



ARTICLE

Flow augmentation from off-channel storage improves salmonid habitat and survival

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Abstract

Objective: In the western United States, juvenile salmon *Oncorhynchus* spp. and steelhead *O. mykiss* are especially vulnerable to streamflow depletion in the dry season. Releasing water from off-channel storage into small streams is a novel restoration strategy to offset impacts from anthropogenic flow alteration on salmonid fishes. To date, no studies have evaluated the ecological effects of small-scale flow augmentations. Here, we quantify the effects of one such augmentation project on habitat connectivity, water quality, invertebrate drift, and juvenile salmonid movement and survival.

Methods: Our study took place in a northern California stream and included an unusually wet summer (2019) and a more typical dry summer (2020). We used categorical and time-series analyses in a before–after, control–impact (BACI) design, along with capture–mark–recapture methods to evaluate the ecological impacts of a 13.9-L/s flow augmentation.

Result: We found that differences in ambient streamflows between the two years mediated the physical and ecological effects of the flow augmentation treatment. In the dry year, habitat connectivity and dissolved oxygen markedly increased at sites over 1.5 km downstream from the point of augmentation, whereas during the wet year, the effects on those variables were negligible. In both years, invertebrate drift marginally increased after augmentation. Interpool movement of wild juvenile steelhead and stocked Coho Salmon *O. kisutch* increased after augmentation during the dry summer but not during the wet summer. Flow augmentation increased the survival probability for salmonids, with a larger effect during the dry summer (24% higher survival for Coho Salmon and 20% higher survival for steelhead) than during the wet summer (no effect was observed for steelhead survival, and Coho Salmon survival increased by 11%).

Conclusion: This study indicates that appropriately designed small-scale flow augmentations can improve conditions for rearing salmonids in small streams, particularly during dry years. More broadly, it provides empirical evidence that efforts to

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restore summer streamflow in small, salmon-bearing streams can yield significant ecological benefits.

KEYWORDS

aquatic ecosystems, ecohydrology, environmental flows, flow augmentation, flow–ecology relationships, food webs

INTRODUCTION

Streamflow alteration is ubiquitous in the United States (Carlisle et al. 2019) and has been identified as a primary stressor for imperiled Pacific salmon and trout *Oncorhynchus* spp. populations in the western United States (Moyle et al. 2017; Crozier et al. 2019). In California, salmonids are particularly vulnerable to flow depletion in the dry season—a period of naturally low flow in which stream habitats contract, water quality conditions often deteriorate, and food resources become limited (Caldwell et al. 2018; Obedzinski et al. 2018; Vander Vorste et al. 2020). A growing body of research from California has shown that for rearing salmonids in many streams, the dry season creates a metabolic knife's edge, where only a few days of hydraulic disconnection, a slight change in dissolved oxygen (DO) levels, or a few degrees of temperature separate profitable from unfavorable habitat conditions (Harvey et al. 2006; Boughton et al. 2009; Sloat and Osterback 2013; Grantham et al. 2014; Hwan and Carlson 2016; Woelfle-Erskine et al. 2017; Obedzinski et al. 2018; Vander Vorste et al. 2020). Water diversions during the dry season can compound these natural stressors, tipping the balance from profitable to stressful or even lethal environments for rearing juvenile salmonids (Deitch et al. 2009; Grantham et al. 2014; Power et al. 2015; Obedzinski et al. 2018). This study explores whether relatively small augmentations to streamflow in the dry season can have a reciprocal effect and improve habitat quality, feeding opportunity, and survival of salmonids.

Streamflow augmentation, defined as adding water to a stream from an external storage source, is a novel restoration strategy that can be used to recover elements of a stream's natural hydrograph in anthropogenically impaired systems. Recently, streamflow augmentation has been implemented opportunistically to benefit salmonids in small, undammed northern California streams (Deitch and Dolman 2017; Ruiz et al. 2019; Russian River Coho Partnership 2022). Unlike large-scale flow regulation, in which water is stored and released from on-channel dams or impoundments, these projects generally use water from off-channel agricultural irrigation ponds or storage tanks specifically to improve streamflow for salmon in small rural watersheds (Ruiz et al. 2019; Russian River Coho Partnership 2022). As of 2023, at least four small-scale

Impact statement

There is growing interest in using novel approaches to offset human-caused impacts on freshwater ecosystems. One approach involves releasing water from off-channel storage directly into small, flow-impaired streams to benefit endangered fishes—especially during the driest times of the year. This study explores how one of these "flow augmentation" projects affects the habitat, prey, and survival of threatened salmon and steelhead in a small coastal California stream.

flow augmentation projects are being implemented in coastal California, and another six are in the planning or permitting stages (A. Benedetti, California Wildlife Conservation Board, personal communication; M. A. King, Trout Unlimited, personal communication).

The ecological effects of streamflow alteration in large, regulated rivers have been well documented (e.g., Carlisle et al. 2019); however, small-scale flow augmentation has received almost no research attention to date. Although initial data suggest that flow augmentation can improve summer habitat conditions for rearing salmonids (Ruiz et al. 2019; Russian River Coho Partnership 2022), no experimental studies have been conducted to quantify the effects of flow augmentation on juvenile salmonid habitat, behavior, and survival in small, undammed streams. Here, we evaluate data from a streamflow augmentation study on Porter Creek, a small, salmon-bearing tributary to the Russian River in northern California. Specifically, this study investigated the survival and movement of summer-rearing salmonids in response to a controlled flow augmentation treatment, as well as evaluating changes in physical and biotic variables that influence salmonid fitness.

The Porter Creek flow augmentation experiment released water from an off-stream pond into the stream channel for 1 month in the summers of 2019 and 2020. We estimated the effects of flow augmentation on DO, water temperature, streamflow, hydraulic connectivity, invertebrate drift, interpool movement of fish, and survival of juvenile steelhead *O. mykiss* and Coho Salmon *O. kisutch*.

We hypothesized that augmentation would increase streamflow and hydraulic connectivity (hypothesis 1 [H1]) and that the effects of augmentation would diminish over space and time (distance downstream from the point of augmentation and as the dry season progressed; H2). We also hypothesized that the augmentation treatments would increase the DO concentration (H3), increase water temperature if augmentation was warmer than ambient flow (and vice versa; H4), and increase invertebrate drift (H5). Finally, we hypothesized that augmentation would increase salmonid movement between pools (H6) and would increase salmonid survival relative to the nonaugmented control reach (H7).

