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Adfluvial salmonids have engineering but not fertilization impacts in tributaries of a central Utah reservoir

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ABSTRACT

Migratory fishes can affect tributary ecosystem properties given their potential to introduce nutrients (fertilize) and physically modify habitat (engineer) during spawning. Nonetheless, migrant effects are frequently context-dependent and it is useful to understand their strength relative to other potential ecosystem drivers. We examined whether tributary ecosystem properties varied in response to migrations of two adfluvial salmonids, taking advantage of differences in migration timing and reproductive strategy between species, as well as hydrogeomorphic differences between a pair of tributaries. For analyses, we used a model comparison approach to evaluate migrant effects relative to other possible drivers. We observed that Bonneville cutthroat trout engineered benthic chlorophyll-*a* in redds, with reduction ($51 \pm 16\%$ decrease) generally occurring during migrations. Contrary to expectations, migrant fertilization effects were not pronounced even in the more retentive tributary during migration by species (kokanee) that exhibited high post-spawning mortality. Based on multi-model comparisons, isolated migrant effects were not the primary influence on measured ecosystem properties. Our findings underscore the need to consider different biotic and abiotic conditions that can mediate migratory fish effects.

INTRODUCTION

Ecologists have long been interested in identifying drivers of ecosystem structure and function, and this interest is intensifying as links are recognized between the provision of beneficial ecosystem services and ecosystem dynamics (Diaz et al. 2006). In rivers, which provide valuable services like nutrient retention (Peterson et al. 2001) and fisheries production (Dugan et al. 2010), abiotic drivers such as flow and temperature are commonly assumed to exert primary control on the distribution and abundance of organisms (e.g., Resh et al. 1988; Caissie 2006). While the influence of physical factors is clear, it is increasingly apparent that stream biota may also regulate riverine ecosystem properties. Recent studies have identified a diverse array of invertebrates (e.g., Atkinson and Vaughn 2015; Snyder et al. 2015) and vertebrates (e.g., Rugenski et al. 2012; Sterrett et al. 2015; Subalusky et al. 2015) that can influence different aspects of stream ecosystem structure and function. Consequently, river ecologists are now considering a broader collection of potential ecosystem drivers.

Among lotic organisms, migratory fishes are especially likely to impact stream ecosystem properties due to their potential to introduce nutrients to recipient habitats and engineer (*sensu* Jones et al. 1994) physical habitat through specific behaviors like spawning (Matthews 1998; Flecker et al. 2010). Migratory fishes can augment dissolved nitrogen (N) and phosphorus (P) pools in recipient habitats through multiple mechanisms, including excretion, gamete deposition, and the decomposition of eggs and carcasses (Figure 1). Migrant-derived N and P may then be incorporated into food webs and subsidize higher trophic levels (periphyton and benthic invertebrates) through bottom-up mechanisms, producing an indirect positive effect of migratory fishes on these organisms. Thus, nutrients contributed by migrants may influence both nutrient limitation of primary producers and nutrient flow through food webs in recipient systems. In contrast to the positive fertilization effects of introduced nutrients, migratory fishes may also have a direct negative effect on different stream biota if migrant behavior substantially engineers physical habitat (Figure 1). For example, anadromous Pacific salmon (*Oncorhynchus* spp.) excavate large (1-17 m²; Groot and Margolis 1991) spawning redds during their migrations, a behavior that can decrease periphyton (Moore and Schindler 2008) and invertebrate (Minakawa and Gara 1999)

standing stocks, and shift stream metabolism such that ecosystem respiration becomes substantially larger than gross primary productivity (Holtgrieve and Schindler 2011). Although initial studies of migratory fish effects largely focused on Pacific salmonids (Janetski et al. 2009 and references therein), more recent studies have demonstrated the potential of other anadromous (e.g., Walters et al. 2009; Hogg et al. 2014; Weaver et al. 2016) and potamodromous (Childress et al. 2014; Tronstad et al. 2015; Jones and Mackereth 2016) species to similarly affect recipient habitats, thereby broadening recognition of the diversity of fishes with the capacity to influence ecosystem dynamics.

Although migratory fish effects in streams can be substantial, they are not ubiquitous. Rather, they are frequently context-dependent, varying over time and space in response to changes in biotic and abiotic conditions (Vanni 2010; Gido et al. 2010). For instance, Janetski et al. (2014) reported ecosystem responses to Pacific salmon migrations within native streams that were very different from those observed in Great Lakes tributaries where many of the same species have been successfully introduced. Such variation also occurs over smaller spatial scales, as researchers studying non-native salmonids in the Great Lakes region have reported conflicting responses of periphyton and dissolved nutrients to migrations (e.g., Schuldt and Hershey 1995; Ivan et al. 2011). Certainly, biotic factors such as body size (Hall et al. 2007) and stoichiometry (Capps and Flecker 2013), biomass (Moore and Schindler 2008), and species identity (Hocking and Reimchen 2009) can all mediate migratory fish effects. Likewise, variation in hydrology (Power et al. 2008), land use patterns (Tiegs et al. 2008), and hydrogeomorphic characteristics that govern system retention of migrant-derived nutrients (Flecker et al. 2010) and susceptibility to engineering (Holtgrieve et al. 2010) all represent abiotic regulators of migratory fish effects. However, temporal or spatial variation of ecosystem properties may be driven by factors other than coincident fish migrations. Only by putting migratory fish effects in the context of other ecosystem drivers can we hope to identify generalizable patterns likely to enhance predictive capabilities regarding migratory fish effects in lotic ecosystems.

Here, we describe a study conducted in two tributaries of a central Utah reservoir that are both used by a pair of introduced salmonids with temporally separated migrations and distinct reproductive strategies.

Our primary objectives were to (1) determine the extent to which a suite of tributary ecosystem properties (benthic chlorophyll-*a*, dissolved nutrients, N incorporation into tributary food webs, autotrophic nutrient limitation patterns) varied in response to fish migrations and (2) examine the level of support for multiple hypotheses related to drivers of measured ecosystem properties, which allowed us to assess migrant effects relative to other possible drivers. As a corollary to our second objective, we evaluated the hypothesis that certain dominant abiotic conditions (particle size and stream retentiveness) and biotic characteristics mediate the ecosystem effects of migratory fishes. To address these objectives, we collected data to estimate migration timing and migrant densities, quantify responses of ecosystem properties to fish migrations, and characterize hydrogeomorphic differences between tributaries that likely influence responses to fish migrations by governing stream retentiveness (Flecker et al. 2010), or ability to retain dissolved or particulate materials (e.g., nutrients, carcasses). We then used a model comparison approach to evaluate support for different hypotheses that contained possible drivers alone or in combination. Given the migratory species and tributaries studied, we predicted that migrants engineered benthic environments, reducing chlorophyll-*a*. However, we also expected this engineering effect to be strongly governed by hydrogeomorphic differences between tributaries. Specifically, we predicted that particle size would mediate the effect of migrants: the more smaller substrates, the stronger the migrant engineering effect. Additionally, we expected any fertilization effects (elevated dissolved nutrient concentrations, incorporation of migrant-derived N into tributary food webs, removal of nutrient limitation) associated with fish migrations to be influenced by both migrant reproductive characteristics and tributary retentiveness. We anticipated that the strongest fertilization effects would be observed in the more retentive tributary and linked with the species that maximizes nutrient delivery to recipient tributaries.

