ARTICLE

The Role of Streamflow and Land Use in Limiting Oversummer Survival of Juvenile Steelhead in California Streams

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Abstract

   Increasing human pressures on freshwater resources have led to global declines in fish populations and have made the protection of instream flows critical to the conservation of riverine ecosystems. However, uncertainty in predicting ecological responses to flow variability has hindered implementation of successful environmental flow management. An improved understanding of the relationships between streamflows and Pacific salmon *Oncorhynchus* spp. population persistence is particularly needed in semiarid regions such as California, where streamflows during the dry season are highly variable and increasingly threatened by withdrawals to meet human water demands. To examine the effects of summer low flows on a threatened salmonid species, we analyzed 9 years of count data for juvenile steelhead *O. mykiss* from nine stream reaches in four coastal California watersheds. We used a Bayesian modeling framework to examine the relative influences of streamflow, land use, and habitat quality on juvenile steelhead oversummer survival. An estimated mean survival of 30% suggested that the dry season is a significant period of stress for juvenile steelhead rearing in tributary streams. The models indicated that the magnitude of summer flow and the duration of low-flow conditions were both important in explaining interannual variation in juvenile survival rates, which showed a consistent increasing trend with higher early and late-summer flows among all sites. The results also suggested an adverse effect of intensive agricultural land use on juvenile steelhead populations, while local habitat suitability had a positive effect. Although additional research is needed to identify the mechanisms by which flow influences fish survival in the dry season, these findings indicate that water quantity is a potential limiting factor to juvenile steelhead survival in coastal California watersheds and suggest that protection of summer streamflows is important for the conservation of threatened salmonid populations.

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Flow regime changes, coupled with habitat loss and degradation, have substantially impaired riverine ecosystems and focused attention on instream flow needs for freshwater biodiversity conservation (Poff et al. 1997; Bunn and Arthington 2002; Annear et al. 2004; Nilsson et al. 2005; Dudgeon et al. 2006). Several innovative approaches have been developed to set instream flow standards for freshwater ecosystems and reduce the adverse effects of water management (Richter et al. 1997; King and Brown 2006; Poff et al. 2010). However, uncertainty in predicting ecological responses to changing flow regimes, together with conflicting water use demands, has hindered the implementation of instream flow protections (Richter et al. 2003; Arthington et al. 2006). The identification of ecological flow relationships is critical for setting water allocation targets but is complicated by the multiple interacting factors that influence the spatial and temporal variation in aquatic communities. Long-term data linking biological and physical conditions are often required to accurately model flow patterns in relation to aquatic species populations, yet most studies are conducted at scales that do not fully account for the range of temporal variability and spatial heterogeneity of stream ecosystems (Webb et al. 2010). Thus, there is a persistent need for data collection efforts that make it possible to infer quantitative relationships between flow variability and ecological responses (Poff and Zimmerman 2010).

The effects of seasonal drought on fish population dynamics have received increased attention in recent years (Hakala and Hartman 2004; Magalhães et al. 2007; Riley et al. 2009), yet surprisingly little is known about the role of dry-season flows in supporting threatened and endangered fishes in the western USA. In California, for example, Central Coast steelhead *Oncorhynchus mykiss*, listed in 1997 as a threatened species under the federal Endangered Species Act, inhabit streams that experience predictable seasonal droughts that vary in year-to-year intensity (Gasith and Resh 1999). The summer low-flow period is associated with the contraction of stream habitat that can concentrate fish into high densities, where they are subject to increased physiological stress and risk of mortality due to competition, predation, and stranding (Magoulick and Kobza 2003; May and Lee 2004; N. R. Bond et al. 2008; Stradmeyer et al. 2008; Irvine et al. 2009). Previous research from California streams also indicates that higher temperatures and reduced hydrologic connectivity in the dry season can result in low to negative growth rates for juvenile steelhead (Boughton et al. 2007; Hayes et al. 2008). Nevertheless, steelhead are often more abundant in intermittent tributary streams in coastal California watersheds despite the availability of perennial main-stem habitats (Boughton et al. 2009). Since body size of steelhead at the time of marine entry is an important determinant of adult returns (M. H. Bond et al. 2008), the environmental conditions experienced in these upland watersheds during the 1–4-year rearing period may be a limiting factor to smolt production (Hayes et al. 2008).

Understanding the relationships between flow conditions during the dry season and juvenile salmon survival is particularly important in California, where the low-flow period coincides with peak agricultural and residential water demands. Like other regions with a Mediterranean climate (Underwood et al. 2009), coastal California watersheds are experiencing extensive land use conversions dominated by the expansion of vineyards and exurban development (Merenlender 2000; Merenlender et al. 2005; Newburn and Berck 2006). The accompanying demands for water are often met by direct abstractions of surface water or shallow groundwater pumping in the vicinity of streams (Deitch et al. 2009). Such water withdrawals have the potential to accelerate stream drying, which decreases the magnitude of flows and increases the duration of the low-flow period, thus limiting the availability of summer rearing habitat for fish. Current growth in water demands, coupled with projected climate change impacts on aquatic ecosystems (Meyer et al. 1999), suggests that California streams will continue to become less suitable for rearing juvenile salmonids during the dry season. Therefore, understanding how streamflow variability, habitat, and land use influence the abundance and oversummer survival of juvenile steelhead is essential to proactively manage and define conservation policies for this threatened freshwater species.

