

Linking resource availability and habitat structure to stream organisms: an experimental and observational assessment

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Abstract. An experiment and a mark-recapture field study of juvenile coho salmon (*Oncorhynchus kisutch*) were conducted to identify controls of key energy flow chains in river food webs. In the small-scale experiment, we investigated the individual and interactive effects of physical habitat structure (PHS) as small wood and resource availability (tissue of adult Chinook salmon, *O. tshawytscha*) on nutrients, algae, invertebrates, and fish predators including juvenile coho. In the field, we quantified the effects of natural variation in prey availability (invertebrate drift biomass), PHS (wood), and local fish density on summer growth of juvenile coho across multiple stream reaches. Adding salmon tissue to experimental channels resulted in strong bottom-up effects on select invertebrates including increased population biomass of chironomids and baetids, the numerically dominant invertebrates, and faster growth of juvenile coho. We link the enhanced growth of coho to chironomid productivity: for instance, adult chironomid flux was 4.3× higher and coho consumption of these animals 3× higher in salmon-subsidized channels. PHS in experimental channels was associated with reduced algal biomass, potentially in response to increased invertebrate consumption, and invertebrate flux or export. The field study revealed coho growth was negatively related to PHS and total fish density and positively related to Diptera drift biomass; however, the effects of fish density and drift biomass on coho growth were relatively weak. The field study also indicated that prey resource availability and coho growth were associated with differences in canopy cover, with prey biomass and coho growth 2–4× higher in reaches receiving more sunlight. As in the experiment, coho in natural stream reaches predominantly fed on adult chironomids and other Diptera, indicating that these taxa and life-stages are a key link between the benthic food web and mobile vertebrate predators. Our study showed that bottom-up processes initiated by salmon subsidies and possibly light flux determined key trophic interactions in the Cedar River food web. Moreover, we speculate that PHS may modify some of these interactions indirectly through its effects on the movement of organisms through the environment.

Key words: anadromous; body size; bottom-up; Chironomidae (Diptera); fish; growth; *Oncorhynchus kisutch* Walbaum; physical habitat structure; resource subsidies; restoration; scale; streams; Washington, USA.

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INTRODUCTION

A major challenge confronting the field of ecology is identifying the suite of factors that modify the flow of energy through food webs (Cross et al. 2011). Understanding these complex relationships is important for predicting how food webs respond to environmental change (Fretwell 1987, Persson et al. 1996, Turchin 2003), such as how changes in nutrient loading or climate warming alter energy flow and ultimately the individual traits and population dynamics of higher trophic levels. Such bottom up or energy flow chains are ecologically important (i.e., they modify individual or population growth rate) pathways of energy movement from basal resources to higher trophic levels and are governed by intrinsic (processes occurring within the defined food web) and extrinsic (energy inputs entering the food web from outside the system) controls (Persson et al. 1996). Although our understanding of energy flow chains is growing (e.g., Grant et al. 2000), there remains much to learn especially with quantifying the relative importance of these controls in predicting food web structure and function when they operate simultaneously. Addressing this uncertainty is especially challenging in open systems with mobile organisms, such as streams and rivers, because organisms in these ecosystems can explore habitats offering a range of growth conditions that result from differences in the type and strength of various controlling agents (Armstrong et al. 2010).

Resource pulses are examples of an extrinsic control that modifies energy flow chains in a variety of ecosystems (Wallace et al. 1999, Grant et al. 2000, Wipfli et al. 2010), and are defined as relatively infrequent episodes of increased resource availability (Yang et al. 2008). Migrations of anadromous fish are a relatively well-studied example of a resource pulse that influences a diversity of ecological characteristics, including trophic productivity and habitat structure, through their spawning activities (Richey et al. 1975, Moore et al. 2007, Jones et al. 2010). Though our understanding of this system is growing (Janetski et al. 2009), there remain some unresolved questions including two that we address

in this paper. First, there is little known with regards to the enrichment potential of low densities (0.1–1.0 kg/m²) of spawning fish (Janetski et al. 2009), which is characteristic of many populations across their native range (Gresh et al. 2000). Second, there is some uncertainty regarding the mechanisms by which adult salmon influence the productivity of higher trophic levels. Specifically, while there is strong evidence supporting the direct transfer of energy (tissue and eggs) from spawning salmon to higher trophic levels (e.g., Armstrong et al. 2010), the evidence supporting the indirect pathway of salmon resources fertilizing food webs via bottom-up processes is mixed (e.g., Lessard and Merritt 2006). One factor that may contribute to these inconsistent results is that most studies sample static measures, such as abundance or biomass, rather than turnover or export, which may be more responsive to salmon subsidies relative to static measures (Lessard and Merritt 2006, Moore et al. 2007, Kiernan et al. 2010).

Physical habitat structure (PHS), consisting of both habitat complexity and heterogeneity (Beck 2000), is potentially another important control on energy flow chains. Since the seminal paper by MacArthur and MacArthur (1961), PHS has been shown to affect population abundance (e.g., Negishi and Richardson 2003), organic matter storage (e.g., Bilby 1981), species diversity (e.g., O'Connor 1991), and biotic interactions (e.g., Crowder and Cooper 1982). For instance, fish abundance and diversity was higher in stream pool habitats with wood, possibly because of increased resource availability and protection from predators (Wright and Flecker 2004). As with resource pulses though, we have a relatively limited mechanistic understanding of how PHS shapes ecosystems (Kovalenko et al. 2012, except see Cardinale et al. 2002) including how it influences the movement of organisms through the environment, a key ecological process (Gaines and Bertness 1993, Bowler and Benton 2005, Kuefler et al. 2010). For example, PHS may modify drift, or the downstream movement of invertebrates in the water column (Benke et al. 1986). Drift is a pervasive feature of lotic ecosystems, and likely influences a variety of ecological processes and patterns including

population dynamics (Bond et al. 2000, Downes and Lancaster 2010), biotic interactions (e. g., Palmer 1995), and energy flow (Bilby 1981, Benke et al. 1984, Benke et al. 1986). Moreover, PHS conceivably interacts with other potential controlling agents, including resource pulses, to modify food web structure and function; yet, studies that explore such interactions are relatively rare (except see Martin et al. 2010).

Therefore, to increase our understanding of energy flow chains, we manipulated resource availability (inputs of adult salmon tissue) and PHS (small pieces of wood) in streamside mesocosms to examine their individual and interactive effects on food web (nutrients, algae, invertebrates, and juvenile coho salmon, *Oncorhynchus kisutch* Walbaum) structure, dynamics, and productivity. We predicted that (1) addition of salmon tissue would enhance the growth, biomass, and turnover of this food web through bottom-up processes mediated by increased availability of essential biomolecules; (2) adding PHS would increase the abundance and diversity of stream invertebrates by increasing available niches; (3) PHS would also modify invertebrate drift; and (4) salmon subsidies would interact with PHS to determine food web attributes.

This experiment allowed us to investigate the effects of resource subsidies and PHS on a food web representative of the Cedar River (Brown et al. 2011), but the relatively small mesocosms lacked many important features of natural systems including variation in fish density and composition and restricted fish movement. In nature, these mobile predators experience a range of growth conditions that are determined by factors besides resource subsidies, such as light flux, temperature, and biotic interactions. Furthermore, PHS in river ecosystems likely delivers functions that are different from those in the mesocosms, including modifying the distribution and abundance of fish populations (Roni and Quinn 2001, Wright and Flecker 2004). Thus, to increase our inference regarding the identification of key energy chains in lotic ecosystems and how abiotic and biotic factors modify these chains, we quantified the effects of drifting invertebrates (prey resource for drift-feeding fish such as juvenile coho), PHS (in-stream wood abundance), and total fish density on juvenile coho growth rate in six reaches of the

Cedar River watershed, WA, USA very near our experimental channels. Based on our understanding of the system (e.g., Pess et al. 2011) and insights from other studies, we predicted that juvenile coho growth would be positively correlated with prey availability (e.g., Rosenfeld et al. 2005) and PHS as represented by in-stream wood (e.g., Solazzi et al. 2000), but negatively correlated with local fish density due to intra- and interspecific competition for resources such as food and space (e.g., Jenkins et al. 1999).

METHODS

Study site

Historically, coho and Chinook (*O. tshawytscha* Walbaum) salmon and steelhead trout (*O. mykiss* Walbaum) were present in the lower portions of the 36,664-ha Cedar River Municipal Watershed (47°38'157" N, 121°95'807" W), a protected watershed that originates in the Cascade Mountains of Western Washington (Fig. 1; see Kiffney et al. 2006, 2009 for further details of study area). However, in 1900 the Landsburg diversion dam blocked upstream migration of adult salmon and anadromous trout, leading to local extirpation of these fishes across 43 km of relatively high quality habitat above the dam. Following installation of a fish ladder in 2003, adult coho and Chinook naturally recolonized this habitat for the first time in over 100 years (Anderson et al. 2008, Kiffney et al. 2009, Pess et al. 2011). Juvenile coho salmon were the focus of our study as they are the numerically dominant salmonid of the Cedar River food web and many other tributaries to the North Pacific, are a species of concern across much of their range (<http://www.nmfs.noaa.gov/pr/species/fish/cohosalmon.htm>), and their extended freshwater rearing period (~12–18 months) is representative of Pacific salmon species with a similar life history (Quinn 2005).

Experiment

Logistics.—Experimental streams (4.8 m long and 0.3 m wide, $n = 16$) were flow-through systems that were partially filled with gravel substrate (10–30 mm median grain size) and received water (temperature range 10–14°C, mean \pm 1 SE = $12 \pm 0.01^\circ\text{C}$; stream flow rate = 1.1 ± 0.03 L/s) containing organic detritus, algae, microbes, and a diverse assemblage of inverte-

