

Pacific salmon (*Oncorhynchus* spp.) are an iconic example of a high-quality pulsed nutrient subsidy. When adult salmon return to their natal rivers to spawn, they bring with them nutrients obtained during their marine residence. These marine-derived nutrients can be released during excretion, spawning, and carcass decomposition, or eggs and carcasses can be directly consumed, contributing to both autotrophic and heterotrophic productivity. For example, the pulse of nutrients from salmon can have positive effects on the production and biomass of biofilm and microbial respiration (Chaloner et al. 2007, Verspoor et al. 2010, Levi et al. 2013a), with subsequent increases in macroinvertebrate (Wipfli et al. 1999) and juvenile salmon abundance (Bilby et al. 1996). Thus, Pacific salmon can facilitate a positive feedback that supports their own population. It is expected that the response of biofilm and subsequent levels

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of the food chain will scale with the number of spawning adults. However, studies illustrate that the direction and magnitude of the response may depend on the environmental conditions of the stream or watershed (Janetski et al. 2009, Bellmore et al. 2014). For example, the effect of salmon on gross primary production (GPP) varies from positive to negative depending on the density of spawners, spawning behavior displayed by different species, and habitat complexity (e.g., available spawning habitat; Holtgrieve and Schindler 2011, Levi et al. 2013a). In contrast, ecosystem respiration (ER) is consistently increased by the decomposition of carcasses and the respiration of the salmon themselves (Holtgrieve and Schindler 2011, Levi et al. 2013a). However, >90% of the studies conducted have been in Alaskan streams with relatively high densities of salmon (>0.1 spawners/m^2; Janetski et al. 2009). Whether spawning salmon can elicit similar responses at lower spawner densities is not known.

In the Pacific Northwest (i.e., Oregon, Washington, and Idaho [USA]), salmon have declined to <10% of their historic population (Nehlsen et al. 1991), resulting in declines of marine derived nutrients once provided by larger salmon runs (Gresh et al. 2000, Moore et al. 2011). Concern exists that diminishing nutrients caused by population declines will result in reduced productivity in natal rivers and less food for juvenile salmon (Bilby et al. 1996, Cederholm et al. 1999). This concern is particularly important in tributaries of the Columbia River because many of them are naturally oligotrophic as a result of the parent geology of the region (Compton et al. 2006). In response, many restoration projects include artificial enrichment of streams and rivers with salmon carcasses, carcass analogs, or inorganic nutrients (Kohler et al. 2012) based on the assumption that large amounts of nutrients will stimulate aquatic productivity. Unfortunately, little is known regarding the existence of positive feedbacks where populations are depauperate. If the salmon can contribute to a positive feedback via bottom-up stimulation, then even when the marine-derived nutrient subsidy is reduced, a subsequent response of the biofilm should still be apparent, and potential for population recovery may still be present. However, failure to detect a response might imply that this organic matter and nutrient subsidy is not an important factor contributing to population growth once returning adult abundance is too low and that some threshold number of spawners is needed before a biologically significant response occurs.

We explored the effects of low densities of naturally spawning Chinook Salmon (*Oncorhynchus tshawytscha*) on ecosystem metabolism. Ecosystem metabolism is well suited for evaluating the effects of salmon on stream autotrophs (GPP) and heterotrophs (ER) because it provides a spatially integrated measure that is comparable across different local reaches and different regions (Williamson et al. 2008). In 3 mid-sized rivers (4th order), we measured ecosystem metabolism continuously before, during, and after the spawning event in reaches with no or minimal spawning and reaches where spawning was concentrated. Based on the assumption that the positive feedback would scale with the density of spawning salmon, we made 2 main predictions. First, we predicted that GPP would be greater in reaches where salmon spawn compared to those with little or no spawning. We expected the effect of salmon on GPP to be positive because limiting nutrients would be provided and the effect of disturbance from redd building would be minimal (i.e., fewer salmon should scour the stream bed less during redd construction). Second, we predicted that ER would be greater in reaches where salmon spawn compared to those where they do not because the excretion and decomposition of carcasses would stimulate heterotrophic activity. Last, we assessed which biotic and abiotic components might be most important in controlling the rates of ecosystem metabolism between spawning (downstream) and no-spawning (upstream) reaches and across all sites in the 3 rivers.

METHODS

Study area and design

We worked in the Methow River, a 5th-order stream in north-central Washington (Fig. 1). The headwaters of

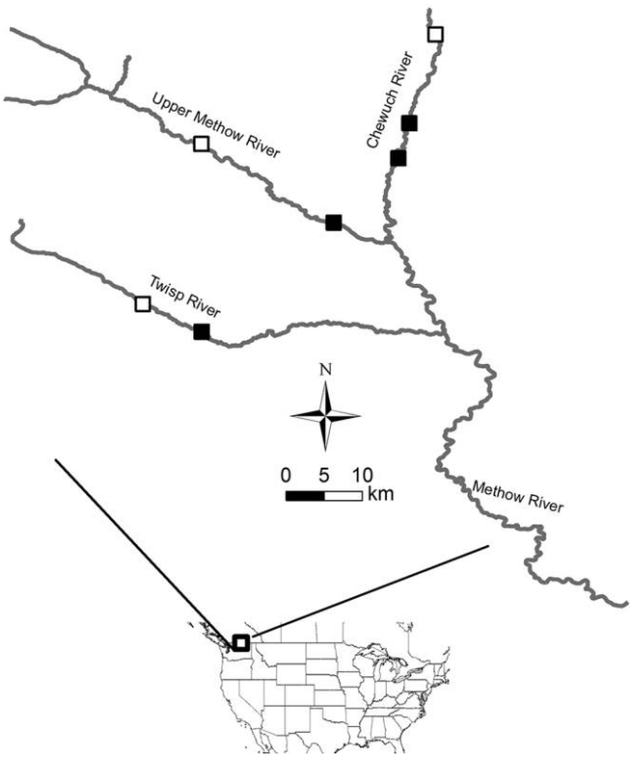

Figure 1. Reaches in the Methow River basin in which spring Chinook Salmon spawning occurred (closed squares) and was low or did not occur (open squares).

the Methow River originate in the North Cascade Mountains and drain south to the confluence with the Columbia River. Precipitation is largely in the form of snowfall, with peak flows occurring in May and June and base flows from July through October. Specifically, we conducted our study in 3 large subbasins of the Methow River: the upper Methow, the Chewuch, and the Twisp Rivers. These 3 subbasins are generally considered to be nutrient limited, based upon very low measurable nutrient concentrations (i.e., dissolved inorganic N [DIN] and P; Konrad et al. 2003). Riparian vegetation in these subbasins consisted of Ponderosa pine (*Pinus ponderosa*), Douglas fir (*Pseudotsuga menziesii)*, alder (*Alnus* spp.), willow (*Salix* spp.), and black cottonwood (*Populus trichocarpa*) along the upper Methow River. Study reaches in the Chewuch and Twisp Rivers were in the Okanogan–Wenatchee National Forest, whereas those in the upper Methow River were on private or state property. Some level of human disturbance has occurred in each of these tributaries, but channel-forming processes are still intact, and the condition of the physical habitat is considered to be good.