METHODS

Study location and project history

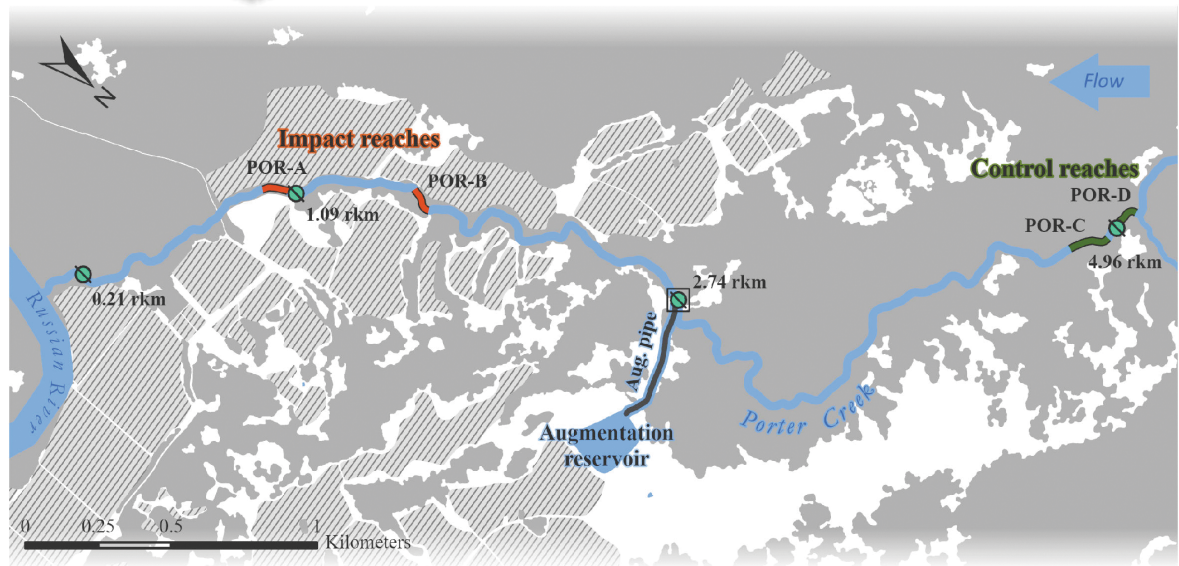
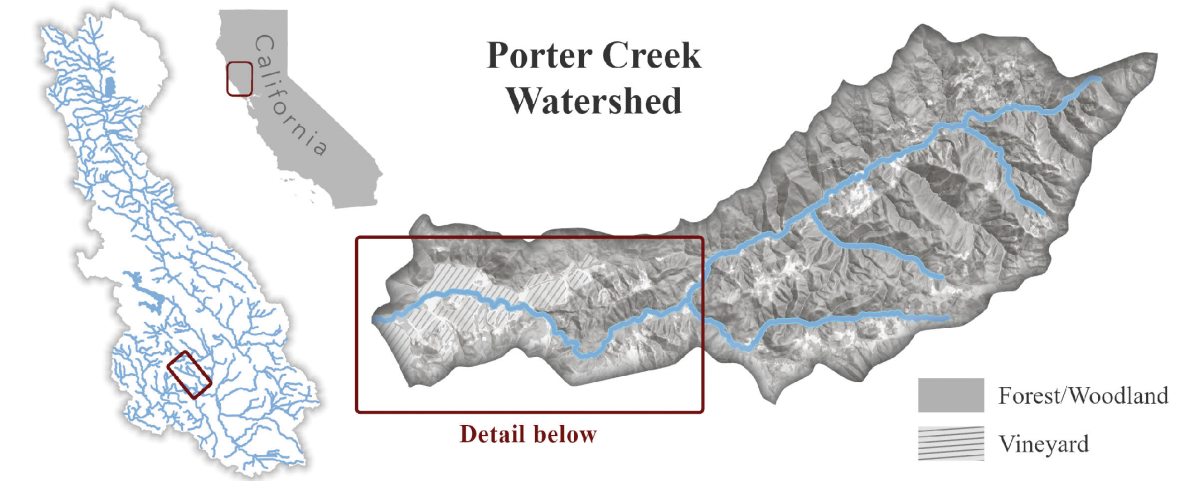
Porter Creek is a tributary to the Russian River in Sonoma County, California (Figure 1). The 19.4-km² watershed is located in California's Coast Range and flows approximately 11.4 km west to east into the Russian River near the town of Healdsburg. The watershed is entirely privately owned and managed for timber, livestock, and premium wine-grape production, with extensive vineyard planting on terraces in the lower 2.3 km of the stream valley. Rural residential development occurs in the upper watershed. The watershed's geology is primarily composed of Franciscan complex mélangé, although the southern slopes and upper watershed are a mix of mélangé and coastal belt shales (Jennings et al. 1977). The Franciscan mélangé geology is regionally associated with sparse deciduous oak and annual grass savanna and limited subsurface storage capacity to sustain streamflows throughout the dry, warm summer season (Hahm et al. 2019).

Streamflow patterns in Porter Creek are characterized by Mediterranean-climate hydrology. More than 90% of the annual rainfall typically occurs during November–April, resulting in flashy winter flows and then steady streamflow recession following the last spring freshets until flows cease completely pending the first fall rains (Deitch et al. 2009). Except in the wettest years, Porter Creek becomes intermittent for much of its length by mid or late summer. For example, by July 1, streamflow was zero at

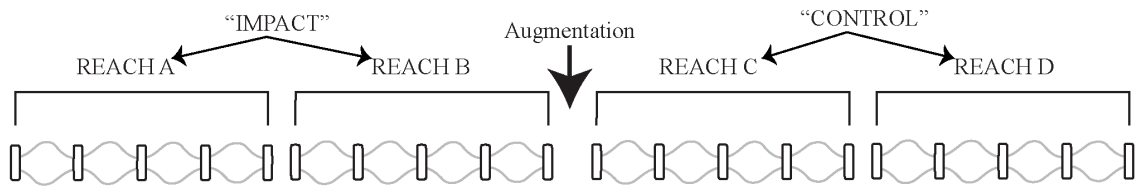
the mouth of Porter Creek and was less than 28 L/s (1 ft³/s) at 2.75 km upstream of the mouth during every year between 2017 and 2022. As flows recede throughout the dry season, riffles dry first, leaving isolated pools, followed by the contraction of wetted pool habitat and, in some stream reaches, complete channel drying by July. Porter Creek supports both wild and conservation hatchery-stocked Coho Salmon, wild steelhead, and a number of native cyprinid fishes (most commonly California Roach *Hesperoleucus symmetricus* and sculpins *Cottus* spp.). Russian River salmonid populations, particularly Coho Salmon, have experienced rapid declines over the past century, with fewer than 10 adult Coho Salmon observed returning each year by the early 2000s. These declines led to state and federal endangered species listings (National Marine Fisheries Service [NMFS] 2012) and prompted a multi-agency conservation hatchery effort that was designed to raise and release juvenile Coho Salmon in key Russian River tributaries (NMFS 2012). Porter Creek was listed in the National Marine Fisheries Service's Coho Salmon Recovery Plan as a priority stream for salmonid restoration and streamflow improvement (NMFS 2012) and has received planted fish from the Don Clausen Fish Hatchery at Warm Springs Dam during most years since 2010.

In 2014, the primary vineyard landowner on Porter Creek entered into a voluntary drought agreement with state management agencies to release water stored in an off-stream reservoir into the stream channel, 2.74 km upstream of the creek outlet, to maintain suitable rearing conditions for juvenile salmon and to facilitate passage of out-migrating smolts (Figure 1). This storage reservoir is filled with water pumped from shallow wells along the Russian River upstream of the confluence with Porter Creek, in addition to annual precipitation recharge. The reservoir elevation is above the augmentation structure, and water is gravity fed into a plumbing array, through a series of butterfly valves, and downslope through a pipe to the augmentation point in Porter Creek (Figure 1; Figures S1 and S2 [available in the Supplemental Materials in the online version of this article]). A programmable controller regulates flow releases from the reservoir (Figure S1) and allows an operator to set the start date and duration of specific augmentation levels. The completed streamflow augmentation system can release up to 61,000 m³ of stored water into the creek each year at a rate of up to 26 L/s (0.9 ft³/s).