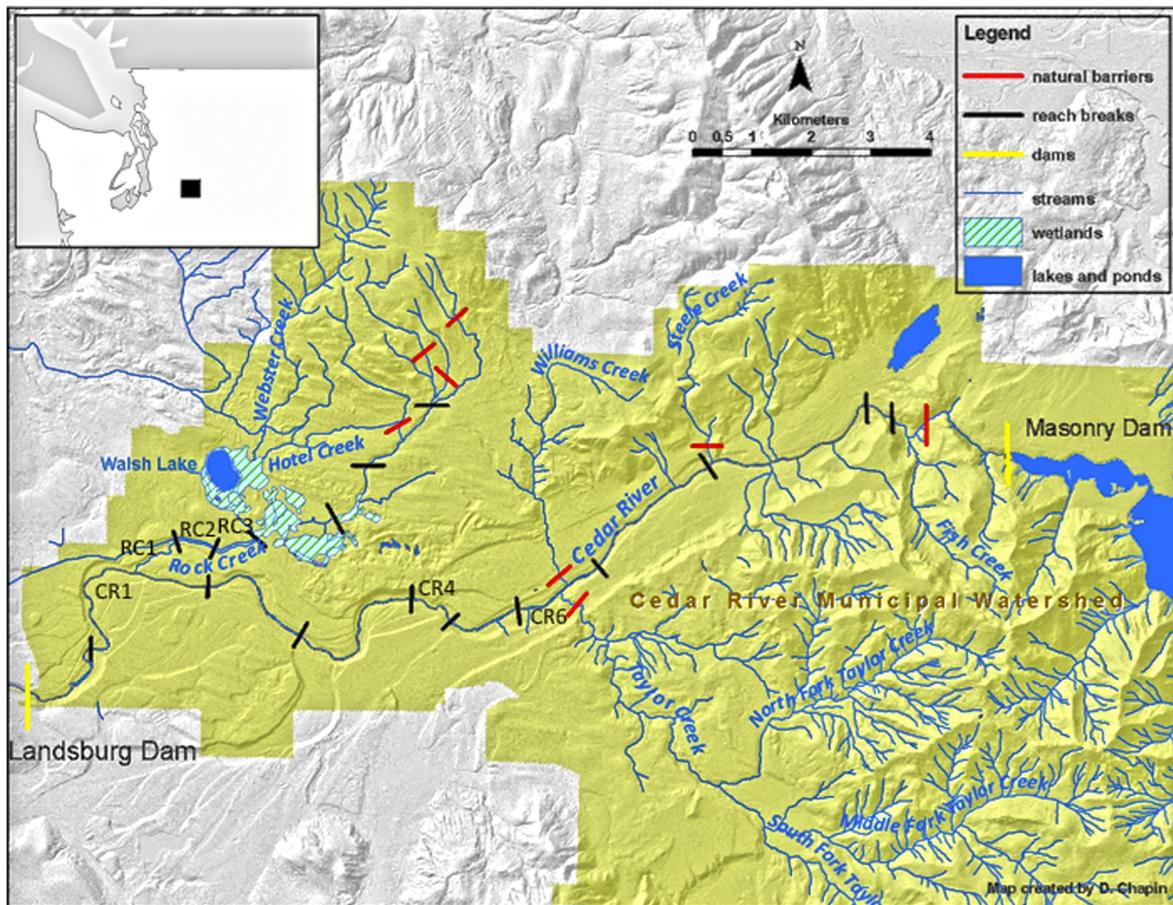


Fig. 1. A map of study area including reach locations for field study; experimental streams were located on the north bank of the river about 250 m west or downstream of Landsburg Dam (dam location represented by solid yellow line bisecting river). Solid black lines indicate different study reaches, while red lines represent natural barriers to upstream fish migration. Reach numbers for Rock Creek (RC) and the Cedar River (CR) increase from downstream to upstream so the first reach (CR1) in the Cedar River begins at the first black line above the dam and ends at the second line above the dam and so on.

brates from the Cedar River (see Cram et al. 2011 for further details). Deposition of eggs by aerial adults may have also contributed to invertebrate populations, but this source of colonists was not quantified. Water was turned on 60 days prior to the start of the experiment to allow the benthic food web to establish (Cram et al. 2011).

After 60 days of water flow, one juvenile coho salmon (length = 66.0 ± 1.5 mm, weight = 4.1 ± 0.3 g) and one torrent sculpin (*Cottus rhotheus* Smith, length = 55.4 ± 1.7 mm, weight = 2.2 ± 0.5 g) collected from the Cedar River were added to each channel. There was no initial treatment difference in weight or length for either species,

and densities (0.70 fish/m²) were within the range observed in nearby streams (Kiffney et al. 2009, Pess et al. 2011). A wire screen (1.75 cm aperture) was placed at the end of each channel to restrict downstream fish movement. Fish acclimated to channels for three days prior to the start of the experiment.

Resource subsidies were represented by adult salmon tissue or salmon analogs (Wipfli et al. 2004, Kohler et al. 2012a), and were added at a density of 0.6 kg/m², which is within the range of spawning biomass observed in natural systems (e.g., Chaloner et al. 2004) but lower than levels used in most salmon-subsidy experiments (Wip-

fli et al. 2004, Janetski et al. 2009). The PHS treatment was represented by small wood (4 pieces/channel, each piece was $\sim 0.02\text{--}0.04$ m in diameter and $0.25\text{--}0.27$ m in length, total wood surface area ~ 0.03 m²), which was gently placed at a 45° angle along each channel the same day analogs were added. Small wood (<0.1 m in diameter and 1.0 m in length) was used, because it is an abundant but understudied habitat element of stream systems including those in the Cedar River watershed (e.g., Wallace et al. 1999; P. Kiffney, *personal observation*). We note that we cannot distinguish the effects of increasing habitat area vs. heterogeneity with our PHS manipulation. Each treatment (C = no wood or analogs, W = wood added, A = analogs added, WA = wood and analogs added) was randomly assigned to four replicate channels. The experiment began (day 0) when analogs and wood were added (18 June 2007) and ended 45 days later (31 August 2007).

Sampling procedures.—Water collected from the downstream end of each channel on days 14 and 45 was measured for total nitrogen and phosphorus and dissolved nutrients (dissolved ammonium-nitrogen [NH₄⁺-N], dissolved nitrate-nitrogen [NO₃⁻-N], soluble reactive phosphorus [SRP]) according to the methods in Valderrama (1981) and UNESCO (1994). Eight unglazed ceramic tiles (0.01 m²), distributed evenly along the length of each channel, were used to sample periphyton and invertebrates. Two of these tiles were randomly selected from each channel on days 14 and 45 and processed for invertebrate abundance and biomass and Simpson's reciprocal index of diversity, which was calculated based on the relative abundance of all taxa (Magurran 1988). A dissection scope with an ocular micrometer and common keys (Merritt and Cummins 2004) were used to identify invertebrates to family and measure head capsule width. Regression equations were then used to convert head capsule width to an estimate of biomass (Burgherr and Meyer 1997, Benke et al. 1999; P. M. Kiffney and S. M. Naman, *unpublished data*). Day 45 tiles were also used to quantify treatment effects on algal biomass (see Kiffney et al. 2003 for further details of algal and invertebrate processing).

On day 14, we determined net invertebrate flux (the number of invertebrates leaving –

number entering each channel) by filtering the entire volume of incoming and outgoing water through drift nets (250 μ m aperture) for 24 hours (Melody and Richardson 2004). Captured animals were stored in 95% ethanol and processed in the same manner as tile invertebrates. Invertebrate flux or export was measured, because turnover can be estimated when flux is combined with benthic densities or biomass (Jackson and Fisher 1986). Invertebrate flux may also serve as a key link between salmon subsidies, the benthic food web, and drift-feeding juvenile coho salmon (Quinn 2005). We note that the number of invertebrates drifting into channels was similar across treatments for all taxa except Simuliidae larvae, which was higher in channels without PHS, so we omitted this taxon from statistical analysis except for body size comparison. Also, invertebrate flux abundance was used because three samples were accidentally destroyed before processing for biomass.

At the end of the experiment, fish were captured and euthanized with an overdose of tricaine methanesulfonate (MS-222). We recaptured fifteen coho but only 12 sculpin, with the analog (A) treatment missing all but one sculpin; therefore, because of the low number of sculpin recaptures, we did not conduct statistical analysis on this species. Coho were weighed (± 0.1 g), measured (± 1.0 mm), and their stomachs removed and placed in 95% ethanol for diet analysis; stomach contents were processed as described for tile and drift invertebrates.

Adult Pacific salmon are enriched in the heavier isotopes of carbon (C) and nitrogen (N) relative to their natal watersheds, and analogs, which were made from adult Chinook salmon, display these isotopic differences (mean $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ of analogs were about -20.1‰ and 10.8‰ , respectively; Kohler et al. 2012a). Thus, to determine the importance of salmon-derived nutrients as an energy source for juvenile coho, mass spectrometry was used to quantify natural abundance stable carbon ($\delta^{13}\text{C}$) and nitrogen ($\delta^{15}\text{N}$) isotope ratios in coho muscle tissue (Reichert et al. 2008). Stable C and N isotope ratios were expressed as $\delta^{13}\text{C}$ or $\delta^{15}\text{N} = [(R_{\text{sample}}/R_{\text{standard}}) - 1] \times 1000$, where R is $^{13}\text{C}/^{12}\text{C}$ or $^{15}\text{N}/^{14}\text{N}$, respectively.

Statistical analysis.—We used an information-theoretic approach and multimodel inference to

test hypotheses regarding the effects of PHS (wood) and resource availability (salmon analogs) on the experimental stream food web. Linear mixed-effects models were used to estimate the fixed effects of analogs (A), wood (W), time (T), and their two-way interactions on variables measured on days 14 and 45, which included nutrient chemistry, benthic invertebrate biomass of dominant taxa (taxa comprising > 0.1 by proportion of total benthic biomass), and Simpson's reciprocal index. All models included a random intercept term (grouped by channel) to account for non-independence of repeated measurements within a channel. Linear models were used to estimate treatment effects on response variables measured only once (net invertebrate flux on day 14; periphyton biomass, and coho growth, body size, and natural abundance levels of C and N isotopes on day 45). Fish size can modify isotopic ratios (e.g., Akin and Winemiller 2008), so final coho body mass (g) was also included as a covariate in models predicting $\delta^{13}\text{C}$ or $\delta^{15}\text{N}$ ratios. Nutrient concentrations and invertebrate biomass were log-transformed before analysis.

To quantify treatment effects on coho growth, we used nonlinear models that capture the well-known dependence of growth rate on size. This approach avoids the difficulties of metrics such as absolute or specific growth rate, which often fail to correct for size-dependence (Sigourney et al. 2008), by instead predicting the final mass M_t of an individual after some period of time Δt using a suitable nonlinear function of initial mass M_0 and environmental covariates. We chose the parabolic growth model (Ostrovsky 1995), which is derived from the simple bioenergetic assumptions of allometric scaling of metabolic rate with mass and proportional scaling of mass growth rate with metabolic rate:

$$M_t = [p\Delta t + M_0]^q \quad (1)$$

with parameters p and q . This model or growth metrics derived from it have been applied to salmonids, including coho (e.g., Quinn et al. 2004). Parabolic growth can be viewed as a special case of the general growth model proposed by Schnute (1981), whose other special cases include the von Bertalanffy model widely used in fisheries (Baker et al. 1991). Given our relatively modest sample size and short growth

interval, we did not pursue model selection on the underlying shape of the growth curve but instead focused on treatment effects, which are expected to change the scale parameter p but not the shape parameter q (Ostrovsky 1995). We used a linear model for $\log(p)$ to ensure that p is positive:

$$\log(p) = p_0 + p_A A + p_W W + p_{A \times W} AW \quad (2)$$

where the dummy treatment indicators A and W take the value 0 or 1. We assumed multiplicative lognormal errors for the observations of final mass, so that $\log(M_t) = \log(\hat{M}_t) + \varepsilon$, where the fitted value is given by Eq. 1 and ε is a normally distributed residual. Attempts to estimate q for the experimental data were unsuccessful due to severe parameter correlation, so we used the model-averaged estimate $q = 0.66$ based on field mark-recapture data (see below, *Field study: Statistical analysis*). Qualitative results were robust to the fixed value of q .

We used Akaike's information criterion corrected for sample size (AIC_c) to rank candidate models that comprised all subsets of the fixed-effect terms (Burnham and Anderson 2002). Interaction terms were allowed only in models that included the corresponding main effects, and the candidate sets included the intercept-only model. Models with $\Delta\text{AIC}_c < 4$ were considered to have strong to considerable support (Burnham and Anderson 2002). We calculated the Akaike weight (w) of each model, an estimate of the probability that it is the best approximating model in the candidate set. For each main effect or interaction, we also calculated the variable weight (i.e., the summed Akaike weights of all candidate models containing that term, where 0 indicates no support and 1 indicates maximum support) and the model-averaged coefficient estimate and its unconditional standard error based on the entire candidate model set (Burnham and Anderson 2002). Analyses were conducted in R (R Development Core Team 2013) using the lme4 (Bates et al. 2013), MuMIn (Barton 2013) and bbmle (Bolker 2012) packages.