We analyzed a long-term biological data set to evaluate the role of dry-season flows as a potentially limiting factor to juvenile steelhead, and assessed other local and landscape factors that may influence oversummer survival. The analysis focused on 9 years of fish count data collected from nine stream reaches in four coastal watersheds of Sonoma County, California (Figure 1), where stream biological monitoring is rare owing to the predominance of private lands (Hilty and Merenlender 2003). Fish surveys were conducted in habitat units with limited surface water connectivity at the beginning and end of the dry season, yielding estimates of apparent survival over the low-flow period. Streamflows were modeled in each of the sampling reaches by using rainfall–runoff relationships, and the dominant land use types in the watershed above each reach were quantified. The fish count and environmental data were then analyzed in Bayesian logistic regression models to examine the influence of multiple environmental variables on oversummer survival, while accounting for potential estimation bias resulting from repeated sampling and spatial clustering of observations. We employed a Bayesian hierarchical modeling approach (Gelman and Hill 2007) because it offers a flexible framework to analyze data from multiple nonreplicate sampling units and can greatly improve inferential strength in the data-poor situations that are common to ecological monitoring (Webb et al. 2010). Our approach makes use of the long-term observation record, repeated-count structure, and spatial stratification of the sampling data to identify the relative effects of streamflow, habitat quality, and land use on the oversummer survival phase of steelhead. Such information is important for guiding the management of freshwater resources and developing effective conservation
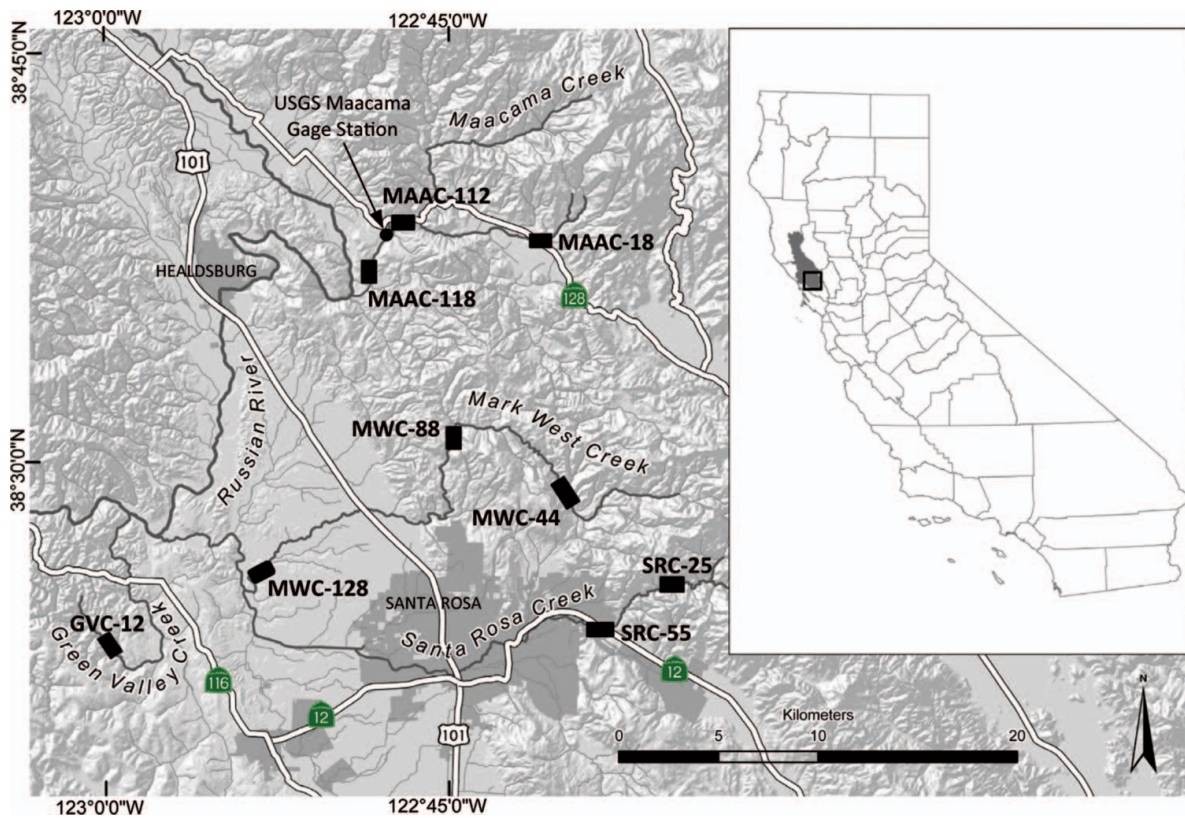
FIGURE 1. Locations of juvenile steelhead survey reaches (black boxes) in Russian River tributary streams, California. Site codes refer to reach location (GVC = Green Valley Creek; MAAC = Maacama Creek; SRC = Santa Rosa Creek; MWC = Mark West Creek) and catchment area (km^2). [Figure available online in color.]

strategies for threatened salmonid populations in the Mediterranean climate of California and other water-stressed regions.