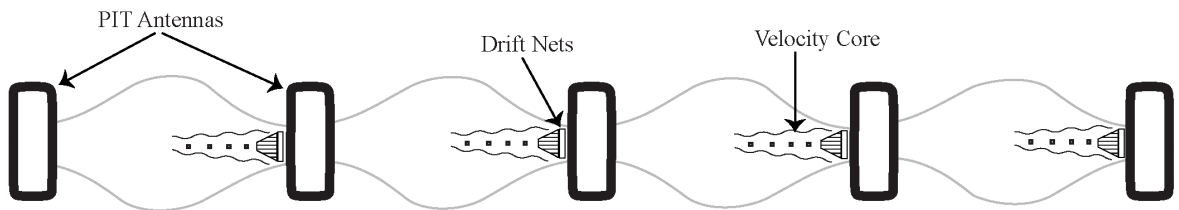
FIGURE 1 The Porter Creek watershed (top panel, right), located in the Russian River watershed in northern California (top panel, left). The study area map of lower Porter Creek (middle panel) shows flow gauging sites, control and impact study reaches (POR-A–D), the off-channel pond, and the augmentation pipe (dark blue line). The study design (bottom panel, reach view) included two “control” and two “impact” study reaches that were separated by the point of augmentation. Each study reach contained four consecutive riffle–pool units (bottom panel, plan view), bounded by a passive integrated transponder (PIT) antenna (see Salmonid movement) and containing a staff plate, a dissolved oxygen logger, and a stage logger in the pool and a second staff plate on the downstream riffle crest (bottom panel, cross section). The drift net (see Invertebrate sampling) and pool velocity measurement locations are also shown (plan view).



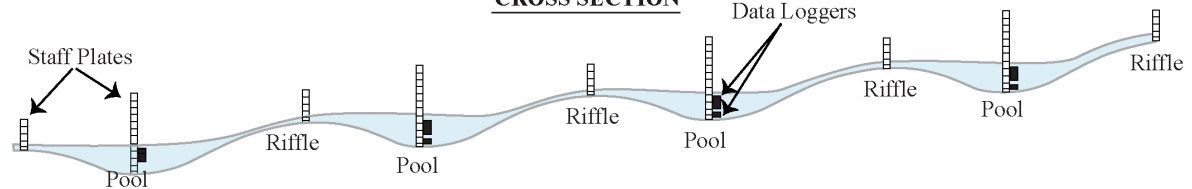
REACH VIEW



PLAN VIEW



CROSS SECTION



Experimental study design

Four study reaches were selected on Porter Creek: two control reaches upstream of augmentation and two impact reaches downstream of augmentation (Figure 1). Each study reach contained four riffle–pool habitat units that served as replicates, resulting in eight “control” units and eight “impact” units (Figure 1, bottom panel). The riffle–pool unit is a ubiquitous geomorphic feature in alluvial streams with slopes between 0.5% and 2.0% (Leopold and Wolman 1957) and provides a discrete habitat unit for evaluating juvenile salmonid rearing and foraging during the low-flow period (Rossi et al. 2021a). During the dry season period, pools approach or reach disconnectivity and are sufficiently isolated to be considered independent units. Study site selection was constrained by landowner access and variation in habitat conditions and therefore was not random. We selected control and impact reaches with similar slope and geomorphic characteristics (morphology, pool dimensions, channel confinement, and substrate) that supported foraging salmonids, and we prioritized sites with simple hydraulic controls so that we could develop robust rating curves at the downstream riffle crest. The control sites were downstream from a small tributary (Press Creek, 2.99 km²), but the tributary was dry during all of our “before” and “after” study periods, and other habitat variables (e.g., pool volume and substrate) were similar in control and impact reaches.

Streamflow gauging and augmentation

Streamflow was gauged at three locations below augmentation (river kilometers [rkm] 2.74, 1.09, and 0.21) and one location upstream (rkm 4.96; Figure 1) to evaluate our hypotheses about the spatial extent of augmentation treatment effects (H1 and H2). We tested the same level of flow augmentation during a wet summer (2019) and a dry summer (2020; Figure 2). Experimental augmentations were timed to occur just prior to riffle–pool disconnection in the control reach of Porter Creek. Based on observations in previous years, we found that when daytime riffle crest depths dropped below 2 cm, disconnectivity in Porter Creek was imminent. To determine when disconnection was imminent during the study, we made weekly site visits in May and June of each year to measure riffle crest depths. In 2019, a large May freshet extended surface connectivity until mid-July in the control reach (Figure 2), and we tested an augmentation treatment of 13.9 L/s, starting on July 12 and continuing through October. This treatment (13.9 L/s) was repeated during the much drier summer of 2020, starting on June 25 and

ending on August 6 (Figure 2). In 2019, augmentation commenced when mean daily flow was 11.5 L/s at rkm 4 (control reach) and 25 L/s at rkm 1.05. In 2020, augmentation commenced when flow was 4.2 L/s at rkm 4 and only 4.3 L/s at rkm 1.05.

Hydraulic habitat measurements

Onset HOBO U20 water level loggers were deployed in all pools within each study reach to measure continuous changes in pool depth. Water level loggers were mounted to rebar and installed near the pool maximum depth (Figure 1, bottom panel). Depth was measured where the thalweg bisects the downstream riffle crest of each pool, a point known as the “riffle crest thalweg” (RCT; Rossi et al. 2021a). The RCT depth served as a proxy for hydraulic connectivity (between pools), although it has also been shown to be a predictor of poor DO concentrations and changes in salmonid foraging behavior (Rossi et al. 2021a, 2021b). The elevation of the RCT was surveyed relative to the elevation of the water level logger and staff plate to allow for a conversion between continuous pool stage and continuous RCT depth (Figure 1, bottom panel). Velocity was measured along the thalweg of the pool (six-tenths of depth) from the upstream point, where water entered the pool at 1-m increments (Figure 1, bottom panel). These velocity profiles served as a proxy for the changing length of feeding zones in pools below riffles due to augmentation (Harvey et al. 2006).

Water quality monitoring

Continuous DO (H3) and stream temperature (H4) were measured using Onset HOBO U26 data loggers in each pool (Figure 1, bottom panel). The DO loggers were laboratory calibrated prior to deployment. Field calibration measurements were taken three times during the study period using a handheld YSI Pro20 meter in each pool, and these values were used to correct the logger output data using HOBOWare Pro's Dissolved Oxygen Assistant software.

Invertebrate sampling

To estimate the effect of streamflow augmentation on prey abundance for salmonids (H6), we sampled benthic macroinvertebrate (BMI) drift entering each pool. Invertebrate drift was sampled 2 weeks before and 2 weeks