Spawning of endangered spring Chinook Salmon occurs annually in the upper Methow, Chewuch, and Twisp Rivers between mid-August and late-September. Spawning densities are consistently different among these 3 major subbasins: lowest in the Twisp, greatest in the Methow, and intermediate in the Chewuch Rivers (Table 1). In general, spawning is limited in the Twisp River because of colder temperatures and larger substrate than that preferred by Chinook Salmon for rearing and redd construction, respectively (Snow et al. 2013). Study reaches were chosen within each of these 3 subbasins to sample a representative distribution of spawning density throughout the Methow River watershed. The densities we observed were more than an order of magnitude lower (<0.001 spawners/m^2) than in Alaskan streams where similar studies have been conducted (>0.1 spawners/m^2). Runs of summer Chinook and Coho Salmon (*Oncorhynchus kisutch*) and Steelhead (*Oncorhynchus mykiss*) are also present, but they spawn at different times from spring Chinook Salmon, and largely in different locations.

To evaluate the effects on ecosystem metabolism of spawning by adult spring Chinook Salmon at low abundances, we used a multiple before–after control–impact (BACI) study design with incomplete blocks (Downes et al. 2002). In each of the 3 subbasins, we had an upstream reach with no or minimal spawning activity and a downstream reach where spawning occurred at higher densities (Table 1, Fig. 1). An additional downstream reach was included in the Chewuch River to provide another spawning location to make a total of 7 study reaches. The range of distances between up- and downstream reaches was 7 to 17 km, and the distance between the 2 spawning reaches in the Chewuch River was 5 km. We conducted the study over a 3.5-mo period from 23 July to 9 November 2012, which allowed us to incorporate periods before, during, and after spawning.

Salmon density

We estimated the density of adult spring Chinook Salmon in our study reaches on the basis of redd counts obtained from surveys conducted by the Washington Department of Fish and Wildlife (Table 1). Redds were surveyed weekly during August and September 2012 by walking the rivers, and each new redd observed was tallied and

Table 1. Mean (SE) reach characteristics and salmon densities measured during the period of the study (2012). For comparison, mean spawner densities also are reported for previous years (2005–2009; Snow et al. 2013). A = the cross-sectional area of the stream, A_s = the transient storage zone.

Metric	Chewuch	Chewuch	Chewuch	Methow	Methow	Twisp	Twisp
Reach location	Up	Middle	Down	Up	Down	Up	Down
Elevation (m)	769	652	650	639	562	916	812
D50 (mm)	8.8	8	4	14.3	6.3	14	10
Temperature (°C)	11.3 (0.4)	11.1 (0.5)	10.7 (0.3)	9.5 (0.3)	10.4 (0.2)	7.5 (0.2)	8.9 (0.3)
Canopy cover (%)	24.8 (2.0)	27.9 (1.2)	32.3 (0.8)	35.5 (0.8)	30.3 (1.6)	24.0 (1.9)	22.9 (0.8)
Depth (cm)	28.7 (2.1)	26.9 (2.3)	36.9 (4.2)	23.5 (1.4)	35.7 (2.7)	24.6 (1.1)	24.1 (2.1)
Width (m)	16.9 (0.8)	23.0 (1.1)	22.7 (1.7)	21.3 (1.4)	21.7 (1.3)	10.6 (0.4)	9.5 (0.7)
Reach length (m)	540	1352	1476	1111	1693	499	707
Discharge (m^3/s)	1.2	1.8	2.7	2.6	3.9	0.9	1.1
A_s/A	0.20	0.22	0.25	0.14	0.25	0.22	0.27
Salmon density 2012 (spawner/$m^2 \times 10^3$)	0.21	1.27	3.35	0.08	1.79	0	1.03
Salmon density 2005–2009 (spawner/$m^2 \times 10^3$)	0.36 (0.18)	0.65 (0.02)	1.28 (0.12)	0.19 (0.05)	1.43 (0.07)	0	0.42 (0.14)

marked (Snow et al. 2013). To estimate salmon density from redd abundance, we assumed a spawner-to-redd ratio of 1.45 (Snow et al. 2013) and a surveyor efficiency of 0.75 (Gallagher and Gallagher 2005).

Nutrients, periphyton, and physical variables

We collected 1 water sample at the downstream end of each reach every 2 to 4 wk, which corresponded with before (26 July 2012), during (27–29 August and 17–20 September 2012) and after (5–7 November 2012) spawning. Samples were filtered (0.45 μm), stored frozen, and analyzed for NH_4^+-N and soluble reactive P (SRP) with a SmartChem 200 autoanalyzer (Unity Scientific, Brookfield, Connecticut) following standard methods (APHA 2005). Detection limit for each constituent was 0.01 mg/L.

On days when water samples were collected, we randomly selected 5 rocks from the active channel at 10-m intervals upstream of where sondes were placed (see below). We scrubbed the surface of each rock, and filtered (preweighed Whatman GF/F; 0.7 μm) and then froze a subsample of the material removed from the rocks until analysis. We traced each rock to estimate surface area (Bergey and Getty 2006). We extracted chlorophyll *a* (Chl *a*; mg/m^2) with 90% acetone and analyzed it with a nonacidification method in a fluorometer (TD-700; Turner Designs, Sunnyvale, California; Welschmeyer 1994). After extraction, we returned the remaining subsample to a crucible and allowed the acetone to evaporate before we processed the filters for ash-free dry mass (AFDM; g/m^2) with the methods published by Davis et al. (2001).

We measured physical variables to assess the similarity of our study sites and for use as potential covariates in our metabolism estimates (Table 1). We measured wetted width (m) and depth (cm) at each site twice during the study, at the beginning and at low flow. We took measurements at 10 transects spaced at 20- to 50-m intervals upstream from the sonde and measured depth at 25, 50, and 75% wetted width. The distance between transects was based on the reach length. We measured canopy cover with a densiometer at every other transect. The composition of sediment on the river bed was quantified once during low flow by measuring the intermediate axis of 100 rocks randomly selected from equally spaced transects upstream of the sonde (Davis et al. 2001). We used these surveys to estimate median substrate size (D50) for each site. We measured discharge at each study reach on the same dates that water and periphyton samples were collected (except on dates when flows were too high).

We measured transient storage via pulse releases of NaCl (Stream Solute Workshop 1990) once during September at each site. Prior to pulse release, we placed a conductivity probe in the thalweg of the channel at a distance downstream (390–950 m) long enough to allow adequate solute mixing (Moore 2005). Conductivity was recorded until the NaCl pulse passed, and conductivity returned to background levels. We used these data in conjunction with One-dimensional Transport with Inflow and Storage (OTIS) and OTIS-*P* software (Runkel 1998) to calculate the cross-sectional area of the stream (A) and the transient storage zone (A_s). The relative importance of storage vs transport properties at each study site was represented by the ratio A_s/A (Harvey and Wagner 2000).

Ecosystem metabolism

We measured stream metabolism with the 1-station, open-channel method (Grace and Imberger 2006). We chose to use a 1-station rather than a 2-station method because it allowed us to increase our sample size, while continuously measuring subtle changes that might occur in response to low densities of spawning salmon. At each of our 7 reaches, we recorded dissolved O_2 (DO) and temperature (Fig. S1A–C) continuously at 10-min intervals for the 3.5 mo of the study with water-quality sondes (YSI 600-OMS; Yellow Springs Instruments, Yellow Springs, Ohio; Hydrolab Data Sonde DS5X, Hach/Hydrolab, Loveland, Colorado) equipped with optical DO probes. We calibrated the sondes based on an air-saturated-water method every 12 to 16 d (Grace and Imberger 2006) and used this calibration to correct for instrument drift.