We also used three descriptive approaches to compare treatment effects on select responses and invertebrate body size distributions measured day 45, and chironomid life-stage transitions or turnover measured on day 14. First, log

Table 1. Measures of central tendency for stream channel width, wood abundance, water temperature, adult Diptera drift biomass, juvenile coho growth rate, total salmonid density, and estimates of cumulative (2003–2007) adult salmon spawning density measured in the six study reaches (see Fig. 1). Means (with 95% CIs in parentheses) are shown except for temperature, which are medians (and minimum and maximum).

Stream-reach	Channel width (m)	Wood abundance (no./km)	Water temperature (°C)	Adult Diptera drift (mg/m ³)	Coho growth rate (g:g ⁻¹ .d ⁻¹)	Total salmonid density (no./m ²)	Adult salmon inputs (kg/m ²)
CR1	21 (18, 24)	65 (42, 89)	11 (9, 13)	0.002 (0, 0.004)	0.008 (-0.003, 0.02) <i>4</i>	0.89 (-0.50, 2.3) <i>7</i>	0.027
CR4	24 (20, 26)	57 (14, 100)	12 (10, 14)	0.007 (0, 0.01)	0.032 <i>1</i>	0.021 (0, 0.05) <i>7</i>	0.01
CR6	22 (19, 24)	176 (19, 332)	12 (10, 13)	0.004 (0, 0.008)	0.004 (0.002, 0.005) <i>13</i>	0.29 (-0.09, 0.70) <i>11</i>	0.007
RC1	4.9 (3.7, 6.2)	381 (232, 531)	14 (11, 17)	0.001 (0, 0.003)	0.0018 (0.0005, 0.003) <i>14</i>	0.64 (-0.20, 1.5) <i>5</i>	0
RC2	4.3 (3.4, 5.1)	294 (200, 332)	14 (11, 17)	0.002 (0, 0.004)	0.0018 (0.001, 0.003) <i>5</i>	0.10 (0.003, 0.20) <i>5</i>	0
RC3	4.1 (3.8, 4.5)	273 (211, 333)	14 (11, 17)	0.001 (0, 0.002)	0.0028 (0.017, 0.0038) <i>24</i>	0.39 (0.02, 0.80) <i>5</i>	0

Notes: Water temperature was measured hourly from 1 July 2007 to 20 August 2007. Numbers in italics represent number of coho recaptured or habitat units surveyed for fish density estimates. Drift biomass was measured in four riffles within each reach except RC3 where three riffles were sampled.

response ratios (i.e., $\log[\text{value in treatment}/\text{mean value in control}]$, $n = 4$ replicates per treatment) were calculated for variables representing all trophic levels (nutrients, algae, invertebrates and fish), with the sign of the log ratio corresponding to the sign of the treatment effect (Harpole et al. 2011). Second, means and 95% confidence intervals were used to compare treatment effects on body size distributions of dominant taxa. Third, chironomids were collected in drift as larvae, pupae and adults, and as larvae and pupae on tiles allowing us to quantify how relatively crude estimates of turnover for this taxon varied across treatments. Estimates of turnover (mean \pm 1 SD) were calculated by dividing the number of pupae (benthic + drift) and adults (drift only) by channel-level estimates of benthic chironomid larvae.

Field study

Logistics.—We examined the relative importance of resource availability as defined by drifting invertebrates, PHS (in-stream wood abundance), and local fish density to juvenile coho growth during summer 2007 across three reaches in Rock Creek (RC1, RC2, RC3; reach length \sim 100 m) and three reaches in the main

stem Cedar River (CR1, CR4, CR6; reach length \sim 1000 m) (Fig. 1, Table 1). Coho growth rates were quantified by capturing and marking fish in June using either electrofishing (RC) or seining (CR) in multiple slow-water habitats (e.g., pools) dispersed across the six reaches, and recapturing a subset of marked fish in September (see Anderson et al. 2008, Pess et al. 2011 for details on capture methods). Captured fish >60 mm ($n = 567$ coho initially tagged; 18 recaptures in the main stem and 46 in Rock Creek) were marked with passive integrated transponders (Prentice et al. 1990). Gastric lavage was used to collect diets from coho captured ($n = 208$ individuals) in study reaches during summer and early fall (2005–2009) (Kamler and Pope 2001).

Prey resource availability (drift biomass concentration [mg/m³], see Leung et al. 2009) was quantified in July 2007 by deploying one drift net (see description of nets in the *Experiment*) for \sim 24 hours at the downstream end of three to four riffles per reach over a seven day period. Riffles were interspersed across the same reaches where coho growth was measured. Reach-scale drift biomass was then estimated by averaging values from individual riffles within a reach. Drift and coho diet samples were processed using the same

methods described in the experiment. To assess whether coho in the experiment and field preferred certain prey items, diet selectivity was determined as $L = r_i - p_i$, where r_i and p_i are the proportions by biomass of prey type i in the diet and drift, respectively (Strauss 1979). When calculating selectivity in channels, we used drift biomass rather than abundance.

Physical habitat structure (wood pieces/km) was quantified by counting large wood (≥ 0.1 m in diameter and ≥ 1 m in length) within the wetted channel of each reach. Total salmonid fish density (no./m²), which included mountain whitefish (*Prosopium williamsoni* Girard), rainbow (*O. mykiss* Walbaum) and coastal cutthroat trout (*O. clarki clarki* Richardson), and juvenile coho and Chinook salmon, was quantified in August 2007 by snorkeling slow-water habitats with characteristics similar to those where coho growth was measured. Reach-scale estimates of fish density were calculated by averaging across values obtained from these individual habitat units (see Kiffney et al. 2009 for details of wood and fish survey methods).

We did not quantify the influence of adult salmon-derived nutrients on juvenile coho growth in the field because reach-scale, cumulative spawning density estimates were extremely low in the main stem and there was no spawning in Rock Creek (Table 1; Burton et al. 2013). Moreover, in previous experiments and field observations in the Cedar River, this range of adult inputs had no detectable effect on nutrient chemistry, algal biomass, invertebrate population biomass, fish growth, and stable isotope ratios of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ of invertebrates or fish (Cram et al. 2011; P. M. Kiffney, unpublished data). Water temperature was also not included as a covariate in statistical modeling, because exploratory analysis showed it was not correlated with coho growth.

Statistical analysis.—To quantify the relationships between environmental factors and the growth of marked coho in the field, we used the parabolic growth model (Ostrovsky 1995) as described above (see *Experiment: Statistical analysis*). We modeled the effects of reach-level covariates on the growth scale parameter as shown in Eq. 2, but here we added a random effect to account for the grouping of growth observations by reach:

$$\log(p) = p_0 + p_F F + p_W W + p_D D + \xi \quad (3)$$

where the mixed-effects model includes the fixed effects of food (adult Diptera drift biomass, F), wood (W) and total salmonid density (D), all measured at the reach level and standardized to have zero means and unit variances, along with a normally distributed reach-specific deviation ξ . Diptera drift biomass was used because exploratory analysis indicated it was more strongly related to coho growth rate than other drift metrics. We assumed multiplicative lognormal errors for the individual observations of final mass, and fit the full model and submodels including all combinations of zero, one, two, or all three covariates using the nlme package in R (Pinheiro and Bates 2000). Candidate models were ranked by AIC_c and variable weights were calculated for each covariate as described for the analysis of experimental stream data.

RESULTS

Experiment

Nutrients.—Analog increased concentrations of most nutrients: on day 45 TP and dissolved NH_4^+ -N concentrations were 1.4× and 2× higher, respectively, in the analog treatment relative to controls (see Table 2 and 3 for summary statistics of response variables measured on day 14 and 45, respectively, and Fig. 2A–L for mean effect sizes of select responses). The highest-ranked models predicting TP and SRP concentrations included analogs as the only covariate, while models with the most support predicting TN and NH_4^+ -N were more complex, including analog and time (TN and NH_4^+ -N), and the analog by time interaction (NH_4^+ -N) (Table 4). Akaike variable weights supported the importance of analogs and, in some cases, time as predictors of nutrient concentrations (Table 5). For example, the variable weight for analogs in models predicting TP was about 2× that of sample day and 4.5× that of wood. Overall, wood was the least important predictor of nutrient concentrations (variable weights of 0.13 to 0.36). The top-ranked models explained 39% (SRP) to 95% (NH_4^+ -N) of the variability in log-transformed nutrient concentrations.

Benthic populations.—In contrast to predictions, chlorophyll *a* biomass was about 3× lower in the analog and 6× lower in the analog plus wood

Table 2. Treatment means (with 95% CIs in parentheses) for nutrients ($\mu\text{g/L}$), invertebrate benthic biomass (mg/tile), invertebrate net flux ($\text{no. channel}^{-1}\text{d}^{-1}$), and Simpson's reciprocal index of invertebrate diversity measured on day 14 (C = controls, W = wood, A = analogs, WA = wood plus analogs, $n = 4$ per treatment).

Response	C	W	A	WA
TP	12 (11, 14)	13 (12, 14)	16 (15, 18)	17 (14, 19)
SRP	4 (3, 6)	5 (3, 6)	6 (5, 7)	7 (4, 9)
TN	232 (189, 274)	219 (180, 257)	285 (205, 366)	250 (154, 345)
$\text{NH}_4^+\text{-N}$	2 (2, 3)	2 (2, 3)	6 (5, 7)	8 (4, 12)
$\text{NO}_3^-\text{-N}$	166 (162, 169)	166 (162, 169)	165 (162, 169)	167 (162, 172)
Baetidae	6 (-3, 15)	13 (-10, 36)	13 (-5, 31)	11 (-4, 26)
Chironomidae larvae	78 (28, 128)	79 (-39, 197)	142 (61, 224)	128 (16, 241)
Chironomidae pupae	4 (2, 5)	3 (-2, 9)	10 (0, 20)	14 (5, 24)
Simuliidae larvae	2 (-4, 8)	4 (-5, 13)	0.3 (-0.5, 1)	0.06 (-0.1, 0.2)
Gastropoda	2.6 (-5, 10)	0.3 (-0.4, 1.0)	1.6 (-1.4, 4.6)	1.0 (-1.0, 2.5)
Total invertebrate biomass	94 (49, 138)	107 (-25, 238)	171 (63, 280)	152 (38, 266)
Simpson's reciprocal index	1.7 (1, 2.4)	2.1 (0.9, 3.3)	1.6 (1.3, 1.9)	2.4 (0.7, 2.4)
Baetidae flux	86 (-36, 208)	7 (-34, 50)	35 (-43, 112)	25 (-7, 57)
Chironomidae larvae flux	402 (-67, 872)	120 (58, 183)	242 (-101, 585)	152 (-106, 411)
Chironomidae pupae flux	48 (-9, 105)	17 (-4, 38)	136 (-31, 304)	79 (-64, 221)
Chironomidae adult flux	41 (-12, 95)	8 (0, 16)	134 (67, 200)	74 (-52, 201)
Total invertebrate flux	738 (-4, 1479)	201 (137, 265)	636 (22, 1251)	399 (-167, 965)

Notes: TP = total phosphorus, SRP = soluble reactive phosphorus, TN = total nitrogen, $\text{NH}_4^+\text{-N}$ = dissolved ammonium-nitrogen, and $\text{NO}_3^-\text{-N}$ = dissolved nitrate-nitrogen in water. Invertebrate taxa that comprised >0.1 by proportion of total benthic biomass (mg) are presented.

treatments relative to controls (Fig. 2C, Table 3). The best approximating model, accounting for 55% of the variation in chlorophyll *a* biomass, included analogs and wood, but this model was only slightly more plausible ($\sim 1.28\times$) than an analog-only model (Table 6). Variable weights indicate that analogs were $1.8\times$ more important than wood in predicting chlorophyll biomass (Table 7).