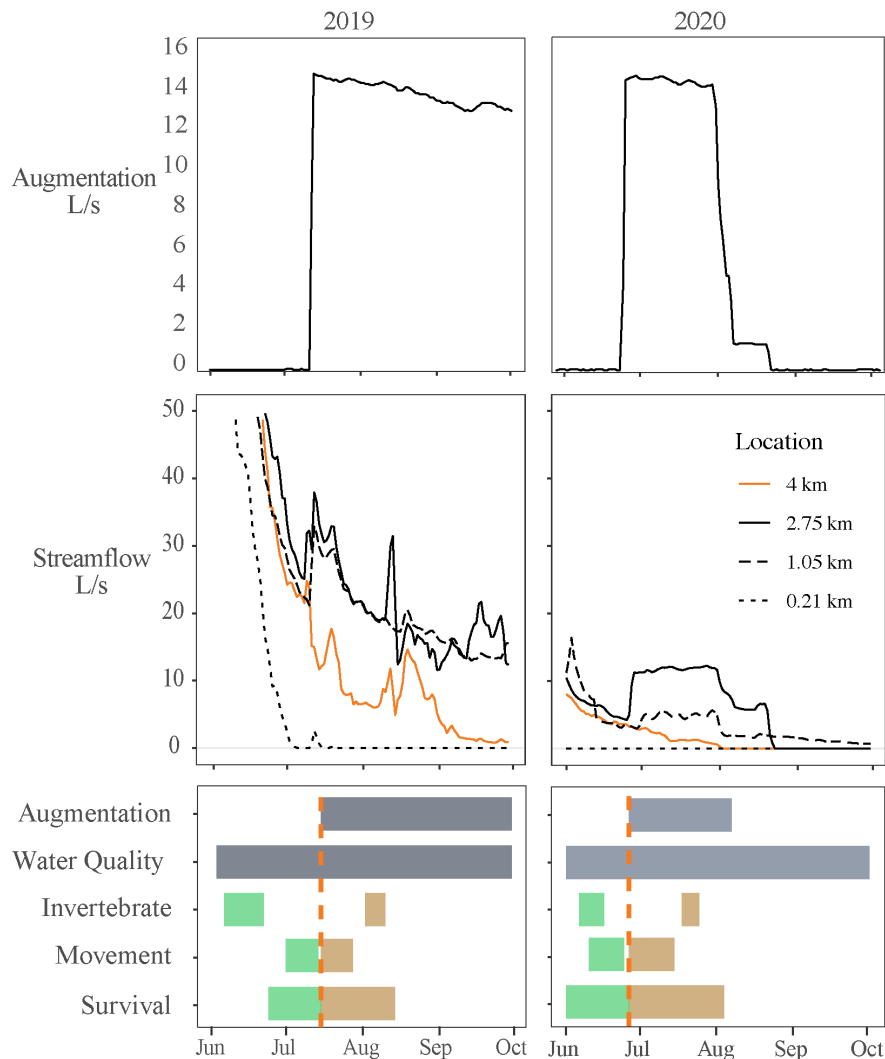


FIGURE 2 Streamflow augmentation schedule (top panels) for Porter Creek during summer 2019 (left) and summer 2020 (right); ambient streamflow (middle panels) above the augmentation (orange solid line, 4 km), at the augmentation (black solid line, 2.75 km), in the impact reach (dashed line, 1.05 km), and near the creek outlet (dotted line, 0.21 km) in 2019 (left) and 2020 (right); and the timing of augmentation relative to data collection (bottom panels) for variables measured in this study during 2019 (left) and 2020 (right).

after augmentation in both years (Figure 2). Sampling took place between 1600 and 1900 hours each day. This timing was selected because the diel peak drift of common invertebrates (especially Baetidae [mayflies] and Chironomidae [midges]) has been reported to occur in the evening period before and during sunset (Waters 1972; Statzner and Mogel 1985; Schreiber 1995, cited in Svendsen et al. 2004). Drift was collected in nets with a 50- \times 20-cm mouth aperture and 500- μ m mesh. The drift net was installed at the water surface at the head of each pool (Figure 1, bottom panel). Cross-stream position of the net was adjusted on each occasion to capture the region of highest velocity at each sampled streamflow. Drift samples were preserved in 100% ethanol in the field. Each invertebrate was measured to the nearest 0.5 mm under a dissecting scope, and biomass (mg dry mass) was estimated from published length-dry mass relationships (Benke et al. 1999; Sabo

et al. 2002). Because our statistical analysis was intended to evaluate the effect of invertebrate availability as a food resource for fish, we removed large (>10-mm) taxa, which made up less than 0.5% of the total drift but skewed the biomass estimates. These larger invertebrates are also rare in the diet of small (e.g., <100-mm), stream-foraging salmonids (Keeley and Grant 2001).

Salmonid monitoring

Salmonid movement (H7) and survival (H8) were evaluated using a population of passive integrated transponder (PIT)-tagged fish. As an initial marking event, Coho Salmon and steelhead juveniles were captured from each study reach (Figure 1) using backpack electrofishing during sampling events on June 24 and 25, 2019, and June

1 and 2, 2020 (Figure 1, bottom panel). Fish larger than 60 mm were fitted with 12-mm PIT tags by creating a small (1-mm) incision in the body cavity on the ventral side and inserting the tag. In addition to the fish that were captured and tagged in the stream environment, tagged juvenile Coho Salmon raised for the Russian River Coho Salmon Captive Broodstock Program at the Don Clausen Fish Hatchery were stocked into reaches A and C (Figure 1) in both years. Approximately 250 Coho Salmon were stocked into each of the two reaches on June 27, 2019, and June 8, 2020 (Table 1). Stocking densities of approximately 0.5–0.8 fish/m were consistent with densities applied by the conservation hatchery program in tributaries to the Russian River over the past decade. Block nets placed at reach boundaries were used to prevent fish from fleeing the reaches immediately after stocking, and the nets were left in place for approximately 1 week to allow fish to acclimate to the natural environment.

Salmonid survival

To estimate reach-specific survival before and after augmentation, we used the robust design capture–mark–recapture model (Kendall et al. 1997), in which secondary sampling occasions are conducted within primary sampling occasions. This model allows survival and recapture probabilities to be decoupled during the last survival interval. Primary sampling occasions consisted of an initial PIT tag marking event prior to augmentation (electrofishing and hatchery release; Table 1) and two subsequent primary recapture occasions each year: one immediately before the onset of augmentation and one following the period of augmentation. Each of the primary recapture occasions consisted of two consecutive days of PIT tag “wandering,” in which biologists waded the full extent of each reach, detecting as many fish as possible by using a portable PIT tag detection system or “wand.” The paired wand surveys served as secondary sampling occasions that were close in time to satisfy the robust design model’s assumption that there is no mortality or emigration between secondary sampling occasions. This sampling approach allowed estimation of survival probability during

an interval of time before augmentation (between the marking event and first primary recapture occasion) as well as an interval after the onset of augmentation (between the two primary recapture occasions; Figure 2).

Salmonid movement

Movement of all PIT-tagged fish was monitored using stationary PIT antenna arrays mounted over riffles between each study pool (Figure 1). Antennas were mounted 30 cm above the water surface on cinder blocks to allow fish to swim freely while maintaining proximity to the antennas for detection. The PIT antennas were connected to power sources and a Biomark IS1001 data logger located on the adjacent terrace. Each reader was programmed to log hourly status reports, which documented the operation of antennas to ensure that they were consistently running. To estimate the effect of augmentation on salmonid movement between pools and riffles, we computed the total number of detections at each antenna per day (in the control and impact reaches) and the number of detections per unique tag per day so that a single mobile fish would not bias the results.

Statistical analysis

Continuous data

All continuous variables (water temperature, DO, RCT depth, and salmonid movement) were analyzed using a multiple before–after, control–impact paired time series (mBACIPS) model (Table 2, group A; Wauchope et al. 2021). This model is appropriate for our study design, which included multiple sites (riffle–pool units) in the control and augmented (impact) reaches and sampling of continuous data before and after treatment (i.e., augmentation). In all before–after, control–impact (BACI) models (including mBACIPS models), the primary term is the interaction of “BA” (before/after augmentation) and “CI” (control/impact reach), which is significant when change occurs in the impact reach but not in the control reach

TABLE 1 Counts of salmonids that were PIT-tagged in Porter Creek, California (Wild) or tagged individuals that were released into Porter Creek from Don Clausen Fish Hatchery in 2019 and 2020. Hatchery Coho Salmon were released only into reaches A and C (Figures 1 and 2).