We used sonde data to calculate the diel change in DO. To quantify GPP and ER, we used a modified version of the daytime regression method (Grace and Imberger 2006, Atkinson et al. 2008):

$$\frac{\Delta[O_2]_i}{\Delta t} = AI_i^p - R\left(\theta^{[temp_i - temp_{mean}]}\right) + K\left(1.024^{[temp_i - temp_{mean}]}\right)D_i, \quad \text{(Eq. 1)}$$

where the photosynthesis term (AI_i^p) includes solar input (I) at time i, ability of primary producers to use incident light (p), and the light use efficiency factor (A). Respiration (R) was temperature-corrected using θ, which was adjusted for every time period and constrained between 1.0 and 1.3. We temperature (*temp*)-corrected reaeration with the atmosphere (K) for every time period i using a constant of 1.024 as recommended by Grace and Imberger (2006). K depended on the deficit or surplus of DO (i.e., the difference between measured O_2 concentration and O_2 concentration at 100% saturation; D_i). We derived values for I, *temp*, and D_i empirically, whereas we solved for values for A, p, R, θ, and K iteratively by minimizing the sums of squares between modeled and measured DO concentrations using a Bayesian framework (Grace et al. 2015). This approach reconstructs the diurnal cycle of DO concentration measured at a single station to estimate daily GPP and ER through 10,000 iterations, after allowing the model to

reach equilibrium (i.e., burn-in), using a Markov Chain Monte Carlo (MCMC) method to estimate values of each parameter. We evaluated daily models on the basis of an R^2, which quantifies the correlation between modeled and measured DO data, and a posterior predictive check (PPC), which measures the overall fit based on the MCMC iterations (Kéry 2010). We used only daily models with $R^2 \geq 0.7$ and PPC between 0.2 and 0.8 (PPC < 0.1 or > 0.9 typically signify poor model fit). The mean R^2 of our models was 0.92 (± 0.004 [SE]) and mean PPC = 0.67 (± 0.006). Similar approaches have been used to provide reasonable metabolism estimates in previous studies (Giling et al. 2013, Griffiths et al. 2013, Levi et al. 2013a, Roley et al. 2014). Estimates of GPP and ER (g O_2 L^{-1} d^{-1}) were converted to areal rates (g O_2 m^{-2} d^{-1}) based on mean stream depth calculated from measured depths or depths from gage heights from stations near each reach (http://waterdata.usgs.gov/wa/nwis/).

Light intensity (lumen/m^2) was measured above the stream surface near each sonde at 10-min intervals (HOBO UA-002; Onset Computer Corporation, Bourne, Massachusetts; Fig. S2A–C). Ideally, we would have measured photosynthetically active radiation (PAR), but logistic considerations prevented us from doing so at all sites. Instead, we used light intensity as a relative measure of the amount of PAR reaching the stream surface. However, we did couple PAR measurements, recorded at 10-min intervals (HOBO H21-002 Micro Station), with light intensity measurements at 1 site (downstream Methow River) to compare model output from the 2 measures of light. Values for GPP and ER were similar between light sources (paired t-test, $p > 0.18$). Similar values were calculated because A in the photosynthesis term (AI_i^p) is adjusted based on the light value used (M. Grace, Monash University; personal communication). Therefore, we continued to use light intensity as the input variable for I in Eq. 1.

Statistical analyses

We used separate models for each nutrient, periphyton, or physical variable to assess any differences between reaches where salmon spawn and reaches where fewer or no salmon spawn. We fit linear mixed models that included river as a fixed blocking variable and a random effect for reach (down- or upstream) nested within river (Littell et al. 2006). To reduce statistical bias, we recorded any concentration of NH_4^+-N or SRP that was below detection limits as ½ the detection limit (0.005 mg/L) for all statistical analyses.

We evaluated the influence of spawning salmon on ecosystem metabolism by first separating the data into 3 periods: before, during, and after spawning. Spawning period was estimated by the first and last redd observations for each river. For example, in the Chewuch River, the first Chinook Salmon redd was observed on 12 August and the last on 19 September. Thus, for the Chewuch River, before spawning included all dates before 12 August, after spawning included all dates after 19 September, and during spawning included all dates between.

We used a mixed-model analysis of variance (ANOVA) to detect changes in GPP and ER as a result of spawning salmon (Schwarz 1998, Downes et al. 2002). Within each model, fixed effects included reach (downstream = spawning, upstream = no/minimal spawning), spawning period (before, during, or after), the reach × spawning-period interaction, and river as a blocking variable. Random effects included the mean effect of sampling date within the spawning period, mean effect of each location within a down- or upstream reach, and their interaction. Under the BACI design, an effect of spawning salmon is measured by the spawning period × reach interaction, which identifies the effect size or magnitude of change. For each response variable, we used a priori contrasts to test our predictions. First, we tested whether the difference between before and during spawning was greater in the down- than in the upstream reaches. Second, we conducted a similar test comparing the difference between before and after spawning periods in the downstream and upstream no spawning reaches. We tested for temporal autocorrelation with the Durbin–Watson test and found positive autocorrelation between daily measures of GPP and ER ($p < 0.01$). Therefore, we used a 1st-order autoregressive structure in the metabolism models to account for variation that would otherwise be attributed to model error (Littell et al. 2006).

For all mixed models, we adjusted the denominator degrees of freedom based on the Kenward–Roger's method, which accounts for estimation of any additional variance and covariance parameters, adjusts for small sample size and unbalanced design, and makes the tests conservative (Littell et al. 2006). If necessary, we ln(x)-transformed variables to meet assumptions of normality and homogeneity of variance. We used SAS to complete our statistical analyses (version 9.3; SAS Institute, Cary, North Carolina).

We used an information-theoretic approach (Burnham and Anderson 2002) in 2 ways to: 1) identify the abiotic and biotic factors that might plausibly explain a significant difference in GPP or ER between down- and upstream reaches based on results from the BACI analysis and 2) assess abiotic and biotic factors that might influence overall rates of GPP and ER across all study sites (henceforth: watershed analysis). We reasoned that the addition of the watershed analysis would provide further support of potential factors controlling GPP and ER across the Methow River basin, while enabling us to evaluate a small gradient of the predictor variables.

For GPP, we developed a suite of 28 candidate models that included combinations of salmon spawner density, weighted distance from the sonde to upstream redds, light

intensity, water temperature, NH_4^+-N, SRP, Chl *a* biomass, and D50. For ER, we developed 36 candidate models that included combinations of spawner density, weighted distance from the sonde to upstream redds, water temperature, transient storage, NH_4^+-N, D50, canopy cover, and discharge. Models were based on influential factors from previous studies (Mulholland et al. 2001, Roberts et al. 2007, Bernot et al. 2010, Beaulieu et al. 2013, Griffiths et al. 2013, Levi et al. 2013a).