STUDY AREA

Maacama, Mark West, Santa Rosa, and Green Valley creeks are tributaries of the Russian River in northern coastal California (Figure 1). These medium-sized watersheds (12–128 km^2) are located in the southeastern portion of the Russian River basin (3,850 km^2) and are not affected by major dams that regulate flows. Elevations range from 15 to 40 m above sea level at the confluence to 400 m in the creek headwaters. The study area is located in the coastal Mediterranean climate region characterized by cool, wet winters and hot, dry summers. Virtually all annual precipitation (mean = 90 cm) occurs between November and March; as a result, streamflows peak in the winter months and gradually recede through the spring to approach or reach intermittency by the end of the dry summer season. Mean dry-season discharges in the larger study basins (>100 km^2) typically range from 0.03 to 0.07 m^3/s, while dry-season discharges in the smaller study basins (<100 km^2) are typically less than 0.02 m^3/s. Mixed-hardwood forests, oak savannas, and grasslands constitute the majority of the natural vegetation cover in the study watersheds. The region is known for its premium wine

grape production, and vineyards are commonly found in valleys and moderately sloped areas. Santa Rosa (with a population of approximately 160,000) and Healdsburg–Windsor (with a population of approximately 30,000) are the major urban centers in the Russian River basin. However, vineyards and exurban use occupy more land area and represent the predominate types of new development in the region (Merenlender et al. 2005; Newburn and Berck 2006).

METHODS

Juvenile steelhead surveys.—Fish sampling was conducted between 1994 and 2002 by fisheries biologists as part of a long-term environmental assessment program funded by the city of Santa Rosa (Merritt-Smith Consulting 2003). The surveys were focused in three sampling reaches of Maacama and Mark West creeks, two reaches of Santa Rosa Creek, and one reach of Green Valley Creek (Figure 1). Reaches located within the same stream were separated by at least 4 km. Mean bankfull channel widths were 3–4 m in the upper reaches (drainage area <25 km^2) and 5–6 m in the middle and lower stream reaches. Stream habitat was classified by the habitat unit approach (Bisson et al. 1982) in which a unit is defined as a continuous portion of the stream of variable length where only one habitat type is present or
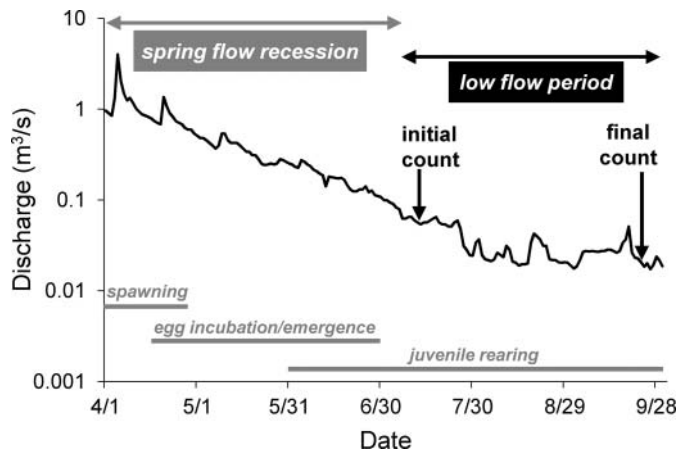
FIGURE 2.   Typical spring–summer hydrograph of streams in coastal California, with discharge plotted on log-transformed axis, illustrating dry-season flow patterns and timing of fish sampling in early and late summer. Gray bars denote life history stages for salmonids in the study region.

dominant. Between 6 and 10 physically discrete habitat units (riffles and pools) were identified in each reach for sampling. Selection of habitat units within a reach was biased toward deep (>0.5 m) habitat units because most fish tended to concentrate in those units during the dry season. In particularly dry years, deep pools offer the only suitable habitat available in the summer months, though they represent a small proportion of the total stream length. The same habitat units were sampled in consecutive years, but occasionally winter storms would modify or eliminate particular units. In those instances, a new habitat unit in the same stream reach would be sampled the following year.

Fish counts were conducted semiannually during the summer rearing period, first in July (approximately 1 month after fry emergence) and again in early fall (October; Figure 2). The first (midsummer) sampling event coincided with the period in which streamflows reached very low (<0.1 m^3/s) or intermittent conditions that generally persisted through October, when the streams were resampled. Under these low-flow conditions, surface water connectivity between habitat units is limited and confines fish to discrete wetted channel areas in an otherwise dry streambed. Therefore, the low surface water connectivity between habitat units was assumed to restrict the movement of fish such that observed declines in abundance between the mid- and late-summer sampling events reflected juvenile fish mortality. This assumption was supported by the fact that among all paired observations (mid- and late-summer counts, $n = 523$) over the 10-year period, less than 10% of samples ($n = 90$) indicated an increase in the number of individuals between sampling events. In the majority of those instances, the count increase was by fewer than five individuals, which may have also been attributed to detection error. Furthermore, of the 90 observations in which no juvenile steelhead were observed in the midsummer sampling event, individuals were detected in the subsequent sampling event in only 10 instances.

All field sampling was conducted by the same two-person team throughout the 9-year period. Fish were collected in each habitat unit by repeated passes through the stream with pole seines, approximately 1.2 m deep × 1.5, 4.5, or 7.5 m long, with a 0.5-cm mesh size. Before sampling, blocking nets were placed across the ends of each habitat unit and any mobile instream objects that could obstruct the nets were temporarily removed. Multiple passes were made with the seines until no individuals were captured. Typically, three to five passes were made, but in structurally complex units up to 10 passes were necessary to exhaustively sample a unit. After each pass with the seine, captured fish were temporarily relocated into buckets containing aerated water and then were sorted by species and counted. Between 50 and 55 habitat units were sampled in each year in the midsummer and late summer, yielding a total of 523 observations over the period of study.

