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ISBN

9798189227189

Author

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Publication Date

2026-06-25

Peer reviewed|Thesis/dissertation

Salmonid Growth in Beaver Dam Analog Habitat

By

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THESIS

Submitted in partial satisfaction of the requirements for the degree of

MASTER OF SCIENCE

in

Ecology

in the

OFFICE OF GRADUATE STUDIES

of the

UNIVERSITY OF CALIFORNIA

DAVIS

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2026

Abstract

Human alteration of stream ecosystems across the western United States has modified channel structure, flow regimes, and floodplain connectivity, contributing to declines in salmonid populations. Beaver dam analogs (BDAs) are increasingly implemented as a process-based restoration strategy in headwater streams to increase water retention, floodplain connectivity, and the development of low-velocity hydraulic habitats. Although these physical responses are well-documented, less is known about how BDAs influence biological performance metrics such as fish growth.

We evaluated the influence of BDA habitat on the growth of salmonids across four streams in the Klamath Mountains and northern Sierra Nevada using a mark–recapture design. Between June 2024 and November 2025, we tagged 4,939 fish and analyzed growth from 652 recaptured individuals, including coho salmon (*Oncorhynchus kisutch*) and resident trout species (brook trout *Salvelinus fontinalis* and brown trout *Salmo trutta*). Observed mean specific growth rates were higher in BDA reaches than in reference reaches in three of four streams.

Specific growth rate was modeled as a function of habitat type (BDA vs. reference), temperature, fish density, and macroinvertebrate drift density using linear mixed-effects models with stream as a random effect. Fish rearing in BDA habitats exhibited higher growth rates than those in reference reaches after accounting for environmental covariates ($\beta = -0.200 \pm 0.030$ SE for reference relative to BDA, $p < 0.001$). Growth declined with increasing temperature and fish density, consistent with metabolic and density-dependent constraints, yet BDA reaches supported higher growth despite being slightly warmer on average. This pattern suggests that temperature alone does not explain observed growth differences and that habitat characteristics associated with BDAs—such as reduced energetic costs of station holding, increased habitat complexity, and altered foraging conditions—may enhance net energy gain.

Our findings indicate that BDAs can enhance growth conditions for salmonids and demonstrate that restoration-driven changes can translate into measurable biological responses. This work highlights the importance of evaluating ecological outcomes alongside physical habitat responses in stream restoration.

Introduction

Human activity has altered the physical characteristics of streams throughout the western United States. As a result, impaired flow regimes, altered sediment supplies, and reduced instream complexity have rapidly changed the structure and function of stream ecosystems (Vannote et al. 1980; Benke 1990; Cluer and Thorne 2014; Wohl 2014; Naiman et al. 1988). These alterations have reduced habitat complexity and limited the range of hydraulic conditions available to aquatic organisms. In many lower order streams, these changes have resulted in the loss of low-velocity habitats (McIntosh et al. 2000).

The loss of aquatic habitat diversity has coincided with the decline of Pacific salmonids (*Oncorhynchus spp.*), with 28 populations currently listed under the federal Endangered Species Act (Williams et al. 2016; Ford 2022). While dwelling in streams, salmonids rely on a mosaic of hydraulic conditions that provide refuge from high velocities while maintaining access to food resources. Low-velocity habitats are particularly important during early life stages, when swimming ability is limited and energetic constraints are high (Chapman and Bjornn 1969; Bjornn and Reiser 1991). This rearing period can represent a critical population bottleneck, especially for anadromous species with relatively longer freshwater residency, such as coho salmon (*O. kisutch*) (Shapovalov and Taft 1954).

Growth in salmonid fishes plays a key role in shaping survival to adulthood, reproductive success, and life history diversity (Quinn 2005). Several studies, across anadromous salmonid species, have demonstrated that larger smolts disproportionately contribute to adult returns (Ward et al. 1989; Zabel and Williams 2002; Zabel and Achord 2004; but see Cordoleani et al. 2021). For instance, Duffy and Beauchamp (2011) found that Chinook salmon (*O. tshawytscha*) smolt size at ocean entry was a strong predictor of survival to adulthood. Differential growth rates can also contribute to life history diversity in salmonid populations, as larger juveniles may emigrate from freshwater habitats earlier than smaller conspecifics (Bosch et al. 2023). In resident salmonids, growth similarly governs key life history traits, influencing the timing and success of reproduction. The phenology of sexual maturation has been linked to size in cutthroat trout (*O. clarkii*), indicating that faster-growing fish are able to reproduce earlier (Downs et al. 1997). Additionally, fecundity in rainbow trout (*O. mykiss*) and brook trout (*Salvelinus fontinalis*) increases with body size (McFadden et al. 1965; Bromage et al. 1990). Thus, stream habitats that provide salmonids with opportunities for enhanced growth may aid in species recovery and build population resiliency (Jeffres et al. 2008; Lusardi et al. 2020).

Somatic growth in ectothermic fishes occurs when energy intake exceeds losses to metabolic demand and waste production (Brett and Groves 1979). Habitats most conducive to growth are those in which food availability is maximized and metabolic costs—associated with temperature and energetic demands such as stream position maintenance—are minimized (Fausch 1984). For rearing salmonids, these conditions are typically found in stream reaches or adjacent habitats that support slow water, cool temperatures and abundant prey. For example, salmonids with access to low-velocity or lentic rearing habitats have been shown to grow faster than individuals restricted to higher-velocity environments (Rosenfeld and Boss 2001; Sethi et al. 2022). Optimal stream temperatures for salmonid growth vary across and within species, regions, and prey availability (Carter 2005; Verhille et al. 2016; Lusardi et al. 2020). Broadly, salmonids achieve maximal growth rates at temperatures between 12 and 20° C (Jonsson 2023). Additionally, growth rates of juvenile salmonids have been shown to increase with invertebrate drift concentration and biomass, reflecting greater energy availability for consumption (Nielsen 1992; Rosenfeld et al. 2005). However, growth in salmonid habitats can also be constrained by competition, as

higher fish densities can reduce per capita food availability and increase energetic costs associated with foraging and interference (Grant and Imre 2005). Because growth-favorable conditions depend on the interaction of flow, temperature, and habitat structure, understanding the processes that create and maintain low-velocity hydraulic habitats is critical for evaluating salmonid growth potential.

Historically, the abundance of slow-water habitat in North American streams was augmented by the activity of beaver (*Castor canadensis*) (Naiman et al. 1988). Through dam-building, beaver impound flow and create low-velocity, deep habitats. For fish occupying beaver ponds, the energetic cost of maintaining position is low (Pollock et al. 2003). Further, beaver dams have been shown to buffer daily stream temperatures during summer (Weber et al. 2017). Where sufficient prey is available, the relatively cool, slow, and deep conditions of beaver ponds can promote net energy gain in salmonids. Although research on prey availability in beaver ponds is variable, several studies have documented greater invertebrate biomass in beaver ponds compared to unimpounded reference sites (Washko et al. 2022). Additionally, macroinvertebrate diversity and emergence phenology can be altered by beaver dam construction (Naiman et al. 1984), with implications for salmonid foraging. For example, Swales and Levings (1989) found that salmonids rearing in beaver ponds exhibited higher growth rates than those in reference habitats. However, centuries of beaver trapping have left populations at a fraction of historical abundance (Johnson and Chance 1974). As a result, widespread losses of slow-water ponded habitats have been documented across streams in the western United States (Johnson and Chance 1974).

Beaver dam analogs (BDAs) have emerged as a process-based technique for restoring habitat in altered stream ecosystems (Goss et al. 2025). This approach typically involves mimicking beaver activity by installing wooden posts into the streambed, weaving willow branches between posts, and packing the structure with fine organic material to promote pond formation (Pollock et al. 2012). Although BDAs are designed to function as surrogates for natural beaver dams, ecosystem responses to these structures can differ substantially from those associated with authentic beaver-built dams (Wohl and Inamdar 2025; Wolf and Hammill 2023).

BDAs have been implemented across numerous watersheds in the Pacific Northwest and beyond, and a growing body of literature demonstrates their effectiveness in reducing channel incision, increasing groundwater elevations, and reconnecting streams with adjacent floodplains (Munir and Westbrook 2021; Pollock et al. 2014; Scamardo and Wohl 2020). Despite these documented geomorphic and hydrologic benefits, relatively little is known about the ecological responses of stream communities to BDAs (Corline et al. 2023). In particular, few studies have evaluated fish growth in BDA-created ponds relative to reference habitats (but see Bouwes et al. 2016 and Halbert and Keeley 2023), and no studies to date have examined their effects on the growth of Pacific salmon.