METHODS

Study area and species

To examine ecosystem responses to migratory salmonids, we collected data in 2012 from two tributaries (Indian Creek and Trout Creek) of Strawberry Reservoir (40°8' N, 111°2' W) in central Utah.

The high-elevation (2317 m) reservoir impounds 69.44 km² and is surrounded primarily by U.S. Forest Service land (Ward and Robinson 2009). Two non-native salmonids spawn in the tributaries and have temporally separated migrations and distinct reproductive strategies. Bonneville cutthroat trout (BCT; *Oncorhynchus clarkii utah*) migrate from the reservoir to tributaries during spring (May-June), often overlapping snowmelt runoff, and are iteroparous. Conversely, semelparous kokanee salmon (KOK; *O. nerka*) migrate during fall baseflow conditions (September-October; Sigler and Sigler 1996; Knight 1997) and exhibit population-wide post-spawning mortality. Both species have the capacity to influence tributary ecosystems through multiple pathways (Figure 1). For example, BCT and KOK both excavate large ($\approx 1 \text{ m}^2$; K. Wheeler, personal observation, 2012) redds during spawning due to their relatively large body sizes and spawning behavior, which may represent substantial benthic engineering. At the same time, these fishes can also introduce nutrients to tributaries via excretion (Wheeler et al. 2015), egg deposition, and carcass decomposition (particularly KOK), and these added nutrients may stimulate production at higher trophic levels through bottom-up fertilization mechanisms.

Study design

To evaluate responses to BCT and KOK, we established two sampling reaches within two different tributaries (Indian Creek and Trout Creek) that consistently serve as primary spawning areas for both species (A. Ward and J. Robinson, Utah Division of Wildlife Resources, Heber City, Utah, personal communication, 2011). Large beaver dams in both systems served as the upstream extent of migrations for both species (K. Wheeler, unpublished data), although the longitudinal distance used by migrants in each tributary ($2919 \pm 323 \text{ m}$ [mean $\pm$ SE]; $n = 4$) was not necessarily the same for both species. We took advantage of these naturally existing migration barriers to establish treatment (i.e., accessible to and used heavily by migrants) and control (i.e., inaccessible to migrants) reaches in each tributary, and counted individuals in these designated reaches 1-2 times weekly during migrations. Although we attempted to minimize bias in our counts, we acknowledge that they were influenced by unaccounted-for error sources, including incomplete detection and undetected migration pulses between successive streamside counts; thus, counts should be interpreted as an index of abundance. To minimize potential confounding effects

of the beaver dams on measured responses, sampling reaches in both tributaries were > 490 m from the barrier dam. No appreciable surface water inputs occurred between control and treatment reaches in either tributary (K. Wheeler, personal observation, 2012).

Field methods: hydrogeomorphic characterization

We measured a suite of abiotic variables to compare hydrogeomorphic conditions between tributaries. We measured discharge just upstream from tributary mouths at irregular intervals depending on hydrologic stage between April and November (interval range = 4-29 days; Indian: $n = 20$; Trout: $n = 21$). Additionally, we roughly estimated channel slope and sinuosity for each tributary. To estimate slope, we divided the elevation difference between the upstream and downstream limits of migrant-accessible habitat by the longitudinal habitat length. For sinuosity, we divided the longitudinal length of migrant-accessible habitat by the straight-line distance between the upstream and downstream limits of this habitat. We measured wetted channel widths along a longitudinal transect at multiple points (Indian: $n = 89$; Trout: $n = 75$) in both channels during July, reasoning that this time period represented average conditions between spring and fall flow extremes. To enable a more complete comparison of hydrogeomorphic conditions, we estimated depth, velocity, channel unit (i.e., riffle, run, pool) availability, and particulate retention by sampling three representative, randomly-selected 100-m reaches in each tributary during baseflow. At each of these reaches, depth and velocity were measured longitudinally along the thalweg at five-meter intervals and then averaged for each reach sampled. Additionally, the proportion of different channel units was estimated visually. We followed procedures outlined by Lamberti and Gregory (2006) to estimate particulate retention rates, which we considered to be an index of a stream's capacity to retain particulate nutrients like carcasses. Abscised and air-dried *Ginkgo biloba* leaves ($n = 500$; soaked overnight prior to release to ensure neutral buoyancy) were released at the upstream end of each reach, and the number of leaves collected at the downstream end was monitored for a specified time period (60 and 30 minutes in Indian and Trout Creeks, respectively). At the conclusion of the collection period, we inventoried retained leaves by counting the number of leaves within each five-meter interval of the reach. When $\geq 25\%$ of the total number of retained leaves was

collected at the downstream end of reaches, we fit leaf retention data to a negative exponential decay model $P_d = P_0 e^{-kd}$ where P_0 is the number of leaves released into the reach, P_d is the number of leaves still in transport at some downstream distance d from the release point, and k is the particulate retention rate. In all other cases, we used the retention inventory (65-94% of released leaves) to calculate a weighted average distance traveled by an individual leaf, and assumed k was the reciprocal of that distance.

Field methods: ecosystem responses

Benthic chlorophyll-a. To evaluate potential benthic engineering by migrants, we measured benthic algal biomass (as periphyton chlorophyll-*a*) on substrates. Weather conditions limited site accessibility until the very end of April, and BCT were already present in the Indian Creek treatment reach by the time sampling was initiated. Thus, for chlorophyll-*a*, we chose to collect data at a single time point when migrant densities were at or near peak values for both species rather than implement a before-after-control-impact design. During the BCT migration, we collected all substrates from our designated treatment reach (downstream of beaver dams) in each tributary. We treated substrates from obvious spawning redds as ‘treatment’ samples and particles from non-spawning areas as ‘control’ samples. In both cases, substrate selection was haphazard. Because spawning redds were less obvious during the KOK migration, we collected substrates from random locations in the designated treatment (downstream of beaver dams) and control (upstream of beaver dams) reaches of each tributary. Although the use of different approaches precludes us from directly comparing BCT with KOK influence on chlorophyll-*a*, we believe each approach reveals an aspect of migrant influence on benthic periphyton. Our BCT data provide an indication of the net outcome of potentially counteracting fertilization and engineering migrant effects since all substrates were subjected to possible fertilization mechanisms but only ‘treatment’ substrates were subjected to relatively recent physical disturbance by migrants. For KOK, the treatment-control contrast is between migrant presence and absence, but there is no certainty that treatment particles were subjected to migrant engineering. We note here that the distinction between treatment and control for KOK chlorophyll-*a* data also existed for other measured responses (see below). Because substrate

