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Effects of flow-related variables on oversummer survival of juvenile Coho Salmon in intermittent streams

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Abstract

While many studies have established the importance of streamflow as a driver of fish population dynamics, few have examined relationships between survival of juvenile salmonids and flow-related variables in intermittent streams. With predictions for higher frequency of drought conditions due to climate change, and the associated increasing human demand for water during the dry season, understanding fish–flow relationships is becoming increasingly important for the protection of sensitive aquatic species. To examine the effects of low streamflow on juvenile salmonids rearing in small intermittent streams, we estimated survival and collected environmental data in four coastal California watersheds from 2011 to 2013. We used an individual-based mark-recapture modeling approach to evaluate the influence of flow-related variables on oversummer survival of PIT-tagged juvenile Coho Salmon stocked into eight stream reaches. Survival was positively associated with streamflow magnitude, wetted volume, and dissolved oxygen, and negatively associated with days of disconnected surface flow (days of disconnection), and temperature. Days of disconnection best explained survival, though the relationship varied by geomorphic reach type. Survival was lower in alluvial reaches as compared to bedrock and clay reaches, and showed a faster rate of decline with increasing days of disconnection and drought condition. In all reaches, the onset of pool disconnection represented a turning point at which water quality, water quantity, and survival declined. For this reason, we suggest that days of disconnection (or the flow magnitude at which pools become disconnected) is a useful metric for identifying flow-impaired reaches, informing streamflow protection strategies, and prioritizing streamflow enhancement efforts designed to benefit sensitive salmonid populations in intermittent streams.

Streamflow is a well-known driver of fish population dynamics, and changes in flow regime have severely impacted freshwater ecosystems over the last century (Power et al. 1995; Bunn and Arthington 2002; Meybeck 2003; Poff et al. 2007; Moyle et al. 2008). Numerous studies have documented relationships between streamflow and fish habitat metrics, particularly in regulated systems (Poff and Zimmerman 2010; Konrad et al. 2011), yet only in recent years have studies begun to quantify the impacts of low streamflow directly on fish population metrics in unregulated intermittent streams (May and Lee 2004; Hodges and Magoulick 2011; Grantham et al. 2012; Hwan and Carlson 2016; Woelfle-Erskine et al. 2017).

Intermittency occurs in over half of the streams in the United States (Nadeau and Rains 2007), reducing the quantity of habitat available to aquatic biota and potentially compromising water quality conditions in remaining habitat. For fish, stream contraction can reduce food availability, restrict movement, increase population density, cause physiological stress due to compromised water quality conditions, and/or cause acute mortality due to stranding (Labbe and Fausch 2000; Magoulick and Kobza 2003; Hakala and Hartman 2004; May and Lee 2004; Harvey et al. 2006; Stradmeyer et al. 2008; Irvine et al. 2009; Hwan and Carlson 2016). Despite these risks, fish are found occupying residual pools of intermittent streams (Bogan et al. 2015) and some studies have found that, while there are high mortality risks during the summer dry season, intermittent streams can offer preferred habitat for juvenile rearing (Wigington et al. 2006) and/or adult spawning (Erman and Hawthorne 1976; Boughton et al. 2009) during the fall and winter wet seasons. Presumably, if fish can survive the high mortality risks of the summer season in intermittent streams, they may gain an advantage of higher survival and growth during the winter season. Understanding such tradeoffs is important in the context of protection and recovery of sensitive species dependent upon these systems.

For threatened steelhead *Oncorhynchus mykiss* and endangered Coho Salmon *Oncorhynchus kisutch* populations at the southern extent of the species' range in coastal California, low streamflow has been identified as a limiting factor to survival (Grantham et al. 2012; NMFS 2012). In tributaries of the Russian River, California, Grantham et al. (2012) found a positive relationship between streamflow and apparent survival of juvenile steelhead, and Woelfle-Erskine et al. (2017) found that flow-related variables (pool size and conductivity) were strongly associated with survival of juvenile steelhead and Coho Salmon rearing in tributaries of Salmon Creek, California. In Woelfle-Erskine et al. (2017), survival of both species was positively associated with pool size (depth for Coho Salmon and surface area for steelhead) and negatively associated with conductivity, which they considered a proxy for dissolved oxygen (DO) levels. These studies take critical steps towards expanding our limited understanding of the complex relationships between streamflow, habitat, and salmonid population responses, but additional work is needed to identify flow-related variables important for the persistence of

fish populations and to inform the development of flow management strategies that support salmonid population recovery.

In the Mediterranean climate of the central California coast, low streamflow typically occurs during the summer dry season at a time when human water demand is high, and surface water diversions and groundwater withdrawals from shallow streamside wells can exacerbate seasonal reductions in discharge (Deitch et al. 2009a; Deitch et al. 2009b; Grantham et al. 2010). Grantham et al. (2012) found that as vineyard cover increased in four California watersheds between 1994 and 2002, there was an associated decrease in apparent oversummer survival of stream-rearing juvenile steelhead, presumably due to increased water extraction. Human water demand is expected to increase with increasing population growth and exurban expansion (Konieczki and Heilman 2004; Laraus 2004; Thompson 2007; Grantham et al. 2010), and climate change is expected to further jeopardize summer streamflows in Mediterranean systems as a result of increased temperatures, reduced precipitation, and changes in rainfall timing (Mannion 1995; Moyle et al. 2008; Karl et al. 2009; MacDonald 2010). Quantifying the relationship between juvenile salmonid survival and streamflow will help us evaluate the impacts of water withdrawals on fish populations and prepare for the anticipated changes resulting from human population growth and climate change.

Addressing widespread streamflow impairment is critical for recovery of stream ecosystems and sensitive species such as threatened and endangered salmonid populations along the West Coast. Over the last few decades, resource managers, non-profit organizations, and private landowners have invested tremendous resources in enhancing habitat for endangered salmonid populations in coastal salmonid streams (NRC 2004; Nielsen-Pincus and Moseley 2010; Roni et al. 2010), yet efforts to improve streamflow have only begun in recent years (Deitch and Dolman 2017). Competing demands for water, as well as the challenges associated with quantifying the effects of low streamflow on fish populations, have thwarted progress in addressing instream flow as a bottleneck to the recovery of imperiled salmonid populations. While many strategies have been developed to identify relevant thresholds that protect streamflow for fish (Reiser et al. 1989; Richter et al. 1997; King et al. 2003; Poff et al. 2010), they are typically aimed at regulated, snow-melt driven systems with continuous flows throughout the summer season. Such strategies do not readily apply to the small coastal streams inhabited by juvenile Coho Salmon, where late summer streamflows are so low that collecting accurate measurements presents a challenge. Further, most models for predicting instream flow requirements are based on discharge–habitat relationships and do not directly consider fish population responses (Stalnaker 1979; McKinney and Taylor 1988; Bovee et al. 1998; Annear et al. 2009; Beecher et al. 2016). This poses a problem for intermittent streams, where streamflow magnitude can fall to zero while residual pools still support rearing fish

through hyporheic flow or groundwater inputs. In these cases, surface flow magnitude may not accurately reflect habitat suitability for fish, and other variables such as pool size, water quality parameters, and thermal regimes become more relevant.

To aid in the identification of flow-impaired stream reaches, set management targets, and prioritize and evaluate streamflow improvement projects, creative approaches are needed to link flow-related variables (i.e., streamflow, water quantity, water quality) to fish population responses in intermittent, salmonid-bearing streams. Between 2011 and 2013, we evaluated oversummer survival of juvenile Coho Salmon in relation to flow-related variables in four tributaries of the Russian River watershed in coastal California. For survival estimation, we used an individual-based mark-recapture approach with a common population of hatchery Coho Salmon stocked in equal densities into eight stream reaches representing three geomorphic reach types. Environmental data were collected in these stream reaches over the same time period and survival was related to specific flow-related variables, including flow magnitude, days of surface flow disconnection, wetted volume, water temperature, and DO.

The following questions were addressed at the reach scale:

1. Does oversummer survival of juvenile Coho Salmon vary by stream, reach, and/or year?
2. Which flow-related variables most influence survival of juvenile Coho Salmon?
3. Do relationships between survival and flow-related variables differ among geomorphic reach types?

METHODS

Study area

Between 2011 and 2013, we sampled reaches of Dutch Bill, Green Valley, Mill, and Grape creeks, tributaries of the lower Russian River located along the central coast of California in Sonoma County (Figure 1). Watershed size of the four streams ranges from 8–58 km^2, and elevations range from 4–39 m above sea level at the stream confluences to 76–214 m at the upper extent of anadromy. Upland areas within the watersheds are generally characterized by Californian Moist Coastal Mixed Evergreen Forest, Californian Coastal Redwood Forest, Californian Broadleaf Forest and Woodland, Californian Coastal-Foothill Seral Scrub, and Californian Annual and Perennial Grassland (USNVC 2016). Vegetation within the riparian corridors consists of coast redwood *Sequoia sempervirens,* Douglas fir *Pseudotsuga menziesii*, California Bay Laurel *Umbellularia californica*, bigleaf maple *Acer macrophyllum*, white alder *Alnus rhombifolia*, and *Salix* spp., with understories of native and non-native shrubs and grasses. Santa Rosa (population 175,155; (USCB 2016)) is the major population center in the

Russian River watershed, and vineyards and rural residential homes occupy much of the landscape in the lower basin. There are no major dams regulating flows on these streams; however, streamflow in Russian River tributaries is frequently influenced by water withdrawals from small-scale direct diversions and streamside wells (Deitch et al. 2009a).