Here, we investigated the effect of BDAs on the growth of stream-dwelling salmonids across four distinct subbasins in the Klamath Mountains and northern Sierra Nevada. We hypothesized that fish rearing in BDA ponds would exhibit higher growth rates than those in untreated reference pools. To test this, we employed a mark-recapture study design to directly estimate individual growth rates while simultaneously collecting data on environmental covariates including water temperature, macroinvertebrate drift density, and salmonid fish density. We then developed a linear mixed-effects model to isolate the effect of BDA habitat on growth and to evaluate the influence of BDAs on the environmental covariates.

Methods

Study Sites

We identified four salmonid-bearing northern California streams where BDAs have been installed between 2014 and 2024 (Figure 1). Two sites are located in French Creek and Sugar Creek, tributaries to the Scott River in Siskiyou County, where rainbow trout/steelhead (*Oncorhynchus mykiss*) and a population of the federally threatened Southern Oregon/Northern California (SONCC) evolutionarily significant unit (ESU) of coho salmon (*Oncorhynchus kisutch*) are present (National Marine Fisheries Service 1997). French Creek and Sugar Creek drain the central Klamath Mountains, originating from sub-alpine lakes sitting between 1,830 and 2,130 m elevation. These systems are primarily driven by rainfall and snowmelt, with peak flows occurring in spring and declining to low baseflows during late summer. Geologically, the watersheds are underlain by a mix of granitic and metamorphic rock characteristic of the Klamath Mountains (Kauffmann et al. 2022). In the nearby town of Callahan (elevation 957 m), mean annual precipitation was 53.14 cm between 1943 and 2016, and mean monthly maximum air temperature ranged from ~7 °C in December to ~32 °C in July (Western Regional Climate Center [WRCC] 2025). Mean daily discharge in August in French Creek and Sugar Creek was 0.011 and 0.063 cubic meters per second (cms), respectively, in 2025 (California Data Exchange Center 2025).

The other two sites were located in Gurnsey Creek, a tributary to Deer Creek in the Sacramento River basin, and Yellow Creek, a tributary to the North Fork Feather River. Resident salmonids in these streams include rainbow trout, introduced brook trout (*Salvelinus fontinalis*), and introduced brown trout (*Salmo trutta*). Gurnsey Creek and Yellow Creek are presently not accessible to anadromous fish, although anadromous species, such as spring-run Chinook salmon, accessed Yellow Creek prior to the construction of impassable dams on the North Fork Feather River in the early 1900s (Yoshiyama et al. 2001). Both streams have headwaters originating between 1,670 m and 1,980 m, with winter and spring flows supported by rainfall and snowmelt and summer baseflows supported by groundwater-fed springs. In contrast to the Klamath sites, these watersheds are influenced by volcanic geology associated with the southern Cascade Range and northern Sierra Nevada (Clynne and Muffler, 2010). Mean annual precipitation in the nearby town of Chester (elevation 1,382 m) was 80.85 cm between 1909 and 2016, and mean monthly maximum air temperature ranged from ~5 °C in January to ~30 °C in July (WRCC 2025). Unlike French Creek and Sugar Creek, Gurnsey Creek and Yellow Creek do not have established gauges allowing for continuous calculation of discharge. However, point measurements were taken during sampling events. Discharge was 0.120 cms in Gurnsey Creek on August 4, 2025 and 0.174 cms in Yellow Creek on August 5, 2025.

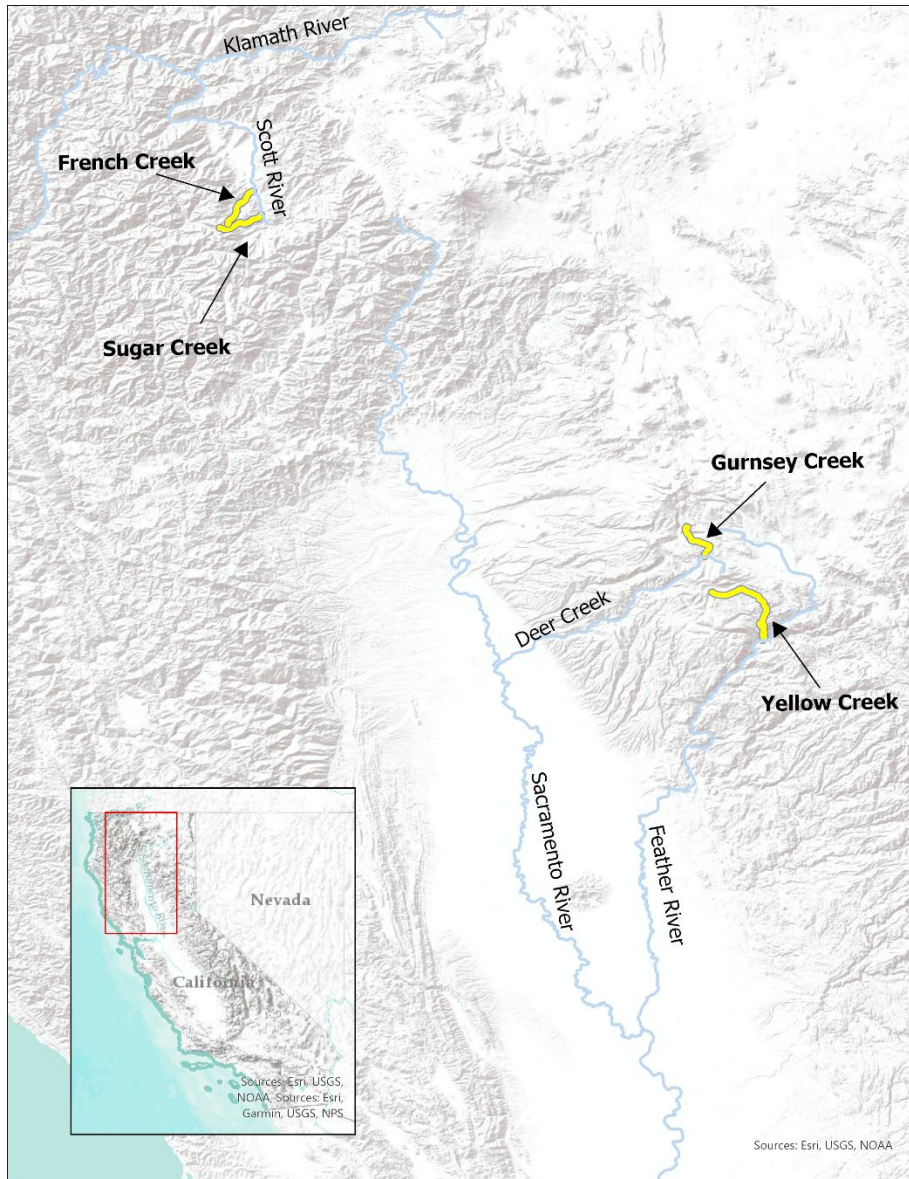


Figure 1. Location of study streams in California.

The BDAs in French Creek and Sugar Creek were installed by the Scott River Watershed Council between 2014 and 2017, while the BDAs in Gurnsey Creek and Yellow Creek were installed by Symbiotic Restoration between 2022 and 2024 (Yokel et al. 2018; Symbiotic Restoration 2025). The structures varied in size and age, but all were formed by weaving thin woody material between a series of posts driven into the substrate and packing with organic material to achieve ponding. In the Scott River watershed, the BDAs were installed primarily to provide habitat for juvenile coho salmon and to address legacy impacts of dredge mining. The Gurnsey Creek and Yellow Creek structures were built to aid in restoring high-elevation meadow habitat impacted by cattle grazing and channel incision.

Experimental design

We conducted this study between June 2024 and November 2025. In each stream, we identified two reaches (approximately 300 m in length), one including three BDA ponds and the other including three

untreated reference pools. We chose reference pools that were representative of hydraulically generated pool habitats found in each stream near its respective BDAs. The position of a reference reach relative to the paired BDA reach varied between streams (Figure 2). In Sugar Creek and Yellow Creek, BDA reaches were downstream of reference reaches. In Gurnsey Creek, the reference reach was downstream of the BDA reach. In French Creek, the BDA reach was in a side channel directly adjacent to the reference reach in the main channel.