Sixteen taxa representing a variety of trophic groups (predators, collector-gatherers, detritivores, herbivores) were observed on tiles, but the collector-gatherers Baetidae (baetid) nymphs and chironomid larvae were the most abundant, comprising 13% and 50%, respectively, of total benthic invertebrate biomass on day 45 (Appendix: Table A1). For a subset of these invertebrates, analogs had positive effects at multiple levels of

Table 3. Treatment means (with 95% CIs in parentheses) for nutrients ($\mu\text{g/L}$), periphyton chlorophyll *a* biomass ($\mu\text{g}/\text{cm}^2$), invertebrate benthic biomass (mg/tile), Simpson's reciprocal index of invertebrate diversity, coho final mass (g), and natural abundance levels (‰) of δC^{13} and δN^{15} in coho tissue measured on day 45.

Response	C	W	A	WA
TP	13 (12, 15)	13 (12, 14)	19 (13, 25)	17 (11, 24)
SRP	5 (4, 6)	5 (4, 7)	6 (6, 7)	5 (4, 7)
TN	259 (234, 284)	265 (250, 280)	422 (48, 770)	331 (143, 521)
$\text{NH}_4^+\text{-N}$	4 (2, 6)	4 (3, 5)	8 (6, 9)	9 (7, 10)
$\text{NO}_3^-\text{-N}$	154 (149, 161)	155 (148, 161)	154 (145, 160)	155 (148, 161)
Chlorophyll <i>a</i>	3 (1, 4)	2 (1, 3)	1 (0, 3)	0.5 (0.1, 1)
Baetidae	19 (-2, 40)	11 (2, 21)	28 (4, 52)	30 (-2, 61)
Ephemerelellidae	2 (-3, 7)	1 (-0.1, 3)	3 (-4, 11)	6 (-15, 27)
Chironomidae larvae	52 (-6, 110)	78 (27, 128)	91 (9, 173)	115 (35, 194)
Chironomidae pupae	4 (-3, 10)	4 (-1, 9)	18 (-11, 46)	14 (-3, 32)
Simuliidae	9 (-7, 26)	19 (-26, 66)	39 (-24, 103)	3 (-5, 11)
Glossosomatidae	3 (-2, 8)	2 (-1, 5)	4 (-5, 13)	1 (-1, 3)
Gastropoda	5 (-1, 12)	5 (-1, 10)	7 (-3, 17)	9 (-11, 30)
Total invertebrate biomass	104 (-4, 212)	112 (54, 171)	169 (86, 250)	198 (4, 393)
Simpson's reciprocal index	3.1 (2.0, 4.2)	3.0 (1.9, 4.3)	3.1 (2.1, 4.0)	2.6 (2.3, 2.9)
Coho final mass	4 (2, 5)	4 (2, 5)	6 (5, 8)	6 (5, 8)
Coho $\delta^{13}\text{C}$	-23 (-24, -21)	-23 (-24, -23)	-21 (-22, -19)	-21 (-22, -20)
Coho $\delta^{15}\text{N}$	6 (5, 7)	5 (5, 6)	9 (7, 10)	9 (8, 10)

Note: See Table 2 for treatment definitions and other details.

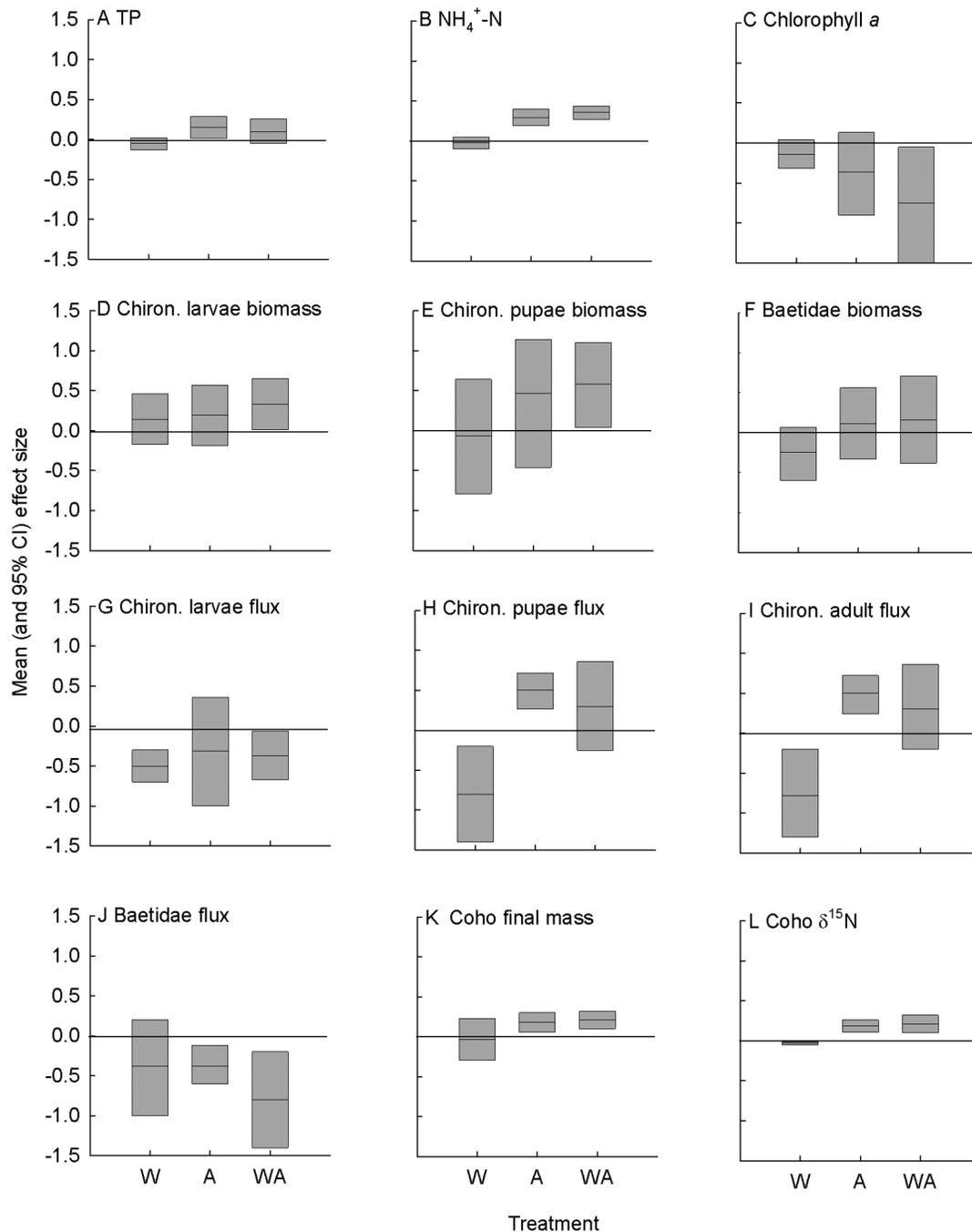


Fig. 2. Mean effect size (and 95% CI) for (A) TP = total phosphorus and (B) NH_4^+ = dissolved $\text{NH}_4^+\text{-N}$ ($\mu\text{g/L}$); (C) periphyton chlorophyll *a* biomass ($\mu\text{g/cm}^2$); (D) Chironomidae larvae, (E) Chironomidae pupae, and (F) Baetidae benthic biomass (mg/tile); (G) Chironomidae larvae, (H) Chironomidae pupae, (I) Chironomidae adult, and (J) Baetidae net flux ($\text{no.}\cdot\text{channel}^{-1}\cdot\text{d}^{-1}$); (K) coho final biomass; and (L) $\delta^{15}\text{N}$ in coho muscle tissue (‰) in the wood (W), analog (A) and wood plus analog (WA) treatments. Response ratios were calculated as follows: $\log(\text{value in treatment}/\text{mean value in control})$, $n = 4$ replicates per treatment. The response ratio of zero (solid line) represents the control, and the box plot represents deviations between experimental and control treatments.

Table 4. Linear mixed-effects models examining the fixed effects of time (T), analog (A), wood (W) and their two-way interactions on nutrient chemistry ($\mu\text{g/L}$), invertebrate benthic biomass (mg/tile), and Simpson's reciprocal index of invertebrate diversity.

Response	Covariates	K	ΔAIC_c	w	R^2
TP	A	4	0	0.371	0.62
	A + T	5	0.7	0.264	0.68
	A + W	5	2.3	0.119	0.63
	A + T + W	6	3.2	0.076	0.67
	A + T + A \times T	6	3.3	0.072	0.69
TN	A + T	5	0	0.386	0.66
	A + T + W	6	1.97	0.144	0.65
	A + T + A \times T	6	2.02	0.141	0.69
	T	4	2.66	0.102	0.72
SRP	A	4	0	0.433	0.39
	A + T + A \times T	6	2.08	0.157	0.46
	A + T	5	2.49	0.128	0.40
	A + W	5	2.82	0.108	0.39
$\text{NH}_4^+\text{-N}$	A + T + A \times T	6	0	0.594	0.95
	A + T + W + A \times T	7	2.14	0.200	0.95
$\text{NO}_3^-\text{-N}$	T	4	0	0.575	0.98
	T + W	5	2.64	0.154	0.98
	A + T	5	2.82	0.141	0.98
Chironomidae larvae	A	4	0	0.437	0.27
	A + T	5	1.89	0.170	0.34
	A + W	5	2.67	0.115	0.26
Chironomidae pupae	A	4	0	0.577	0.46
	A + W	5	2.73	0.147	0.46
	A + T	5	2.79	0.143	0.46
Baetidae	T	4	0	0.331	0.43
	A + T	5	0.06	0.321	0.38
	T + W	5	2.80	0.082	0.43
	A + T + A \times T	6	2.91	0.077	0.41
	A + T + W	6	3.11	0.070	0.38
EphemereIIDae	T	4	0	0.515	0.35
	A + T	5	1.95	0.194	0.37
	T + W	5	2.83	0.125	0.35
Glossosomatidae	T	4	0	0.510	0.31
	W + T	5	2.71	0.132	0.32
	A + T	5	2.77	0.128	0.31
	T + W + T \times W	6	3.13	0.107	0.38
Gastropoda	T	4	0	0.543	0.71
	A + T	5	2.52	0.154	0.70
	T + W	5	2.62	0.147	0.71
Total benthic biomass	A	4	0	0.475	0.52
	A + T	5	1.97	0.177	0.56
	A + W	5	2.86	0.114	0.52
Simpson's diversity	T	4	0	0.427	0.79
	A + T	5	1.07	0.250	0.78
	T + W	5	2.01	0.105	0.78
	A + T + A \times T	6	3.85	0.062	0.79