Streamflow variables.—To estimate flow conditions at each of the reaches during the 9 years of fish sampling, we developed a rainfall–runoff regression model that predicted mean daily flows (m^3/s) based on daily rainfall records. We used U.S. Geological Survey (USGS) flow data from Maacama Creek (USGS station 11463900; 1961–1980) and Santa Rosa Creek (USGS station 11465800; 1959–1970) and rainfall records from a nearby precipitation station (Healdsburg, California) to fit a log-linear regression model of mean daily flows to rainfall occurring in antecedent periods (e.g., previous 1–7 d, 8–15 d, 16–30 d, and so on). Precipitation records from the study period (1994–2002) were then used to estimate daily flows at the study sites, scaling by differences in drainage area and precipitation between the study sites and reference gauges. Model performance was assessed by comparing predicted daily flow with discharge measurements made at each reach after the study period (2003–2006). There was a significant correlation ($r > 0.90$, $P < 0.01$) between predicted and measured flow values at all sites based on at least 12 flow measurements.

Multiple hydrologic metrics were generated from the modeled flow data to represent interannual and seasonal variation in summer streamflow characteristics (1 July to 30 September). The analysis was focused on metrics that described the annual dry-season flow recession by the magnitude of early summer flows and severity of low-flow conditions (Table 1). Because flows recede from the beginning to the end of the dry season (Figure 2), the upper part of the frequency distribution of daily flows represents early season flow conditions, while the lower part of the distribution represents late-season flow conditions. Therefore, the 90th and 75th percentiles, median, and mean of daily flows were used to characterize the magnitude of early summer flow at each site in each year. The severity of late-season low-flow conditions was represented by the 25th and 10th percentile of daily flows and minimum mean flows that occurred over 7-, 15-, and 30-d periods. Although the early season and low-flow metrics are calculated from the same distribution of daily flows, they are not always positively correlated. For example, in a given year it is possible to have high flows in

TABLE 1. Flow variables used in the analysis of juvenile steelhead survival patterns in Russian River tributary streams, California. Flow metrics are calculated from the distribution of daily summer flows (1 July–30 September) for each reach in each year. All metrics (dimensionless) are scaled by the long-term (1961–1980) annual mean daily discharge to allow comparisons among reaches with different drainage areas.

Flow metric	Mean	SD	Minimum	Maximum
Early summer flow magnitude				
90th percentile of daily flow	3.20	2.49	0.38	11.73
75th percentile of daily flow	2.31	1.88	0.14	10.48
Median daily flow	1.32	1.16	0.01	7.44
Mean daily flow	1.60	1.20	0.18	6.69
Low-flow severity				
25th percentile of daily flow	0.64	0.46	0.00	2.24
10th percentile of daily flow	0.47	0.36	0.00	2.21
Minimum mean 7-d flow	0.40	0.32	0.00	1.70
Minimum mean 15-d flow	0.45	0.35	0.00	2.23
Minimum mean 30-d flow	0.56	0.41	0.00	2.45

the early summer followed by a steep flow recession and severe low-flows in the late summer. In another year, lower early summer flows could be followed by a moderate flow recession and mild low-flow period. Thus, the early season flow and low-flow metrics vary in each year of the study depending on the particular form of the summer hydrograph. To allow comparisons of flow dynamics among reaches with different drainage areas, all metrics were expressed as a percentage of the annual mean daily discharge (Table 2), which was estimated at each site from the long-term USGS summer flow records for Maacama Creek (1961–1980), scaling by drainage area and precipitation.

Land use and habitat variables.—To quantify the potential effects of land use on oversummer survival, we measured vineyard land cover, rural residential development density, and road density in the watersheds above each study reach (Table 2). These variables were selected to reflect the dominant land uses in the study watersheds that have previously been shown to influence streamflow and habitat quality (Lohse et al. 2008; Deitch et al. 2009). Vineyard land cover was measured within a geo-

graphical information system (GIS) based on aerial photographs taken in 1993, 2000, and 2002. Total vineyard land cover was divided by the drainage area above each study reach to obtain percent vineyard land use. To estimate the change in vineyard land cover for each year of the study (1994–2002), the differences in percent cover observed in the three time periods of the photographs were calculated. Assuming a constant rate of land use change for each study reach, the observed difference in vineyard cover was divided by the elapsed years between aerial photographs. In 1994, vineyard land cover in the watersheds of the study reaches ranged from 0.74% to 5.70%. There was evidence of vineyard expansion in all watersheds, and by 2002 the range of vineyard land cover percentages had increased to 0.98–7.34% (Table 2). The density of rural residential development calculated from county parcel maps was between 0.2 and 2.8 housing units/km^2. Road densities were calculated within a GIS based on 1:24,000-scale U.S. Forest Service Cartographic Feature Files published in 2002. Road densities in the study watersheds ranged from 0.45 to 1.60 km/km^2. Data were not

TABLE 2. Annual discharge and variation in land use within catchments above the sampling reaches in Russian River tributary streams, California. Study site codes refer to reach location within each creek (GVC = Green Valley Creek; MAAC = Maacama Creek; SRC = Santa Rosa Creek; MWC = Mark West Creek) and drainage area (km^2).