We reasoned that the magnitude of the observed response might be related to the proximity of the sonde to upstream redds in addition to the predicted effect of absolute spawner density on stream metabolism. We assumed that the influence of salmon on metabolism would be strongest in close proximity to spawning sites because: 1) adults excrete nutrients while guarding redds, 2) salmon carcasses are likely to be deposited nearby, 3) recently scoured redd locations may have high algal turnover rates, and 4) nutrients can be leached from the redds themselves (Rice and Bailey 1980, Wright et al. 1995). Therefore, we created an index that weighted redds based on their distance from the location of the sonde, where redds closer the sonde carried a greater weight than redds further upstream. We created the index by first calculating the inverse distance from the sonde to each upstream redd *i* in the study reach *j*, and then taking the sum of the inverse distances ($\Sigma[1/distance_{ij}]$).

Model selection under the information-theoretic approach identifies the best approximating model and produces a weight of evidence for each model. We evaluated the fit of each candidate model by examining residual plots, used a likelihood ratio test of the deviance (Littell et al. 2006), and found no evidence of heterogeneous variance. Performing diagnostics on the candidate models instead of the global model is preferred if the global model has too many parameters relative to the sample size (Burnham et al. 2011). We used Akaike's information criterion adjusted for small sample size (AIC_c) to rank each set of candidate models, calculated Akaike weights (w_i) to assess the relative plausibility of each model given the data, and report a confidence set of models that includes those with relative likelihood $\geq 1/8^{th}$ that of the best approximating model (Burnham and Anderson 2002). We estimated the importance of each parameter by summing Akaike weights of each model containing that parameter. In each model set, we included all 1- and 2-variable models, which produces a more balanced set and allows unbiased estimation of importance weights (Doherty et al. 2011).

RESULTS

Nutrients, periphyton biomass, and most physical variables were similar between downstream (spawning salmon; $n = 4$) and upstream reaches (fewer or no spawning salmon; $n = 3$) (mixed-model ANOVA). No difference in NH_4^+-N was detected between down- and upstream reaches ($p > 0.16$; Table 2). All values for SRP were below detection limits, so we removed this variable from further analyses. Chl *a* biomass and AFDM were similar between up- and downstream reaches ($p > 0.28$), as were temperature, canopy cover, depth, width, and discharge ($p \geq 0.10$; Table 1). However, D50 was consistently smaller in down- than in upstream reaches ($p = 0.03$).

Differences in ecosystem metabolism

On average, the difference in GPP between before and during spawning was 46% greater in the down- than in the upstream reaches (before vs during spawning BACI contrast, $p = 0.03$), supporting our prediction (Fig. 2A). The increase in GPP in downstream reaches from before to during spawning was a result of responses in the Chewuch (86% increase; Fig. 3A, B) and Methow (31% increase; Fig. 3C, D) Rivers that offset the 24% decrease in GPP in the Twisp River (Figs. 3E, F). The difference in GPP before and after spawning did not differ between down- and upstream reaches (before vs after spawning BACI contrast, $p = 0.24$). GPP differed among rivers ($p = 0.04$). The Twisp River (range: 0.03–0.49 g O_2 m^{-2} d^{-1}) had the lowest rates and the Chewuch (0.04–1.5 g O_2 m^{-2} d^{-1}) and Methow Rivers (0.03–1.21 g O_2 m^{-2} d^{-1}) had higher rates (Fig. 3A–F).

The difference in ER before and during spawning (before vs during spawning BACI contrast, $p = 0.06$) and before and after spawning did not differ between down- and upstream reaches (before vs after spawning BACI contrast, $p = 0.27$; Fig. 2B). Rates of ER were similar among the Twisp (range: –11.23 to –1.08 g O_2 m^{-2} d^{-1}), Chewuch (range: –8.39 to –1.32 g O_2 m^{-2} d^{-1}), and Methow Rivers (range: –12.20 to –0.64 g O_2 m^{-2} d^{-1}) (Fig. 4A–F).

Abiotic and biotic factors driving differences in ecosystem metabolism

Water temperature, salmon density, and the weighted distance of Chinook Salmon redds from the sonde were important variables explaining the difference in rates of GPP before and during spawning between up- and downstream sites (Table 3). Water temperature was present in 2 of the 4 top models, including the best approximating model with temperature alone. Moreover, water temperature was ranked as an important variable (cumulative $w_i = 0.59$). Change in temperature before and during spawning was negatively related to difference in GPP before and during spawning (Fig. 5A). Salmon density was present in 2 of the 4 top models and was ranked as an important variable (cumulative $w_i = 0.48$). The summed weighted distance of each redd alone was present in the confidence set, but this variable showed little evidence of an effect (cumulative $w_i = 0.19$). As expected, the difference in GPP before and during spawning was positively related to salmon density

Table 2. Mean (SE) NH_4^+-N, chlorophyll *a* biomass (Chl *a*), and ash-free dry mass (AFDM) in periphyton for each sampling period in the upstream (Up) little or no spawning reaches and the middle or downstream (Down) spawning reaches. BDL = Below detection limit.

River	Location	Month	NH_4^+-N (mg/L)	Chl *a* (mg/m^2)	AFDM (g/m^2)
Chewuch	Up	July	0.032	15.33 (1.95)	0.72 (0.31)
		August	0.013	16.95 (3.27)	1.11 (0.28)
		September	0.010	29.00 (13.14)	0.67 (0.26)
		November	0.024	14.85 (1.82)	0.43 (0.11)
	Middle	July	0.036	9.99 (3.91)	0.93 (0.30)
		August	BDL	9.67 (2.50)	0.65 (0.21)
		September	0.015	21.14 (4.14)	0.79 (0.29)
		November	0.011	24.31 (6.96)	0.34 (0.22)
	Down	July	0.011	10.71 (2.27)	0.81 (0.22)
		August	0.014	26.16 (4.57)	0.87 (0.38)
		September	BDL	13.36 (2.71)	0.47 (0.29)
		November	0.016	40.60 (9.80)	0.87 (0.30)
Methow	Up	July	0.010	2.26 (0.61)	0.39 (0.19)
		August	0.019	6.17 (2.03)	0.54 (0.17)
		September	0.014	4.55 (0.62)	0.40 (0.18)
		November	0.015	9.05 (0.53)	0.23 (0.14)
	Down	July	0.016	13.76 (0.89)	1.58 (0.37)
		August	0.019	83.08 (13.97)	0.81 (0.13)
		September	BDL	22.18 (6.46)	0.45 (0.12)
		November	0.010	17.97 (5.20)	0.38 (0.17)
Twisp	Up	July	0.014	7.18 (2.10)	0.22 (0.15)
		August	0.014	12.65 (4.55)	0.32 (0.15)
		September	0.019	16.37 (6.29)	0.38 (0.10)
		November	0.013	31.22 (5.73)	0.56 (0.18)
	Down	July	BDL	2.98 (0.31)	0.18 (0.18)
		August	0.012	4.75 (0.46)	0.13 (0.13)
		September	0.023	3.73 (0.70)	0.34 (0.20)
		November	BDL	22.00 (2.76)	0.31 (0.15)

and proximity to redds (Fig. 5B, C). NH_4^+-N was present in the 1 of the top models in the confidence set together with salmon density, which probably inflated the importance of NH_4^+-N (cumulative w_i = 0.23). Little evidence was found for an effect of light intensity, Chl *a* biomass, or D50 (cumulative $w_i \leq 0.03$).