Species	2019			2020		
	Wild	Hatchery	Total	Wild	Hatchery	Total
Steelhead	186	0	186	174	0	174
Coho Salmon	5	517	522	166	497	663

TABLE 2 Statistical design used to evaluate each response variable by group type in the flow augmentation experiment conducted in Porter Creek, California. Abbreviations: BMI, benthic macroinvertebrate; mBACI, multiple before–after, control–impact; mBACIPS, multiple before–after, control–impact paired time series; RCT, riffle crest thalweg.

Group	Variable	Type	Analysis
A	Water temperature Dissolved oxygen RCT depth Fish movement	Continuous logger or antenna detections	mBACIPS linear mixed-effects model: Variable ~ (Treatment × Reach × Time) + (1 Site) + (1 Date)
B	Pool velocity Pool depth BMI drift	Categorical (manual measurement)	mBACI linear mixed-effects model: Variable ~ (Treatment × Reach) + (1 Site)
C	Fish survival (by species)	Categorical (capture–mark–recapture)	MARK analysis: ^a 1. Null 2. Treatment 3. Year 4. Treatment and Year

^aModels were run separately for each species (Coho Salmon or steelhead).

(e.g. Popescu et al. 2012; Smokorowski and Randall 2017). In the continuous mBACIPS models, a three-way interaction among BA, CI, and Time (day) determines whether the impact also caused a change in the time series trends. A random effect of site was also added to the mBACIPS models. Models were constructed separately for each year (2019 and 2020). We constructed mBACIPS time series models following the methods described by Wauchope et al. (2021, their supplemental S3):

$$\text{Variable} \sim \text{Time} + \text{BA} + \text{CI} + (\text{BA} \times \text{CI}) + (\text{BA} \times \text{Time}) + (\text{CI} \times \text{Time}) + (\text{BA} \times \text{CI} \times \text{Time}), \quad (1)$$

where Time is a daily time step centered on the day of augmentation, BA is a categorical variable of either before or after, and CI is a categorical variable of either control or impact.

An assumption of the mBACIPS models is that the trends prior to the treatment are similar in both the control and impact sites. We evaluated this visually by plotting the “before” data from all sites.

Categorical data

For categorical data (Table 2, group B), we used the same model as Equation (1) (except without the continuous Time variable) configured as a multiple BACI model (Wauchope et al. 2021). Site (riffle–pool unit) was added as a random effect in all models. For both time series and categorical data (Table 2, groups B and C), we used linear mixed-effects models with the LMER command in R version 3.5.1. To determine an augmentation treatment effect, we used the BA × CI interaction as the response variable (Table 2, group C); to determine an augmentation trend

effect, we used the Time × BA × CI interaction (Table 2, group C; Wauchope et al. 2021).

Mark–recapture data

For survival analysis (Table 2, group C), we used a model evaluation approach (Lebreton et al. 1992) to determine whether survival probability differed between control and impact reaches before and after augmentation. For each species, we constrained the parameters of the robust design model (Kendall et al. 1997) in program MARK (White and Burnham 1999) to arrive at a set of candidate models for evaluating hypotheses (H7). The model set for each species included models that allowed survival to vary by treatment (control or impact), year (2019 or 2020), or treatment and year. We also included a null model that held survival constant across treatment and year. In all models, we estimated survival probability during the intervals before and after the onset of augmentation. Detection probability was allowed to vary by reach and survey date to account for the potential influence of flow or other factors (e.g., surveyor experience and time of day) on detection efficiency. Akaike's information criterion corrected for small sample size (AIC_c) was used to evaluate model support, and models were considered to show similar support if they were within 0–2 AIC_c units and/or carried over 10% of total model weight (Burnham and Anderson 2002). For the models with the highest support, we estimated the effect size for each reach–year combination by subtracting the survival probability before augmentation from the survival probability after augmentation, and we calculated 95% confidence intervals using the equation $1.96 \times \sqrt{\text{var}(\text{after}) + \text{var}(\text{before}) - 2\text{cov}(\text{after}, \text{before})}$, following methods described by Cooch and White (2019).

RESULTS

Connectivity and hydraulic habitat

The effects of augmentation on streamflow varied between years, with greater longitudinal loss of flow during the dry summer of 2020 and complete loss of flow at rkm 0.21 during both years. Streamflow effects were strongly coupled with changes in habitat connectivity as measured by RCT depth (Figure 2). During the wet summer of 2019, augmentation caused a small increase in riffle crest depths (+0.23-cm mean; +0.02-cm/day trend) and pool depths (+0.27-cm mean), although there was no change in habitat connectivity (all units remained connected in the impact reach) or pool velocity (Table 3). During the dry summer of 2020, four of the eight impact sites had become disconnected prior to augmentation.

Augmentation in 2020 had a large effect on riffle crest depth (+3.4-cm increase in RCT depth; +0.155-cm/day trend) and pool depth (+4.4-cm mean) and restored surface connectivity in the impact reach. Pool velocity also increased (+6.3 cm/s) due to augmentation in the dry summer (Table 3). Even with augmentation, however, stream drying consistently occurred in some low-gradient reaches, characterized by alluvial gravel deposits and wide bar-riffle morphology, especially downstream of rkm 0.5 and also between rkm 1.75 and 4.0 in the drier summer of 2020 (Figure S4).

Water quality

Augmentation increased DO in the impact sites during both years, although the effect size was much larger

TABLE 3 Results from mixed modeling for before–after, control–impact (BACI; comparison of means) and before–after, control–impact paired time series (BACIPS; comparison of trends) effects from flow augmentation in Porter Creek, California, during 2019 and 2020; *p*-values in bold are considered significant. Abbreviation: BMI, benthic macroinvertebrate.

Year	Variable (units)	Fixed effect	Estimate	SE	<i>p</i>
2019	Dissolved oxygen (mg/L)	BACI (means)	0.232	0.036	<0.001
		BACIPS (trends, day)	0.004	0.005	0.468
	Water temperature (°C)	BACI (means)	−0.413	0.049	<0.001
		BACIPS (trends, day)	0.043	0.006	<0.001
	Riffle crest depth (cm)	BACI (means)	0.228	0.077	0.003
		BACIPS (trends, day)	0.020	0.011	0.073
	Pool depth (cm)	BACI (means)	0.266	0.099	0.008
	Pool velocity (cm/s)	BACI (means)	−2.112	4.073	0.612
	BMI drift (mg/h)	BACI (means)	3.253	2.669	0.243
	Steelhead movement (detections·tag ^{−1} ·day ^{−1})	BACI (means)	3.0957	2.9663	0.297
		BACIPS (trends, day)	0.7104	0.3861	0.066
	Coho Salmon movement (detections·tag ^{−1} ·day ^{−1})	BACI (means)	1.293	2.232	0.563
BACIPS (trends, day)		0.873	0.278	0.002	
2020	Dissolved oxygen (mg/L)	BACI (means)	2.264	0.302	<0.001
		BACIPS (trends, day)	0.151	0.034	<0.001
	Water temperature (°C)	BACI (means)	1.344	0.192	0.000
		BACIPS (trends, day)	−0.016	0.021	0.457
	Riffle crest depth (cm)	BACI (means)	3.410	0.225	<0.001
		BACIPS (trends, day)	0.155	0.029	<0.001
	Pool depth (cm)	BACI (means)	4.410	0.362	<0.001
	Pool velocity (cm/s)	BACI (means)	6.293	1.670	0.002
	BMI drift (mg/h)	BACI (means)	3.300	1.539	0.050
	Steelhead movement (detections·tag ^{−1} ·day ^{−1})	BACI (means)	4.178	2.058	0.043
		BACIPS (trends, day)	0.372	0.278	0.181
	Coho Salmon movement (detections·tag ^{−1} ·day ^{−1})	BACI (means)	2.067	0.730	0.005
BACIPS (trends, day)		−0.094	0.112	0.401	