The study area is characterized by a Mediterranean climate in which nearly all precipitation occurs in the form of rainfall between November and April, resulting in peak streamflows during the winter season that slowly recede through the spring and summer and commonly reach an intermittent state during the dry season. Air temperatures drop to an average low of 2.5°C in winter and reach an average high of 28.5°C during summer (NOAA 2017).

Over the study period (2011 to 2013) drought conditions in the Russian River watershed progressed from no drought in 2011, to abnormally dry in 2012, to severe drought in 2013 (NDMC 2017), and annual streamflow in the Russian River also decreased progressively over that period (USGS 2017). In all four study streams, we observed a general decline in streamflow conditions between June 15 and September 30 over the years studied, with total discharge decreasing each year from 2011 to 2013 (Figure 2).

Study reaches

Within each of the four study streams, two reaches were selected (Figure 1) based on Coho Salmon habitat suitability and accessibility to streams across privately-owned land. Target reach length was 250 m; however, because reach boundaries were placed at habitat unit breaks which did not always fall at 250 m, this varied somewhat (range 210–310 m; Table 1). Catchment area among reaches ranged from 7.4–43.0 km^2, and slope ranged from 0.3–1.9%. Due to the potential influence of geomorphic setting on oversummer survival (May and Lee 2004), we assigned each reach to one of three geomorphic categories based on visual observations: alluvial (all pools characterized by loose alluvial material), bedrock (bedrock visible beneath gravel/cobble substrate in the majority of pools), or clay (clay visible beneath gravel/cobble substrate in the majority of pools).

For each reach, we classified channel types based on geomorphological characteristics, including entrenchment, gradient, width–depth ratio, sinuosity, and bed substrate (Rosgen 1994). We also conducted an initial survey each year in June to classify habitat units as pool, riffle, or flatwater habitat types (Flosi et al. 2004). As a measure of relative habitat suitability for rearing juvenile Coho Salmon, we assigned a shelter value to all pool and flatwater units based on the composition and quality of available shelter (0–3, with 3 being the highest complexity), and multiplied this value by the estimated percentage of instream cover in the unit to calculate

an instream shelter rating (Flosi et al. 2004). We also assessed over-channel canopy cover on all habitat units greater than six meters in length using a handheld, spherical densitometer.

In general, reaches were similar in both channel type and habitat quality (Table 1). All but one reach was characterized as an F channel type (relatively entrenched, meandering, low gradient, riffle-pool channels with high width–depth ratios, generally subject to high erosion rates), and dominated by small cobble (F3) or gravel (F4) substrates. One reach on Green Valley Creek (GRE-13.40) was classified as B4; a moderately entrenched, moderate gradient, riffle-dominated channel with infrequently spaced pools, very stable banks and channel profiles, and gravel substrate. Average canopy cover ± SD was high in all reaches, ranging from 81.3 ± 2.4% to 98.1 ± 0.9%, and instream cover was available in all reaches, with shelter rating ± SD ranging from 10.2 ± 2.0 to 34.3 ± 17.3. The total number of pool and flatwater units varied among years and ranged from 7–8 in MIL-6.10 to 12–16 in GRP-1.14. Over the three study years, average discharge between June and October in the study reaches ranged from 0–44 L/s (0–1.6 ft^3/s). Common fish species occurring within the study reaches include Coho Salmon, steelhead, Sculpin *Cottus* spp., and California Roach *Lavinia symmetricus*.

Study Population

The Russian River watershed falls within the Central California Coast Evolutionarily Significant Unit for federally-endangered Coho Salmon and is near the southern extent of the species' range. In the early 2000s, fewer than 10 adult Coho Salmon were known to return to the Russian River watershed each year. In response to this decline, a multiagency partnership initiated a conservation hatchery program in which juvenile Coho Salmon were captured each year from Russian River tributaries, raised to the adult stage, and spawned at Don Clausen Fish Hatchery at Warm Springs Dam. Broodstock were genotyped and spawned according to a matrix that maximized genetic diversity of offspring. Beginning in 2004, progeny of these broodstock were released annually into Russian River tributaries. Releases of juvenile Coho Salmon during the spring season provided an opportunity to compare oversummer survival in relation to flow-related variables among specific stream reaches using a common population of experimental fish similar in size and genetic composition.

In late May or early June each year, hatchery-raised age-0 Coho Salmon were measured for fork length and weight, and fish ≥ 56 mm and ≥ 2 g were tagged with 12.5 mm full-duplex passive integrative transponder (PIT) tags using the methods of Gries and Letcher (2002). Following tagging, the fish were held in tanks for two weeks before approximately 500 fish were released into each study reach in mid-June. Average fork length ± SD and average weight ± SD at the time of tagging were 68.7 ± 5.8 mm and 3.9 ± 1.2 g, 66.4 ± 6.5 mm and 3.6 ± 1.4 g,

and 66.1 ± 6.4 mm and 3.5 ± 1.1 g in years 2011, 2012, and 2013, respectively. During each stocking event, the fish were transported in aerated backpack containers from the hatchery truck to the target stream reaches and stocked into individual pools and flatwater units. The stocking density (approximately two fish per meter) was consistent with stocking densities applied by the conservation hatchery program in tributaries to the Russian River. Prior to stocking fish, an initial snorkeling survey was conducted in each reach to determine the presence of wild juvenile Coho Salmon. If wild fish were present in a reach, the number of hatchery fish released was reduced for that reach to maintain a similar density of two fish per meter. Wild fish were not included in the survival estimates.

Juvenile Coho Salmon surveys

In order to estimate survival of experimental fish between June and October, we completed a series of surveys on each reach using a portable PIT-tag detection system, or "wand" (O'Donnell et al. 2010). We used the robust design mark-recapture model in which secondary sampling occasions are conducted within primary sampling occasions (Kendall et al. 1997). This approach allowed for estimation of abundance on each primary sampling occasion and estimation of survival between primary occasions.

Primary sampling occasions occurred approximately monthly between June and late-September or early-October. The number of primary occasions varied from three to six per year, depending on reach and year. Each primary occasion was comprised of a pair of wand surveys (secondary sampling occasions) conducted in each reach over two consecutive days (one wand survey/day). Each pair of wand surveys was conducted close in time in order to satisfy the assumption of the robust design model that there is no mortality between the secondary sampling occasions comprising a given primary sampling occasion. On each wand survey, we waded every pool and flatwater habitat unit in each reach from downstream to upstream, moving the wand through the water column in an attempt to detect PIT-tagged fish. Detected tags were recorded on a PIT transceiver attached to the wand.

We placed stationary PIT antennas at the downstream end of each stocked reach for the duration of the study in order to account for downstream emigration from the study reaches. When resources allowed, we also operated antennas at the upstream boundaries of stocked stream reaches (6 of 17 reach/year combinations). To account for upstream movement out of the reaches at times when an upstream antenna was not operated, we conducted additional wand surveys upstream of the reach to a point where PIT tags were no longer detected.

In previous stocking events in these tributaries, we often observed fish exhibiting a "flight" response in which up to half of the fish moved either upstream or downstream of the

stocking reach during the first few days following the release. To prevent this from occurring in our study reaches, we placed block nets at the boundaries of each reach to prevent the fish from immediately leaving. The nets were kept in place and tended daily for 15–17 days, after which we considered any fish movements to be for reasons other than an initial flight response.

Because mortality of fish and PIT tag loss can result in tags that become lodged in the streambed ("ghost tags"), on each sampling occasion we identified PIT tag codes of individuals thought to have perished (or shed a tag) since the previous sampling occasion. We recorded a tag as a ghost tag when it remained stationary despite vigorous disturbance with the wand immediately above an open streambed surface. Because we had no way of determining whether or not the fish had died or shed its tag, we assumed that all ghost tags were mortalities. Although misclassification of shed tags as mortalities could lead to survival estimates that are biased low, for two reasons we are confident that tag loss was negligible. First, we employed the PIT-tagging methods of Gries and Letcher (2002) who observed high tag retention rates (99.8%) in juvenile Atlantic salmon tagged and subsequently held in a hatchery for approximately 9 months. Second, tag retention data based on a secondary mark (collected in our study reaches at the end of each season during subsequent electrofishing surveys) indicated that PIT tag retention rates were 99.4%.

Environmental data collection

Between June and October of years 2011 through 2013, we collected streamflow, water temperature, DO, and wetted volume data in each reach. Streamflow and temperature data were collected at the reach level. DO and wetted volume data were collected at the habitat unit level (DO for pools and wetted volume for pool and flatwater units) and averaged for all units within the reach for reach-scale analyses.