Rates of ER were similar in both up- and downstream reaches before, during, and after the salmon run, so we did not use AIC_c to assess biotic and abiotic factors that might explain differences among time periods.

Watershed models

In the watershed analysis, GPP was strongly associated with weighted distance of Chinook Salmon redds upstream from the sonde, which was present in all of the models in the confidence set (Table 4). The importance of weighted redd distance was further supported by its high cumulative weight (w_i = 0.97). D50 was present in only 1 model in the confidence set, but it was identified as important (cumulative w_i = 0.34). Salmon density was present in 1 model in the confidence set, but only when coupled with weighted redd distance and had little evidence for an effect (cumulative w_i = 0.09). Similarly, little evidence was found that other variables had important effects on GPP across the sites in the Methow River watershed (cumulative $w_i \leq 0.08$).

Temperature was the only variable related to ER across the watershed. Temperature was included in all 4 models in the confidence set (Table 4). In addition, temperature had the highest cumulative weight (w_i = 0.98). Weighted redd distance and salmon density had moderate cumulative weights (w_i = 0.37 and 0.19, respectively), but their importance probably was influenced by being coupled with temperature in models in the confidence set. Little evidence was found that other variables had important effects

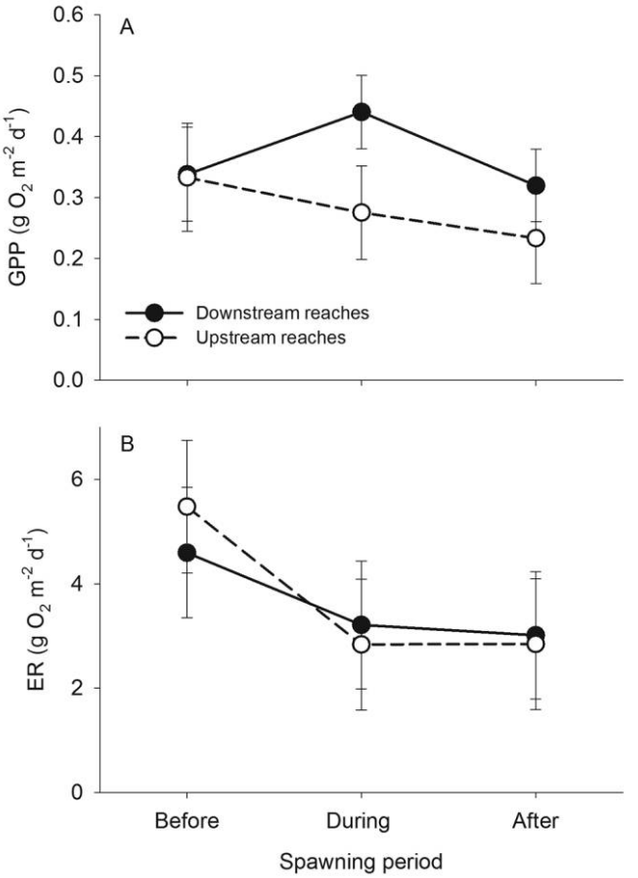

Figure 2. Least squares mean (±1 SE) estimates of gross primary production (GPP) (A) and ecosystem respiration (ER) (B) in upstream (little or no spawning) reaches (n = 3) and downstream (spawning) reaches (n = 4) before, during, and after spawning.

on ER across the sites in the Methow River watershed (cumulative $w_i \leq 0.09$).

DISCUSSION

Even with low densities of naturally spawning Chinook Salmon, differences in ecosystem metabolism can exist. In the Methow River basin, low densities of spawning salmon increased GPP by 46% during spawning in downstream compared to upstream reaches. The magnitude of this difference suggests that it is ecologically significant because basal resources available to higher trophic levels nearly doubled. Moreover, even after accounting for other biotic and abiotic factors, the influence of salmon on the differences in GPP remained apparent. In contrast to our initial prediction, ER did not differ between down- and upstream reaches. By exploring the effect natural spawning salmon have on ecosystem metabolism, we have helped to fill 3 important gaps. First and foremost, few investigators have evaluated the response of river ecosystems to low spawner densities (Janetski et al. 2009) that are typical over much of the range of Chinook Salmon. Our results suggest that the positive feedback created by salmon and their marine-derived nutrients may operate across a range of salmon densities. Second, the influence of naturally spawning salmon on ecosystem processes has been understudied (Naiman et al. 2002). Our results contribute to the short list of studies (Lessard et al. 2009, Holtgrieve and Schindler 2011, Levi et al. 2013a, b) on this topic. Third, most studies have been concentrated in a small percentage of the region used by Chinook Salmon (Janetski et al. 2009), and the interior Columbia River has been largely underrepresented in the existing studies.

Our findings are consistent with those of investigators who observed a positive response of GPP to naturally spawning salmon (128% increase; Levi et al. 2013a) and carcass analog added to streams (59% increase; Ebel et al. 2014), but are counter to those of Holtgrieve and Schindler (2011) who observed a negative response (28% reduction). The discrepancy in the response was most probably caused by differences in available spawning habitat and the disturbance to the sediment and accompanying biofilm during redd construction, which can be influenced by density of spawners or behavioral differences in redd building among salmon species. That is, when a negative effect was observed, salmon built redds throughout the stream (Holtgrieve and Schindler 2011), and when a positive effect was observed, streambed geomorphology prevented salmon from constructing redds in some parts of the stream (Levi et al. 2013a) or bed disturbance did not accompany nutrient addition (Ebel et al. 2014). Modeling efforts corroborate these findings, but suggest that positive effects of salmon on GPP would occur only when background nutrient concentrations were low (<0.002 mg SRP/L and 0.02 mg DIN/L; Bellmore et al. 2014). In our study, reduced bed disturbance consequent to small numbers of spawning Chinook Salmon coupled with oligotrophic condition of the rivers may explain why we observed an increase in GPP. However, this effect was short term and did not continue once spawning was finished, which is consistent with observations in streams that had higher densities of spawning salmon (Holtgrieve and Schindler 2011). Thus, in our study reaches, nutrients delivered via excretion might be more important than those from carcasses (Tiegs et al. 2011).