size can influence periphyton response to migratory fishes (Holtgrieve et al. 2010; Bellmore et al. 2014), we used pebble counts (Wolman 1954) of 100-200 particles in each reach to establish substrate size quartiles based on *B*-axis length (2nd longest side). Although the pebble counts were made relatively soon after BCT migrations had initiated, we acknowledge the possibility that counts were influenced by spawning behavior (e.g., Kondolf et al. 1993). During sampling events, we collected three to eight particle ‘samples’ from each of the four size quartiles, grouping multiple particles from the same size quartile to form composite samples in some cases. We categorized all substrates < 9 mm (*B*-axis) as fines and, where necessary, collected required samples by sliding a plastic spatula under an inverted specimen cup (area = 33.18 cm²) inserted into benthic substrates (Hoellein et al. 2009). We scrubbed the exposed surface area of collected particles, rinsed them with tributary water, and recorded the total volume of the generated periphyton slurry. We then filtered a known slurry volume onto pre-ashed Whatman GF/F filters, wrapped filters in aluminum foil, and froze them. For fines, which could not be scrubbed individually, we added a known volume of tributary water to sample containers, shook them vigorously for one minute, allowed settling for 90 seconds, and used a syringe to extract a known supernatant volume for filtration. The methodological differences used to estimate chlorophyll-*a*, while necessary, could have introduced bias; thus comparisons between fines and other size classes should be interpreted cautiously. In the lab, we extracted chlorophyll-*a* from filters for 24 hours at 4°C in 95% ethanol following a five-minute hot (78°C) water bath (Biggs and Kilroy 2000) and analyzed samples fluorometrically (Aquafluor fluorometer, Turner Designs, Sunnyvale, CA). To express chlorophyll-*a* on an areal basis, we used digital photographs of the exposed 2-D area of each substrate particle to estimate surface area in Image J (Rasband, ImageJ), summing multiple particle surface areas for all composite samples.

Dissolved nutrients. To assess potential nutrient delivery by spawning migrants, we collected water column samples ($n = 2-3$) from the thalweg in the downstream end of treatment and control reaches every 1-3 weeks between April and November (Indian: $n = 14$; Trout: $n = 15$). We filtered samples in the field through pre-ashed Whatman GF/F filters into acid-washed Nalgene bottles, stored them on ice in the dark,

and froze them (within four hours) until analysis. Samples were analyzed spectrophotometrically for $\text{NH}_4\text{-N}$, $\text{NO}_3\text{-N}$, and soluble reactive phosphorus (SRP) (3020 Autoanalyzer, Astoria-Pacific Inc., Clackamas, OR) at the Utah State University Aquatic Biogeochemistry Lab (Logan, UT).

$\delta^{15}\text{N}$. We used stable isotope ($\delta^{15}\text{N}$) measurements to determine whether migrant-derived N was incorporated into tributary food webs. We focused our stable isotope analyses on periphyton and scraper invertebrates, reasoning that fertilization effects from spawning migrants would appear first in basal resources (i.e., periphyton) prior to ingestion by primary consumers (i.e., scrapers). We collected stable isotope samples of periphyton and scrapers from control and treatment reaches in both tributaries.

Additionally, we evaluated temporal variation in isotopic data by collecting replicate ($n = 3$) periphyton and scraper samples at each one of five time points; we targeted pre-, during, and post-migration sampling for each species (BCT and KOK), with the post-BCT and pre-KOK samples occurring at the same point. Also, BCT had been present for approximately 1 week in the Indian Creek treatment reach before sampling was conducted. We generated periphyton replicates by haphazardly collecting six substrate particles from each third of every sampling (i.e., treatment or control) reach. We scrubbed particles in the field and considered each composite slurry (from six particles) as a replicate. Slurries were placed on ice and frozen within four hours until analysis. To prepare periphyton samples for isotopic analyses, we thawed slurries and homogenized them before withdrawing a subsample that was dried to constant mass at 60°C in a glass container. At each sampling reach, we used a Surber sampler (mesh = $500\text{ }\mu\text{m}$) to collect invertebrates from nine randomly selected riffle habitats and formed a single composite sample. From each of these composite samples, we generated replicates by identifying scrapers common to the treatment and control reaches in each tributary (Indian Creek: *Optioservus* spp. [Elmidae] larvae; Trout Creek: Heptageniidae larvae; Merritt et al. 2008) and drying three groups of multiple individuals to constant mass at 60°C in glass containers. Dried periphyton and scraper samples were homogenized and weighed in tin capsules (Costech Analytical Technologies Inc., Valencia, CA), then shipped for natural abundance $\delta^{15}\text{N}$ analysis at the University of California at Davis Stable Isotope Facility (PDZ Europa

ANCA-GSL elemental analyzer interfaced to a PDZ Europa 20-20 isotope ratio mass spectrometer, Sercon Ltd., Cheshire, UK). Values are reported as the difference between stable isotope ratios of samples and international lab standards (atmosphere N_2 for $\delta^{15}N$) and are referred to as delta (δ) values in units of per mil (‰).

NDS. Finally, we used nutrient-diffusing substrates (NDS) to determine if BCT or KOK altered autotrophic nutrient limitation patterns across space and time. NDS were constructed by filling plastic cups with approximately 30 mL of agar, which was either untreated (i.e., no nutrients added) or amended with NH_4 -N (0.5 M NH_4Cl), PO_4 -P (0.5 M KH_2PO_4), or $NH_4 + PO_4$ (Tank et al. 2006). Additionally, a fritted glass disc (area = 2.85 cm²) was placed on top of the agar in each cup as physical substrate for autotrophic growth. We used NH_4 and PO_4 because they are the primary inorganic forms of N and P excreted by freshwater fishes (Wood 1995; Vanni 2002). For deployment, we attached NDS to plastic bars in random order and nailed the bars into benthic substrates in a riffle area, placing them perpendicular to flow. To evaluate spatial and temporal changes in limitation, we deployed replicates ($n = 5-7$) of each NDS treatment in treatment and control reaches of both tributaries at three different times: during BCT spawning, between BCT and KOK spawning, and during KOK spawning. Additional NDS deployments were not possible given suggested incubation times (18-22 d; Tank et al. 2006), the temporal length of spawning migrations, and weather constraints that restricted site access prior to BCT migrations. At the end of each incubation period, we placed discs in individual plastic containers, put them on ice, and froze them (within two hours) until analysis. We measured chlorophyll-*a* on each disc following a 20-hour extraction in 95% ethanol at room temperature, using a non-acidification method (Welschmeyer 1994) for fluorometric analysis (10-AU fluorometer, Turner Designs, Sunnyvale, CA).