For streamflow data collection, we deployed and operated Azonde 2220 or In-Situ Level TROLL 500 pressure transducers in or near (within 300 m of) each reach. Each gauge recorded water stage every fifteen minutes for the duration of the study period. Streamflow was measured approximately one time each month in every reach using a USGS Price Pygmy Current Meter. Measured streamflow values were correlated with stage data at the time of measurement to create rating curves according to standard USGS protocols (Rantz et al. 1982), and the equations of these curves were used to estimate streamflow (L/s) at fifteen-minute intervals for all stage data.

To document stream temperature, we deployed Onset HOBO U22 Water Temp Pro v2 continuously-recording temperature loggers in a representative pool within each of the study

reaches between June 15 and October 15 each year. Temperature loggers were calibrated using a NIST thermometer prior to deployment and recorded water temperature at 60-min intervals.

Dissolved oxygen surveys were conducted on the same dates as PIT-tag wand surveys in each study reach using a YSI handheld DO meter with a polarographic sensor (YSI 55D or YSI Pro20, depending on year). We measured DO concentrations between 0850 and 1130 hours at a consistent depth (approximately 25 cm below the water surface) at the location of the maximum depth in each pool. DO sensors were calibrated prior to each survey and membranes were inspected and changed, as needed, following guidelines in the manufacturer's operations manuals.

Data for estimating wetted volume in each pool and flatwater unit were collected during habitat surveys conducted within one to two days of PIT-tag wand surveys. Following habitat-type classification of individual units (pool, flatwater, or riffle) during initial habitat surveys in June of each year, we established transects within each unit at two to six points (depending on unit size and configuration) that served as fixed locations for measuring wetted width and depth. Wetted length, average wetted width, and average depth were multiplied to calculate the wetted volume of each pool and flatwater unit.

Observations of surface flow disconnection during habitat surveys were related to discharge data to estimate a flow level at which pools become disconnected (connectivity threshold). Although connectivity thresholds appeared to vary by stream, we found that in almost all reaches, pools were disconnected when discharge dropped to 0.28 L/s (0.01 ft^3/s). This threshold was used to estimate the number of days that pools were disconnected in each reach.

Data Analysis

Survival estimation approach.—PIT tag detections recorded during each paired wand survey were used to construct an encounter history for each individual detected during the June survey. We used the robust design mark-recapture model (Kendall et al. 1997) in Program MARK (White and Burnham 1999) to estimate survival at the reach scale. Program MARK uses general linear modeling to estimate beta parameters, and these beta parameter estimates are combined using a sub-model (e.g., sin link, logit link) to estimate real parameters of interest (i.e., survival). This statistical approach allowed for incorporation of environmental covariates in the robust design models. By using the principals of multimodel inference (Burnham and Anderson 2002), we were able to formally evaluate the relative influence of covariates on survival.

Individuals that were detected leaving (or upstream of) the study reach during the oversummer period were assumed to have permanently emigrated and were removed from the model likelihood following the date of their last wand detection within the study reach.

We accomplished this by changing the frequency of each emigrant's encounter history to negative one. This allowed us to fix the movement parameters in the robust design to zero for all intervals. Additionally, all detections classified as ghost tags were converted from detections (1s) to non-detections (0s) beginning on the sample in which the presumed mortality was documented.

Prior to evaluating our study questions, we were interested in understanding the range in survival among reaches and years. To accomplish this, we ran a robust design model for each reach/year combination (eight reaches x three years = 24 individual models) to estimate reach- and year-specific survival. To compare among reaches and years, we standardized the survival interval to June 15 through October 15 (122 days) by adjusting the survival estimate for a given reach to the desired timeframe: standardized $\hat{S}$ = unstandardized $\hat{S}^{1/(i/122)}$), where i = the actual number of days in the study interval for the given reach.

Statistical evaluation of study questions.—Our general statistical approach was to construct model sets to evaluate specific study questions. We evaluated the strength of models within a given model set based on Akaike information criteria (AIC). To evaluate model support, we used the following guidelines (Burnham and Anderson 2002): ΔAICc within 0–2 indicated substantial support for both models; differences of 4–7 indicated considerably less support for the model with the higher ΔAICc; and differences greater than 10 indicated essentially no support for the model with the higher ΔAICc.

For environmental covariate models with high AIC support, we examined the beta associated with that covariate to determine whether the 95% confidence interval overlapped zero. For covariates where 95% confidence intervals did not overlap zero, we used the betas to estimate a function describing the relationship between that covariate and survival.

[C]*Survival in relation to stream, reach, and year (Objective 1).*—To determine whether survival varied among streams, reaches, and/or years, we evaluated a model set that included six general models: a model that constrained variation in survival among streams, reaches, and years ($S_{*,*}$), models that allowed for variation in survival among streams, reaches, or years ($S_{s,*}$; $S_{r,*}$; $S_{*,y}$), a model that allowed for variation in survival among both streams and years ($S_{s,y}$), and a model that allowed for variation in survival among both reaches and years ($S_{r,y}$). Because the number of primary sampling occasions varied by reach and year (range 3–6), we limited our dataset for this analysis to the first and last primary sampling occasions of each reach/year combination.

Survival in relation to flow-related variables (Objective 2).—We calculated multiple hydrologic metrics from the streamflow dataset to characterize the magnitude and duration of flow conditions hypothesized to impact survival. Multiple hydrologic metrics from Olden and Poff (2003) were considered for representation of critical attributes of the summer flow regime. These included average, minimum, and maximum flow conditions, as well as duration of surface flow disconnection. We also considered metrics to represent three additional flow-related variables known to influence stream salmonid populations; water temperature, DO, and wetted volume (Herrmann et al. 1962; Bjornn and Reiser 1991; Welsh et al. 2001; Woelfle-Erskine et al. 2017).

Our first step was to select a single metric to represent each of the seven flow-related variables of interest (average flow, minimum flow, maximum flow, duration of surface flow disconnection, DO, wetted volume, and water temperature). To accomplish this, we proceeded by constructing a covariate model for each candidate metric using the robust design model as previously described. For each covariate model we included the data for a given metric summarized by reach and year and used the same wand dataset as was used for the general models.

To select the metric that best represented each flow-related variable, we considered variable-specific model sets that included candidate metric models for each variable. For example, to select a metric to represent minimum flow, we considered eight models; one model for each of eight candidate metrics normalized by catchment area: average minimum daily flow; minimum 7-, 15-, and 30-day average flows; minimum 7-, 15-, and 30-day minimum flows; and 10th percentile average daily flow. The covariate in the model with highest AIC support was selected as the metric to represent minimum flow. This process was repeated for each of the seven flow-related variables resulting in seven representative metrics used for further analyses.

Our second step was to evaluate which of the seven flow-related variables had the strongest influence on survival. We used a standard normal transformation to standardize each metric and the resultant transformed values (Z scores) were included as covariates in a single robust design model that included all reaches and years as well as multiple covariates. Prior to transformation and inclusion in the model, each metric representing a given flow-related variable was tested for correlation with the remaining six representative metrics, and we excluded those that were highly correlated. For each covariate included in the final model, we examined the estimated beta ($\hat{\beta}$) and its 95% confidence interval to evaluate whether the covariate influenced survival. If the confidence interval for the beta did not overlap with zero,

we concluded that the covariate influenced survival and assessed whether the relationship was positive ($\hat{\beta} > 0$) or negative ($\hat{\beta} < 0$).

Comparison of alluvial, bedrock, and clay reaches (Objective 3).—To evaluate whether geomorphic setting affected survival, we compared a model that included geomorphic reach type (alluvial, bedrock or clay; $S_{g,*}$) with the general model $S_{*,*}$. For this analysis, we used the same wand dataset as was used for the general models representing all reaches and years (first and last primary sampling occasions only).

To further explore variation in survival among geomorphic reach types, we developed reach- and year-specific survival models for reaches representing alluvial (GRP-0.16), bedrock (GRP-1.14), and clay (GRE-13.40) geomorphic types. For this analysis, we included wand and environmental data from all reach/year combinations in which we collected data on five primary sampling occasions (four survival intervals) over the summer period (2011 to 2012 for the alluvial reach, and 2011 to 2013 for bedrock and clay reaches). For each reach, we modelled survival as a function of metrics that demonstrated a strong influence on survival from the Objective 2 analysis. For each covariate model, we combined the point estimates of the betas through the logit link to depict survival over a range of covariate values.

RESULTS

Approximately 500 juvenile Coho Salmon were stocked into each reach in each year, with the exception of GRE-13.40 in 2012 and 2013, and GRP-1.14 in 2013 when the number of fish released was reduced due to the presence of wild fish (Table 2). In 2013, we did not stock GRE-8.69 and GRP-0.16 because we presumed that water in all habitat units would disappear due to progressing drought conditions; as expected, these two reaches became completely dry. Because environmental data was collected for these two reaches in 2013, we were able to include them in our model sets by fixing survival to zero.

The average proportion (range) of fish that emigrated from the study reaches over all three years was 0.07 (0.01–0.36); in only three cases, the proportion that emigrated was > 0.10 (Table 2). Ghost tags were documented in all reaches and the number detected in each reach/year combination ranged from 15–97 (Table 2).