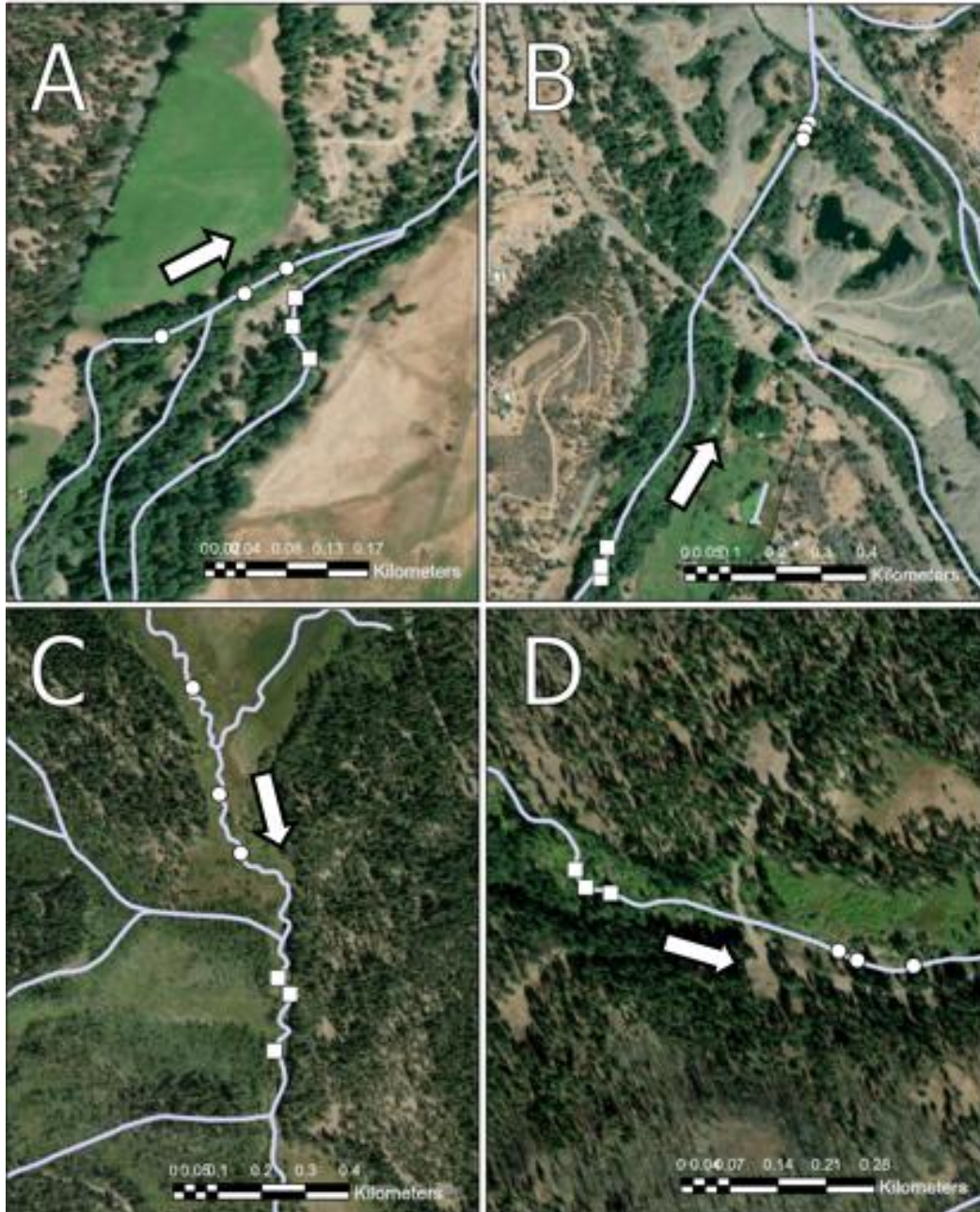


Figure 2. Position of BDA vs reference pools. A is French Creek, B is Sugar Creek, C is Gurnsey Creek and D is Yellow Creek. Circles represent BDA ponds and squares represent reference pools. Arrows represent the direction of flow.

We employed a mark-recapture study design, wherein we repeatedly visited our sites, tagging fish and identifying recaptures at each sampling event. Timing of sampling varied by site (Table 1). Between August 2024 and March 2025, we sampled French Creek and Sugar Creek every 4-8 weeks. We resumed sampling French Creek monthly between August and November 2025, although the furthest upstream BDA pond remained dry through the sampling period, meaning only two units were sampled in the BDA reach during this period. Sampling at Sugar Creek did not occur after March 2025, as all fish were relocated from the BDA reach in August 2025, prior to a channel reconfiguration project being implemented. We sampled Gurnsey Creek and Yellow Creek every 4-8 weeks between June and November of 2024 and 2025.

Table 1. Period and frequency of sampling at each study stream.

Stream(s)	Sampling Period	Sampling Frequency
French Creek & Sugar Creek	August 2024–March 2025	Every 4–8 weeks
French Creek	August 2025–November 2025	Every 4 weeks
Gurnsey Creek & Yellow Creek	June–November, 2024 and 2025	Every 4–8 weeks

Fish sampling

To evaluate the effects of BDA habitat on salmonid growth rates, we repeatedly sampled fish populations in each study stream. Methods used to capture fish varied based on study site and time of year. In French Creek and Sugar Creek, a beach seine was used to capture fish between August and November. In each unit, we repeatedly pulled the seine through the pool until the catch diminished. Captured fish were placed into buckets filled with aerated water until seining was complete. Between November and March, increased depths and velocities precluded the use of beach seines as an effective sampling method. Instead, in each habitat unit we distributed minnow traps baited with cured salmon roe in the late afternoon. We left the traps to soak overnight, returning to process the catch the following morning. In Gurnsey Creek and Yellow Creek, we collected fish using an Apex backpack electrofisher (Smith-Root Inc., Vancouver, WA, USA). Blocknets were set up at the upstream and downstream end of each pool, and two passes were made with an electrofisher to remove all fish from the habitat unit. Stunned fish were captured with dip nets and placed into buckets filled with aerated water until the electrofishing was complete.

All captured fish were placed into aerated buckets of water prior to processing. Captured salmonids were anesthetized in a carbon dioxide (CO₂) bath before being identified to species and measured for fork length (± 1 mm). All salmonids exceeding 69 mm were scanned using a handheld PIT reader to determine if the fish had been previously tagged and recaptured (Biomark Inc., Boise, Idaho, USA). Individuals 70 mm or greater that were not already tagged received a 12 mm full-duplex passive integrated transponder (PIT) tag (Biomark Inc., Boise, Idaho, USA) implanted in the abdominal cavity,

between the pectoral and pelvic fins. We recorded mass (± 0.01 g) following tag insertion or recapture detection. After processing, fish were allowed to recover in an aerated bucket before being returned to the pool from which they were taken.

Environmental variables

To better understand the predictors of growth rate in each type of habitat, we collected data on the physical characteristics of the pools. Water temperature ($^{\circ}\text{C}$) was recorded at 30-minute intervals using a Tidbit logger (Onset Computer Corporation, Bourne, Massachusetts, USA) submerged in two BDA and two reference pools in each stream throughout the duration of the study.

We quantified the abundance and community composition of drifting aquatic macroinvertebrate prey in BDA and reference pools. Due to limitations on our ability to process samples, only one sample was collected from each pool in August 2024 by setting a drift net (1m length, 30.5cm x 29.5cm opening; 250 μm mesh) for a 30-minute interval near the center of the pool. At each drift net location, depth and current velocity were measured at the beginning ($t=0$ minutes) and end ($t=30$ minutes) of the set. Macroinvertebrates collected in the nets were elutriated into containers, stored in 70% ethanol (EtOH) solution, and returned to the laboratory for processing. Samples were picked, identified to family and enumerated using a dissection microscope (Merritt and Cummins 2019; Thorp and Covich 2009).

Data analysis

Growth Rate

We calculated specific growth rate (G) for all individuals only recaptured within the reach in which they were tagged. Many individuals were tagged and recaptured in different pools, but only four fish were encountered in both the BDA and reference reach of their respective streams. We arrived at specific growth rate by dividing the mass at recapture (w_2) by the mass at tagging event (w_1), exponentiating that to the inverse of the number of days elapsed between encounters (Δt), then subtracting 1 from that value and multiplying by 100 to yield the percent increase in mass per day (Crane et al. 2020):

$$\left(\frac{w_2}{w_1}\right)^{\frac{1}{\Delta t}} = e^g \quad G = 100(e^g - 1)$$

From these individual values, mean specific growth rate for each BDA and reference reach was calculated.