Statistical analyses

To determine the strength of migrant effects on chlorophyll-*a*, we calculated log response ratios ($LRR = \log(\bar{x}_{TRMT}/\bar{x}_{CTRL})$; Cooper et al. 1990; Hedges et al. 1999), where $\bar{x}_{TRMT}$ and $\bar{x}_{CTRL}$ are treatment and control group means, respectively. When possible, we used *t*-tests ($\alpha = 0.05$) to compare

hydrogeomorphic characteristics between tributaries. We relied on multi-model comparisons to evaluate competing hypotheses about the relative importance of factors driving responses of benthic chlorophyll-*a*, dissolved nutrients, and $\delta^{15}\text{N}$. We used a linear mixed modeling approach with our raw data and considered five potential drivers: migrants, tributary, time, particle size, and biota. Potential drivers were always used as fixed effects in models. We opted to represent migrants categorically in models for all responses because of the elevated frequency of zero density values. For chlorophyll-*a*, we built separate candidate model sets for BCT and KOK because of our different sampling protocols. Consequently, the migrants fixed effect in these models represented two categories (migrant presence, migrant absence). Conversely, repeated sampling associated with nutrient and isotope data permitted differentiation among three migrant categories (i.e., BCT, KOK, or none). The tributary fixed effect reflected differences (e.g., hydrologic, geomorphic, and/or thermal) between Indian and Trout Creeks and was included in models for all responses. For the nutrient and isotope data, we evaluated the effect of time, which reflected temporal differences within tributaries, by considering the Julian date of sampling; actual values were standardized between 0 (first sampling date) and 1 (final sampling date) to facilitate model fitting. Particle size was included as a categorical fixed effect (size quartiles) in only the chlorophyll-*a* models because we anticipated different responses among different size classes. Similarly, we included a categorical fixed effect (biota: periphyton or scrapers) in only the isotope models to reflect possible differences between biota sampled. In all models, we also included a random effect on model intercepts to account for underlying differences in sampling locations ($n = 2$ [BCT chlorophyll-*a* model only] or 4) that were not represented by other measured covariates.

To construct candidate model sets, we considered all possible additive and two-way interactive effects of fixed effect terms. We also included null (i.e., intercept + random effect only) and global models in each candidate set. We calculated Akaike's Information Criterion adjusted for small sample size (AIC_c) for each model and used differences (ΔAIC_c) and model weights (w_i) to compare models and identify the best-approximating model (minimum AIC_c ; $\Delta\text{AIC}_c = 0$) for each response (Burnham and Anderson 2002).

Additionally, we established a credible model set ($0 \leq \Delta AIC_c \leq 2$) for each response and interpreted estimated coefficients as covariate effects. We used the *lmer* function in package *lme4* (Bates et al. 2015) in R (version 3.2.3; R Development Core Team, 2015) for all mixed model analyses and considered all non-zero (i.e., 95% confidence intervals do not overlap zero) model coefficients to be statistically significant.

Following Tank et al. (2006), we used two-way ANOVA to determine nutrient limitation of autotrophic growth during each of the three NDS deployments, with the presence and absence of each nutrient (N and P) serving as factors. When replicates were not completely balanced among treatments due to damaged or displaced cups, we used the *car* package (Fox and Weisburg 2011) in R to calculate type III sums of squares for analyses.

RESULTS

Hydrogeomorphic differences between tributaries

Hydrogeomorphic conditions differed significantly between Indian and Trout Creeks, with estimated values consistently suggesting higher retentiveness in Indian Creek. Mean discharge, velocity (maximum and baseflow), channel slope, and proportion of riffle habitat were all lower in Indian Creek ($P \leq 0.013$; Table 1), while sinuosity, average wetted channel width, depth during baseflow, proportion of pool and run habitats, and particulate retention were all higher in Indian Creek ($P \leq 0.042$; Table 1). Pebble counts revealed additional differences between tributaries with respect to particle size distribution (Table 2).

Indian Creek had a higher (approximately 40% in both reaches) proportion of fine (< 9 mm *B*-axis) substrates than Trout Creek (approximately 15% in both reaches) while the treatment reach of Trout Creek had a lower proportion of large (> 50 mm *B*-axis) particles than other reaches.

Migrant density patterns

Temporal patterns of migrant density indices (density hereafter) also differed between Indian and Trout Creeks, although neither tributary had consistently higher densities than the other. Average live BCT (5.8 ± 1.1 ind 100 m^{-2} ; mean $\pm$ SE) and carcass (1.0 ± 0.3 ind 100 m^{-2}) densities were 1.6 and 14 times higher in Indian Creek, respectively, but the mean density of live KOK (11.1 ± 2.0 ind 100 m^{-2}) was

2.6 times higher in Trout Creek (Figure 2). Average KOK carcass density (1.7 ± 0.3 ind 100 m^{-2}) was similar in both tributaries. Between species, mean densities of live KOK (7.0 ± 1.3 ind 100 m^{-2}) and KOK carcasses were 1.4 and 3 times higher than corresponding BCT densities.

Ecosystem responses

Benthic chlorophyll-a. BCT spawning appeared to engineer benthic substrates in treatment reaches, as mean periphyton chlorophyll-*a* values were generally lower ($51 \pm 16\%$ decrease [mean $\pm$ SE]; $n = 8$) on redd particles than on non-redd particles (Figure 3) and the mean *LRR* was negative (-1.24 ± 0.45). Additionally, the BCT engineering effect appeared to be independent of tributary, as the best-approximating model included a migrant $\times$ particle size interaction but not migrant $\times$ tributary (Tables 3, S1). These model results suggested that the engineering effect of BCT was strongest on size class C (51st-75th percentiles) and that the isolated effect of BCT was negative, although imprecisely estimated (Table 3). In contrast, KOK presence had no discernable effect on periphyton chlorophyll-*a*; there was no general trend ($0 \pm 25\%$) associated with KOK presence, and there was no evidence that mean *LRR* (-0.24 ± 0.28) was statistically different from zero. Furthermore, model comparisons suggested particle size and tributary were more influential drivers of chlorophyll-*a* biomass than KOK. The isolated KOK fixed effect appeared in only one of the best-approximating chlorophyll-*a* models and its magnitude, while negative, was relatively low and imprecisely estimated (Table 4). Conversely, we observed non-zero particle size and tributary fixed effects in both of the best-approximating KOK chlorophyll-*a* models: biomass was highest on the largest particles and was higher in Indian Creek than in Trout Creek (Table 4, Figure 3). Although a migrant $\times$ tributary interaction was not part of the best-approximating chlorophyll-*a* models (Table S1), mean *LRR* values suggested stronger migrant effects in Indian than in Trout Creek for BCT (Ind: -1.80 ± 0.68 ; Trout: -0.68 ± 0.51 ; $n = 4$) and, to a lesser degree, KOK (Ind: -0.58 ± 0.38 ; Trout: 0.11 ± 0.35).