Capture probability averaged 0.66 over all wand surveys and ranged from 0.45–0.88. Survival of juvenile Coho Salmon between June 15 and October 15 ranged from 0–0.88 over reaches and years and decreased progressively with decreasing summer discharge from 2011 to 2013 (Figure 2, Figure 3).

Survival in Relation to Stream, Reach, and Year (Objective 1)

The reach- and year-specific model ($S_{r,y}$) had the highest AIC support when compared with all other general models in the model set (AICc weight = 1.0), indicating that survival was influenced by both reach and year. For all other models, ΔAICc was greater than 100.

Survival in Relation to Flow-Related Variables (Objective 2)

For six of the seven flow-related variables, a single metric demonstrated high support when compared with other candidate metrics within that variable (Table 3). The exception was temperature, in which MWMT and MWAT demonstrated similar support.

Survival of Coho Salmon increased as streamflow, DO, and wetted volume increased, and survival decreased with increasing days of disconnection and increasing temperature; however, the relationship with temperature was weak (Figure 4).

Following tests for correlation among flow-related variables, we chose to include days of disconnection, maximum flow, and wetted volume in the model with multiple covariates. DO was excluded because it was correlated with days of disconnection (r = 0.82, $P < 0.001$) and had a weaker relationship with survival than days of disconnection. Temperature was excluded because it was correlated with wetted volume (r = 0.51, $P < 0.05$) and had a weaker relationship with survival than wetted volume. Because of strong correlations among average, minimum, and maximum flow, we selected maximum flow as the metric to representative flow magnitude because it had a stronger relationship with survival than average or minimum flow. Correlations for all other comparisons were low (r < 0.5). When the three remaining flow-related variables were included in a single model, the betas for days of disconnection, maximum flow, and wetted volume all differed from zero, and days of disconnection had the strongest effect on survival (Figure 5).

Comparison of Alluvial, Bedrock, and Clay Reaches (Objective 3)

Overall, we observed lower survival in the three alluvial reaches (GRP-0.16, GRE-8.69, and DUT-3.87) as compared to their upstream counterparts in bedrock or clay reaches (GRP-1.14, GRE-13.40, and DUT-6.51, respectively) (Figure 3). There was strong support for the model that included geomorphic reach type ($S_{g,*}$; AICc weight = 1.0), and the point estimate for the probability of survival in alluvial reaches was 0.16 lower than in bedrock reaches and 0.38 lower than in the clay reach.

Because days of disconnection demonstrated the strongest effect on survival in our Objective 2 analysis, we explored the influence of this metric in the reach- and interval-specific survival models for the alluvial (GRP-0.16), bedrock (GRP-1.14), and clay (GRE-13.40) reaches in which primary sampling occurred on five occasions each year. Because it is likely that DO is one of the driving mechanisms behind the negative relationship between survival and days of disconnection (Figure 4), we also explored reach and interval-specific relationships between survival and DO.

With the progression of drought conditions from 2011 to 2013 (Figure 2), the number of days of disconnection increased each summer in each reach; in 2011 all reaches remained connected by surface flow, but by 2013 all reaches had extended periods of pool disconnection (Figure 6). Disconnection occurred most extensively in the alluvial reach, was intermediate in the bedrock reach, and occurred only in 2013 in the clay reach.

We also observed a general decline in DO levels in each of the different geomorphic reach types between 2011 and 2013, as well as an overall decrease in DO levels within each study season (mid-June to late-September) (Figure 7). DO levels were highest in the clay reach in nearly all intervals and years, and lowest in late-season intervals in the alluvial reach. Annual and seasonal declines in DO were most pronounced in the alluvial reach.

In general, survival remained above 0.5 in all reaches during intervals when surface flow was present, and fell below this level during intervals with extended periods of surface flow disconnection (i.e., surface flow < 0.28 L/s) (Figure 8). In most reaches and years, the lowest survival occurred during the last interval of the season, between late-August and mid-September. The clay reach had the highest survival in years 2011 and 2012, and in 2013 survival remained high until the last interval when it fell precipitously following an extended period of disconnection. Though survival in the bedrock reach was more variable than in the clay reach, it showed a similar pattern, with an extreme decline during the last interval in 2013. The alluvial reach responded differently than the other reaches; in 2011 survival fluctuated among intervals and was generally lower than in the clay and bedrock reaches, and in 2012 there was a general decline in survival over the study period even when surface flow was present. No survival data was collected in the alluvial reach in 2013; however, the reach was intermittent in June and dry in September so we can assume that, had fish been released, they all would have perished.

While the relationship between survival and days of disconnection was negative in all cases, the shape of the relationship varied among reaches and was lower in the alluvial reach (Figure 9). For example, based on our data, the model predicted that survival in the alluvial reach would drop to 0.5 following two weeks of disconnection, whereas in the bedrock and clay reaches it would take over four weeks before survival dropped to 0.5. If disconnection persists

for a long enough period of time, however, we expect survival to drop to 0 regardless of reach type. We found a positive relationship between survival and DO in all reaches (Figure 9) but survival in the alluvial reach was always lower for a given DO concentration when compared to the bedrock and clay reaches.

DISCUSSION

The results of this study advance our understanding of which flow-related variables are appropriate for describing fish–flow relationships in intermittent streams, and offer insight to managers for the development of flow-related recovery and protection strategies for sensitive salmonid species in small coastal streams. By stocking experimental fish of similar size and genetic composition at common densities, we controlled for some of the potential confounding factors affecting survival (e.g., prior residence, size, genetic composition) and we were able to look more directly at the influence of flow-related variables on survival. In almost all reaches and years, emigration from the study reaches was minimal, and our ability to account for emigration using PIT tag detection systems allowed us to estimate true rather than apparent survival.

Our finding that oversummer survival of juvenile Coho Salmon is positively associated with streamflow magnitude, wetted volume, and DO concentrations is consistent with the results of recent studies in coastal California streams (Grantham et al. 2012; Woelfle-Erskine et al. 2017). In addition, we found that the number of days of surface flow disconnection was the strongest driver of survival of juvenile Coho Salmon at the reach scale, with survival decreasing as a function of increasing days of disconnection. Furthermore, survival and its relationship to days of disconnection varied by geomorphic reach type; in an alluvial reach, survival was lower and declined more rapidly following surface flow disconnection than in either a bedrock or clay reach. Though our multiple-interval study was limited to one reach of each geomorphic type, this outcome verifies the results of May and Lee (2004) who showed higher apparent survival of juvenile salmonids in bedrock-dominated pools where more water remained for the duration of the summer season than in alluvial pools.

Influence of Flow-Related Variables on Survival of Juvenile Coho Salmon

For each flow-related variable in which multiple candidate metrics were considered, with the exception of temperature, a single metric demonstrated high model support (Table 2), and we suggest using these top metrics for future studies in intermittent streams. Most notable was the high support for the model that included the number of days that *minimum* flow fell

below 0.28 L/s (flow level at which habitat units disconnected from surface flow) when compared to the model that included the number of days that *average* flow fell below 0.28 L/s (Table 2). This suggests that even daily fluctuations to flow levels that disconnect habitat units can have a negative influence on survival, thus highlighting the importance of maintaining continuous surface flow connection to support summer-rearing salmonids.

Similar to Grantham et al. (2012), we found that variables representing streamflow magnitude (average, minimum, and maximum) are positively associated with oversummer survival of juvenile Coho Salmon. Our analysis, however, revealed a potential problem with relying on flow magnitude alone to explain fish population metrics in intermittent streams. The issue is evident in the estimated relationships between survival and flow-related variables (Figure 4) in which survival was greater than zero when flow magnitude variables were zero. This can be explained by our observation that pools held water even after surface flow dropped to zero, allowing fish to survive in residual pools. For this reason, other flow-related metrics (i.e., DO, wetted volume, and temperature) are more likely to accurately represent the conditions that fish continue to experience even after surface flow drops to zero. Indeed, we found that survival was positively associated with DO and wetted volume and negatively associated with temperature (Figure 4).

In our study, days of disconnection best explained survival (Figure 5). This metric likely represents an integration of multiple environmental and biological factors that fish directly experience, including water quality, water quantity, predation, food availability, and competition. Presumably, the longer that pools are disconnected from surface flow, the greater the probability that fish will experience mortality due to physiological stress, predation, resource availability, and/or stranding.

DO, which was highly correlated with days of disconnection, also demonstrated a strong positive relationship with survival. However, relationships between survival and wetted volume and survival and temperature demonstrated lower model support than expected given that they represent factors directly experienced by fish. We suspect this was due to increased habitat unit-level variability in these metrics following surface flow disconnection. Because our analysis was at the reach scale, important relationships occurring at the habitat unit-level may have been obscured. Further studies are needed that examine fish–flow relationships at the habitat unit-, reach-, and watershed-scales representing a broader range of streamflow, temperature, and geomorphic reach types. This would likely strengthen some of the conclusions and allow for broader management application.