Fish Density

We estimated the abundance of taggable ($\geq 70\text{mm}$) salmonids in each reach to explore possible effects of fish density on growth rate. We used the R package RMark (Laake and Rexstad 2008) to construct models for program MARK (White and Burnham 1999). Specifically, we used the POPAN formulation of a Jolly-Seber model (Schwarz and Arnason 1996). For each reach, we created a series of models in which apparent survival, capture probability, and probability of new individuals entering the taggable population were either held constant or allowed to vary over time. We compared the candidate models using Akaike's information criterion adjusted for small sample size (AICc) (Burnham and Anderson 2004). For each reach, we extracted occasion-specific abundance estimates from the model with the lowest

AICc value. We converted these values to densities by dividing the estimated abundance by the summed length of the sampled habitats in the reach. We assigned a density value to each recapture by taking the mean of the density estimates for all of the occasions that occurred within the growth interval for that fish (excluding the first and last occasion due to POPAN limitations).

In the case of Gurnsey Creek and Yellow Creek, where tagged resident salmonids were possibly recaptured over the full study period, we created models using the entire set of capture histories. For French Creek, where coho salmon outmigrate each spring, we separated capture histories by sampling season (before and after July 2025) and created two distinct model sets. This approach would have also been used in Sugar Creek, but the deconstruction of the BDAs precluded this, resulting in the creation of one model set using all Sugar Creek capture histories. We calculated a mean density for each stream, reach and year combination by taking the mean of all occasion-specific abundance estimates for a combination, again excluding the first and last estimates.

Environmental variables

To arrive at reach-level metrics of water temperature, we combined the data from two temperature sensors in each reach by taking the mean of the water temperature values at each 30 minute interval. We calculated the daily mean water temperature and maximum weekly average temperature (MWAT) from the combined data. For each recapture, we calculated the MWAT and the average of daily mean water temperature over the period between the first and last encounter.

We calculated the density of macroinvertebrate drift to allow for comparison across sites. Drift density was calculated by dividing the number of captured individuals by the volume of water (m^3) that passed through the net during sampling. Drift density for each reach was calculated by taking the mean of the densities from each pool. The mean drift density value for each reach was assigned to recaptures in that reach, regardless of the period over which the growth took place.

Results

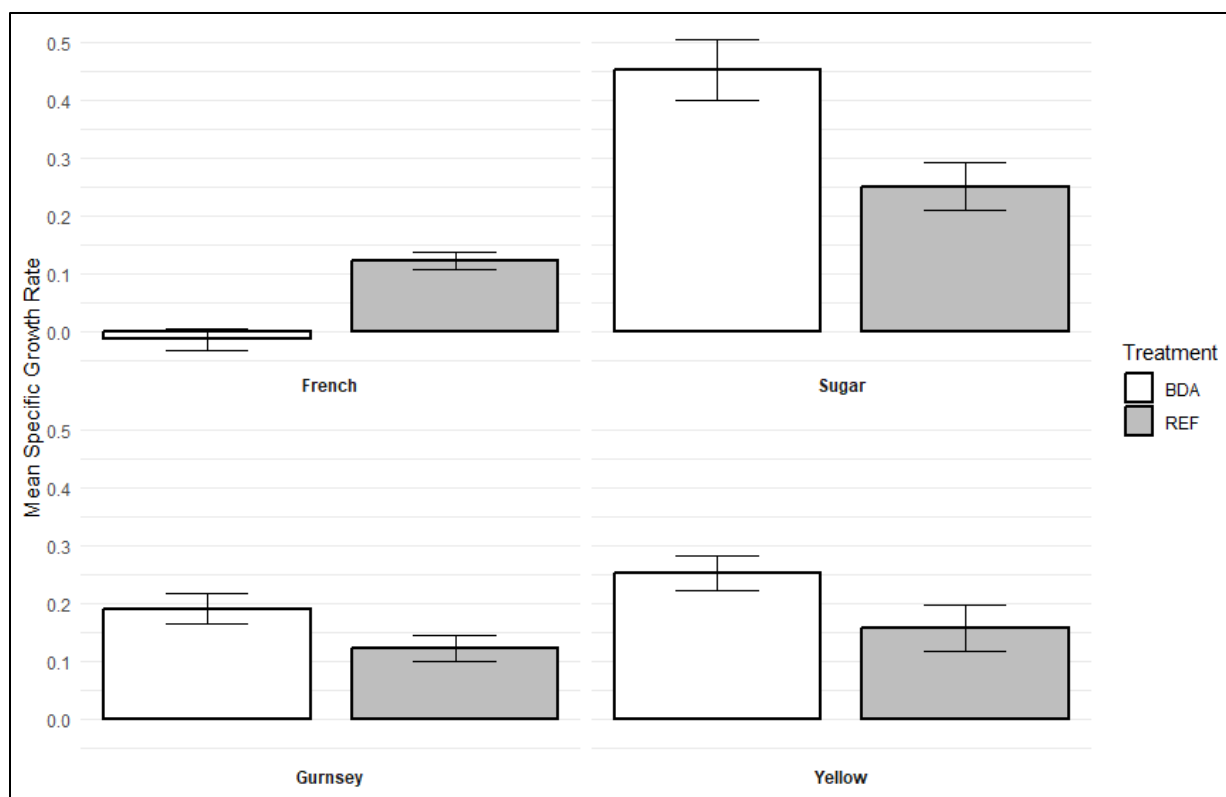


Figure 3. Mean specific growth rate of salmonids in BDA and reference reaches across four study streams. Error bars indicate ± 1 standard error

While growth rates in the French Creek reference reach were higher than the BDA reach when looking at the total study period, during the first season of sampling (August 2024 – March 2025) the opposite pattern was seen (Supplement Figure 1). Fish in the BDA reach exhibited higher growth rates than those in the reference reach during this period.

Fish Density

Estimated densities of taggable ($\geq 70\text{mm}$) salmonids varied among streams, sampling periods, and reaches (Figure 4). In French Creek during the 2024–2025 sampling period, estimated densities were greater in the reference reach (9.5 ± 1.8 SE individuals/m) than in the BDA reach (8.7 ± 5.0 individuals/m). During the 2025 sampling period this pattern persisted, with densities averaging 5.4 ± 0.5 individuals/m in the BDA reach and 7.2 ± 2.4 individuals/m in the reference reach.

In Gurnsey Creek, Yellow Creek and Sugar Creek, estimated densities were higher in BDA reaches than reference reaches. Mean density in the Gurnsey BDA reach was estimates to be 7.2 ± 3.4 individuals/m, and 4.7 ± 1.6 individuals/m in the reference reach. Sugar Creek exhibited mean densities of 12.3 ± 0.4 individuals/m in the BDA reach and 3.0 ± 1.2 individuals/m in the reference reach, while Yellow Creek densities averaged 5.0 ± 1.1 individuals/m and 3.9 ± 1.3 individuals/m in BDA and reference reaches, respectively.

Although these reach-scale density estimates are presented to illustrate overall differences among habitats, density covariates incorporated into growth models were calculated individually for each recaptured fish by averaging occasion-specific density estimates across the corresponding growth interval. This approach allowed modeled density values to reflect the conditions experienced by fish during the period over which growth occurred.