Dissolved nutrients. We found no evidence suggesting that migrants increased dissolved nutrient concentrations in Strawberry Reservoir tributaries during our sampling interval. Instead, modeling results indicated the likely influence of the interaction between time and tributary on all three nutrients (Table

S2). The interaction was the same for NH_4 and NO_3 : concentrations of both nutrients decreased over time in Indian Creek, whereas there was little evidence of concentration changes in Trout Creek over the study period (Figure 4; Tables 5 and 6). SRP concentrations displayed the opposite pattern (more evidence for decrease over time in Trout Creek; Figure 4), although there was also evidence that SRP concentrations were independent of drivers examined as part of this study (Table 7). In the one instance where the isolated migrant effect was a part of the credible model set for dissolved nutrients, SRP tended to be highest during periods without migrants, although the migrant effects were imprecisely estimated (Table 7).

$\delta^{15}\text{N}$. Our modeling results did not suggest a strong influence of migrants on periphyton or scraper $\delta^{15}\text{N}$ signatures (Table S3). Similar to dissolved nutrient dynamics, the day $\times$ tributary interaction appeared to be the primary driver of N isotopic signatures; $\delta^{15}\text{N}$ decreased over time in Indian Creek and remained relatively constant in Trout Creek (Table 8; Figure 5).

NDS. Salmonid migrations did not appear to consistently alter patterns in autotrophic nutrient limitation over the study period, with one potential exception: during BCT migrations in Trout Creek, NH_4 limitation observed in the upstream control reach may have been removed in the treatment reach (Figure 6). During other NDS incubations in the same tributary, responses were generally similar in treatment and control reaches and indicated that neither NH_4 nor SRP availability was limiting autotrophic production. In Indian Creek, we observed stronger positive responses to nutrient addition than in Trout Creek. While these responses indicated a higher probability of nutrient (especially NH_4) limitation in this tributary, they also appeared to be largely independent of migrant presence; patterns of autotrophic response to NDS were essentially the same in treatment and control reaches during all three NDS incubations (Figure 6).

DISCUSSION

Effects of stream biota on riverine ecosystem dynamics are increasingly recognized as case studies document the considerable influence of a wide variety of organisms. Our study adds to growing evidence

that ecosystem properties respond to migratory fishes by demonstrating the potential of spawning BCT to engineer benthic sediments in redds, reducing benthic chlorophyll-*a* biomass. At the same time, our results did not provide evidence that fertilization effects of migrants were stronger where hydrogeomorphic conditions suggested increased retentiveness, nor did they support the hypothesis that migrants alone influenced measured ecosystem properties other than periphyton chlorophyll-*a*. Instead, our findings lead us to hypothesize that migrant effects either depended on or acted in concert with abiotic drivers (e.g., particle size, patterns of nutrient supply and demand) and that scenarios where biota overwhelm or act in isolation of other drivers are likely less common than scenarios in which biotic effects are context-dependent, both of which support a growing body of literature that illustrates different magnitudes and directions of fish effects in streams.

Engineering effects on benthic chlorophyll-a

Our original expectation that migrations of adfluvial salmonids represented a disturbance to benthic environments in spawning tributaries was borne out by our BCT chlorophyll-*a* data and modeling results, which indicated negative (though imprecisely estimated) effects of spawning on benthic chlorophyll-*a* in redds. Benthic chlorophyll-*a* response to spawning salmonids is the outcome of two counteracting yet coincident processes (Figure 1; Bellmore et al. 2014): biomass reduction associated with spawning activity (i.e., engineering) and increased biomass linked with the uptake and incorporation of dissolved inorganic nutrients translocated by the fishes (i.e., fertilization). Our focal taxa are both large relative to most fishes found in streams (Strawberry River fish trap size estimates [mean TL, mm/g]: BCT = 488/872, KOK = 450/886; A. Ward and J. Robinson, unpublished data, 2012) and exhibit spawning behaviors involving repeated contact with benthic particles (Sigler and Sigler 1996), while the spawning tributaries used by these fishes at Strawberry Reservoir feature relatively small benthic particle sizes. This combination of characteristics provided a potential for engineering that we believed would outweigh any potential fertilization effects of the migrants on benthic chlorophyll-*a*, even though the capacity of these same species to provide substantial nutrient inputs to spawning tributaries via excretion is documented (Wheeler et al. 2015).

We found mixed support for expected interactions governing chlorophyll-*a* response to migrants. We predicted stronger (i.e., more negative) benthic chlorophyll-*a* responses in Indian Creek, where the proportion of fine (< 9 mm *B*-axis) substrates was approximately 2.7 times higher than in Trout Creek. This prediction was supported for BCT migrations when we compared *LRRs*, for which the benthic chlorophyll-*a* response was negative and non-zero (based on 95% confidence intervals) in Indian but not Trout Creek. However, the same pattern was not observed during the KOK migration, where neither effect size estimate could be distinguished from zero. Additionally, credible model sets for both species revealed essentially no support for a migrant $\times$ tributary interaction indicative of different chlorophyll-*a* responses to migrants between tributaries. We also predicted that particle size would mediate migrant effects on chlorophyll-*a*, and the expected migrant $\times$ particle size interaction was part of the best-approximating BCT model. The result was counterintuitive, however, as BCT appeared to most strongly reduce chlorophyll-*a* biomass on size class C rather than the smaller size classes (i.e., A or B). Furthermore, modeling results indicated the effect of KOK on chlorophyll-*a* biomass was independent of particle size. Consequently, we conclude that migratory fishes and particle size, while influential, do not solely dictate benthic chlorophyll-*a* biomass in our study systems, even during migration periods.

There are several other factors that may have individually or collectively influenced our chlorophyll-*a* estimates. First, If BCT and KOK spawning activity was patchily distributed in treatment reaches, we were more likely to accurately characterize BCT engineering effects because we collected BCT ‘treatment’ samples from obvious redds, whereas KOK ‘treatment’ samples were collected from random locations within the treatment reach that may or may not have been the site of redd construction. Beyond this methodological factor, species-level variation in engineering effects could be related to body size differences, which did not appear prominent, or density differences, which could have been important. Average BCT densities were 1.6 times higher in Indian than in Trout Creek, a difference that was also reflected by counts made 1-2 days prior to the collection of BCT chlorophyll-*a* data. However, if the effect of density differences on chlorophyll-*a* was consistent, then it seems likely that KOK effects would have been stronger in Trout Creek, where average densities were 2.6 times higher than in Indian Creek.

Likewise, counts made one day before KOK chlorophyll-*a* data were collected indicated migrant densities 8 times higher in Trout Creek than in Indian Creek. Reproductive trait differences between BCT and KOK could have also played a role, as has been documented for other Pacific salmon (Hocking and Reimchen 2009). Unlike BCT, KOK exhibit population-wide post-spawning mortality, which creates the potential for elevated nutrient loading via carcasses. It is thus possible that KOK engineering effects on chlorophyll-*a* may be dampened (i.e., less negative) relative to BCT due to this larger nutrient addition, a result consistent with our species-level effect size estimates that indicated negative, non-zero effects of BCT but not KOK. Finally, abiotic factors such as temperature, light, and nutrient concentrations can also influence benthic chlorophyll-*a* levels (Allan and Castillo 2007). While we did not have sufficient data to include these factors as fixed effects in our models, we instead assumed they were collectively represented as part of the tributary fixed effect, which did appear in both of the best-approximating chlorophyll-*a* models for KOK.