Notes: All models included a random intercept term (grouped by channel) to account for non-independence of repeated measurements within a channel ($n = 16$). K = number of parameters in the model, $\Delta\text{AIC}_c = \text{AIC}_c$ deviation relative to the best model for each response variable, and w = Akaike weights (an estimate of the probability that the model is the best approximating model in the candidate set). Only models with $\Delta\text{AIC}_c < 4$ are shown, ranked in order of decreasing support. Nutrient concentrations and invertebrate biomass were log-transformed prior to analysis. See Table 2 for other details.

biological organization. At the individual level, six of seven taxa were larger (both central tendency and maximum values) in the analog treatment (Table 8). For example, chironomid larvae and pupae and Simuliidae larvae were, on average, about 2 \times larger in the analog treatment. At the population level, the benthic biomass of chironomid larvae (1.6 \times) and pupae (4 \times), and

baetid nymphs (1.9 \times) was higher on day 45 in the analog treatment relative to other treatments (Fig. 2D–F). In agreement with these observations, the most plausible models predicting benthic chironomid (larvae and pupae) and baetid biomass included analog or analog and time as covariates (Table 4), and analog had a higher variable weight than other covariates,

Table 5. Model-averaged parameter estimates (with unconditional SE in parentheses) for nutrient chemistry ($\mu\text{g/L}$), invertebrate benthic biomass (mg/tile), and Simpson's reciprocal index of invertebrate diversity based on all candidate models. Predictor variables include: analog (A), time (T), wood (W), and their two-way interactions. Variable weights, which are Akaike weights (w) summed over all candidate models that include a given covariate, are shown in italics.

Response	Intercept	A	T	W	A \times T	A \times W	W \times T
TP	2.5 (0.07)	0.28 (0.06)	0.05 (0.04)	-0.01 (0.04)	0.05 (0.07)	-0.02 (0.08)	-0.07 (0.07)
		<i>1</i>	<i>0.48</i>	<i>0.29</i>	<i>0.10</i>	<i>0.05</i>	<i>0.03</i>
TN	5.2 (0.15)	0.18 (0.16)	0.20 (0.08)	-0.08 (0.12)	0.13 (0.12)	-0.14 (0.16)	0.02 (0.13)
		<i>0.85</i>	<i>0.96</i>	<i>0.34</i>	<i>0.21</i>	<i>0.06</i>	<i>0.05</i>
SRP	1.5 (0.10)	0.30 (0.14)	0.08 (0.08)	0.03 (0.08)	-0.19 (0.10)	-0.14 (0.10)	-0.07 (0.10)
		<i>1</i>	<i>0.39</i>	<i>0.27</i>	<i>0.21</i>	<i>0.09</i>	<i>0.02</i>
NH_4^+ -N	0.28 (0.14)	1.4 (0.20)	0.49 (0.08)	0.07 (0.10)	-0.32 (0.10)	0.18 (0.40)	-0.06 (0.10)
		<i>1</i>	<i>1</i>	<i>0.36</i>	<i>0.92</i>	<i>0.09</i>	<i>0.06</i>
NO_3^- -N	5.2 (0.007)	0.001 (0.009)	-0.07 (0.002)	0.004 (0.009)	-0.002 (0.005)	0.005 (0.02)	-0.002 (0.005)
		<i>0.23</i>	<i>1</i>	<i>0.25</i>	<i>0.05</i>	<i>0.01</i>	<i>0.04</i>
Chironomidae larvae	4.2 (0.34)	0.65 (0.28)	-0.24 (0.26)	-0.11 (0.53)	-0.19 (0.40)	-0.02 (0.43)	0.69 (0.37)
		<i>0.89</i>	<i>0.35</i>	<i>0.27</i>	<i>0.06</i>	<i>0.04</i>	<i>0.05</i>
Chironomidae pupae	1.3 (0.25)	1.1 (0.27)	0.05 (0.24)	0.04 (0.29)	0.07 (0.45)	0.37 (0.45)	0.14 (0.45)
		<i>1</i>	<i>0.23</i>	<i>0.25</i>	<i>0.04</i>	<i>0.05</i>	<i>0.01</i>
Baetidae	1.1 (0.58)	0.44 (0.48)	0.90 (0.30)	-0.01 (0.48)	0.28 (0.55)	-0.20 (0.56)	-0.21 (0.56)
		<i>0.54</i>	<i>0.95</i>	<i>0.23</i>	<i>0.10</i>	<i>0.02</i>	<i>0.04</i>
Ephemerelellidae	-0.82 (0.38)	0.10 (0.41)	0.86 (0.23)	-0.02 (0.37)	0.32 (0.42)	0.18 (0.42)	0.21 (0.43)
		<i>0.33</i>	<i>1</i>	<i>0.23</i>	<i>0.07</i>	<i>0.01</i>	<i>0.04</i>
Glossosomatidae	-0.56 (0.38)	0.04 (0.36)	0.77 (0.23)	0.33 (0.61)	-0.27 (0.38)	-0.34 (0.37)	-0.61 (0.37)
		<i>0.24</i>	<i>1</i>	<i>0.24</i>	<i>0.05</i>	<i>0.02</i>	<i>0.14</i>
Gastropoda	-0.59 (0.44)	0.16 (0.26)	1.1 (0.24)	-0.34 (0.57)	0.15 (0.47)	0.20 (0.67)	0.47 (0.46)
		<i>0.26</i>	<i>1</i>	<i>0.27</i>	<i>0.04</i>	<i>0.01</i>	<i>0.07</i>
Total benthic biomass	4.4 (0.24)	0.59 (0.23)	0.15 (0.23)	-0.05 (0.29)	-0.04 (0.32)	-0.03 (0.40)	0.35 (0.31)
		<i>0.90</i>	<i>0.31</i>	<i>0.23</i>	<i>0.05</i>	<i>0.03</i>	<i>0.02</i>
Simpson's diversity	0.29 (0.10)	-0.13 (0.11)	0.02 (0.002)	0.03 (0.13)	0.002 (0.004)	-0.19 (0.18)	-0.004 (0.004)
		<i>0.43</i>	<i>1.0</i>	<i>0.26</i>	<i>0.08</i>	<i>0.03</i>	<i>0.07</i>

Notes: See Table 2 for other details.

especially for chironomids (Table 5). Salmon subsidies also increased the likelihood of chironomids transitioning from one life stage to the next: apparent stage-specific survival or turnover (larvae to adults, larvae to pupae) was 3 to 5 \times higher in channels with analogs (Fig. 3). Analog also had small but positive effects on Ephemerelellidae, Glossosomatidae and Gastropoda benthic biomass, and Simpson's diversity index, but overall, sample day was the most important predictor for these invertebrates (Tables 4 and 5).

Although it was included in all candidate models predicting benthic invertebrate biomass, wood had small to moderate effects (both

positive and negative) relative to analogs and time. Specifically, the top-ranked models never included wood as a covariate and there was little to no change in the coefficient of determination for models that included wood as a covariate relative to models without this predictor. The variable weights for wood were also often lower than the variable weights for analog or time. Models with the most overall support explained 27–71% of the variability in log-transformed invertebrate benthic biomass, indicating a substantial range of unexplained variation (Table 4).

Analog and wood had significant but contrasting effects on invertebrate flux, a key

Table 6. Linear models of the fixed effects of analog (A), wood (W) and their interaction on chlorophyll *a* biomass ($\mu\text{g}/\text{cm}^2$), invertebrate net flux ($\text{no.}\cdot\text{channel}^{-1}\cdot\text{d}^{-1}$), coho final mass (g), and natural abundance levels (‰) of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ in coho muscle tissue. Nonlinear parabolic growth models are shown for coho final mass (g). Coho final mass (M) was also included as a covariate in models predicting $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ isotope ratios.

Response	Covariates	<i>K</i>	ΔAIC_c	<i>w</i>	<i>R</i> ²
Chlorophyll <i>a</i>	A + W	4	0	0.507	0.55
	A	3	0.49	0.397	0.42
Chironomidae larvae flux	W	3	0	0.451	0.21
	Intercept only	2	0.46	0.358	0
	A + W	4	3.21	0.091	0.25
	A	3	3.33	0.085	0.02
Chironomidae pupae flux	A	3	0	0.514	0.31
	A + W	4	1.65	0.225	0.40
	Intercept only	2	2.40	0.155	0
	W	3	3.69	0.081	0.11
Chironomidae adult flux	A + W	4	0	0.696	0.70
	A	3	2.46	0.204	0.54
	A + W + A × W	5	3.99	0.095	0.71
	W	3	0	0.400	0.19
Baetidae flux	Intercept only	2	0.01	0.398	0
	A	3	2.85	0.096	0.02
	A + W	4	3.19	0.081	0.22
	W	3	0	0.658	0.32
Total invertebrate flux	Intercept only	2	2.54	0.185	0
	A + W	4	3.76	0.100	0.32
	A	3	0	0.570	0.63
	A + W + A × W	5	1.85	0.230	0.73
Coho final mass	A + W	4	2.91	0.130	0.63
	A + M	4	0	0.690	0.91
Coho $\delta^{13}\text{C}$	A	3	2.63	0.190	0.87
	A + M	4	0	0.507	0.91
Coho $\delta^{15}\text{N}$	A	3	1.12	0.290	0.88
	A + M + W	5	3.02	0.112	0.92
	A + W	4	3.92	0.072	0.88
	Intercept only	2	0	0.000	0.00

Notes: See Table 4 notes for explanation of column headings.

ecosystem process. On average, the flux of chironomid pupae (4.5×) and adults (3.4×) was substantially higher in the analog treatment; in contrast, wood reduced their net export (2–3×), as well as that of chironomid larvae (2.3×) and baetid mayflies (5.2×) (Fig. 2G–J, Table 2). The best models predicting flux of chironomid pupae and adults included analogs (pupae) or analogs and wood (adults) as covariates, and these models were 2.3× (pupae) and 3.4× (adults) more plausible than the second ranked models (Table 6). Wood was the only covariate in the top models predicting the flux of chironomid larvae and baetid nymphs, with these models only slightly more plausible than the intercept-only model. Akaike variable weights indicated that wood was relatively more important than analogs in predicting invertebrate flux, especially for baetid nymphs and chironomid larvae (Table 7). Similar to benthic invertebrate biomass, there was a wide range in the amount of variation explained by models predicting flux rates rang-

ing from 19% for baetids to 70% for chironomid pupae.

Coho.—Salmon analogs had strong positive effects on juvenile coho: on average, coho were larger (1.6×) and were more enriched in ^{15}N (1.6×) and ^{13}C (1.1×) in the analog treatment than controls (Table 3, Fig. 2K–L). The best parabolic growth model predicting coho final mass included a positive effect of analogs, while the top-ranked models predicting $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ included the positive effects of analogs and final mass (Table 6). Overall, analogs had very high variable weights in models predicting coho growth (0.93) and stable isotope enrichment (1.0; Table 7). Wood had negative effects on coho growth and $\delta^{15}\text{N}$, but its variable weight was low (≤ 0.38); likewise, there was relatively weak support for an interaction between analogs and wood. Covariates predicting final coho mass and stable isotope ratios explained considerable model variation ranging from 63–92%.