during the dry summer of 2020 (+2.26 mg/L) than during the wet summer of 2019 (+0.23 mg/L) and the trend was only significant in 2020 (+0.15 mg·L⁻¹·day⁻¹; $p < 0.001$; Table 3). During the wet summer (2019), augmentation had a negligible cooling effect on daily average water temperature (-0.41°C), although the trend was positive (+0.043°C/day). During the dry summer, augmentation increased the water temperature (+1.34°C; $p < 0.001$), although water temperature stayed within suitable ranges for rearing salmonids. There was no effect on the trend in 2020. Overall, the effects of augmentation on DO and riffle crest depth were large in the dry year (2020), and effects on temperature were negligible in both years (e.g., as illustrated for a single impact site in Figure 3).

Stream invertebrates

Although drifting invertebrates were near annual minimums by midsummer in Porter Creek (Rossi et al. 2022), the BMI drift rate in the impact reaches declined less

(2019) or increased (2020) after augmentation relative to the control reaches (Figure 4). After augmentation in 2020, drifting invertebrate flux increased in the impact reach by 3.3 mg/h ($p = 0.05$) relative to the control site (Table 3). In 2020, following augmentation in the impact reach, we observed increases in chironomids and baetids, which are vulnerable to predation by juvenile salmonids (Figure S5). The mean biomass of drifting invertebrates was nearly identical between control and impact reaches prior to augmentation, but mean biomass decreased more in the control reaches after augmentation (Table S1 [available in the Supplemental Materials in the online version of this article]).

Salmonid movement

Movement rates of tagged steelhead and Coho Salmon were higher in the wet summer of 2019 than in the dry summer of 2020. In 2019, augmentation had no effect on total detections per tag for salmonids at riffle antennas,

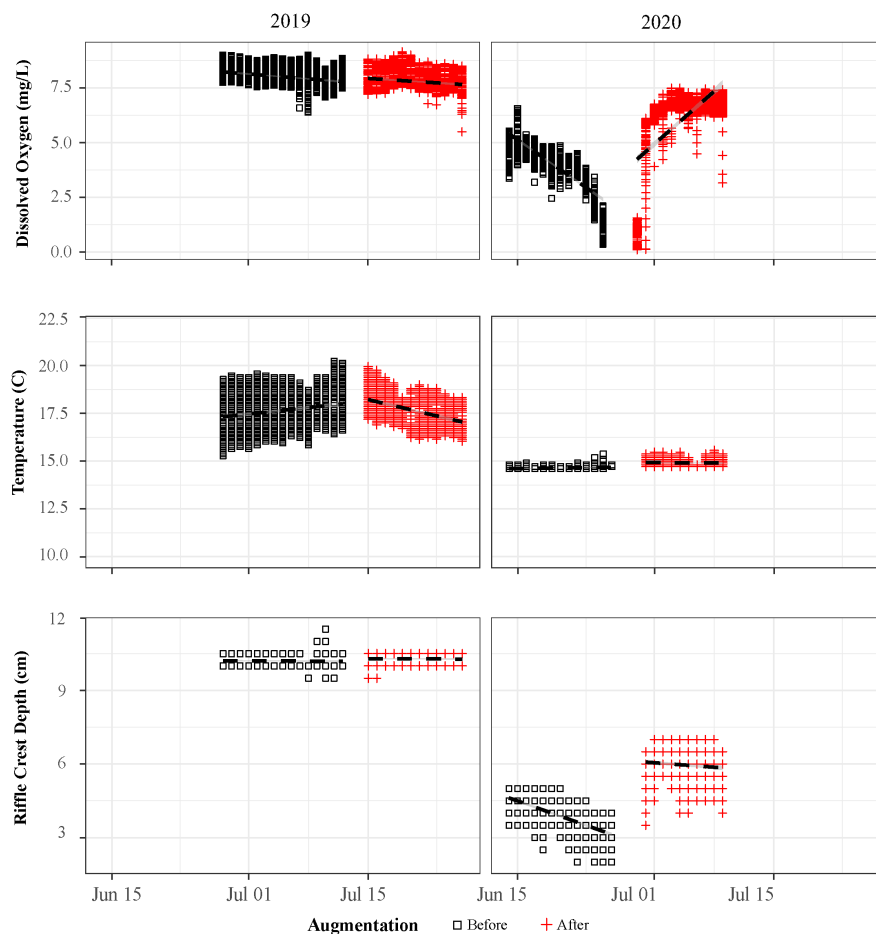


FIGURE 3 Dissolved oxygen (mg/L; top panels), water temperature (°C; middle panels), and riffle crest depth (cm; bottom panels), shown for a representative impact site in reach B of Porter Creek (Figure 1) to illustrate the before (black) and after (red) periods in both 2019 (left) and 2020 (right).

but the rate of detections per tag per day (trend) increased after augmentation for both steelhead (+0.71 detections·tag⁻¹·day; $p=0.06$) and Coho Salmon (+0.87 detections·tag⁻¹·day; $p=0.002$; Table 3). During the dry

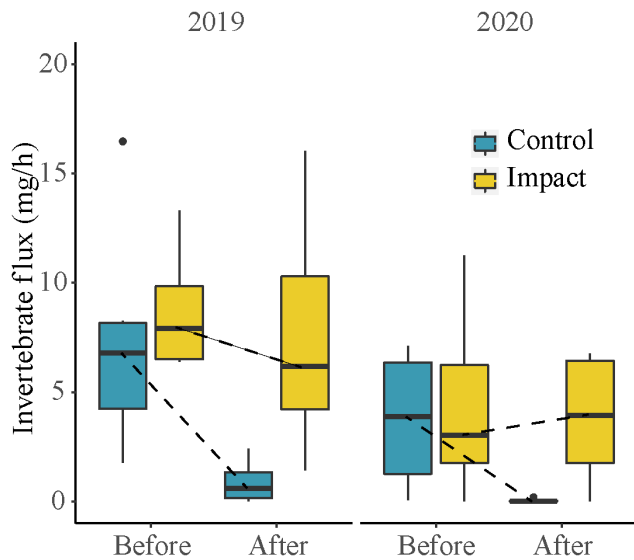


FIGURE 4 Midsummer benthic macroinvertebrate drift (mg/h) before and after the onset of flow augmentation in Porter Creek for the control (blue) and treatment (yellow) reaches during a wet year (2019) and a dry year (2020). Box plots are connected at the median values, and boxes show the 25th–75th quartile range. Whiskers show the 95th percentile range.

summer of 2020, augmentation significantly increased the total detections per tag for juvenile steelhead (by 4.2 detections/tag) and Coho Salmon (by 2.1 detections/tag) but had no effect on trend for either species (Table 3). In total, we detected 50% of the tagged steelhead (93 of 186) among all reaches in 2019 and 40% of the tagged steelhead (69 of 174) in 2020. We detected 39% of the tagged Coho Salmon (202 of 522) among all reaches in 2019 and 22% of the tagged Coho Salmon (144 of 663) in 2020.