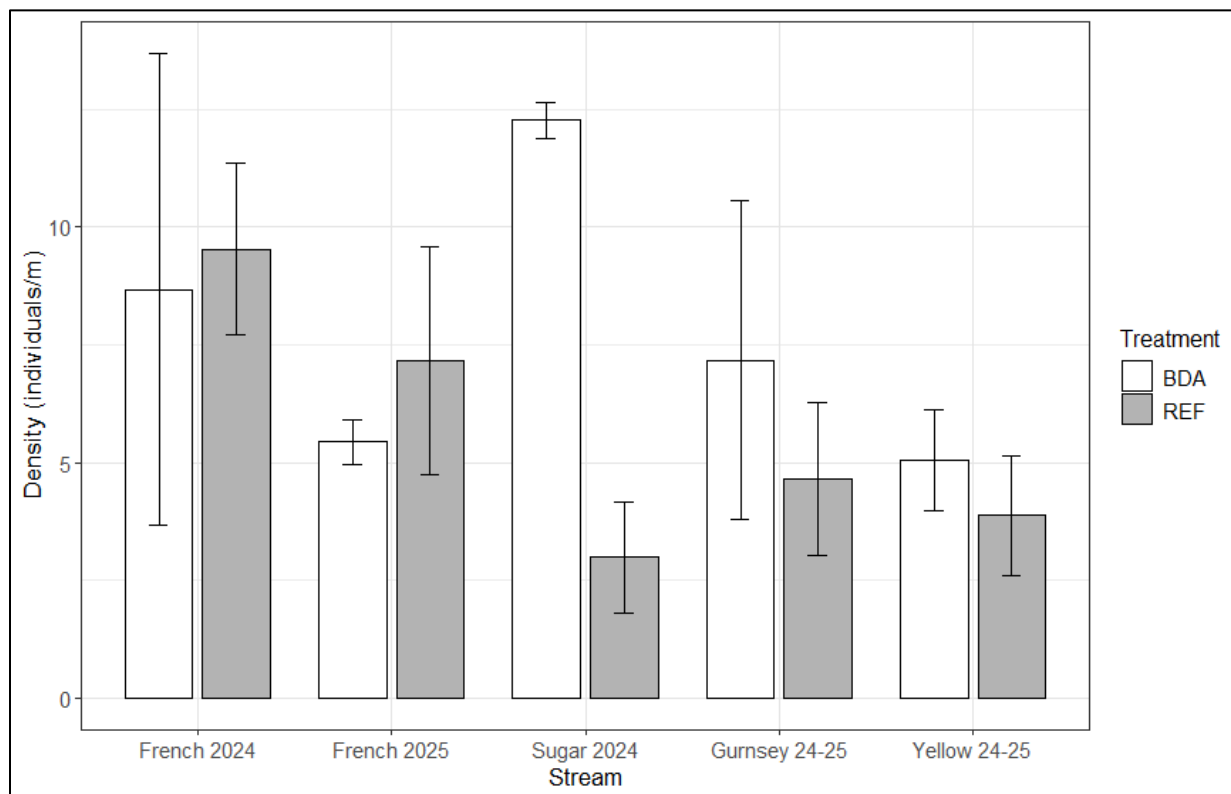


Figure 4. Estimated reach-scale density of taggable salmonids (≥ 70 mm) in BDA and reference reaches across study streams and sampling periods. Density estimates were derived from POPAN mark-recapture models and standardized by sampled habitat length (individuals/m). Error bars represent ± 1 standard error.

Water Temperature

Mean daily water temperatures exhibited strong seasonal patterns across all study streams, with temperatures generally peaking during mid- to late-summer and declining to near 0 °C during winter months (Figure 5). Seasonal temperature patterns were broadly similar between BDA and reference reaches within streams, although some differences in summer thermal regimes were observed.

Visual inspection of mean daily temperature time series suggested that BDA reaches in Sugar Creek and Gurnsey Creek tended to exhibit warmer summer temperatures than reference reaches. Differences between reaches appeared to be minimal in French Creek and Yellow Creek. Winter temperatures in all streams approached 0 °C for extended periods, particularly in Gurnsey Creek and Yellow Creek, indicating prolonged cold-water conditions during the winter months. Both Yellow Creek and Sugar Creek experienced periods in which winter water temperature in BDA reaches exceeded temperatures in reference reaches.

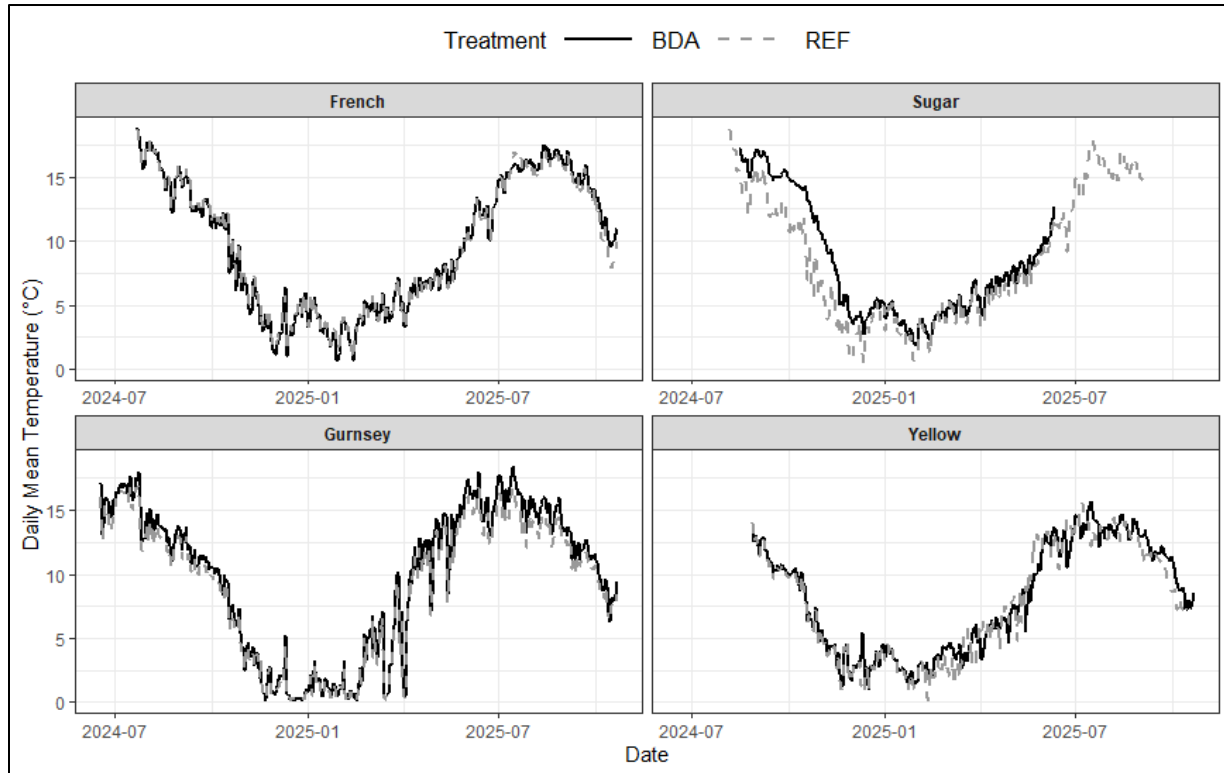


Figure 5. Mean daily water temperature (°C) recorded in each study reach during the study period.

Maximum weekly average temperature (MWAT) values ranged from 14.8 to 17.5 °C across all reaches (Table 3). For each stream, these values were only calculated for the period in which both reaches had loggers installed. The highest MWAT was observed in the Gurnsey Creek BDA reach (17.5 °C) during the period from July 11–17, 2025. French Creek BDA and reference reaches both exhibited MWAT values of 17.4 °C between July 31 and August 6, 2024. The Sugar Creek reference reach reached an MWAT of 15.1 °C between August 27 and September 2, 2024, while the Sugar Creek BDA reach exhibited a much higher MWAT of 16.9 °C in a similar period (August 29–September 4, 2024). In Yellow Creek, MWAT values were comparatively lower and similar between reaches, reaching 15.0 °C in the BDA reach and 14.8 °C in the reference reach during July 11–17, 2025.

Table 3. Maximum weekly average temperature (MWAT; °C) observed in each study reach during the study period, and the corresponding 7-day window over which MWAT was calculated.

Reach	MWAT (°C)	MWAT Window Start	MWAT Window End
French BDA	17.4	7/31/2024	8/6/2024
French REF	17.4	7/31/2024	8/6/2024
Gurnsey BDA	17.5	7/11/2025	7/17/2025
Gurnsey REF	16.4	7/6/2024	7/12/2024
Sugar BDA	16.9	8/29/2024	9/4/2024
Sugar REF	15.1	8/27/2024	9/2/2024
Yellow BDA	15.0	7/11/2025	7/17/2025
Yellow REF	14.8	7/11/2025	7/17/2025

Drift

Macroinvertebrate drift composition varied among streams and habitat types (Figure 6). Drift samples from French Creek were dominated by Chydoridae, particularly in the BDA reach, whereas samples from Gurnsey Creek and Yellow Creek contained greater proportions of dipteran taxa such as Chironomidae and Simuliidae. Baetidae were also abundant in several reaches, particularly in Yellow Creek. Sugar Creek generally exhibited lower total abundances across families than the other study streams.