Surprisingly, we found juvenile Coho Salmon surviving in pools with DO concentrations below documented daily minimum tolerance thresholds of 3.8–4.3 mg/L (WSDE 2002; Carter

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2005) and, at times, below lab-based survival thresholds of 3.0–3.5 mg/L (Davison et al. 1959; Herrmann et al. 1962; Warren 1973; WSDE 2002). It is important to recognize that our DO measurements, while consistent in terms of measurement location and time of day, only represented reach-scale averages of point location measurements and did not account for spatial variation within pools or diel fluctuations that might vary over the course of the summer. It is also possible that when DO levels declined in study reaches, juveniles were keying in to locations in pools with higher DO levels than those observed at our spot measurement locations. In other stream systems, fish have been documented moving to locations of preferred temperatures (Nielsen et al. 1994; Matthews and Berg 1997), and it would be informative to learn whether similar behavior occurs in relation to DO. While we are confident in our result that there is a positive relationship between survival and DO, further study is needed to examine microhabitat-scale relationships between continuous DO levels and fish survival, growth, and movement.

Implications for Management

The results of this study have important implications for streamflow management and salmonid recovery efforts. Our observation that juvenile Coho Salmon were able to survive at flows below 3 L/s (approximately 0.1 ft^3/s), so long as pools remained hydrologically connected, suggests that streamflow improvement projects contributing even a few L/s could allow rearing juveniles to survive the summer bottleneck in intermittent streams. Our findings also underscore the importance of considering the size, character, and geomorphic context of a watershed when estimating the benefits of a potential streamflow improvement project on fish populations. For larger, snowmelt-driven systems, a streamflow enhancement project that repurposes a few L/s to the stream is likely trivial; however, in small, coastal headwater streams that have a tendency towards intermittency, this small quantity of water could mean the difference between complete loss of a year-class of endangered salmonids versus survival to seasons of higher opportunity.

Based on the results of this study, we conclude that the number of days of surface flow disconnection is a potentially useful metric for setting management targets to prevent extirpation of juvenile salmonids rearing in intermittent streams. Although we observed reach variation in the rate at which survival declined in relation to pool disconnection, in all reaches the onset of pool disconnection represented a turning point for which water quality, water quantity, and survival all declined. In cases where flow magnitude thresholds are being developed with the goal of sustaining or recovering salmonid populations, we suggest identifying the flow (or stage) at which pools become disconnected in the stream or reach of

interest and using that value as the threshold at which the risk of mortality substantially increases.

Surviving versus Thriving

Although survival is a useful metric for examining how environmental variables affect fish populations, survival should not be the single biological response considered in the context of population recovery. Ensuring that sufficient flow is available for growth and production is also important. In this study, we determined that streamflow magnitude is positively associated with oversummer survival of juveniles and that, given suitable habitat and water quality conditions, maintaining stream connectivity has the potential to allow juvenile Coho Salmon to persist through the summer. We did not evaluate the size or condition of the fish, nor determine their fate to the smolt and/or adult stages.

We view the minimum streamflows required to maintain pool connectivity as flow levels that should be sustained in order to minimize flow-related mortality; however, such flows are likely not high enough for achieving target size thresholds or production goals. Studies have shown that reductions in streamflow decrease drift rates of invertebrate prey (Poff and Ward 1991), and that there is a positive correlation between streamflow and juvenile salmonid growth (Harvey et al. 2006; Nislow et al. 2004). Summer growth opportunity may result in larger size which, in turn, can have implications for survival to later life stages (Quinn and Peterson 1996; Ebersole et al. 2006; Bond et al. 2008; Claiborne et al. 2011). To inform the development of flow thresholds that support sufficient growth and production in intermittent streams, further work is needed to track the size and condition of summer-rearing fish, as well as their fate following the summer season. An individual-based approach that uses PIT tags and PIT tag detection systems lends itself to this type of evaluation. With the expected increase in drought frequency due to climate change and the associated increasing demand on water supply, such studies will be essential for informing strategies aimed at protecting and restoring threatened and endangered salmonid populations in intermittent streams.

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Figure 1. Locations of juvenile Coho Salmon survival study reaches (black lines) and study watersheds in the Russian River basin, California. Study reach codes refer to stream name (DUT = Dutch Bill Creek, GRE = Green Valley Creek, MIL = Mill Creek, GRP = Grape Creek) and the distance of the downstream end of each reach along the stream course (river kilometers) from the confluence.
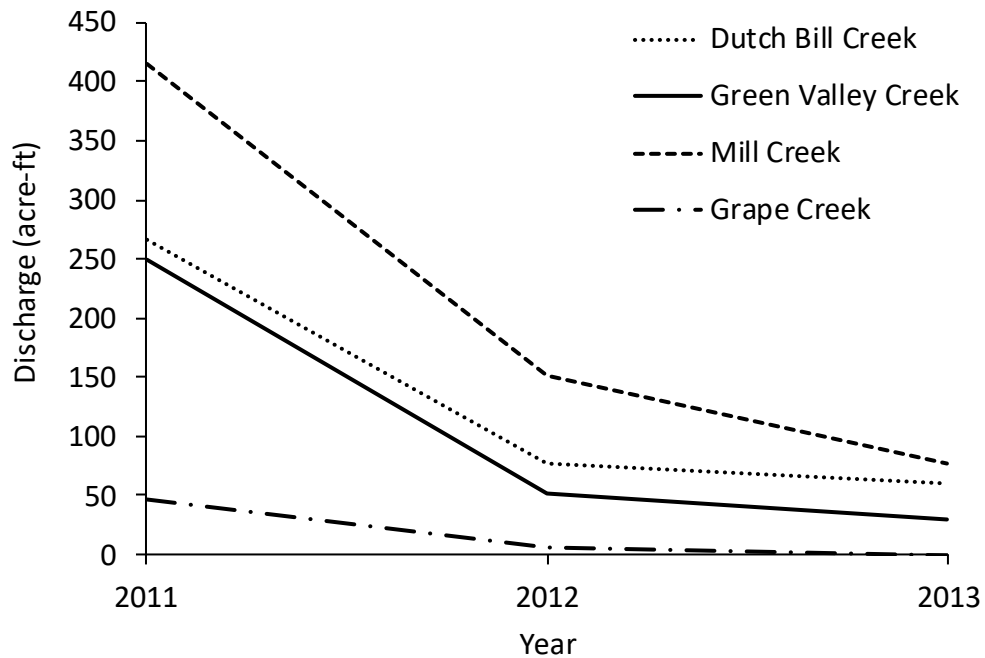
Figure 2. Total stream discharge between June 15 and September 30 by study stream, years 2011–2013 (1 acre-foot = .23 cubic decameters). Stage and streamflow data were collected at river kilometers 4.37 in Dutch Bill Creek, 9.39 in Green Valley Creek, 6.44 in Mill Creek, and 0.54 in Grape Creek.

Table 1. Characteristics of study reaches within Dutch Bill, Green Valley, Mill, and Grape creeks. Study reach codes refer to stream name (DUT = Dutch Bill Creek, GRE = Green Valley Creek, MIL = Mill Creek, GRP = Grape Creek) and the distance of the downstream end of each reach along the stream course (river kilometers) from the confluence.

Reach	Length (m)	Catchment area (km^2)	Slope (%)	Geomorphic reach type	Channel type[a]	Number[b] of pool and/or flatwater units	Average[b] shelter rating[c] ± 1 SD	Average[b] canopy (%) ± 1 SD
DUT-3.87	290	24.8	0.4	alluvial	F4	9–10	16.0 ± 0.9	93.5 ± 1.3
DUT-6.51	260	14.9	1.3	bedrock	F3	8–9	18.0 ± 3.7	96.5 ± 1.3
GRE-8.69	310	43.0	0.5	alluvial	F3	10–12	10.2 ± 2.0	90.6 ± 3.7
GRE-13.40	220	8.0	0.3	clay	B4	12–13	34.3 ± 17.3	98.0 ± 1.1
MIL-6.10	210	30.0	0.7	bedrock	F4	7–8	18.4 ± 3.4	90.4 ± 3.0
MIL-12.39	240	10.4	1.1	bedrock	F4	11–15	32.3 ± 3.8	81.3 ± 2.4
GRP-0.16	230	8.2	0.7	alluvial	F4	12	12.2 ± 4.5	92.4 ± 1.8
GRP-1.14	230	7.4	1.9	bedrock	F4	12–16	29.8 ± 5.9	98.1 ± 0.9

[a] Rosgen stream channel classification (Rosgen 1994).

[b] Reach-scale range or average over summer study periods between 2011 and 2013.

[c] Shelter composition value (0–3, with 3 being the highest complexity) multiplied by percent instream cover (Flosi et al. 2004).

Table 2. Summary of the juvenile Coho Salmon released, the number and proportion emigrating during the study period, and the number of ghost tags (i.e., mortalities or shed tags) detected in each study reach and year combination.