If increased nutrients from salmon excretion was the mechanism, then why did we not observe an increase in N or P where salmon spawn? At least 3 possible reasons can be found. First, in oligotrophic rivers like those in our study, nutrient limitation may be so great that nutrients are taken up rapidly (Davis and Minshall 1999), and even modest nutrient input may be enough to stimulate primary production (Bilby et al. 1996, Childress et al. 2014). This reasoning may explain why one of the candidate models to explain changes in GPP during spawning included salmon density

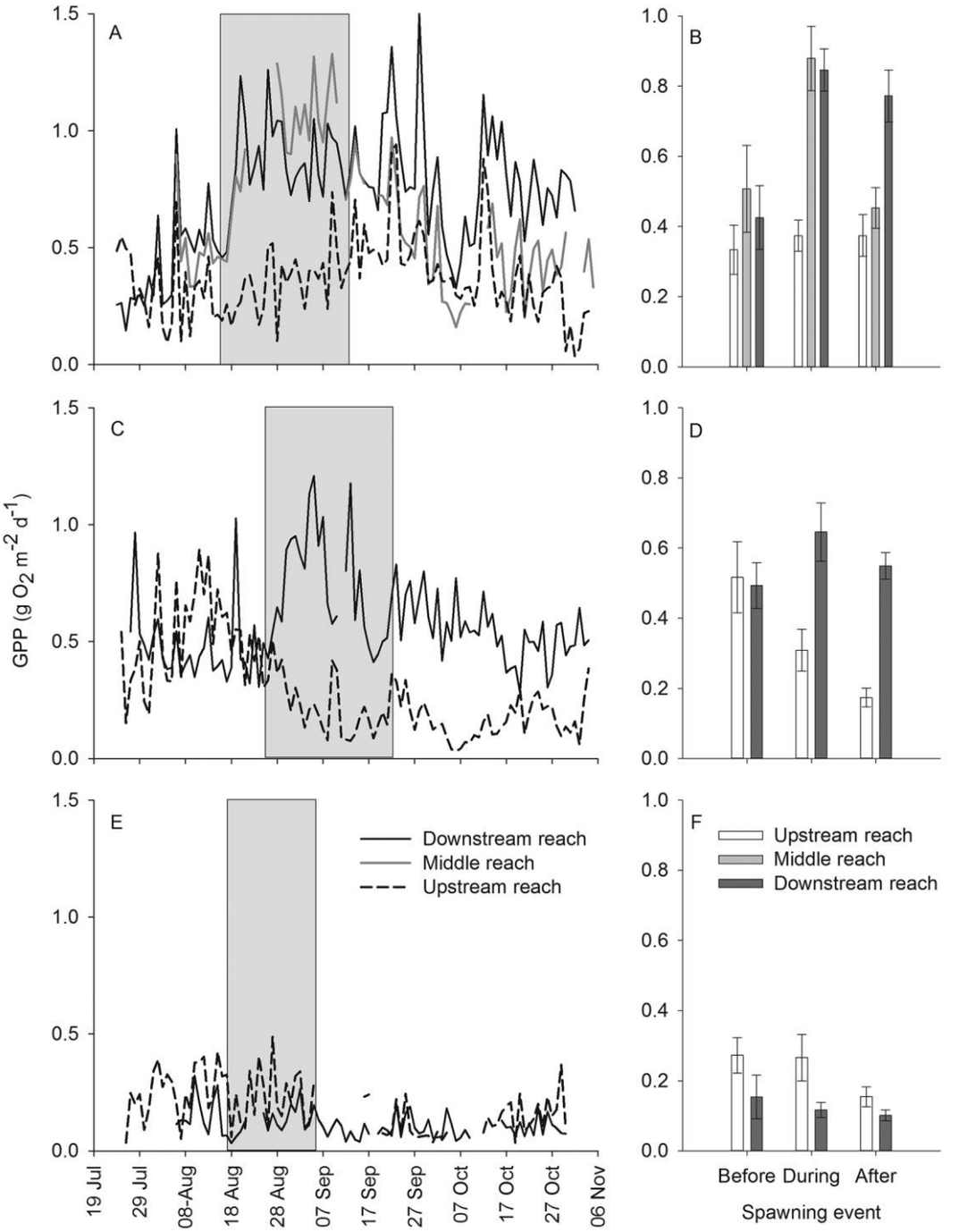

Figure 3. Daily (A, C, E) and mean (±95% CI) (B, D, F) gross primary production (GPP) in upstream (little or no spawning) reaches (n = 3) and downstream (spawning) reaches in the Chewuch (A, B), Methow (C, D), and Twisp (E, F) Rivers before, during, and after spawning. Shaded areas represent approximate windows of active Chinook Salmon spawning in the river based on the dates when the first and last redds were observed.

and NH_4^+-N. Second, increased dissolved organic C, such as that provided by salmon carcasses, could increase the assimilative demand for nutrients, thereby reducing the concentration in the water column (Bernhardt and Likens 2002, Fellows et al. 2006). Third, increases in nutrients from salmon can be brief (Holtgrieve and Schindler 2011, Marcarelli et al. 2014), and the timing of our nutrient samples at the onset and end of spawning may not have coin-