There were several lines of evidence to suggest

Table 7. Model-averaged parameter estimates (with unconditional SE in parentheses) for chlorophyll *a* biomass ($\mu\text{g}/\text{cm}^2$), invertebrate net flux ($\text{no.}\cdot\text{channel}^{-1}\cdot\text{d}^{-1}$), coho final mass (g), and natural abundance levels (‰) of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ in coho muscle tissue based on all candidate models. Predictors include analog (A), wood (W), the A \times W interaction, and final coho mass (M) in g (for stable isotope ratios only). Variable weights, which are Akaike weights (*w*) summed over all candidate models that include a given covariate, are shown in italics.

Response	Intercept	A	W	A \times W	M
Chlorophyll <i>a</i>	2.35 (0.40)	-1.28 (0.43)	-0.71 (0.43)	-0.13 (0.85)	
		<i>0.96</i>	<i>0.57</i>	<i>0.06</i>	
Chironomidae larvae flux	290.8 (87.5)	-72.9 (124.4)	-191.9 (112.4)	192.9 (230.4)	
		<i>0.19</i>	<i>0.56</i>	<i>0.02</i>	
Chironomidae pupae flux	48.3 (32.2)	78.6 (36.5)	-43.4 (38.3)	-26.3 (74.2)	
		<i>0.76</i>	<i>0.33</i>	<i>0.02</i>	
Chironomidae adult flux	42.1 (19.3)	81.0 (21.0)	-45.2 (20.1)		
		<i>1</i>	<i>0.77</i>		
Baetidae flux	51.8 (22.6)	-15.7 (31.5)	-47.5 (30.3)	69.3 (58.0)	
		<i>0.20</i>	<i>0.51</i>	<i>0.02</i>	
Total invertebrate flux	642.8 (149.9)	29.9 (210.2)	-403.9 (184.4)	299.5 (387.4)	
		<i>0.16</i>	<i>0.77</i>	<i>0.02</i>	
Coho final mass	-3.16 (0.51)	1.22 (0.62)	-2.14 (13.71)	2.10 (13.73)	
		<i>0.93</i>	<i>0.38</i>	<i>0.23</i>	
Coho $\delta^{13}\text{C}$	-24.4 (0.70)	1.8 (0.51)	-0.05 (0.27)	-0.07 (0.56)	0.32 (0.15)
		<i>1.0</i>	<i>0.12</i>	<i>0.01</i>	<i>0.78</i>
Coho $\delta^{15}\text{N}$	4.7 (0.95)	2.7 (0.67)	-0.29 (0.36)	0.08 (0.74)	0.38 (0.19)
		<i>1.0</i>	<i>0.20</i>	<i>0.02</i>	<i>0.68</i>

Table 8. Treatment means (with 95% CIs in parentheses) for individual body size (mg) of dominant invertebrate taxa on day 45. Number in italics represents number of individuals measured in each treatment.

Taxa	C	W	A	WA
Ephemerelellidae	0.09 (0.03, 0.15)	0.05 (0.03, 0.07)	0.13 (0.03, 0.23)	1.7 (-1.8, 5.1)
	<i>22</i>	<i>42</i>	<i>11</i>	<i>10</i>
Baetidae	0.08 (0.07, 0.1)	0.09 (0.08, 0.10)	0.09 (0.08, 0.10)	0.09 (0.07, 0.10)
	<i>195</i>	<i>202</i>	<i>180</i>	<i>153</i>
Glossosomatidae	0.24 (0.16, 0.32)	0.27 (0.02, 0.51)	0.45 (0.21, 0.69)	0.13 (0.09, 0.18)
	<i>20</i>	<i>23</i>	<i>8</i>	<i>24</i>
Chironomidae larvae	0.18 (0.15, 0.21)	0.08 (0.05, 0.10)	0.25 (0.21, 0.30)	0.31 (0.24, 0.38)
	<i>228</i>	<i>230</i>	<i>212</i>	<i>154</i>
Chironomidae pupae	0.39 (0.31, 0.47)	0.28 (0.20, 0.36)	0.68 (0.54, 0.82)	0.59 (0.47, 0.71)
	<i>19</i>	<i>16</i>	<i>21</i>	<i>25</i>
Simuliidae	0.10 (0.08, 0.13)	0.05 (0.04, 0.07)	0.21 (0.18, 0.23)	0.07 (0.06, 0.08)
	<i>115</i>	<i>71</i>	<i>162</i>	<i>101</i>
Gastropoda	1.50 (0.49, 2.60)	1.48 (0.19, 2.76)	2.52 (-0.26, 5.3)	2.20 (0.11, 4.23)
	<i>18</i>	<i>13</i>	<i>11</i>	<i>13</i>

Notes: See Table 2 for treatment definitions.

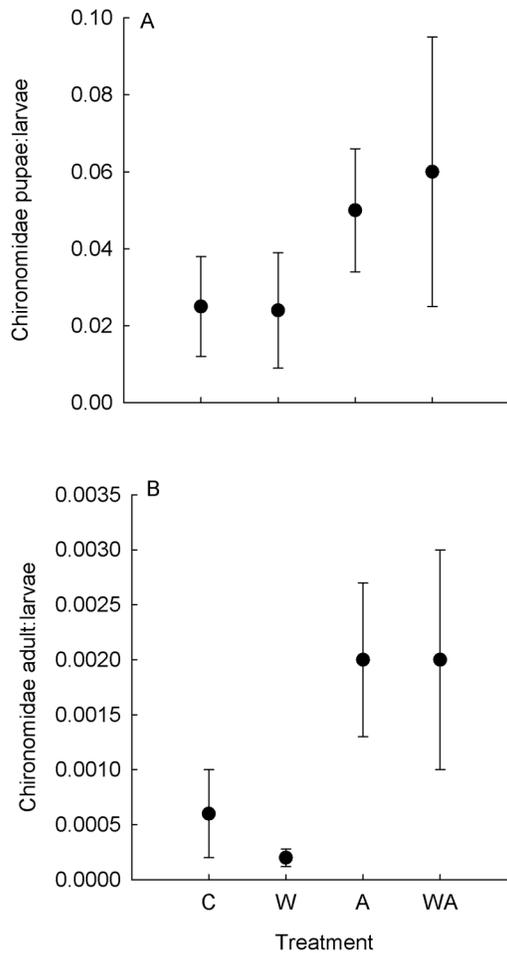


Fig. 3. Mean (± 1 SD) for (A) Chironomidae pupal abundance (benthic + flux) and (B) Chironomidae adult abundance divided by channel level estimates of benthic Chironomidae larval abundance in the different treatments on day 14 (see Fig. 2 for treatment definitions).

that the increased availability of chironomids was the key trophic link between analogs and coho growth rate. First, the net flux and turnover of chironomid pupae and adults increased in tandem with coho growth in the analog treatment. Second, there was a strong positive relationship between coho final body mass and adult chironomid flux when using data from all channels ($r = 0.62$, $n = 15$). Third, the proportion by biomass of chironomid adults in coho diets was $\sim 3\times$ higher in channels with analogs (Fig. 4). Fourth, coho in experimental streams were selectively consuming chironomid pupae and

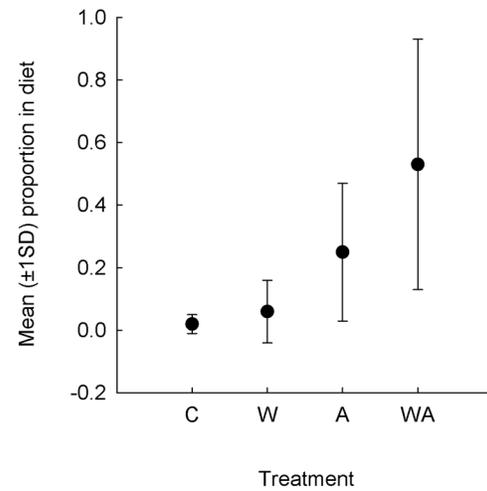


Fig. 4. Mean (± 1 SD) proportion by biomass (mg) of Chironomidae adults in coho diets in the different treatments on day 45 (see Fig. 2 for treatment definitions).

adults relative to their availability in drift (Appendix: Table A2).

Field study

At the reach scale, we found strong support for a negative relationship between coho growth and in-channel wood abundance. Of the eight candidate parabolic growth models, all four with $\Delta AIC_c < 4$ included wood abundance with a negative estimated effect, and the overall variable weight for wood was 0.92 (Table 9). There was somewhat weaker evidence of intra- or interspecific density dependence in coho growth, with a negative effect of total salmonid density appearing in the top-ranked model (overall variable weight 0.59). Adult Diptera drift biomass was weakly positively related to coho growth, appearing in two of the top four models (variable weight 0.40). However, adult Diptera drift was also negatively correlated with wood abundance at the reach level ($r = -0.67$, $n = 6$), making it difficult to distinguish the effects of these two factors on coho growth. In general, the parabolic growth model described coho growth well, explaining 87–89% of the variance in log-transformed final mass and producing residuals that appeared independent of initial or final mass. The covariates explained most of the among-reach variation in the growth rate scale param-

Table 9. Nonlinear mixed-effects models of coho growth ($n = 64$) in the field mark-recapture study ranked in order of descending support by ΔAIC_c . Point estimates and SE are given for the parabolic growth shape parameter (q) and the intercept and effects of total salmonid density (D), adult Diptera biomass flux (F), and wood (W) on the log of the growth rate scale parameter p (see Eq. 1).

K	Intercept	D	F	W	q	ΔAIC_c	w	R^2
6	-3.17 (0.76)	-0.19 (0.09)		-0.48 (0.1)	0.62 (0.15)	0	0.45	0.88
6	-3.68 (0.76)		0.17 (0.09)	-0.37 (0.12)	0.73 (0.19)	1.62	0.20	0.88
5	-3.48 (0.75)			-0.46 (0.09)	0.69 (0.17)	2.24	0.15	0.87
7	-3.18 (0.9)	-0.18 (0.16)	0.01 (0.16)	-0.47 (0.16)	0.62 (0.18)	2.56	0.12	0.88

Notes: All models include a reach-level random effect on the intercept of $\log(p)$. Only models with $\Delta\text{AIC}_c < 4$ are shown. Variable weights, which are Akaike weights (w) summed over all candidate models that include a given covariate, are 0.59 for total salmonid density, 0.4 for adult Diptera biomass flux, and 0.92 for wood.

eter, reducing the estimated standard deviation of the random effect from 0.71 in the null (intercept-only) model to near zero (3.1×10^{-6}) when salmonid density, wood abundance, and adult Diptera drift were included in the model.

Each of the reach-scale variables exhibited a range of values, but, on average, main stem reaches were wider and cooler and had less wood, higher invertebrate drift biomass, and faster coho growth than Rock Creek, while total salmonid density was similar between streams (Table 1). The proportions (by biomass) of various invertebrate taxa in coho diets were variable, but chironomid larvae ($\sim 27\%$ of total diet biomass) and adults (32% of diet biomass) were the most important prey items. Similar to the channel experiment, coho showed positive selectivity for chironomid adults and pupae relative to their availability in drift (Appendix: Table A3).