Year	Reach	Number of fish released	Number (proportion) of emigrants	Number of ghost tags
2011	DUT-3.87	508	12 (0.02)	30
2011	DUT-6.51	508	49 (0.10)	24
2011	GRE-8.69	510	49 (0.10)	15
2011	GRE-13.40	508	27 (0.05)	26
2011	MIL-6.10	507	9 (0.02)	17
2011	MIL-12.39	507	52 (0.10)	24
2011	GRP-0.16	510	7 (0.01)	75
2011	GRP-1.14	509	8 (0.02)	48
2012	DUT-3.87	536	28 (0.05)	97
2012	DUT-6.51	506	9 (0.02)	63
2012	GRE-8.69	510	96 (0.19)	18
2012	GRE-13.40	358 [a]	5 (0.01)	26
2012	MIL-6.10	509	16 (0.03)	35
2012	MIL-12.39	509	11 (0.02)	17
2012	GRP-0.16	508	22 (0.04)	62
2012	GRP-1.14	508	8 (0.02)	63
2013	DUT-3.87	507	78 (0.15)	84
2013	DUT-6.51	495	176 (0.36)	51
2013	GRE-8.69	0 [b]	NA	NA
2013	GRE-13.40	209 [a]	5 (0.02)	45
2013	MIL-6.10	509	53 (0.10)	62
2013	MIL-12.39	502	7 (0.01)	50
2013	GRP-0.16	0 [b]	NA	NA
2013	GRP-1.14	410 [a]	14 (0.03)	76

[a] To maintain a stocking density consistent with other reaches, the number of fish released was reduced due to presence of wild fish.

[b] No fish were released because we presumed that water in all habitat units would disappear due to progressing drought conditions.
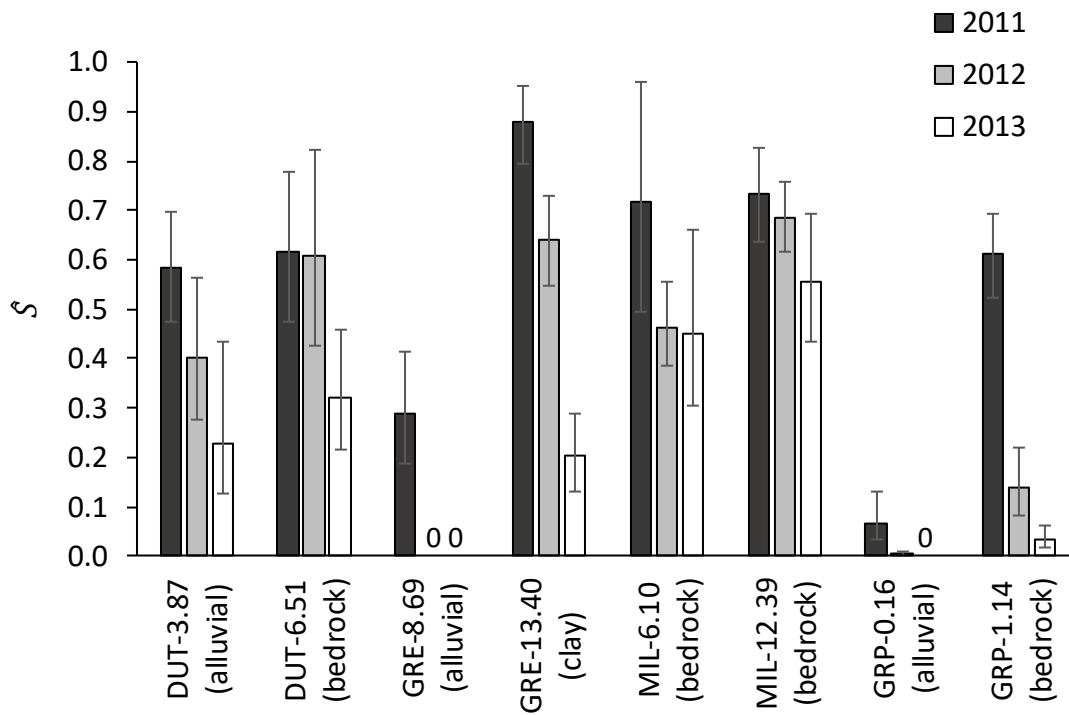
Figure 3. Estimated juvenile Coho Salmon survival ($\widehat{S}$; error bars show the 95% CI) based on PIT-tag wand data collected in study reaches between June 15 and October 15, years 2011–2013. Reach codes refer to stream names (DUT = Dutch Bill Creek, GRE = Green Valley Creek, MIL = Mill Creek, GRP = Grape Creek) and the distance of the downstream end of each reach along the stream course (river kilometers) from the confluence. Alluvial, bedrock, or clay indicates the geomorphic setting of the reach.

Table 3. Flow-related variables and metrics evaluated for use as covariates in juvenile Coho Salmon oversummer survival models. Metrics highlighted in bold italics had the highest AIC support within each variable and were used as covariates in subsequent analyses.

Variable	Metric	Units	AICc weight	ΔAICc
Average flow	*Average daily flow/catchment area*	$L \cdot s^{-1} \cdot km^{-2}$	*1.0*	*0.0*
	Median daily flow/catchment area	$L \cdot s^{-1} \cdot km^{-2}$	0.0	29.9
Minimum flow	*Minimum 30 day minimum flow/catchment area*	$L \cdot s^{-1} \cdot km^{-2}$	*1.0*	*0.0*
	Minimum 15 day minimum flow/catchment area	$L \cdot s^{-1} \cdot km^{-2}$	0.0	8.4
	Minimum 30 day average flow/catchment area	$L \cdot s^{-1} \cdot km^{-2}$	0.0	13.6
	Minimum 7 day minimum flow/catchment area	$L \cdot s^{-1} \cdot km^{-2}$	0.0	16.9
	Minimum 7 day average flow/catchment area	$L \cdot s^{-1} \cdot km^{-2}$	0.0	21.5
	10th percentile average daily flow/catchment area	$L \cdot s^{-1} \cdot km^{-2}$	0.0	23.1
	Minimum 15 day average flow/catchment area	$L \cdot s^{-1} \cdot km^{-2}$	0.0	29.5
	Average minimum daily flow/catchment area	$L \cdot s^{-1} \cdot km^{-2}$	0.0	40.9
Maximum flow	*Average maximum daily flow/catchment area*	$L \cdot s^{-1} \cdot km^{-2}$	*1.0*	*0.0*
	75th percentile average daily flow/catchment area	$L \cdot s^{-1} \cdot km^{-2}$	0.0	103.9
	90th percentile average daily flow/catchment area	$L \cdot s^{-1} \cdot km^{-2}$	0.0	135.3
Days of disconnection	*Number of days minimum daily flow < 0.28 L/s*	*days*	*1.0*	*0.0*
	Number of days average daily flow < 0.28 L/s	days	0.0	127.8
Dissolved oxygen	*Average of the minimum DO measurements recorded in each pool*	*mg/L*	*1.0*	*0.0*
	Average of all pool-level DO measurements	mg/L	0.0	44.4
Wetted volume	*Total wetted volume (average of all seasonal surveys)/catchment area [a]*	m^3/km^2	*1.0*	*0.0*
	Lowest total wetted volume of the summer season/catchment area [a]	m^3/km^2	0.0	14.0
Temperature	*Maximum weekly maximum temperature (MWMT)*	*°C*	*0.8*	*0.0*
	Maximum weekly average temperature (MWAT)	°C	0.2	2.3