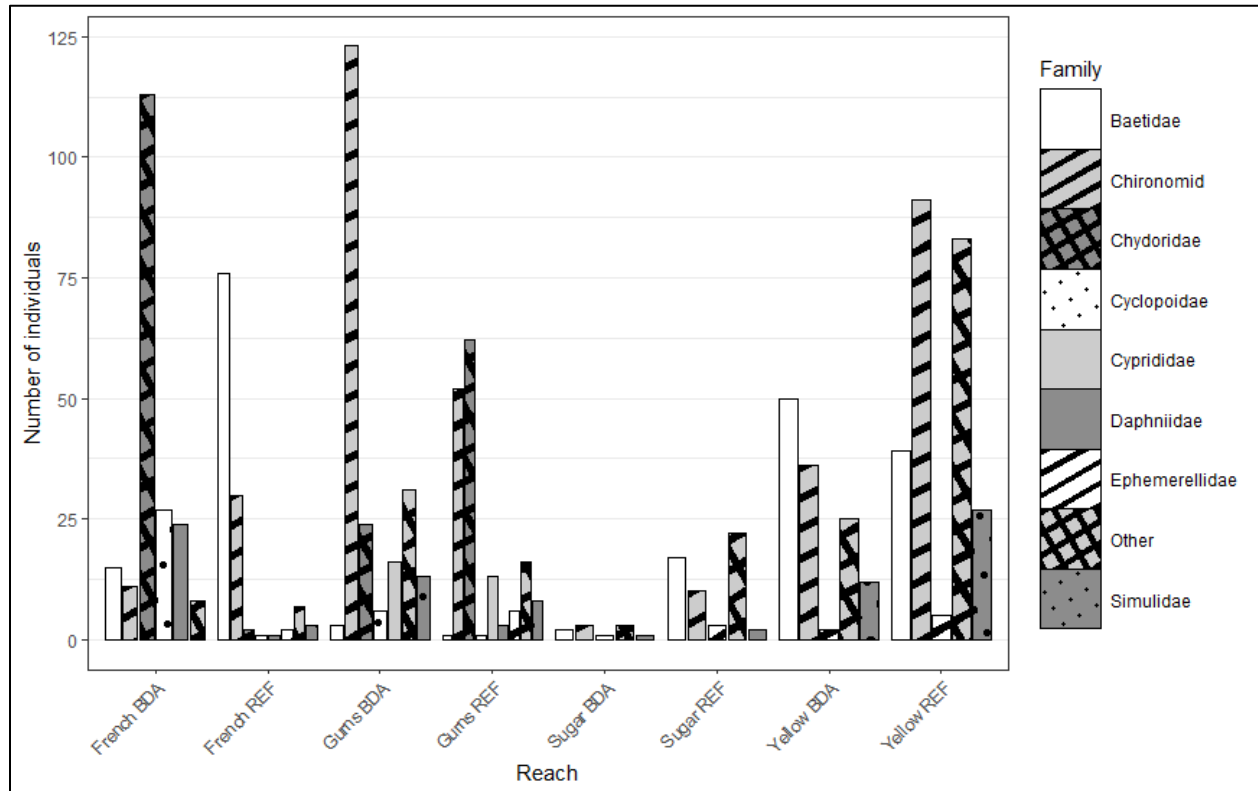


Figure 6. Counts of macroinvertebrates by family collected from drift samples in each study reach during August 2024.

Drift density also varied substantially among streams and habitat types (Figure 7). French Creek exhibited the highest drift densities observed in the study, with densities averaging approximately 72 individuals/m³ in the BDA reach compared to approximately 6 individuals/m³ in the reference reach. Gurnsey Creek exhibited intermediate drift densities, averaging approximately 13 individuals/m³ in the BDA reach and 7 individuals/m³ in the reference reach. In contrast, Sugar Creek exhibited lower drift densities overall, with densities averaging approximately 3 individuals/m³ in the BDA reach and 7 individuals/m³ in the reference reach. Drift densities in Yellow Creek were relatively similar between habitat types, averaging approximately 7 individuals/m³ in the BDA reach and 4 individuals/m³ in the reference reach.

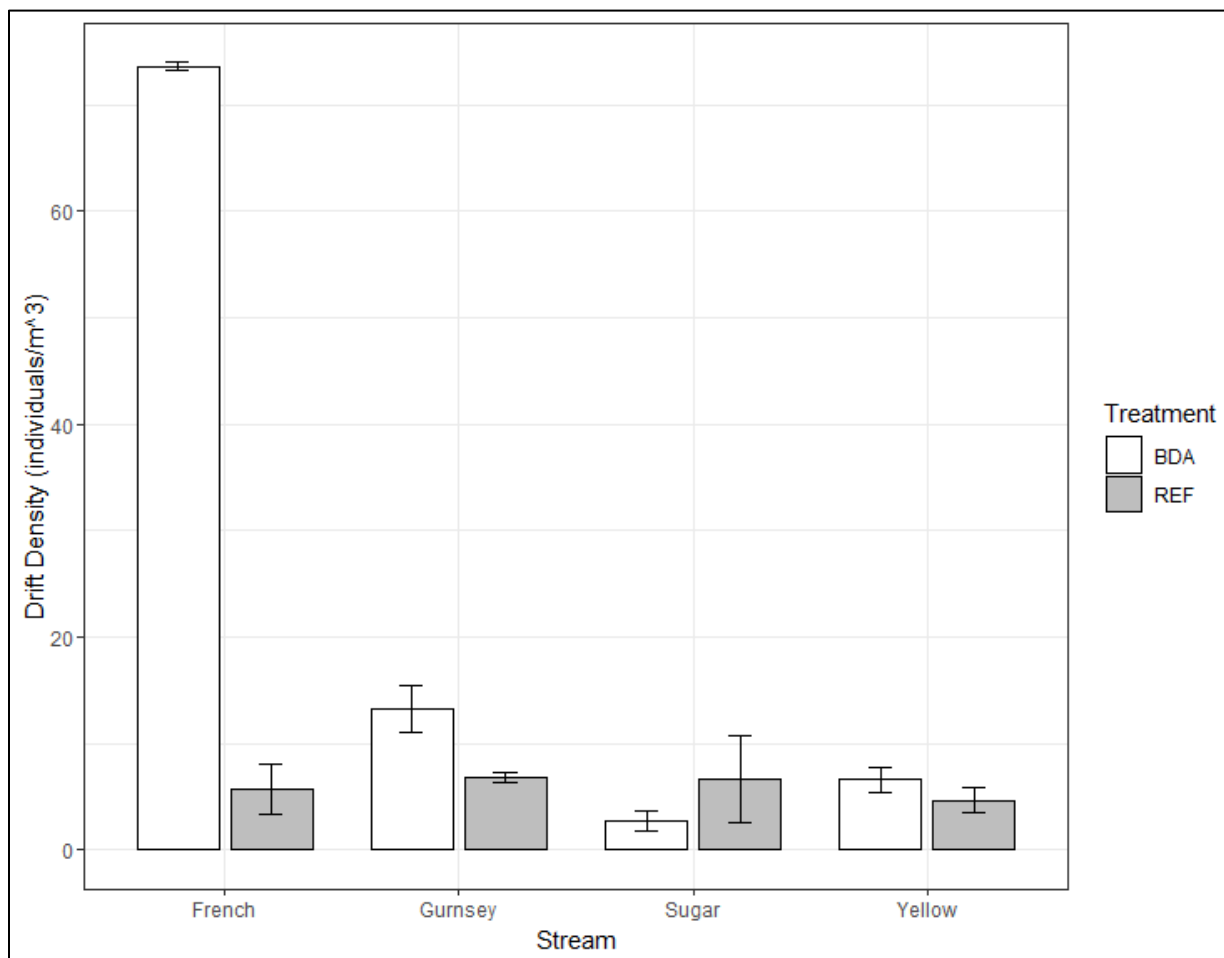


Figure 7. Densities of drifting macroinvertebrates in each study reach during August 2024. Plotted values are the mean densities of three drift samples collected in each reach.

Mixed-effects Modeling

Model Development

We used a linear mixed-effects modeling approach to explore differences in growth rates between BDA and reference reaches. Using the *lme4* package (Bates et al. 2015), we fit a global mixed-effects model with reach (BDA vs. reference), species, fish density, drift density, and mean water temperature as fixed effects and stream included as a random effect. We initially evaluated MWAT as an additional metric, but

models incorporating daily mean temperature provided a substantially better fit than those including MWAT (Supplement Figure 2). We verified that our global model met the assumptions of residual normality by visually inspecting a qq plot, a scatterplot of plotted residuals against fitted values, and a histogram of residuals to confirm variance homogeneity. All continuous parameters were centered prior to analysis, and fish density and drift density were log-transformed. Multicollinearity among predictors was assessed using variance inflation factors (VIF), and all retained predictors exhibited low collinearity ($VIF < 3$).