Study site	Mean annual discharge (m^3/s)	Vineyard cover 1994 (%)	Vineyard cover 2002 (%)	Rural density (parcels/km^2)	Road density (km/km^2)	Mean habitat score (rating)
GVC-12	0.28	3.02	3.35	0.27	1.29	1.00
MAAC-18	0.36	2.89	5.93	0.02	0.40	0.81
SRC-25	0.59	0.97	0.99	0.03	0.48	0.93
MWC-44	0.98	1.37	1.78	0.42	0.99	0.60
SRC-55	1.10	0.74	0.95	0.52	1.41	0.85
MWC-88	1.90	1.05	1.46	0.98	1.02	0.87
MAAC-112	2.37	3.48	5.98	0.10	0.36	0.74
MAAC-118	2.47	4.99	7.34	0.22	0.45	0.32
MWC-128	2.50	5.70	6.83	2.84	1.59	0.66

available to calculate the temporal changes in rural residential development or road densities over the study period.

A habitat assessment was conducted in 1994 for all study reaches by the fish survey team. Each sampled habitat unit was mapped and a qualitative summer habitat suitability score was assigned based on the presence of preferred features of rearing juvenile steelhead at least 1 month postemergence (fork length > 30 mm). Habitat units were assigned a score from 1 to 3 (with 3 representing the highest habitat suitability) based on the availability of instream shelter (e.g., woody debris, rootwads, or overhanging banks) and presence of riparian vegetation cover that provided shade to the stream channel. To ensure consistency and minimize potential observer bias (Poole et al. 1997), all surveys were performed by a single individual who was experienced in fish habitat classification. Owing to the nature of the assessment method, the potential effects of different habitat components on fish abundance and survival could not be evaluated independently. The number of units with a rating of 3 ($n = 329$) was substantially greater than units with ratings of 1 ($n = 63$) and 2 ($n = 49$), so for regression purposes the habitat rating was transformed into a dichotomous variable representing high (scores of 3) and low (scores of 1 and 2) summer habitat suitability.

Modeling of oversummer survival.—We used a hierarchical modeling framework (Gelman and Hill 2007) to identify the effects of streamflow variability, habitat, and land use on apparent oversummer survival of juvenile steelhead. The analysis was focused on young-of-the-year (age-0) steelhead, which were distinguished from fish of older age-classes (age 0 +) based on fork length. Survival probability (ϕ) of fish within each habitat unit was estimated using a binomial distribution of the number of surviving fish (S) sampled from those counted in the early summer survey (N),

$$S_{ijt} \sim \text{Binomial}(N_{ijt}, \ \phi_{ijt}), \qquad (1)$$

where ϕ_{ijt} is the estimated survival of individuals in habitat unit i in reach j and year t. The population in each unit is assumed to be closed to immigration and emigration between sampling events, and counts on the same unit in different years are considered independent. Initial fish counts with no fish present ($n = 90$) were excluded to yield 443 paired (midsummer and late-summer) observations. The logit link function was then used to express survival probability for the unit as a linear function of the explanatory variables,

$$\text{logit}(\phi_{ijt}) = \beta_0 + \sum \beta_k X_k + b_j, \qquad (2)$$

where β_0 is the model coefficient for the mean intercept and β_k are the coefficients for the explanatory variables. The reach-specific random effect b_j was included to account for clustering of observations and potential influence of unobserved covariates within each reach. The random effects account for dependencies

in the data to provide robust SE estimates of the regression coefficients.

The analysis was done in a Bayesian framework, which is well suited to fit hierarchical models that accommodate variation in the data due to nonindependence of observations (Congdon 2006). We conducted model fitting with Monte Carlo Markov chain (MCMC) methods (Gilks et al. 1996) using WinBUGS (Spiegelhalter et al. 2003). Prior distributions for regression coefficients were normal with means of zero and SDs of 1,000. The random effects were assumed to be drawn from a normal distribution with mean of zero and a SD that was estimated from the data. Priors for the SDs of the random effects were uniform between 0 and 100. The vague priors specified in the model meant that they had little influence on the posterior distributions of the parameters. For each model, three Monte Carlo Markov chains with different initial values were simulated for 100,000 iterations after a burn-in of 25,000 iterations, thinning by a factor of 10 to reduce autocorrelation in the sample. The burn-in was more than sufficient to ensure that the MCMC samples were being drawn from the stationary distribution, based on visual inspection of chain convergence and Gelman–Rubin diagnostics (Gelman and Rubin 1992). To improve the efficiency of the MCMC sampling, all explanatory variables were centered by subtracting the mean. The focus of our analysis was on the resulting posterior distributions of parameters of the survival models. For each parameter, the mean and 2.5th and 97.5th percentiles of the posterior distribution are reported. This interval represents a 95% Bayesian credible interval (CI), which expresses the level of uncertainty in the parameter estimate. If working within the null-hypothesis testing framework, a parameter with a 95% CI that does not encompass zero is similar to rejection of the null hypothesis of no effect.

We evaluated candidate models with different combinations of flow, land use, and habitat variables (Tables 1, 2). Early summer fish density (number of individuals per unit length) and a categorical variable for habitat unit type (pool or riffle) were also included as covariables to control for their potential effects on oversummer survival. To identify the flow metrics that best explained patterns in survival, the effects of all individual and paired variables (consisting of a seasonal summer flow magnitude and a low-flow variable) were evaluated (Table 1). Before assessing the significance of variable pairs in the models, all pairs of highly correlated ($r > 0.70$) flow metrics were eliminated in order to limit redundancy among variables (Olden and Poff 2003) and minimize model selection bias due to multicollinearity (Zar 1999). Correlation among all other variables within each candidate model was less than 0.50. The fit of the models to the data was assessed by using the deviance information criterion (DIC; Spiegelhalter et al. 2002). The DIC value of a model reflects the trade-off between the fit of a model and its complexity, with smaller values indicating a better model. When DIC values differ by less than 2, this indicates that the models are largely indistinguishable; DIC difference values of 3

or greater indicate that the model with the smaller DIC is likely to be superior.