Fertilization effects on nutrients, NDS, and isotopes

Our observations that neither BCT nor KOK increased dissolved nutrient concentrations, removed autotrophic nutrient limitation, or enriched basal resource or consumer N in spawning tributaries are consistent with some previous studies of adfluvial salmonids (e.g., Rand et al. 1992; Sarica et al. 2004; Ivan et al. 2011; Janetski et al. 2014) but opposite others (e.g., Richey et al. 1975; Schuldt and Hershey 1995; Collins et al. 2011; Ruegg et al. 2011), thereby highlighting the role of context for migratory fish effects. Our collected data strongly suggested that Indian Creek was far more retentive than Trout Creek so we expected stronger fertilization effects (elevated nutrient concentrations, food web incorporation of migrant-derived nutrients, removal of nutrient limitation) there (Flecker et al. 2010). Additionally, we expected stronger fertilization responses to one of our focal species (KOK) due to population-wide post-spawning mortality producing substantial carcass loading in spawning tributaries. Our results did not support either prediction, although we know from previous studies that migrant excretion met at least a portion of the nutrient demand in these tributaries in 2012 (Wheeler et al. 2015). However, to observe elevated dissolved nutrient concentrations or removal of nutrient limitation using NDS assays, nutrient

addition by migrants would need to exceed nutrient demand. Rather, Wheeler et al. (2015) found that in these two tributaries, excretion by migratory fishes met or exceeded demand only for N, but not P, and only in Trout Creek. We conclude that ambient nutrient dynamics played a strong role in mediating tributary fertilization responses to adfluvial migrants in Strawberry Reservoir tributaries. If this is true, then larger migrations of BCT or KOK could overcome nutrient limitation and enhance primary production in Indian Creek via excretion and other nutrient delivery pathways (Childress and McIntyre 2015), but would be less likely to influence primary production in Trout Creek, where factors other than nutrients likely exert more control on benthic algae production.

Our isotope results were similar to those for dissolved nutrients and NDS in that they did not support our original expectation of stronger fertilization effects in Indian Creek during KOK migrations. Muscle tissue from KOK carcasses had $\delta^{15}\text{N} = 14.5 \pm 0.1$ (mean $\pm$ SE, $n = 5$). Assuming relatively similar values for BCT, we expected higher $\delta^{15}\text{N}$ enrichment of periphyton and scrapers in Indian Creek, either because elevated retention permitted more assimilation or because N more likely limited production in this system and thus is more likely to be assimilated and retained by biota (Sterner and Elser 2002). Instead, modeling results indicated $\delta^{15}\text{N}$ depletion over time in Indian Creek but not Trout Creek, as well as persistent differences in $\delta^{15}\text{N}$ between tributaries (Indian > Trout) that were independent of migration timing. One possible explanation for our results is that uptake of migrant-derived N by periphyton and scrapers occurs from tissues other than muscles (e.g., gonadal tissue such as milt or eggs), meaning that our collected samples may not represent the source of migrant-derived N used by resident stream biota. Gender- and time-dependent differences in $\delta^{15}\text{N}$ values between muscle and gonadal tissues have been noted in other freshwater fishes (Jardine et al. 2005) and tissue-dependent isotopic changes in migrating salmonids have been documented (Doucett et al. 1999). Some more recent work on migratory fish effects has focused on migrant eggs as a relevant nutrient source (Childress and McIntyre 2015; Jones and Mackereth 2016), and we suggest future studies focused on the incorporation of migrant-derived nutrients into stream food webs would benefit from comparing multiple tissue types.

Addressing context

Our results add to evidence suggesting that potential effects of migratory salmonids are highly dependent on existing abiotic conditions in spawning streams as well as biological characteristics of the migratory species. Results from published studies indicate that migratory salmonid effects are likely most pronounced when migrants have relatively large body sizes, reach high densities, and spawn in streams where nutrient demand exceeds availability (Flecker et al. 2010). Additionally, particle size distributions within spawning streams can govern whether migrants reduce or increase periphyton biomass (e.g., Holtgrieve et al. 2010). In our study, the small particle sizes in Indian and Trout Creeks, relative to native salmon streams in the Pacific Northwest, help to explain why BCT tended to reduce benthic chlorophyll-*a* biomass in redds. Additionally, the engineering effects we observed may have been lower than those measured elsewhere as a result of the small body sizes and densities of BCT and KOK relative to other studies of Pacific salmonids (e.g., Collins et al. 2011), although we cannot rule out potential effects resulting from our chlorophyll-*a* sampling protocols. The lack of fertilization responses we observed is consistent with other studies of migratory salmonids (e.g., Rand et al. 1992; Sarica et al. 2004; Ivan et al. 2011; Janetski et al. 2014) despite relatively low ambient nutrient concentrations in our study tributaries. Thus, we suggest that the balance between migrant nutrient fluxes and ecosystem nutrient demand may be a better indicator of potential fertilization effects than background nutrient levels, and may help to explain why there are other instances where migratory salmonids do have more pronounced fertilization effects (e.g., Richey et al. 1975; Schuldt and Hershey 1995; Collins et al. 2011; Ruegg et al. 2011).

Studies demonstrating salmonid effects have been instrumental in fostering appreciation for the functional role of migratory fishes in lotic ecosystems, but numerous taxa, possible responses, and contextual questions remain understudied or unanswered. As recent studies illustrate, a variety of non-salmonid fishes also have the capacity to affect ecosystem properties in both temperate (e.g., Childress et al. 2014) and tropical (e.g., Capps and Flecker 2013) streams and rivers, including other anadromous species like alewife (*Alosa pseudoharengus*; Walters et al. 2009) and sea lamprey (*Petromyzon marinus*; Hogg et al. 2014; Weaver et al. 2016). Additionally, researchers are only beginning to explore how

migratory fishes, in addition to affecting standing crops of materials and resources (e.g., nutrients, periphyton), may also influence a variety of process-oriented ecosystem properties like metabolism (e.g., Taylor et al. 2006; Holtgrieve and Schindler 2011), decomposition (e.g., Walters et al. 2009), and nutrient cycling (e.g., Tronstad et al. 2015). Given the prevalence of migratory life cycles among freshwater fishes (Flecker et al. 2010) and the myriad pathways by which these fishes can elicit some type of ecosystem response (Matthews 1998), future work will shed additional light on the particular scenarios in which migratory fishes shape ecosystem properties. As individual case studies accumulate, there is also the opportunity to quantitatively synthesize the existing body of work to identify relevant drivers of observed dynamics (e.g., Janetski et al. 2009; Wheeler 2015), thereby enabling a more complete understanding of context.