We used a single-term deletion test on the global model, which indicated that species identity did not significantly improve model fit and was removed from subsequent analyses. Comparing additive and interaction models using likelihood ratio tests (LRTs) indicated that an interaction between water temperature and drift density significantly improved model fit. Additional mixed-effects models showed that reach type (BDA vs. reference) significantly influenced mean water temperature, fish density, and drift density, with stream included as a random effect in all models. All analyses were conducted in R (R Core Team 2024). Statistical significance was evaluated at $\alpha = 0.05$.

Model Results

The final model included reach, mean water temperature, log-transformed fish density, log-transformed drift density, and an interaction between temperature and drift density as fixed effects, with stream included as a random intercept (Table 4).

Table 4. Results of the linear mixed-effects model evaluating the effects of habitat type (reference vs. BDA), mean water temperature, fish density, and drift density on specific growth rate of salmonids.

Predictor	β (Estimate)	SE	t	df	p
Intercept	0.243	0.0278	8.75	3.97	0.001
Mean water temperature (°C)	-0.0161	0.003	-5.40	646.56	<0.001
Log drift density	-0.131	0.0156	-8.41	65.27	<0.001
Log fish density	-0.103	0.0257	-4.01	267.61	<0.001
Reach type (REF vs BDA)	-0.200	0.0299	-6.69	82.35	<0.001
Mean water temp × drift density	-0.0157	0.00237	-6.63	650.91	<0.001
Random effect	Variance	SD			
Stream (intercept)	0.00242	0.049			
Residual	0.047	0.217			

After accounting for temperature, fish density, drift density, and the interaction between temperature and drift density, reach type remained a strong predictor of growth. Growth rates were significantly lower in reference reaches than in BDA reaches ($\beta = -0.200 \pm 0.030$ SE, $p < 0.001$), indicating that fish rearing in BDA habitats exhibited higher growth independent of other modeled covariates. Likelihood ratio tests confirmed that inclusion of reach significantly improved model fit ($\chi^2 = 41.26$, $df = 1$, $p < 0.001$).

The model predicted that specific growth rate would decline with increasing mean temperature ($\beta = -0.0161 \pm 0.0030$ SE, $p < 0.001$), increasing fish density ($\beta = -0.103 \pm 0.0257$ SE, $p < 0.001$), and increasing drift density ($\beta = -0.131 \pm 0.0156$ SE, $p < 0.001$). A significant interaction between temperature and drift density was detected ($\beta = -0.0157 \pm 0.0024$ SE, $p < 0.001$), with the model predicting that the effect of increasing temperature on growth would become more negative at higher drift densities.

Effect of Reach Type on Environmental Variables

Likelihood ratio tests were used to determine whether reach type (BDA vs. reference) was a significant predictor of environmental parameters included in the final model. Mean water temperature differed between reaches, such that reference reaches were significantly cooler than BDA reaches after accounting for variation among streams ($\beta = -1.24 \pm 0.24$ SE, $p < 0.001$). Fish density did not differ significantly between reaches (LRT $p = 0.74$), but estimated drift density did, with reference reaches exhibiting substantially lower drift densities than BDA reaches ($\beta = -1.54 \pm 0.05$ SE, $p < 0.001$). However, because drift density estimates were derived from a single sampling period, these results should be interpreted cautiously.

Discussion

This study evaluated the influence of BDA habitat on the growth of stream-dwelling salmonids across four streams in northern California. We hypothesized that fish rearing in BDA ponds would exhibit higher growth rates than those occupying untreated reference pools. Although mean growth varied among streams, mixed-effects modeling revealed a consistent positive association between BDA habitat and growth after accounting for environmental covariates and among-stream variation. Specifically, fish rearing in BDA reaches exhibited significantly higher growth rates than those rearing in reference reaches when temperature, fish density, and drift density were held constant.

Collectively, these findings suggest that BDAs can create habitat conditions that promote enhanced somatic growth in stream-dwelling salmonids. Importantly, this relationship appears robust to variation in key environmental drivers, indicating that the structural and hydraulic characteristics of BDA habitats may provide growth advantages beyond those explained by local abiotic and biotic conditions alone.

At the stream level, mean growth rates were higher in BDA reaches in three of four streams, although these differences were not statistically significant in all cases. French Creek was the exception, where growth was significantly greater in the reference reach during part of the study period. However, prior to our second sampling season (beginning August 2025), mean specific growth rate was significantly higher in the French Creek BDA reach than in the reference reach, indicating a temporal shift in relative growth patterns.

The shift in growth rates may be explained by the reconfiguration of a logjam in French Creek where the mainstem splits into the BDA and reference channels. Observations from landowners and local watershed partners suggested that the proportion of flow entering the BDA reach decreased between sampling seasons. A reduction in discharge through the BDA reach would likely have reduced available habitat volume, potentially intensifying density-dependent interactions and constraining growth rates. Importantly, fish density was estimated based on linear sampling distances established at the study's

outset. As a result, any reduction in wetted habitat areas or volume would not have been captured by this metric, potentially obscuring increases in effective fish density within this BDA reach.

Variability in growth response is not unexpected given differences in hydrology, structure age, and species composition among study systems. To account for heterogeneity in study sites, we incorporated stream as a random intercept in a mixed-effects framework, allowing estimation of the overall effect of habitat type across systems. The persistence of a strong positive treatment effect in the model indicates that, despite site-specific variability, BDA habitat was consistently associated with enhanced growth.

Fish density was negatively associated with growth in our model, consistent with density-dependent competition. Such relationships are well documented in salmonids, where higher densities increase competition for food and space and can reduce individual growth rates (Grant and Imre 2005). However, fish density did not differ significantly between BDA and reference reaches, suggesting that density-dependent processes do not explain the observed differences in growth between habitats. The persistence of a strong positive treatment effect after accounting for density further indicates that enhanced growth in BDA reaches was not simply a function of lower fish abundance but instead reflects habitat-mediated differences in growth conditions.

Water temperature emerged as a strong predictor of growth in our models, with growth declining as mean temperature increased relative to the centered value. This negative relationship is consistent with established physiological theory: temperatures exceeding species-specific optima elevate metabolic demand and can reduce net energy gain (Brett and Groves 1979; Verhille et al. 2016). During the study period, mean temperatures in some reaches likely exceeded the optimal range for sustained growth, particularly during summer months. Salmonids are able to continue growing in habitats with elevated water temperatures, but only if food resources are abundant (Lusardi et al. 2020). Consequently, the relationship between temperature and growth is often context dependent, with the effects of warming varying according to local prey availability and energetic conditions.

BDA reaches were associated with slightly warmer temperatures than reference reaches. This finding contrasts with studies suggesting that beaver ponds can buffer stream temperatures during summer growth periods (Weber et al. 2017), although warming effects linked to increased residence time and solar exposure have also been documented (Majerova et al. 2015). Despite these warmer conditions, fish in BDA reaches exhibited higher modeled growth rates. This pattern suggests that temperature differences alone do not explain the observed growth responses and that other habitat characteristics associated with BDAs likely offset potential metabolic costs associated with warmer water (Lusardi et al. 2020). Such characteristics may include increased prey availability, reduced energetic costs of station holding, or enhance foraging efficiency in low-velocity habitats (Fausch 1984; Rosenfeld and Boss 2001).

For fish that continued growing through fall and winter, the warmer thermal regime in BDA habitats may have extended the period during which temperatures remained within a range favorable for growth. Enhanced growth in BDA reaches may reflect seasonally advantageous thermal conditions in combination with other features of ponded environments. Reduced current velocity likely lowers the energetic costs of position maintenance, allowing greater allocation of energy to somatic growth. In addition, increased depth and structural complexity may enhance predator avoidance and improve foraging opportunities, further contributing to growth potential (Fausch 1984; Fausch 1993).

Density of drifting macroinvertebrates was negatively correlated with growth in our model. This pattern may reflect limitations of our drift dataset, specifically the use of only one set of samples collected in August 2025, and the lack of quantification of drift biomass or community composition. However, it may also indicate shifts in foraging modes within habitats with low current velocities. For stream-dwelling salmonids, drift foraging is a well-documented and efficient means of prey acquisition (Fausch 1984; Hughes and Dill 1990). However, BDA installation may reduce current velocities to the extent that drift no longer accurately represents resource availability. Under these conditions, salmonids may shift from drift feeding to alternative strategies such as actively foraging on prey in the water column or benthos (Harvey and Railsback 2014). Consequently, fish occupying habitats with low measured drift densities may still have access to abundant food resources not captured by this metric. Additionally, beaver ponds and similar habitats can alter macroinvertebrate community composition relative to adjacent free-flowing stream reaches (Corline et al. 2023; Washko et al. 2022). Because macroinvertebrate species vary in energetic value to predatory fish (Cummins and Wuycheck 1971), habitats supporting fewer but more energetically profitable prey items may promote higher growth rates than habitats with greater overall prey densities.