Based on the parameter coefficients from the best models, we assessed the relative influence of each variable on oversummer survival. The multiplicative effect (E_k) was calculated as the ratio of predicted maximum and minimum survival probabilities evaluated over the range of the data for each explanatory variable from the following equation:

$$E_k = \frac{\phi_{max}}{\phi_{min}} = \frac{1 + e^{-[\bar{\beta}_0 + (\beta_k \times \min k) + \bar{\beta}_1 \bar{X}_1 + ... + \bar{\beta}_5 \bar{X}_5]}}{1 + e^{-[\bar{\beta}_0 + (\beta_k \times \max k) + \bar{\beta}_1 \bar{X}_1 + ... + \bar{\beta}_5 \bar{X}_5]}}, \quad (3)$$

where ϕ_{max} and ϕ_{min} are survival estimates for the maximum and minimum data values, respectively, of each of the k explanatory variables (X) over the 95% CI of the parameter estimate (β_k), holding all other variables and their respective data constant at their mean values. A multiplicative effect of less than 1 indicates a decrease in the response variable, while an effect greater than 1 indicates an increase. The magnitude of the effects reflects the predicted change in the response variable evaluated over the range of the explanatory variable. The 95% CI shows the range of plausible values for the multiplicative effect of a variable, with an effect of 1 indicating no change in survival probability (i.e., no detectable effect).

RESULTS

Seasonal and Annual Variation in Fish Counts

Over 90% of individual salmonids captured during sampling were age-0 steelhead, and few individuals of older age-classes were present. The mean $\pm$ SD length of captured age-0 steelhead was 69.1 ± 10.6 mm in the early summer and 79.2 ± 9.6 mm in the late summer. The mean $\pm$ SD density of age-0 steelhead in the early summer was 1.6 ± 2.4 fish/m of stream length, and the density range was 0–27 fish/m (minimum–maximum) based on 443 habitat unit observations over the study period. Mean fish densities in the early summer varied among reaches (Figure 3A) but were more constant among years and consistently fell between 0.9 and 2.0 fish/m (Figure 3B). Middle and upper stream reaches with smaller drainage areas (<100 km^2) supported higher steelhead densities than lower stream reaches (drainage areas > 100 km^2). Between the early and late-summer counts, fish densities declined, on average, by 1.1 fish/m (or 68%). Variation in fish densities also decreased; the late-summer density SD was 1.0 fish/m and ranged from 0 to 11 fish/m (minimum–maximum). Variation in fish densities among reaches was consistent in the early and late-summer surveys, such that reaches with higher fish densities in the early summer also tended to have higher fish densities in the late summer (Figure 3A). However, changes in fish densities among years were less predictable, and years with the highest early summer fish densities were not necessarily those with the highest late-summer fish densities (Figure 3B).
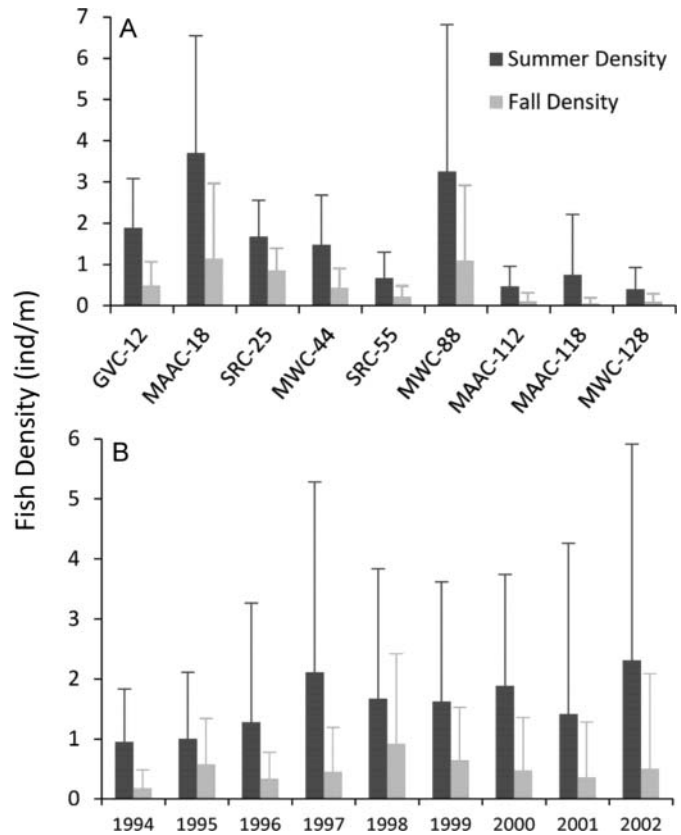

FIGURE 3. Observed early summer and late-summer (fall) densities (individuals [ind]/m) of juvenile steelhead **(A)** among reaches on Maacama Creek (MAAC), Mark West Creek (MWC), Santa Rosa Creek (SRC), and Green Valley Creek (GVC); and **(B)** among years. Numbers in site codes indicate the drainage area (km^2) above each reach. Whiskers on bars represent 1 SD from the mean. Data are from repeated fish surveys conducted in isolated habitat units ($n = 38$–56 per year) in the early and late summer over a 9-year period (1994–2002).