[a] The total wetted volume on a given survey was the sum of the wetted volume of all pool and flatwater units within a reach.
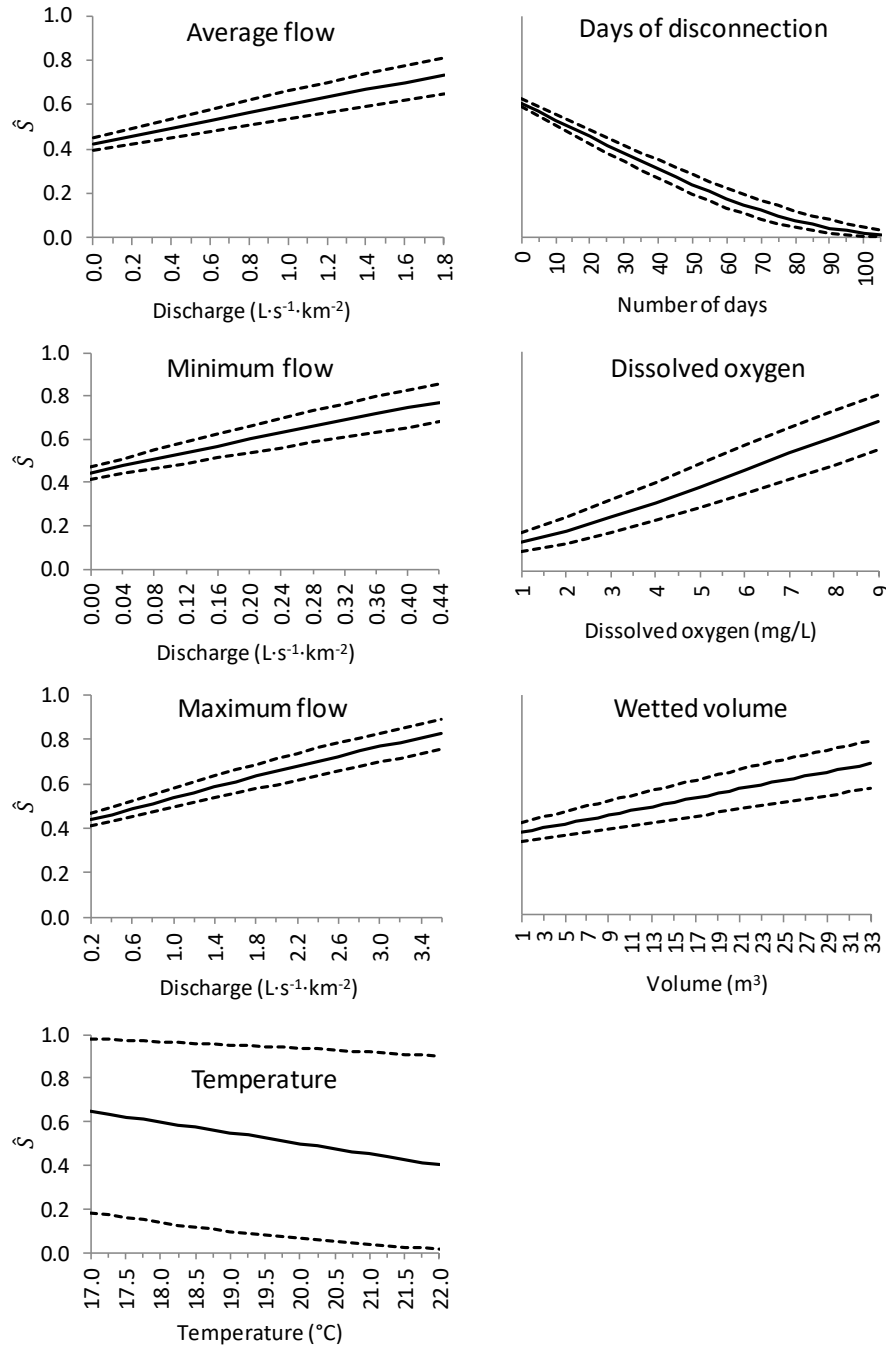
Figure 4. Estimated Coho Salmon survival ($\hat{S}$) as a function of flow-related variables based on data collected in Dutch Bill, Green Valley, Mill, and Grape creeks between June 15 and October 15, years 2011–2013. Solid lines represent estimated survival functions and dashed lines represent the 95% confidence intervals of estimated survival functions. Specific metrics are defined in Table 2. Covariate ranges reflect empirical ranges during the study period.
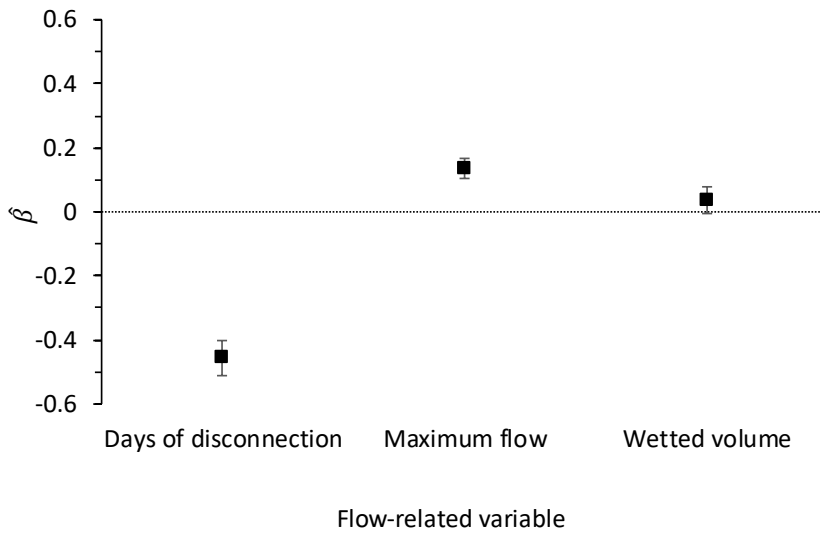
Figure 5. Estimated beta values ($\hat{\beta}$; error bars show 95% Cis) of flow-related covariates showing positive (above x-axis) or negative (below x-axis) relationships with oversummer survival of juvenile Coho Salmon, years 2011–2013 in Dutch Bill, Green Valley, Mill, and Grape creeks.
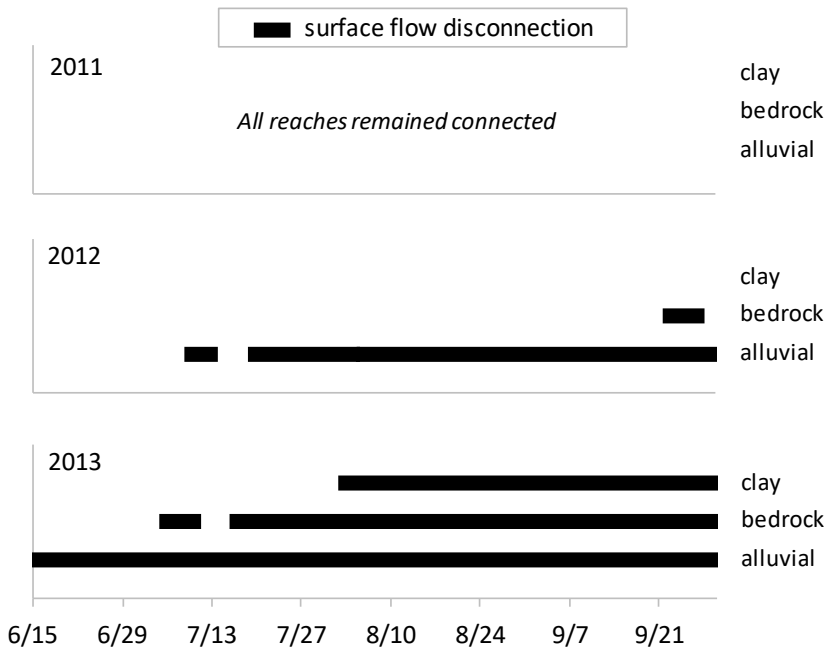
Figure 6. Days of disconnection in alluvial (GRP-0.16), bedrock (GRP-1.14), and clay (GRE-13.40) reaches between June 15 and September 30, years 2011–2013.
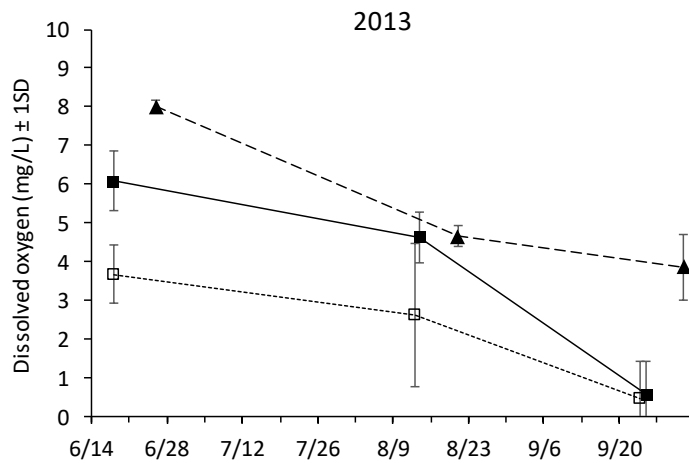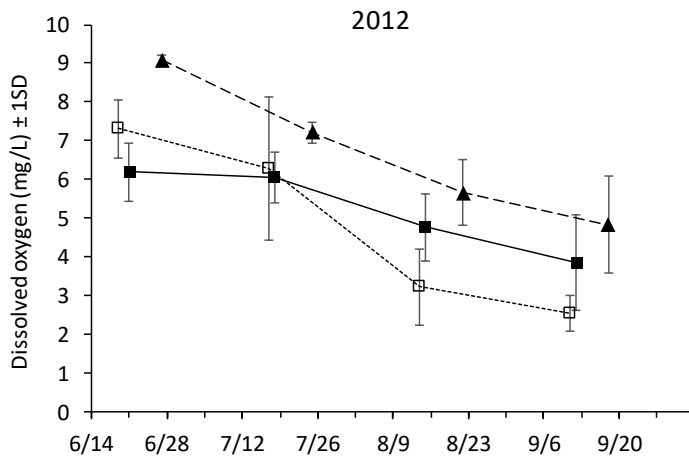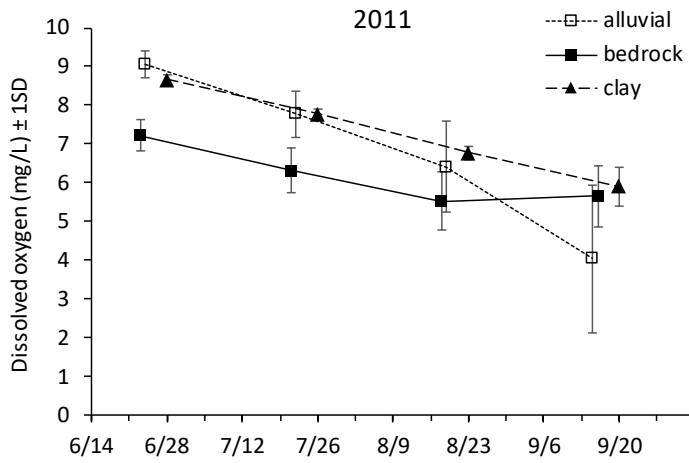