A likely explanation for the patterns observed in this study is the increased habitat heterogeneity created by instream restoration. By varying structure size and spacing, BDA complexes can generate a diverse array of hydraulic habitats, including ponded margins, backwater, slow glides, and higher-velocity connecting channels. The movement of tagged fish among pool habitats within restored reaches suggests that individuals were utilizing multiple habitat types across the restored habitat mosaic. Within such a network, fish may experience an “energy landscape” (Wilson et al. 2011) in which the costs of maintaining position, acquiring prey, and accessing refuge vary over short spatial scales. Low-velocity habitats can function as energetically efficient rearing environments for salmonids, reducing swimming costs while maintaining access to prey resources (Rosenfeld and Boss 2001; Sethi et al. 2022). More broadly, beaver-related restoration has been shown to increase pool frequency and side-channel habitat, reconnect floodplain surfaces, and expand slow-water habitat, all of which can improve rearing conditions for stream-dwelling fishes (Pollock et al. 2012; Bouwes et al. 2016). Collectively, these changes in habitat availability and energetic opportunity may have contributed to the positive treatment effect detected in our model.

Our findings also suggest that BDA habitats may influence not only average growth rates, but also subsequent life-history trajectories. If BDA habitats consistently promote faster juvenile growth, they may contribute to larger body sizes at key life-history transitions, including over-winter survival, smoltification, and sexual maturation. In anadromous salmonids, larger smolt size is often associated with higher survival to adulthood, while in resident fishes, body size can influence maturation schedules and fecundity (Ward et al. 1989; Zabel and Williams 2002; Quinn 2005; Downs et al. 1997). By creating a heterogeneous mosaic of habitats that differ in energetic conditions and resource availability, BDA complexes may also generate a wider range of growth opportunities among individuals. This variation could contribute to greater diversity in body size and life-history trajectories within populations. From this perspective, the benefits of BDA habitats may extend beyond short-term individual performance by increasing the range of phenotypes expressed within a watershed and potentially enhancing population resilience to environmental change.

These results have broader implications for restoration and management. Much of the motivation for BDA implementation has focused on geomorphic and hydrologic outcomes, such as increasing floodplain

connectivity, slowing incision, and increasing groundwater levels (Pollock et al. 2012). Our findings suggest that these habitat changes can also translate into measurable biological benefits at the individual level. For managers, this is important because fish growth rate integrates multiple ecological processes (e.g., temperature, food availability, and energetic costs) and can serve as an early indicator of restoration effectiveness before longer-term demographic responses become apparent. At the same time, our results caution against assuming that habitat responses to BDAs will be uniformly beneficial or consistent across streams. As demonstrated by French Creek, variation in local hydrologic configuration can alter habitat function and potentially reverse expected outcomes.

Several directions for future research emerge from this study. First, repeated sampling of drifting and benthic macroinvertebrates across seasons, coupled with an analyses of macroinvertebrate biomass and community composition, would strengthen inference regarding the role of food availability in mediating growth responses in BDA habitats. Second, direct quantification of hydraulic conditions—including velocity, depth, and seasonal changes in wetted habitat area—would improve understanding of the energetic pathways linking BDAs to fish growth. Finally, linking juvenile growth to subsequent survival, movement, smolt size, or maturation would help determine whether the individual-level responses observed here translate into population-level restoration benefits.

Overall, this study provides evidence that BDA habitats can enhance growth conditions for salmonids across diverse stream systems. Although responses were not uniformly positive across all study reaches, the positive effects observed in most systems suggest that BDAs can create ecological conditions that improve juvenile fish performance. By restoring ecological processes historically associated with beaver activity, these structures may help rebuild the habitat complexity and energetic opportunities that support salmonid growth and persistence. In systems where the loss of slow water habitat has constrained rearing opportunities, such effects may have meaningful consequences for resilience and recovery. Collectively, these findings suggest that BDAs can provide not only physical habitat benefits but also measurable biological responses, supporting their use as a process-based restoration strategy in degraded stream networks.

Acknowledgments

This study was made possible by Betsy and Michael Stapleton, Sally Painter, Dennis Jensen and Collins Pine Company allowing us to collect data on their properties. Ivie Foster, Jaya Hanning, Juliana Aristizabal, Alex Ginez, McKenzie Ginther, Brandy Smith, Kristin Rank, Ethan Lange, Aidan Reynolds, Linda Bailey, David Goodwin and Aidan Fernandez all assisted with data collection. Staff from the Scott River Watershed Council, especially Charnna Gilmore and Erich Yokel, provided equipment and local expertise that was crucial to this study. Kate Laskowski, Caroline Gengo, Rosealea Bond and Kelly Goedde-Matthews provided data analysis support. Rob Lusardi, Tyson Hallbert, Sarah Yarnell and Carson Jeffres reviewed and provided useful feedback on this manuscript. Funding for this study was provided by the California Department of Fish and Wildlife Agreement #Q2296025.

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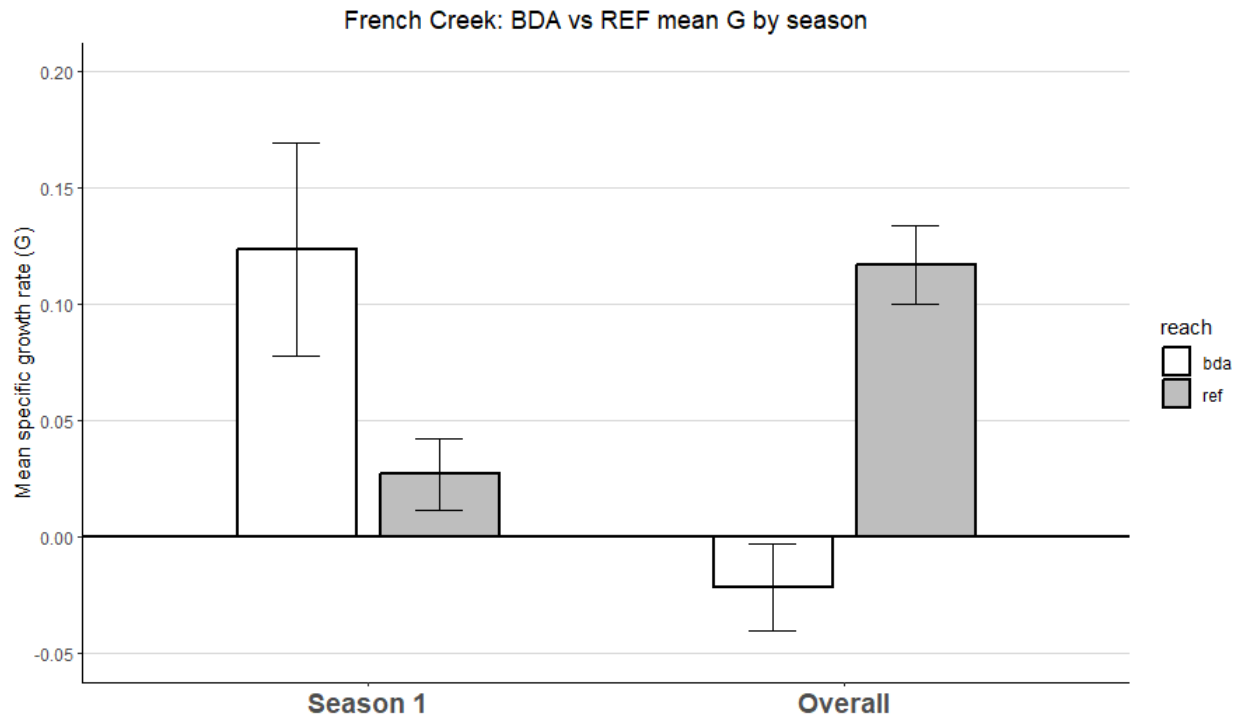
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Supplement



Supplement Figure 1. French Creek mean specific growth rates at the end of season 1 (March 2025) versus the end of the study. Error bars indicate ± 1 standard error.

Supplement Table 1. AIC model comparison of global model using mean daily temperature versus MWAT.

Model	Temperature metric	df	AIC	Δ AIC
m_mean	Mean daily temperature	7	-78.06	0.00
m_mwat	MWAT	7	-55.58	22.47