Juvenile Steelhead Oversummer Survival

Survival models were evaluated for the age-0 steelhead count data. The limited number of observations and low number of individuals made it infeasible to examine fish of older age-classes in the same modeling framework. Model selection using DIC values identified one model that was superior to all other candidate models. The best model contained variables for summer flow dynamics (75th and 10th percentiles of daily flows), vineyard use, initial fish density, habitat suitability, and the pool categorical variable (Table 3). Survival estimates of juvenile steelhead from early to late summer ranged from 2% to 71%, with a mean $\pm$ SD of 30 ± 14% across all sampled units.

The models provided support for a strong response in juvenile steelhead survival to the magnitude of summer flows and severity of low-flow conditions. The apparent positive response in survival to flow was observed for all pairs of flow metrics (Table 1), but the models with the 75th and 10th percentile flow variables provided the best fit to the data based on the comparison of DIC values. The final model predicted a multiplicative effect

TABLE 3. Estimated coefficients (mean, SD, and 95% Bayesian credible interval [95% CI]) of a logistic regression model for oversummer survival of juvenile steelhead in Russian River tributaries ($n = 396$).

Variable	Mean	SD	95% CI	
			Lower limit	Upper limit
Constant	−1.363	0.332	−2.022	−0.691
Summer fish density (fish/m)	−0.024	0.006	−0.035	−0.012
75th percentile summer flow[a]	0.320	0.017	0.287	0.354
10th percentile summer flow[a]	0.450	0.121	0.212	0.687
Vineyard land cover (%)	−0.295	0.044	−0.383	−0.208
Pool[b]	0.169	0.049	0.074	0.264
Habitat suitability (high)[c]	0.369	0.082	0.209	0.531

[a]The 75th and 10th percentile flow metrics represent early summer flow conditions and late-season low-flow conditions, respectively; both metrics (dimensionless) were scaled by annual discharge at each site to allow comparisons among reaches with different drainage areas.

[b]Categorical variable that distinguishes between pool and riffle habitat units.

[c]Categorical habitat variable that distinguishes between units with high and low summer habitat suitability based on the availability of instream shelter and the presence of riparian canopy cover.

of approximately 5.1 (95% CI = 4.8–5.3), indicating a five-fold increase in mean survival rates when comparing years with the lowest to highest early summer flows, represented by the 75th percentile of daily flows (Figure 4). The severity of late-summer low flows (represented by the 10th percentile of daily flows) also had a strong positive relationship with survival, with a multiplicative effect of 1.9 (95% CI = 1.4–2.5). The model predicted a significant increasing trend across the range of observed early summer flow and low-flow conditions (Figure 5A, B). The positive trend of increasing flows was consistent across reaches with different drainage areas, although reaches with larger watershed areas (90–130 km^2) had consistently lower survival rates than reaches with smaller watershed areas (<90 km^2; Figure 5A, B). The reaches located in the upper watershed (area < 40 km^2) also tended to have higher survival rates than the reaches with moderately sized watersheds (40–90 km^2).
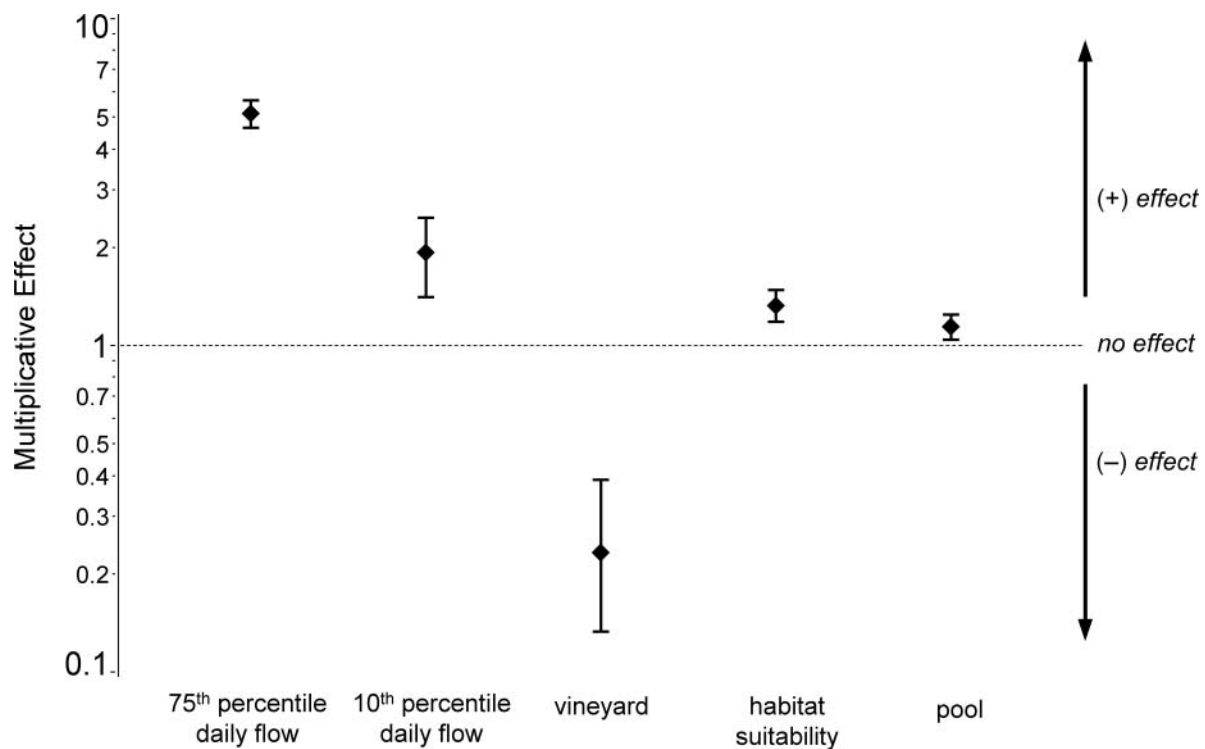