Salmonid survival

In the wet summer of 2019, the probability of survival for Coho Salmon increased more in the impact reach than in the control reach during the interval in which flow augmentation occurred (Figure 5). The probability of survival for steelhead declined in the control reaches and remained the same in the impact reaches during 2019, although there was high overlap in the 95% confidence intervals. In 2020 (the dry year), we observed a decline in survival probability from the preaugmentation interval to the postaugmentation interval in almost all reaches; however, for both species the decline was greater in the control reaches. For juvenile Coho Salmon, the effect of rearing in the augmentation reach was an increase in survival probability of 0.11 in 2019 (wet year) and 0.24 in 2020 (dry year; Figure 6). For steelhead, there was no effect of rearing in the augmentation

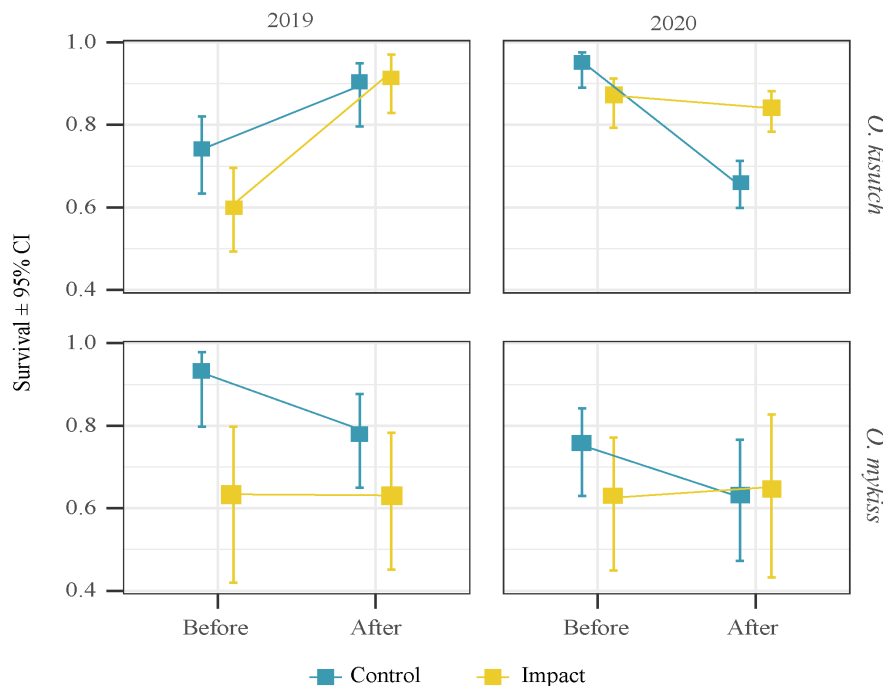


FIGURE 5 Probability of juvenile salmonid (Coho Salmon: top panels; steelhead: bottom panels) summer survival (standardized to month; ±95% confidence interval [CI]) before and after the onset of flow augmentation in Porter Creek during a wet year (2019) and a dry year (2020).

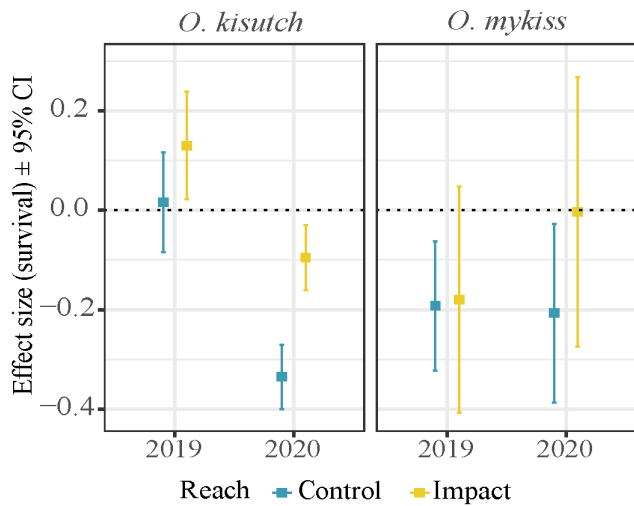


FIGURE 6 Effect size of juvenile salmonid (Coho Salmon: left panel; steelhead: right panel) survival ($\pm 95\%$ confidence interval [CI]) before and after flow augmentation in control and impact reaches of Porter Creek during a wet year (2019) and a dry year (2020).

reach during 2019, whereas rearing in the augmentation reach increased survival probability by 0.20 in 2020.

DISCUSSION

Our hypotheses for the flow augmentation experiment were generally supported. In both years of the study, the treatment increased downstream flows and hydraulic habitat parameters (H1), including pool velocities and riffle and pool depths; however, the effect size of these impacts was much larger in the dry summer (2020). Habitat connectivity was only increased during the dry summer. We also observed a decreasing influence of augmentation on flows with downstream distance, as expected (H2). The flow augmentation treatment had detectable effects on water quality variables, especially increasing DO (H3), with marginal effects on stream temperature (H4). Augmentation also modestly increased BMI drift during the dry summer (H5). Observed changes in flow, hydraulic habitat, water quality, and BMI drift were associated with modest increases in movement (H6) and higher survival (H7) of juvenile salmonids during the treatment period. Overall, the findings of our experiment show that small-scale flow augmentation had a positive and ecologically significant effect on dry season habitat conditions for rearing salmonids.

Spatial and temporal effects of augmentation on connectivity and hydraulic habitat

The effects of dry season augmentation on most variables were mediated by ambient streamflow conditions. This

was particularly evident for hydraulic habitat indicators. In 2019, for example, ambient flow remained relatively high throughout the treatment period, and we observed small but measurable effects on RCT depths, pool depths, and pool velocities. In 2020, however, significant drying occurred prior to augmentation, especially in reaches with deep, porous gravel deposits (e.g., near rkm 2.0 and downstream of rkm 0.6; Figure S4). As the dry season progresses, such reaches are more likely to become disconnected as flows drain into the subsurface, as has been observed in other coastal California streams (Lovill et al. 2018; Moidu et al. 2021). Future augmentation projects should consider locating discharge points away from deep alluvial deposits if impacting surface flow is a primary objective. In 2020, 1 month of augmentation at 13.9 L/s was able to re-wet most of the downstream channel in Porter Creek except for the stream confluence (Figure S4). The augmentation also increased riffle crest depths by over 3 cm, on average, which corresponds to the common body depth of juvenile steelhead and Coho Salmon (Negus 2003) and likely facilitated their movement into riffles and between pools. Similarly, the observed increases in riffle depths and pool head velocities during 2020 suggest that augmentation created more favorable habitat for drift-feeding salmonids (Harvey et al. 2006; Rossi et al. 2021b).

Augmentation effects on water quality

We found that flow augmentation increased DO, but like the hydraulic variables, a much greater effect was observed in 2020. In the 2 weeks prior to the 2020 augmentation, DO in the impact reaches had lowered to levels (median = 4.2 mg/L; SD = 2.6) known to impair swimming performance and food conversion efficiency for juvenile Coho Salmon and steelhead (U.S. Environmental Protection Agency [USEPA] 1986; Bjornn and Reiser 1991). However, augmentation increased DO to a median of 6.6 mg/L (SE = 1.52), a level at which juvenile salmonids have been shown to experience minimal impairment (USEPA 1986). Synoptic tests of DO from the pipe effluent were always near 100% saturation (DO > 9 mg/L at 18°C), likely a result of aeration as water passed through the pipe. Thus, one explanation for the increase in DO is that the mass of augmented streamflow started with and retained high levels of DO between the augmentation point and our downstream study sites. The decreased residence time of flow in the hyporheic zone (within alluvial bars) and in pools may have also contributed to maintaining the higher DO levels as flow moved downstream. Residence time of flow is directly related to interaction time with decomposers on the benthos and in the hyporheic zone, which are key drivers of carbon cycling in intermittent streams (Burrows et al.