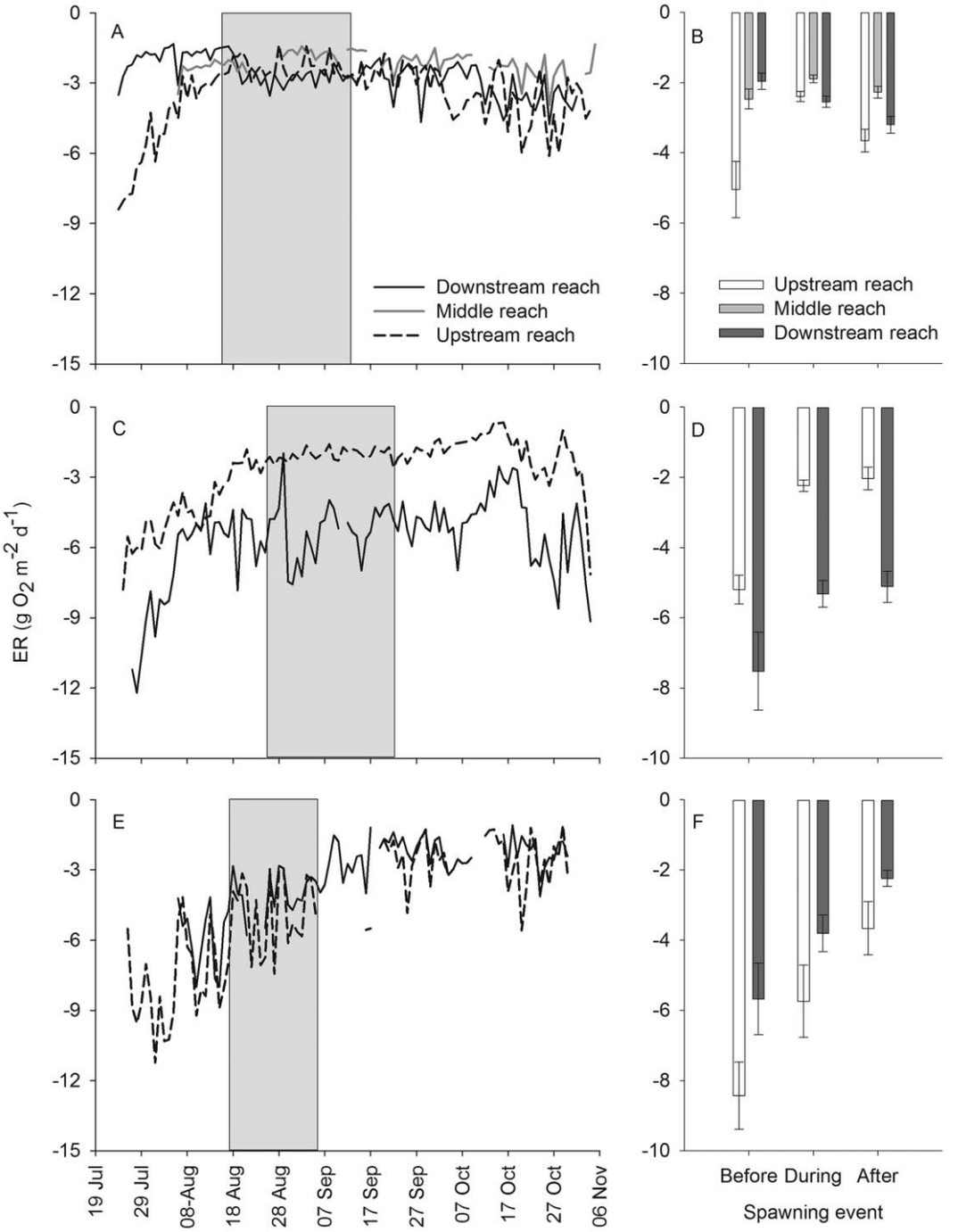

Figure 4. Daily (A, C, E) and mean (±95% CI) (B, D, F) ecosystem respiration (ER) in upstream (little or no spawning) reaches (n = 3) and downstream (spawning) reaches in the Chewuch (A, B), Methow (C, D), and Twisp (E, F) Rivers before, during, and after spawning. Shaded areas represent approximate windows of active Chinook Salmon spawning in the river based on the dates when the first and last redds were observed.

cided with the peak of nutrient concentration. Moreover, our nutrient sampling was conducted at only 1 location, and did not incorporate potential spatial variability in nutrient response.

The difference we observed in GPP between down- and upstream reaches was primarily caused by the density of spawning salmon based on the cumulative weights from our model-selection analysis. Similarly, in the watershed

Table 3. The top 10 candidate models to explain the difference in gross primary production (GPP) before and during spawning between up- (n = 3) and downstream (n = 4) reaches. The −2 log-likelihood (2Log$L$), Akaike's Information Criterion adjusted for small sample size (AIC_c), difference in AIC_c (ΔAIC_c), and Akaike weights (w_i) are shown. Larger weights indicate more plausible models. Models in bold represent those in the confidence set. Redd distance is the sum of the inverse distance to each upstream redd within the study site ($\Sigma[1/distance_{ij}]$).

Model	−2Log$L$	AIC_c	ΔAIC_c	w_i
Temperature	**−5.1**	**29.3**	**0.0**	**0.28**
Salmon density, temperature	**−12.6**	**29.4**	**0.1**	**0.26**
Salmon density, NH_4^+-N	**−12.0**	**30.0**	**0.7**	**0.19**
Redd distance	**−3.6**	**30.7**	**1.4**	**0.14**
Redd distance, light intensity	−7.6	34.4	5.1	0.02
Salmon density	0.4	34.8	5.5	0.02
NH_4^+-N	0.8	35.2	5.9	0.01
Redd distance, temperature	−6.6	35.4	6.1	0.01
Temperature, chlorophyll *a* biomass	−6.6	35.4	6.1	0.01
Temperature, D50	−5.6	36.4	7.1	0.01

analysis, proximity to redds was the most important variable. Taken together, these analyses support the prediction that salmon can affect GPP even at low densities. The observed increase in GPP with salmon density was predicted, but how the pattern may respond at greater densities of salmon in these rivers is unknown. We were unable to identify a mechanism behind this pattern, but the most likely mechanism is an increase in nutrient availability, which we were unable to detect. Redds may provide areas where GPP is concentrated because of available surface for new algal growth after redd construction, continued excretion of labile nutrients by adults building and guarding redds, and N leaching from the redd (Rice and Bailey 1980, Wright et al. 1995) and deposited salmon carcasses. Moreover, the 1-station approach to estimating metabolism may be biased toward events occurring closest to the sonde (Reichert et al. 2009). Thus, closer redds may provide more immediate measures of GPP and have more weight in the overall estimate. Studies are needed to explicitly test the effect of nutrient additions at different and cumulative distances from DO sensors used to estimate metabolism.

In contrast to other studies with higher densities of naturally spawning salmon (Holtgrieve and Schindler 2011, Levi et al. 2013a) or with carcass analogs (Ebel et al. 2014), we did not observe a difference in ER between down- and upstream reaches. Salmon can affect ER in multiple ways including contributing to O_2 demand via respiration and increasing heterotrophic activity via carcass decomposition or excretion (i.e., organic C; Janetski et al. 2009, Holtgrieve and Schindler 2011). The daily patterns of ER we observed were relatively consistent between down- and upstream reaches and among the reaches in the 3 rivers. The number of returning spawners probably was not sufficient to increase ER, or other factors may have been more important. For instance, temperature was the primary factor controlling ER in all 7 reaches, a result that is consistent with those of other studies in streams and rivers (Hunt et al. 2012, Griffiths et al. 2013) and across ecosystems (Yvon-Durocher et al. 2012). However, temperature alone often does not explain all of the variation in ER (Sinsabaugh 1997) and typically covaries with additions of organic C, such as salmon carcasses or leaf litter (Mulholland et al. 2001, Bernot et al. 2010, Griffiths et al. 2013), which we either did not detect or did not measure.

Our no-spawning and spawning reaches were up- and downstream, so our observations might be explained by upstream–downstream differences in other environmental or biotic factors (Mulholland et al. 2001, Roberts et al. 2007, Bernot et al. 2010). We did measure and test a suite of metrics that can be important in controlling metabolism. However, the only variable that differed between up- and downstream reaches was substrate size, which was greater in up- than in downstream reaches and may explain why spawning was limited in the upstream reaches. Most of the environmental changes experienced in these rivers, such as light availability and water temperature, followed a similar seasonal pattern at both up- and downstream reaches (Figs S1A–C, S2A–C). Moreover, we observed similar rates of GPP and ER between up- and downstream reaches before and after salmon spawned, which lends support that the response observed during spawning was caused by salmon. In addition, the BACI design we used should have accounted for the spatial and temporal differences in biological, chemical, and physical factors between the downstream and upstream reaches (Downes et al. 2002). Even when the variation in covariates was con-