Figure 7. Mean ± SD DO levels collected on multiple dates in alluvial (GRP-0.16), bedrock (GRP-1.14), and clay (GRE-13.40) reaches during the summer dry season, years 2011–2013.
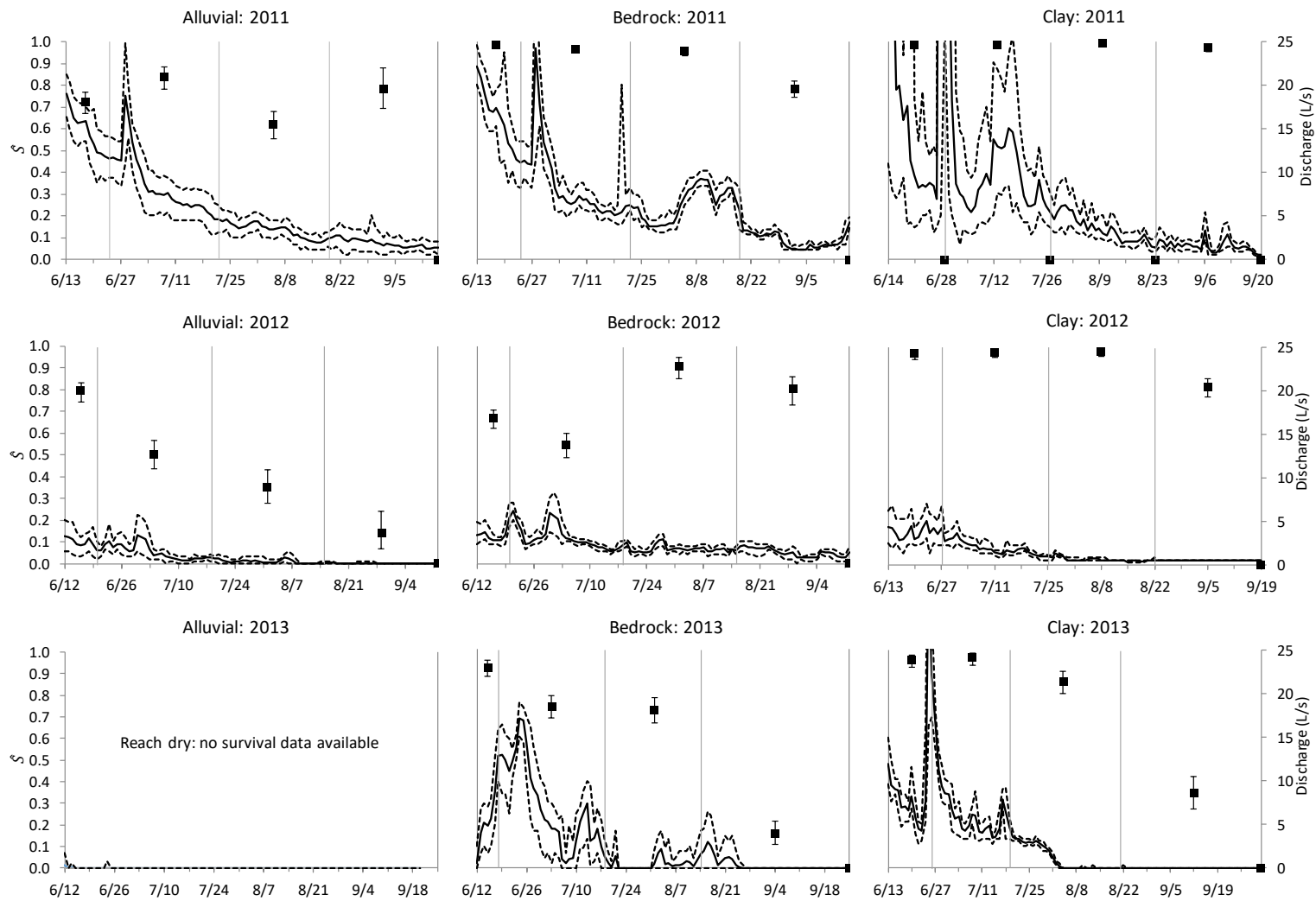
Figure 8. Average daily discharge (solid line), and minimum and maximum daily discharge (dashed lines) in relation to estimated juvenile oversummer survival ($\hat{S}$, black squares; error bars show 95% CIs) in an alluvial reach (GRP-0.16), a bedrock reach (GRP-1.14) and a clay reach (GRE-13.40), years 2011–2013. Gray vertical lines represent timing of PIT-tag wand surveys.
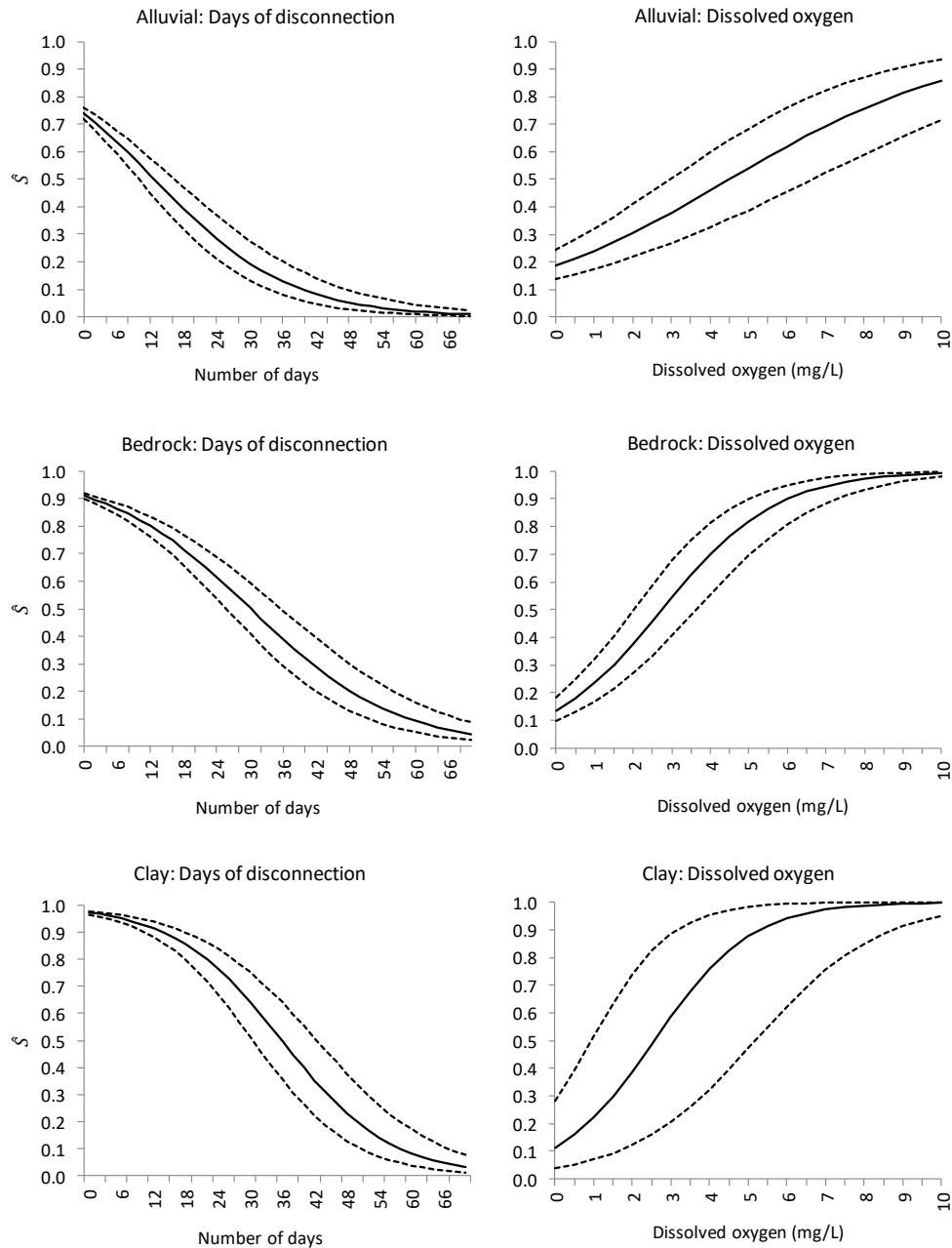
Figure 9. Estimated survival ($\hat{S}$) of juvenile Coho Salmon as a function of days of disconnection and average DO levels in alluvial (GRP-0.16), bedrock (GRP-1.14), and clay (GRE-13.40) reaches based on data collected between mid-June through September, years 2011–2012 (GRP-0.16) or 2011–2013 (GRP-1.14 and GRE-13.40). The solid lines represent estimated survival functions, and the dashed lines represent the 95% confidence intervals of estimated survival functions. Covariate ranges extend from the minimum value observed in one or more reaches to the maximum value in one or more reaches (see Figure 6 and Figure 7).