2017). Decreased interaction time between decomposers and the volume of flowing water could lead to decreased organismal oxygen consumption, thus maintaining DO. However, we did not measure residence time in this study, and more work is needed to understand the mechanisms that may be driving the effects of flow on DO in coastal streams during the dry season.

We found that augmentation had marginal effects on water temperature. Because augmentation resulted in a small change in the total volume of water in the channel, we suspect that atmospheric and within-channel transport processes largely controlled stream water temperature downstream from the point of augmentation and buffered the effects of the warmer augmentation water source at downstream study sites. Despite some warming in 2020, temperatures at all of our sites remained below the stressful physiological tolerance limits of salmonids. However, we acknowledge the potential for augmentation to significantly affect stream temperatures under different site conditions, including initial temperatures (from the pond), flow release rates, flow in the receiving water bodies, and other local environmental factors (Ficklin et al. 2012).

Augmentation effects on stream invertebrate drift

The biomass of BMI drift increased relative to control reaches after the onset of augmentation, consistent with previous studies, which have shown that increased wetted area and riffle velocity can increase the production, hydraulic transport, and behavioral drift of invertebrate species (Annear et al. 2004; Naman et al. 2016). However, the natural phenology of invertebrate drift in Porter Creek was near its annual minimum by midsummer (Rossi et al. 2022), and the relative increase in BMI drift (<4 mg/h) represents a small change in the growth potential of foraging salmonids. For example, Porter Creek drift rates in April 2018 were between 100 and 200 mg/h, excluding large or rare invertebrates (Rossi et al. 2022). Using published energy densities for freshwater invertebrates (e.g., 3072 J/g; Thompson and Beauchamp 2016), an additional 4 mg/h would contribute a negligible amount (~12.3 J/h) of potential energy for salmonids. Late-summer growth rates for salmonids are naturally near zero in many California coastal streams (Kelson and Carlson 2019; Rossi et al. 2022). Thus, we suspect that potential benefits to survival from this level of augmentation (13.9 L/s) in midsummer are more likely due to decreased metabolic stress from increased DO or perhaps increased mobility of fish rather than being due to higher food availability from this modestly increased drift rate.

Augmentation effects on salmonid movement and survival

Augmentation was associated with increased movement between pools, measured as detections per tag in both years, although the impact was much larger in the dry summer of 2020. This was not surprising because hydraulic connectivity and suitable DO concentrations were largely maintained in 2019, whereas the increase in riffle crest depth and DO after augmentation in 2020 significantly improved the hydraulic and metabolic environment for fish movement. We chose the “number of detections per tag” as our response variable to indicate interpool movement because we observed that some animals were detected much more frequently than others. Swimming performance of salmonids significantly declines at DO levels below 5 mg/L (USEPA 1986; Bjornn and Reiser 1991), and the decreased metabolic cost of swimming is a potential mechanism for the increased movement we saw in 2020. A further analysis of covariates with detections (e.g., DO, riffle crest depth, and velocity) and their interactions would greatly aid our understanding of the mechanisms by which streamflow augmentation affects salmonid movement. Because PIT antennas were placed over riffle habitats and away from pools and because riffles had become very shallow by late summer, we reasoned that most detections were associated with movement between pools; however, we cannot rule out that some detections were related to foraging movements into riffles and not movement between pools.

Perhaps the most consequential finding of this study was the significant increase in oversummer survival during flow augmentation for both juvenile Coho Salmon (+24%) and steelhead (+20%) in 2020 and for juvenile Coho Salmon (+11%) in 2019. Obedzinski et al. (2018) found a negative relationship between oversummer survival of juvenile Coho Salmon in Russian River tributaries and the number of days of stream disconnectivity (intermittent flow). Those authors also found a positive relationship between survival and flow, DO, and wetted pool volume (Obedzinski et al. 2018). Our study suggests that augmentation, particularly during the dry summer of 2020, strongly affected those variables that were closely associated with salmonid survival (i.e., stream connectivity and DO). Although our study did not directly investigate mechanisms for mortality, longer periods of disconnection and decreased DO are likely associated with physiological stress, increased competition for resources, and increased vulnerability to terrestrial predators, all of which have the potential to reduce survival (Hwan et al. 2018; Obedzinski et al. 2018; Vander Vorste et al. 2020).

Management implications for future streamflow augmentation projects

To mitigate the ecological impacts of flow impairment in undammed streams, there is growing interest in novel management approaches, including changes in agricultural water diversion schedules (Grantham et al. 2014); actions to promote groundwater recharge (Woelfle-Erskine et al. 2017); and the direct release of water into streams from off-stream storage (Deitch and Dolman 2017; Ruiz et al. 2019), as illustrated in this study. To our knowledge, this is the first controlled flow manipulation experiment to quantify the effects of flow augmentation from off-channel storage on juvenile salmonids. However, questions remain over the magnitude, timing, and duration of flow restoration that would be required to produce a meaningful ecological benefit. The findings of increased oversummer survival of Coho Salmon and steelhead in flow-augmented reaches are promising, but more work is needed to understand the life cycle consequences of these effects (e.g., at the population level) and their dependencies on ambient environmental conditions. Although 2020 was a dry year, it is uncertain whether this level of flow augmentation would confer the same benefits in critically dry years or how the physical and biological effects that we measured potentially scale with augmentation rates. More work is also needed to monitor the effects of augmentation on nontarget species (e.g., stream amphibians and nonsalmonid fishes), the ecological effects of altering intermittent stream hydrology over many years, and the potential consequences of augmentation on adult returns and population dynamics. Nonetheless, given the dire state of salmonid populations in California (Moyle et al. 2017), the increased development of small-scale water storage in the study region (Deitch et al. 2013), and new models of collaboration between agriculture and wildlife conservation (Holmes et al. 2021), the findings of this study suggest that flow augmentation may become an important tool to improve stream habitat as part of a broader salmonid conservation strategy.

Flow alteration is a pervasive driver of river ecosystem degradation worldwide (Reid et al. 2019) and in California (Zimmerman et al. 2018), and the recovery and protection of streamflows are essential for “bending the curve” of freshwater biodiversity loss (Tickner et al. 2020). Although it is self-evident that flow-impaired streams should benefit from augmentation, few studies have quantified the ecological responses to flow restoration in small, undammed streams (Davies et al. 2014; Gillespie et al. 2015). Our study provides empirical evidence that a well-timed, short-duration, low-volume flow augmentation measurably improved habitat quality and the survival of summer-rearing salmonids. It suggests

that in systems like Porter Creek, even slight increases in streamflow (e.g., 10–20 L/s) during critical periods can move salmonids away from the knife’s edge of survival and potentially aid in the recovery of imperiled populations. More broadly, this project provides a template for how to monitor the effects of flow enhancement in small streams, highlights critical areas for further study, and suggests that management actions to effectively restore streamflow in small, salmon-bearing streams can yield significant ecological benefits.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Data are available at <https://datadryad.org/stash/share/SNsDJsHRQCAtpV0QGJnCbhLK6fY5W9ZnbmfOFPTwPIQ>.

ETHICS STATEMENT

All animals used in this study were approved by the Institutional Animal Care and Use Committee under permit S12020.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.