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711 **TABLE 1.** Comparison of hydrogeomorphic characteristics between Indian and Trout Creeks. When
 712 multiple measurements were made, data are presented as means (SE). Characteristics with * indicate
 713 measurements made during baseflow conditions. Statistically significant ($\alpha = 0.05$) differences between
 714 streams in bold. Q, discharge; U_{MAX}, maximum velocity observed during discharge measurements;
 715 WCW, wetted channel width; z, depth; U, velocity; k, particulate retention

	Q (m ³ s ⁻¹)	U _{MAX} (m s ⁻¹)	Slope	Sinuosity	WCW (m)	z* (m)	U* (m s ⁻¹)	Pool* %	Riffle* %	Run* %	k* (m ⁻¹)
Indian Creek	0.065 (0.012)	0.36 (0.03)	0.01	1.64	3.01 (0.09)	0.24 (0.03)	0.15 (0.04)	15 (2)	34 (8)	51 (6)	0.0192 (0.0026)
Trout Creek	0.094 (0.003)	0.69 (0.03)	0.03	1.18	1.97 (0.07)	0.14 (0.01)	0.69 (0.04)	0 (0)	95 (2)	5 (2)	0.0062 (0.0021)
<i>t</i>	-2.60	-7.57	---	---	9.10	2.94	-9.48	6.38	-7.29	6.79	3.93
df	39	39	---	---	162	4	4	4	4	4	4
<i>P</i>	0.013	<0.001	---	---	<0.001	0.042	<0.001	0.003	0.002	0.002	0.017

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717 **TABLE 2.** Benthic particle size quartiles in Strawberry Reservoir tributaries. Measurements of 100-200
 718 particles were made in two reaches (TRMT = accessible to migrants downstream of beaver dam; CTRL =
 719 inaccessible to migrants upstream of beaver dam) of each tributary. Particles < 9 mm *B*-axis were
 720 classified as fines (f).

Percentile range	<i>B</i> -axis range (mm)			
	Indian,TRMT	Indian,CTRL	Trout,TRMT	Trout,CTRL
0-25 (A)	f	f	f - 14	f - 14
26-50 (B)	f - 19	f - 17	15 - 24	15 - 27
51-75 (C)	20 - 54	18 - 58	25 - 40	28 - 56
76-100 (D)	> 54	> 58	> 40	> 56

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TABLE 3. Summary of the credible model set ($\Delta AIC_c \leq 2$) for benthic chlorophyll-*a* biomass during the Bonneville cutthroat trout migration. Bold font denotes non-zero coefficients (i.e., 95% confidence intervals do not overlap zero). AIC_c , ΔAIC_c , and w_i values were calculated and interpreted following Burnham and Anderson (2002). $n = 81$ observations. Location ($n = 2$) is a random effect to account for variation between sample collection areas that is not reflected in the tributary fixed effect. mig = migrants (present or absent); ps = particle size (quartiles; Table 2).

best-approximating model: mig $\times$ ps + (1 location); $w_i = 0.777$, $\Delta AIC_c = 0.000$					
<i>Fixed effects:</i>			<i>Random effects:</i>		
	estimate	SE	<i>t</i>		variance
Intercept	1.798	0.650	2.766	location (intercept)	0.003
mig (present)	-1.508	0.918	-1.643	residual	2.529
ps B	0.277	0.795	0.349		
ps C	2.862	0.807	3.546		
ps D	0.868	0.807	1.076		
mig (present) $\times$ ps B	0.119	1.124	0.106		
mig (present) $\times$ ps C	-2.524	1.151	2.192		
mig (present) $\times$ ps D	0.723	1.126	0.642		

TABLE 4. Summary of the credible model set ($\Delta AIC_c \leq 2$) for benthic chlorophyll-*a* biomass during the kokanee salmon migration. Bold font denotes non-zero coefficients (i.e., 95% confidence intervals do not overlap zero). AIC_c , ΔAIC_c , and w_i values were calculated and interpreted following Burnham and Anderson (2002). $n = 88$ observations. Location ($n = 4$) is a random effect to account for variation among sample collection areas that is not reflected by the tributary fixed effect. ps = particle size (quartiles; Table 2); trib = tributary; mig = migrants (present or absent).

best-approximating model: ps + trib + (1 location); $w_i = 0.543$, $\Delta AIC_c = 0.000$					
<i>Fixed effects:</i>			<i>Random effects:</i>		
	estimate	SE	<i>t</i>		variance
intercept	2.089	0.365	5.731	location (intercept)	0.036
ps B	-0.632	0.411	-1.540	residual	1.799
ps C	0.313	0.411	0.763		
ps D	1.359	0.415	3.275		
trib (Trout)	-1.429	0.344	-4.154		
2 nd best-approximating model: mig + ps + trib + (1 location); $w_i = 0.273$, $\Delta AIC_c = 1.374$					
intercept	2.257	0.379	5.949	location (intercept)	0.009
mig (present)	-0.331	0.301	-1.097	residual	1.799
ps B	-0.635	0.411	-1.546		
ps C	0.311	0.411	0.756		
ps D	1.354	0.415	3.263		
trib (Trout)	-1.445	0.301	-4.794		

TABLE 5. Summary of the credible model set ($\Delta AIC_c \leq 2$) for dissolved NH_4 over time. Bold font denotes non-zero coefficients (i.e., 95% confidence intervals do not overlap zero). AIC_c , ΔAIC_c , and w_i values were calculated and interpreted following Burnham and Anderson (2002). $n = 58$ observations. Location ($n = 4$) is a random effect to account for variation among sample collection areas that is not reflected by the tributary fixed effect. day = time (standardized between 0 and 1); trib = tributary.

best-approximating model: day $\times$ trib + (1 location); $w_i = 0.655$, $\Delta AIC_c = 0.000$					
<i>Fixed effects:</i>			<i>Random effects:</i>		
	estimate	SE	<i>t</i>		variance
intercept	17.603	1.942	9.063	location (intercept)	4.232
day	-9.578	2.130	-4.496	residual	12.242
trib (Trout)	-3.982	2.682	-1.485		
day $\times$ trib (Trout)	8.250	2.892	2.853		

TABLE 6. Summary of the credible model set ($\Delta AIC_c \leq 2$) for dissolved NO_3 over time. Bold font denotes non-zero coefficients (i.e., 95% confidence intervals do not overlap zero). AIC_c , ΔAIC_c , and w_i values were calculated and interpreted following Burnham and Anderson (2002). $n = 58$ observations. Location ($n = 4$) is a random effect to account for variation among sample collection areas that is not reflected by the tributary fixed effect. day = time (standardized between 0 and 1); trib = tributary.

best-approximating model: day $\times$ trib + (1 location); $w_i = 0.841$, $\Delta AIC_c = 0.000$					
<i>Fixed effects:</i>			<i>Random effects:</i>		
	estimate	SE	<i>t</i>		variance
intercept	38.807	25.465	1.524	location (intercept)	1233.6
day	-36.720	9.316	-3.941	residual	234.2
trib (Trout)	828.794	35.920	23.074		
day $\times$ trib (Trout)	55.238	12.649	4.367		