DISCUSSION

Experiment

One of the most salient results from the channel experiment was establishing the key energy chain between salmon analogs, select invertebrates, and juvenile coho. We observed that the bottom-up effect of analogs on lower trophic levels was primarily manifested in chironomids and baetids, the two numerically dominant invertebrates. Chironomids exhibited the most striking bottom-up effect, as they responded rapidly to salmon analogs (after 14 days), and were affected at the individual, population, and ecosystem-level (i.e., increases in chironomid pupae and adult biomass flux). There was strong evidence linking these changes

in chironomid dynamics to increased growth of juvenile coho, a linkage recently proposed (i.e., Lessard et al. 2009) but not revealed until now. Production and drift flux of Chironomidae, along with Simuliidae, were also a key trophic link supporting rainbow trout production in the Colorado River, USA (Cross et al. 2011). Thus, Chironomidae may be a key source of energy supporting freshwater salmonid production.

The isotopic enrichment of coho in channels with analogs also provided evidence for the energy flow chain between salmon tissue, chironomids, and coho. This enrichment indicates a greater reliance of a marine-based energy pathway (i.e., salmon analogs) that was potentially mediated by coho consumption of chironomids. Consistent with this mechanism was the positive correlation between coho $\delta^{15}\text{N}$ and biomass of adult chironomids in coho diets ($r = 0.56$, $n = 15$).

Also consistent with this mechanism were results from an experimental stream study in Alaska, where chironomids were the most isotopically enriched invertebrate in channels augmented with salmon tissue and likely a key pathway for the trophic transfer of marine-derived nutrients delivered by spawning salmon (Chaloner et al. 2002). Direct consumption of analogs may also explain some of the variation in coho growth and isotopic enrichment, as analog fragments and adult salmon tissue and eggs are consumed by coho (Armstrong et al. 2010, Wipfli et al. 2010, Cram et al. 2011, Kohler et al. 2012b). However, our diet analysis provided no evidence of direct consumption of analogs, although this may reflect the fact that coho diets were only sampled once and at a different time (day 45) than invertebrate flux (day 14)

We hypothesize that some of the variability in

how stream organisms, including chironomids and baetids, respond to salmon subsidies was due to differences in mobility and growth or developmental rates. Chironomids and baetids are opportunistic species displaying high rates of dispersal and population growth (Jackson and Fisher 1986, Mihuc and Minshall 1995), characteristics of consumers predicted to respond robustly to resource pulses such as those provided by spawning salmon (Ostfeld and Keesing 2000). The especially vigorous response by chironomids may also be due to the species colonizing channels, which were those with physiological or developmental traits that allowed for the efficient transfer of nutrients and energy from analogs into accelerated growth and reproductive development, ultimately leading to increased turnover. Supporting this hypothesis is the observation that salmon analogs greatly increased ratios of pupae and adults relative to larvae compared to other treatments, with this response occurring in only 14 days. Although our inference regarding the effect of salmon analogs on chironomid flux and turnover and coho growth is limited because drift was sampled only once, a recent study also observed higher flux of chironomid pupae paralleled by increased juvenile salmonid growth in experimental streams enriched with adult salmon tissue (Kiernan et al. 2010).

In contrast to the robust response of chironomids and baetids, other invertebrate consumers, including stone-cased caddis flies (Glossosomatidae) and snails, responded weakly to analogs, perhaps because of armor that protects them from predators but limits their mobility and ability to react quickly to resource pulses. Relative mobility was found to be a key trait predicting whether invertebrate consumers were able to gain access to resources efficiently when nutrient limitation was experimentally removed (Peckarsky et al. 2013). Thus, our results support the hypothesis that mobility and growth or developmental rates are potentially key predictors for how consumers respond to resource pulses (Marczak and Richardson 2008, Peckarsky et al. 2013).

Bottom-up processes likely mediated the increased trophic productivity we observed in the analog treatment, as evidenced by higher concentrations of elements known to limit ecosystem

productivity (total P and N, $\text{NH}_4^+\text{-N}$, and SRP) (e.g., Johnston et al. 2004). Numerous studies have shown that concentrations of limiting nutrients increase following inputs of resource subsidies such as periodic inputs of seaweed to islands (e.g., Spiller et al. 2010), salmon or carcass analogs to streams (Johnston et al. 2004, Kohler et al. 2012b) or cicadas to terrestrial ecosystems (Yang 2004). Higher nutrient levels following these resource pulses sometimes translate into increased primary productivity (Johnston et al. 2004, Yang 2004), but not always (Ambrose et al. 2004, Verspoor et al. 2010). The algal response we observed was in agreement with these latter studies, as despite higher nutrient levels, primary producer biomass was lower in the presence of analogs, and lowest in channels with both analogs and wood ($C > W > A > WA$ for mean chlorophyll *a* biomass; see Fig. 2C). Though our evidence is indirect, we attribute these patterns to increased consumption by primary consumers because treatment differences in the benthic biomass of chironomid larvae, the dominant primary consumer, were the mirror opposite of algal biomass ($C < W < A < WA$), while light, temperature, disturbance, and discharge were similar across treatments. The negative correlation between chironomid larvae and chlorophyll *a* biomass is consistent with the hypothesis of top-down control of benthic algae (Pearson's correlation coefficient, $r = -0.99$, $n = 4$, using treatment means). Therefore, in the absence of disturbance, top-down control of algal biomass may be more pronounced in habitats with increased resource availability and greater physical heterogeneity because of larger consumer populations. Similarly, Taniguchi and Tokeshi (2004) found that algal chlorophyll *a* biomass declined as habitat complexity increased, possibly due to increased consumption by larger grazer populations in complex habitats. Additionally, grazers may allocate more time to foraging in complex habitats because they provide protection from predators (e.g., Langelotto and Denno 2004).

Physical habitat structure, such as that provided by wood in streams, may contribute to top-down control of algal biomass by modifying how organisms move through the landscape thereby temporarily influencing local abundances and the intensity of biotic or trophic interactions.

Specifically, PHS (small wood) may have indirectly supported top-down effects on benthic algae by reducing drift flux (56%), thereby aggregating consumers contributing to larger consumer populations and increased consumption. Physical habitat structure can concentrate consumers by serving as attachment or oviposition sites (e.g., Peckarsky et al. 2000), increasing resource availability (e.g., Schneider and Winemiller 2008), and providing a refuge from predators (e.g., Crowder and Cooper 1982). In addition, PHS can create dead zones where particles exit the flow of water or air, thereby increasing the settlement rate of invertebrates in transport (Eckman 1983, Bond et al. 2000, Downes and Lancaster 2010). A similar set of mechanisms may be operating in our experiment where PHS created dead zones or attachment sites for drifting invertebrates thus reducing invertebrate flux. There is evidence from other ecosystems supporting the observation that PHS alters how invertebrates move through the landscape: the movement rate of a wetland butterfly (*Satyroides appalachia*) was lower in complex riparian and wetland habitats relative to simple, open habitats (Kuefler et al. 2010).

The observation that PHS had relatively small effects on benthic invertebrate biomass or diversity was surprising given the moderate to strong effects PHS had on algal biomass and net invertebrate flux. This observation was also surprising because a number of studies have demonstrated substantial changes in benthic invertebrate structure and function after manipulation of PHS (Angermeier and Karr 1984, Wallace et al. 1999, Schneider and Winemiller 2008, except see Lepori et al. 2005). For example, one study showed that logs added to a North Carolina stream resulted in major changes in physical conditions, with a concomitant change in benthic invertebrate community structure (Wallace et al. 1995). We suggest sampling and experimental design issues may partly explain the weak ecological effect of PHS on benthic invertebrate populations in our experiment. First, we assumed that any increase in benthic invertebrate populations as a result of manipulating PHS would be detected on tiles (i.e., a spillover effect). A more direct approach would have been to sample wood (Benke et al. 1984, Schneider and Winemiller 2008, Coe et al. 2009) as we did for

tiles. Second, the amount added may have been too little, the experiment too short, or the replication too low for PHS to have measureable effects on benthic invertebrates as observed in other studies (Wallace et al. 1995, Wallace et al. 1999, Negishi and Richardson 2003).

There was also little support for the hypothesis that PHS modified the effects of analogs (i.e., A × W interaction). Recent studies have demonstrated both strong (Flecker et al. 2002, Kiffney 2008, Indermaur et al. 2010) and weak support for interactive effects (Griffen and Drake 2008, Weis et al. 2008) when simultaneously testing the influence of multiple factors on ecological systems. The lack of evidence supporting treatment interactions in our study may be due to the sampling and experimental issues described above. Moreover, manipulating PHS and analogs along gradients rather than simple presence-absence might reveal a threshold at which interactions occur (e.g., Kiffney 2008). There was stronger support that some responses (i.e., nutrients, baetid biomass, Simpson's diversity) were temporally dynamic over the time scale of our experiment; however, except for dissolved $\text{NH}_4^+\text{-N}$, these fluctuations were relatively small.

Overall, these experimental results are important for at least three reasons. The strong trophic linkage between analogs, chironomids, and coho growth agrees with theoretical and empirical studies that suggest energy flow in food webs consist of a few key trophic interactions (Persson et al. 1996, Cross et al. 2011). Our results are also important because of the connections between body size and population dynamics (Lomnicki 1988, Turchin 2003), and population dynamics and ecosystem processes (Loreau 2010). For example, larger juvenile coho emigrating to the ocean may survive at a higher rate, leading to larger adult returns and nutrient inputs enriching stream food webs that support juvenile salmon, thereby constituting a positive feedback loop. Finally, PHS in the form of small wood appears to play an important role in affecting the downstream movement of stream invertebrates, which may have consequences for population dynamics and trophic interactions.

Field study

In general, results from the mark-recapture field study supported a priori predictions,

experimental results, and observations from similar studies. First of all, local fish density had negative effects on juvenile coho growth rate, confirming the importance of density-dependent growth in stream-dwelling salmonid populations (Jenkins et al. 1999, Grant and Imre 2005). Secondly, the negative growth effect we observed occurred at relatively low fish densities ($\sim 0.02\text{--}0.9$ fish/m²), a pattern observed in other studies (see Jenkins et al. 1999). Thirdly, the positive effect of prey availability (in this case, adult Diptera drift) on coho growth confirmed experimental results, and results from similar investigations (Wilzbach et al. 1986, Rosenfeld et al. 2005, Ward et al. 2009). Fourthly, coho in the field showed a strong preference for chironomid pupae and adults relative to their availability, a relationship also observed in the experiment. A number of studies have demonstrated that Chironomidae, and Diptera in general, are a key source of energy for a variety of predators including fishes (Loftus and Lenon 1977, our study), ground beetles (Hering and Platcher 1997), bats (Kellner and Harestad 2005), and birds (Gardarsson and Einarsson 2004, Pearce-Higgins 2010). The trophic significance of this taxon is likely due to their global distribution, high species and functional diversity, and productivity (Armitage et al. 1995). Predators, such as juvenile coho in our study, may also preferentially consume chironomid pupae and adults because these life stages have energy-rich reproductive structures providing more energy per individual consumed relative to immature life stages: McCarthy et al. (2009) showed that the energy density of winged insects (combined Ephemeroptera, Plecoptera, Trichoptera, and Diptera adults) was 1.5 \times higher than the energy density of Diptera larvae.