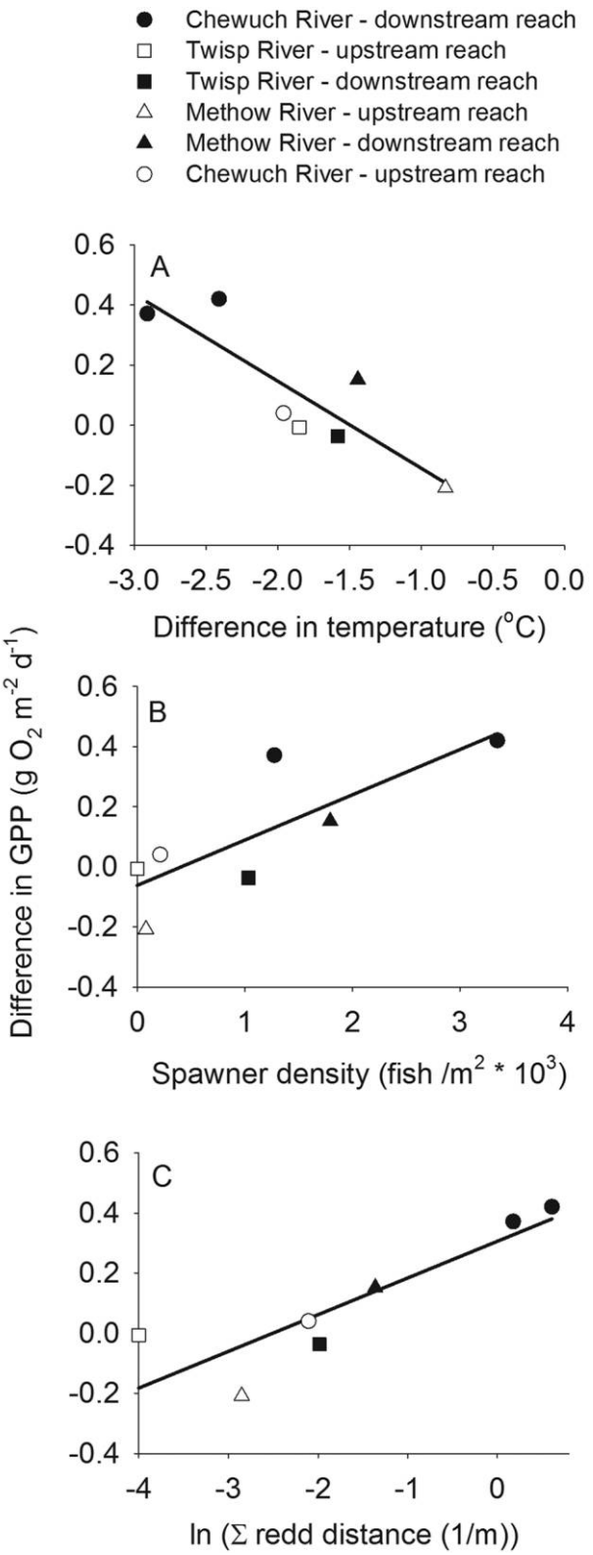

Figure 5. Relationships between the difference in gross primary production (GPP) before and during spawning and the difference in temperature before and during spawning (A), spawning Chinook Salmon density (B), and the distance of Chinook Salmon redds upstream of sonde (C).

sidered, we still observed a strong influence of salmon on GPP that was evident in statistical models used in the BACI analysis and in the analyses of reaches across the watershed.

Given our finding, an important question to address is: If low densities of salmon spawners increase stream productivity, then why do salmon populations in the Methow River not increase gradually? The first possibility is that when returning adult numbers are too low the amount of energy transferred up the food chain is insufficient to increase fish productivity measurably. To evaluate this possibility, we conducted a thought experiment using a simple trophic efficiency model whereby we assumed that: 1) observed differences in GPP between up- and downstream sites was strictly from spawning salmon, 2) 50% of GPP goes to autotrophic respiration (Webster and Meyer 1997), 3) 10% of the production is transferred to the next trophic level (Lindeman 1942), and 4) fish are 2 trophic levels above primary producers. Based on these assumptions, we calculated a 10% increase in fish capacity in the downstream reaches where salmon spawn compared to in upstream sites where no spawning occurs. This result suggests that the positive feedback once created by large salmon runs may still be present, but is drastically reduced from historical conditions. A 2nd possibility is that other feedbacks created by salmon may be lost. For example, larger numbers of spawners can reorganize streambed substrate or habitat, thereby releasing and transporting sediment stored in interstitial spaces and opening new habitat for biofilm and invertebrates (Janetski et al. 2009). These mobilized nutrients and macroinvertebrates also may benefit downstream recipient communities (Albers and Petticrew 2012). A 3rd possibility is that the ecosystem may have entered a new stable state because of years of declining numbers of salmon returns (Yang et al. 2008). If so, a different community could be present that may provide lower-quality food for juvenile salmon (Wipfli et al. 1999) or functional processes may be behaving differently. The 4th possibility is that downstream conditions in the Columbia River or in the ocean, such as dam passage by juveniles and overharvesting (Nehlsen et al. 1991), may limit salmon more than habitat and food availability in natal rivers.

Our findings add to the limited number of studies in which investigators evaluated the effects of naturally spawning salmon (Holtgrieve and Schindler 2011, Levi et al. 2013a) and salmon carcass additions (Ebel et al. 2014) on ecosystem metabolism. We contribute to these studies by showing that even at low densities, salmon in oligotrophic rivers can increase basal productivity. Despite our results and those of others, whether a lower threshold exists where salmon are no longer able to sustain their population via a positive feedback (Moore et al. 2011) or this feedback can be reinstated following nutrient augmentation remains unclear. As the positive feedback paradigm predicts, increases in primary production caused by salmon may ben-

Table 4. The top 10 candidate models of abiotic and biotic controls on gross primary production (GPP) and ecosystem respiration (ER) across 7 sites in the Methow River watershed. The −2 log-likelihood (−2Log*L*), Akaike's Information Criterion adjusted for small sample size (AIC_c), difference in AIC_c (ΔAIC_c), and Akaike weights (w_i) are shown. Larger w_is indicate more plausible models. Models in bold are those in the confidence set. Redd distance is the sum of the inverse distance to each upstream redd within the study site ($\Sigma[1/distance_{ij}]$).

Response variable	Model	−2Log*L*	AIC_c	ΔAIC_c	w_i
GPP	**Redd distance**	**−30.8**	**−11.2**	**0.0**	**0.34**
	Redd distance, D50	**−34.7**	**−11.1**	**0.1**	**0.32**
	Redd distance, salmon density	**−31.8**	**−8.2**	**3.0**	**0.08**
	Redd distance, light intensity	**−31.8**	**−8.2**	**3.0**	**0.08**
	Redd distance, chlorophyll *a* biomass	**−31.4**	**−7.8**	**3.4**	**0.06**
	Redd distance, NH_4^+-N	**−31.0**	**−7.4**	**3.8**	**0.05**
	Redd distance, temperature	**−30.8**	**−7.3**	**3.9**	**0.05**
	D50	−22.8	−3.2	8.0	0.01
	Salmon density, D50	−26.5	−2.9	8.3	0.01
	Salmon density	−22.3	−2.7	8.5	0.00
ER	**Redd distance, temperature**	**77.6**	**101.1**	**0.0**	**0.37**
	Temperature	**82.6**	**102.2**	**1.1**	**0.21**
	Salmon density, temperature	**78.9**	**102.5**	**1.4**	**0.18**
	Temperature, D50	**80.4**	**104.0**	**2.9**	**0.09**
	Temperature, storage	81.8	105.4	4.3	0.04
	Temperature, NH_4^+-N	82.3	105.9	4.8	0.03
	Temperature, discharge	82.5	106.1	5.0	0.03
	Temperature, canopy cover	82.6	106.2	5.1	0.03
	Salmon density	91.6	111.2	10.1	0.00
	Discharge	92.3	111.9	10.8	0.00

efit macroinvertebrate and fish production, but most studies, including ours, have been focused on 1 or 2 trophic levels and not the full food web (but see Kohler et al. 2012). Perhaps the lack of whole-foodweb studies is a result of logistic constraints. An alternative approach would be to develop models that could simulate potential responses to spawning salmon, and help develop hypotheses to be tested. A systems dynamic model to identify how environmental context mediates the potential effects of salmon on primary production has been developed (Bellmore et al. 2014), and an expansion of this model to explore potential effects on the rest of the food web is underway.

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