TABLE 7. Summary of the credible model set ($\Delta AIC_c \leq 2$) for soluble reactive phosphorus (SRP) over time. Bold font denotes non-zero coefficients (i.e., 95% confidence intervals do not overlap zero). AIC_c , ΔAIC_c , and w_i values were calculated and interpreted following Burnham and Anderson (2002). $n = 58$ observations. Location ($n = 4$) is a random effect to account for variation among sample collection areas that is not reflected by the tributary fixed effect. day = time (standardized between 0 and 1); trib = tributary; mig = migrant (BCT, KOK, or none).

best-approximating model: $1 + (1 \mid \text{location})$; $w_i = 0.326$, $\Delta AIC_c = 0.000$					
<i>Fixed effects:</i>			<i>Random effects:</i>		
	estimate	SE	<i>t</i>		variance
intercept	2.663	0.170	15.680	location (intercept)	0.054
				residual	0.891
2 nd best-approximating model: $\text{day} \times \text{trib} + (1 \mid \text{location})$; $w_i = 0.139$, $\Delta AIC_c = 1.701$					
intercept	2.236	0.368	6.082	location (intercept)	0.052
day	1.000	0.547	1.826	residual	0.809
trib (Trout)	0.695	0.497	1.398		
day $\times$ trib (Trout)	-1.735	0.743	-2.334		
3 rd best-approximating model: $\text{mig} + (1 \mid \text{location})$; $w_i = 0.137$, $\Delta AIC_c = 1.744$					
intercept	2.153	0.297	7.244	location (intercept)	0.000
mig (KOK)	0.409	0.446	0.918	residual	0.884
mig (none)	0.655	0.332	1.971		

755 **TABLE 8.** Summary of the credible model set ($\Delta AIC_c \leq 2$) for $\delta^{15}N$ over time. Bold font denotes non-
 756 zero coefficients (i.e., 95% confidence intervals do not overlap zero). AIC_c , ΔAIC_c , and w_i values were
 757 calculated and interpreted following Burnham and Anderson (2002). $n = 40$ observations. Location ($n =$
 758 4) is a random effect to account for variation among sample collection areas that is not reflected by the
 759 tributary fixed effect. day = time (standardized between 0 and 1); trib = tributary.

best-approximating model: day $\times$ trib + (1 location); $w_i = 0.699$, $\Delta AIC_c = 0.000$					
<i>Fixed effects:</i>			<i>Random effects:</i>		
	estimate	SE	<i>t</i>		variance
intercept	8.848	0.377	23.549	location (intercept)	0.009
day	-2.301	0.586	-3.923	residual	0.955
trib (Trout)	-7.945	0.533	-14.899		
day $\times$ trib (Trout)	2.616	0.829	3.156		

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FIGURE 1. Pathways by which non-feeding migratory fishes may affect stream ecosystem properties. Solid grey lines indicate direct effects of migrants whereas darker dashed lines depict indirect migrant effects. Black boxes and solid lines represent stream nutrients and biota and their trophic relationships. Grey boxes indicate ecosystem properties that may be altered in response to fish migrations. Note that pathways depicted here are not necessarily exhaustive. N = nitrogen, P = phosphorus. Bonneville cutthroat trout illustration drawn and provided by Joseph R. Tomelleri.

FIGURE 2. Live migrant and carcass density indices in Indian and Trout Creeks during 2012. Spring migrants are Bonneville cutthroat trout (BCT; *O.clarkii utah*) and fall migrants are kokanee salmon (KOK; *O.nerka*). Density indices are based on streamside migrant counts and reflect areas associated with designated treatment reaches in each tributary. Dashed lines depict average live migrant densities during each migration. Bonneville cutthroat trout and kokanee salmon illustrations drawn and provided by Joseph R. Tomelleri.

FIGURE 3. Benthic substrate chlorophyll-*a* biomass during 2012 migrations in Strawberry Reservoir tributaries. Substrates were sampled during periods at or near peak migrant densities for Bonneville cutthroat trout (BCT; *O.clarkii utah*) and kokanee salmon (KOK; *O.nerka*) in Indian (Ind) and Trout Creeks. Migrants were present and actively spawning in areas where treatment (TRMT) particles were collected and absent or not spawning in locations where control (CTRL) particles were collected (see Methods). Particle size classes were delineated using quartiles based on *B*-axis length (Table 2) and reflect increasing size from A to D. Mean values + 1 SE are plotted.

FIGURE 4. Dissolved nutrient concentrations during 2012 migrations in Strawberry Reservoir tributaries. Samples were collected periodically from treatment (TRMT; accessible to migrants) and control (CTRL; inaccessible to migrants) reaches in Indian and Trout Creeks. Shaded areas in each panel denote migration periods in each tributary: Bonneville cutthroat trout (BCT; *O.clarkii utah*) migrate during the spring and kokanee salmon (KOK; *O.nerka*) migrate during the fall. Note difference in y-axis scales for NO₃. Mean nutrient concentrations ± 1 SE are plotted.

FIGURE 5. Nitrogen ($\delta^{15}\text{N}$) isotopic signatures of periphyton (P) and scraper invertebrates (S) during 2012 migrations in Strawberry Reservoir tributaries. Samples were collected periodically from treatment (TRMT; accessible to migrants) and control (CTRL; inaccessible to migrants) reaches in Indian and Trout Creeks. Shaded areas in each panel denote migration periods in each tributary: Bonneville cutthroat trout

(BCT; *O.clarkii utah*) migrate during the spring and kokanee salmon (KOK; *O.nerka*) migrate during the fall. Mean isotopic signatures ± 1 SE are plotted.

FIGURE 6. Chlorophyll-*a* measured during nutrient-diffusing substrate (NDS) incubations in Strawberry Reservoir tributaries. NDS incubations were carried out during three separate time periods in Indian (Ind) and Trout Creeks: during the Bonneville cutthroat trout migrations (BCT), between the Bonneville cutthroat trout and kokanee salmon migrations (bw), and during the kokanee salmon migrations (KOK). Incubations took place in treatment (TRMT; accessible to migrants) and control (CTRL; inaccessible to migrants) reaches in both tributaries and consisted of four nutrient treatments: control (CTRL; i.e., no nutrients added), NH₄-nitrogen alone (N), soluble reactive phosphorus alone (P), and N and P added together (N+P). Asterisks indicate a significant ($\alpha = 0.05$) limiting effect of particular treatment(s) and text reflects interpretation of these results (following Tank and Dodds 2003). Mean values ± 1 SE are plotted. 1° = primary, 2° = secondary

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FIGURE 1.

FIGURE 2.

FIGURE 3.

FIGURE 4.

FIGURE 5.

FIGURE 6.