Surprisingly though, the effects of fish density and adult Diptera drift on coho growth were less important than the negative effect of PHS or in-channel wood, which was puzzling because there is substantial evidence that wood improves habitat conditions for fish (Roni and Quinn 2001, Wright and Flecker 2004, Johnson et al. 2005). We hypothesize that the negative effect of wood on coho growth was also due to density dependent interactions resulting from the positive effects of wood on fish density. Specifically, we speculate that the relatively scarce wood

structures in the Cedar River aggregate fish, especially juvenile coho, increasing local densities, leading to lower growth rates via competition for food or space, as reflected in the negative association between total fish density and coho growth. Partially supporting our hypothesis are summer surveys in the Cedar River that have consistently shown a positive correlation between wood abundance and total salmonid density at the habitat unit scale (P. M. Kiffney, *unpublished data*), a relationship observed in other studies (e.g., Roni and Quinn 2001). These wood structures also increase the density of predators, such as large trout (>200 mm in total length), which may contribute to lower growth rates because juvenile coho are allocating more energy to predator avoidance. By contrast, in the experiment where the effect of wood on coho growth was also negative but much weaker, density dependence and predator effects were eliminated because each channel contained only one individual, and coho were food-limited.

The unexpected negative relationship between wood and coho growth may also be an outcome of a mismatch in the scales of observation and the scale at which mobile organisms perceive the environment, and statistical constraints. For example, coho were collected for growth at the habitat unit scale ($>10\text{--}100$ m² in surface area), while wood abundance was a reach-level ($>1,000\text{--}10,000$ m²) cumulative count, potentially resulting in a mismatch of scales (Wiens 1989). Our field study was also subject to statistical issues common to large-scale field surveys, including confounding factors and small sample size, potentially leading to spurious effects (Anderson 2008). Notwithstanding the issues of scale and statistical constraints, our models showed that prey availability as drift biomass, wood abundance, and local fish density explained almost 88% of the variation in coho growth measured at the reach-scale, emphasizing the importance of these covariates on coho performance in the Cedar River above Landsburg Dam, a relatively pristine ecosystem representative of coarse-bottom, cold water streams of the Pacific Northwest.

Despite the relative weak effect of Diptera drift biomass on coho growth, we present other evidence supporting the hypothesis that their growth was constrained by prey availability,

whose productivity may have been limited by light. Rock Creek is narrower than the main stem (~4 m vs. 22 m wide), resulting in riparian vegetation shading more of the stream surface from incoming solar radiation: canopy closure was about 54% in the main stem and 86% in Rock Creek (P. M. Kiffney, *unpublished data*). This difference in canopy cover is important because the trophic productivity of many temperate forest streams is primarily limited by light, which is largely a function of riparian shading (Murphy et al. 1986, Hill et al. 1995, Kiffney et al. 2003). Our field data support this link between light and trophic production. Specifically, Diptera drift biomass averaged across the sunlit main stem was 4× higher and coho growth 2× higher than in heavily shaded Rock Creek. Thus, relatively pristine stream reaches receiving more light may exhibit higher prey availability because of increased invertebrate turnover resulting from bottom up effects, ultimately leading to higher growth rates of drift-feeding fish (Wilzbach et al. 1986, Ward et al. 2009), as well as other predators associated with streams including spiders, bats, birds and lizards (e.g., Jackson and Fisher 1986).

Synthesis and implications

Our multi-scale study provided several insights into the structure and function of river ecosystems. In the small-scale experiment, we observed the bottom-up effects of salmon subsidies on the growth potential of juvenile coho in the absence of density-dependent interactions and light limitation. This result was consistent with the positive, albeit weaker, effect of adult Diptera drift biomass on coho growth rate in the large-scale field study, where light flux potentially constrained trophic productivity. The unexpected negative effect of wood on coho growth complicated the interpretation of results from the field study; nonetheless, we hypothesize this result was due to fish aggregating around wood structures intensifying the strength of density-dependent interactions. Wood may have had analogous effects on trophic interactions in the experiment by concentrating drifting invertebrates leading to local increases of the dominant primary consumers (i.e., chironomids) and corresponding reductions in algal biomass. Collectively, our study indicates that individual performance (body size, growth rate) and the

structure and function of river food webs were modified by multiple intrinsic (e.g., species traits, biotic interactions) and extrinsic factors (salmon subsidies, light flux, PHS) operating simultaneously, which is likely a common scenario of ecological systems (Persson et al. 1996).

Our results also suggest that management, conservation, and restoration of river ecosystems require a multi-factorial approach including, but not limited to, identifying key energy chains, the role of PHS, biotic interactions, as well as assessing whether these potential controlling agents interact (e.g., Rosenfeld et al. 2005). The key energy chain we identified in the experiment was initiated by salmon subsidies, which is important from a conservation and management perspective because the highest reach-scale biomass density of salmon spawning above Landsburg Dam was 0.027 kg/m², 22× lower than the density of salmon analogs added to stream channels. Low returns of spawning anadromous fish are widespread: the flux of nutrients and energy delivered by spawning salmon to some tributaries of the North Pacific is about 95% lower than historic levels (Gresh et al. 2000). These reductions alter a range of ecological processes, including nutrient dynamics, sediment flux, and trophic production, from headwater streams to near-shore habitats (Johnston et al. 2004, Moore et al. 2007, Wipfli and Baxter 2010). Therefore, management or restoration actions that increase the number of spawning adults or mimic their enrichment and physical effects may improve the individual and population growth of a variety of organisms, including juvenile salmon, in tributaries with low adult returns (e.g., Wipfli et al. 2004). In fact, we showed that a salmon-loading of 0.6 kg/m² had strong positive effects on trophic production during summer including accelerating coho growth.

It is necessary to emphasize that the ecological effectiveness of restoring salmon subsidies or restoration in general will depend on a host of factors such as water temperature, water quality (e.g., nutrient levels), and PHS (Compton et al. 2006, Wipfli and Baxter 2010). With this in mind, our research in the Cedar River highlights the potential importance of species composition, light availability, density-dependent interactions, and season in affecting the response of river food webs to nutrient enrichment (e.g., increasing

adult salmon escapement). With respect to season, we observed strong bottom-up effects of enriching channels with salmon tissue on coho growth in summer, while there were no effects of adding up to 4 kg/m² of adult salmon tissue on juvenile coho in the same set of experimental channels during fall and early winter, which we attribute to cool water temperatures and low light flux limiting trophic production (Cram et al. 2011).

Similar to reductions in anadromous fish populations, the homogenization of river ecosystems is widespread (Cardinale et al. 2002), so increasing PHS by adding wood or large boulders is a popular method of restoring this lost complexity (Roni and Quinn 2001, Lepori et al. 2005, Roni et al. 2008). Clearly, many aquatic ecosystems would benefit from restoration of habitat complexity; unfortunately, these efforts may not improve demographic rates of threatened species, especially in resource-limited systems, if PHS also intensifies density-dependent interactions by aggregating organisms. Possibly exacerbating this scenario is the release of hatchery fish, which is commonly used to augment salmon populations (e.g., Einum et al. 2009). Artificial supplementation of fish populations or other species has clear benefits when they face immediate risk of extinction (Young 1999), but in resource-limited systems it may have negative demographic consequences for wild populations because territorial species, such as stream-dwelling salmonids, are strongly affected by density-dependent interactions (our study, Jenkins et al. 1999, Grant and Imre 2005, Buhle et al. 2009, Einum et al. 2009).

We conclude by supporting the proposal made by others that understanding food web dynamics, especially ecological conditions that modify the flow of energy to higher trophic levels, is fundamental to predicting how these food webs respond to environmental change including river restoration and conservation efforts (Rosenfeld et al. 2005, Wipfli and Baxter 2010, Cross et al. 2011, Bellmore et al. 2013). Facilitating this understanding are multi-scale experiments, observational studies, and modeling exercises that investigate multiple limiting factors rather than focusing on a single limiting condition (e.g., Peckarsky et al. 2013).

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SUPPLEMENTAL MATERIAL

APPENDIX

Table A1. The relative proportion (means with 95% CIs in parentheses) of total benthic biomass of invertebrates collected on tiles.

Response	Day 14	Day 45
Ephemerelellidae	<0.001	0.02 (0.006, 0.03)
Baetidae	0.08 (0.04, 0.12)	0.13 (0.10, 0.16)
Heptageniidae	<0.001	0.001 (0.0003, 0.003)
Chironomidae larvae	0.77 (0.68, 0.86)	0.50 (0.42, 0.59)
Chironomidae pupae	0.06 (0.03, 0.08)	0.05 (0.03, 0.08)
Simuliidae larvae	0.04 (0, 0.10)	0.11 (0.03, 0.19)
Glossosomatidae	0.003 (0, 0.005)	0.02 (0.004, 0.03)
Hydropsychidae	0.0008 (0, 0.002)	0.007 (0.002, 0.01)
Plecoptera	<0.001	0.001 (0, 0.003)
Gastropoda	0.01 (0, 0.02)	0.05 (0.02, 0.07)

Table A2. The relative proportion (means with 95% CIs in parentheses) of total biomass of invertebrates in drift and coho diets in experimental streams. Diet selectivity was estimated by subtracting mean diet biomass from mean drift biomass for each taxon.

Response	Drift	Diet	Diet selectivity
EphemereIIDae	<0.001	<0.001	
Baetidae	0.06 (0.03, 0.10)	0.16 (0.008, 0.31)	0.1
Heptageniidae	<0.001	0	
Chironomidae	0.47 (0.39, 0.55)	0.11 (0.004, 0.22)	-0.37
Simuliidae	0.11 (0.06, 0.17)	0.03 (-0.03, 0.09)	-0.08
Adult Chironomidae†	0.27 (0.17, 0.37)	0.63 (0.42, 0.84)	0.36
Trichoptera	<0.001	0	
Plecoptera	<0.001	0	
Terrestrial	0.007 (0.001, 0.01)	0.09 (-0.01, 19)	0.083

† Adult Chironomidae includes both winged adults and pupae.

Table A3. The relative proportion (means with 95% CIs in parentheses) of total biomass of invertebrates in drift and coho diets in the Cedar River and Rock Creek. Diet selectivity was estimated by subtracting mean diet biomass from mean drift biomass for each taxon.

Response	Drift	Diet	Diet selectivity
EphemereIIDae	0.03 (0.007, 0.06)	0.01 (0.005, 0.023)	-0.02
Baetidae	0.31 (0.22, 0.40)	0.10 (0.06, 0.13)	-0.21
Heptageniidae	0.04 (0.003, 0.07)	0.004 (0.0009, 0.007)	-0.036
Chironomidae	0.05 (0.02, 0.07)	0.27 (0.23, 0.31)	0.22
Simuliidae	0.13 (0.07, 0.18)	0.06 (0.04, 0.08)	-0.06
Adult Chironomidae†	0.04 (0.02, 0.05)	0.32 (0.27, 0.37)	0.28
Trichoptera	0.13 (0.05, 0.22)	0.14 (0.1, 0.18)	0.01
Plecoptera	0.06 (0.02, 0.09)	0.05 (0.03, 0.07)	-0.01
Terrestrial	0.06 (0.02, 0.1)	0.11 (0.08, 0.14)	0.05

† Adult Chironomidae includes both winged adults and pupae.