FIGURE 4. Mean multiplicative effects (± 95% Bayesian credible interval) of 75th and 10th percentile daily summer flows, vineyard land cover, habitat suitability, and habitat type (pool versus riffle) on juvenile steelhead oversummer survival calculated from logistic regression model coefficients (Table 3), indicating the predicted magnitude of change in the response variable over the range of each explanatory variable.
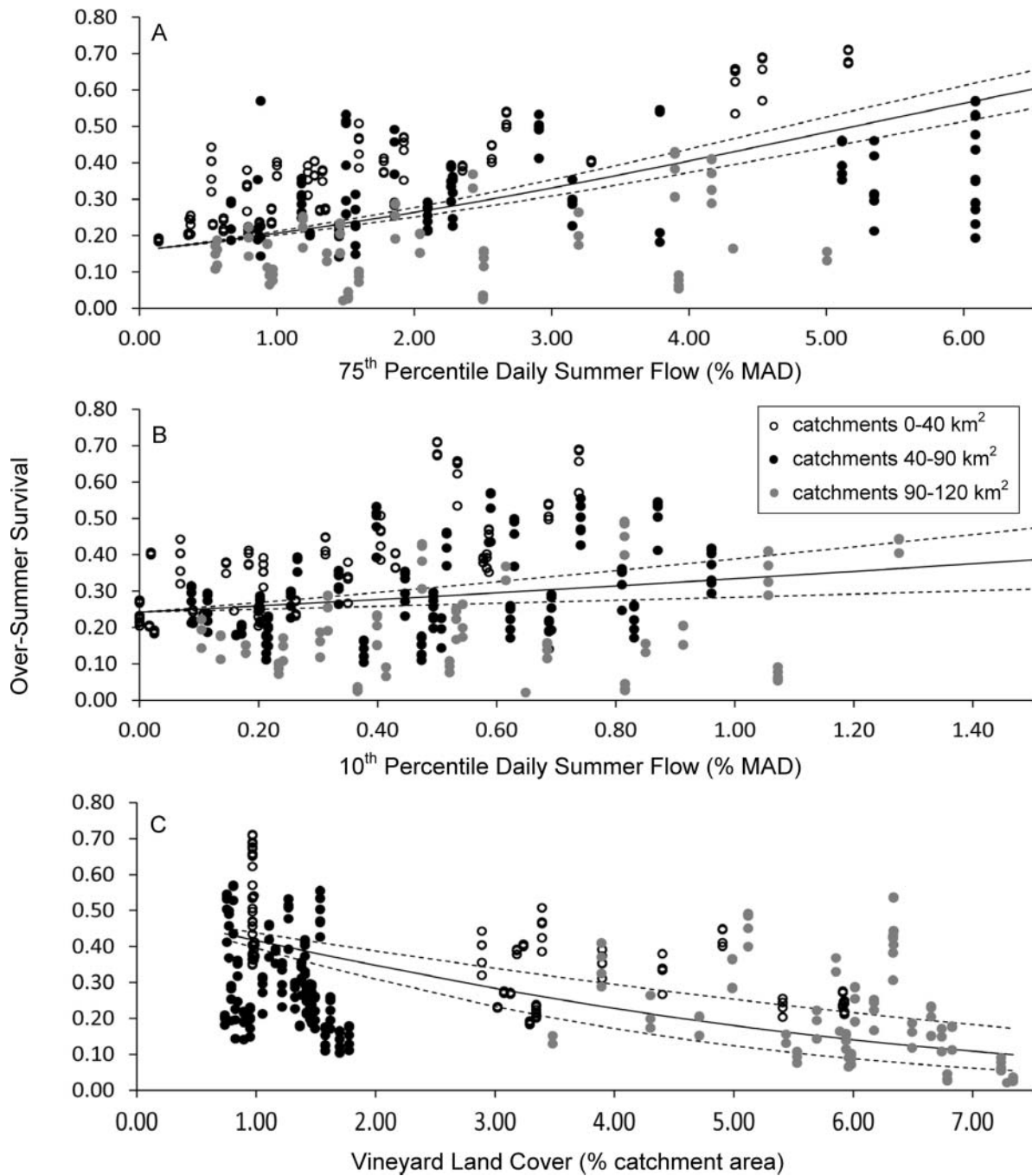
FIGURE 5. Predicted relationship of juvenile steelhead oversummer survival to **(A)** 75th percentile of daily summer flow, **(B)** 10th percentile of daily summer flow, and **(C)** vineyard land use, conditional on the mean value of all other variables and logistic regression model coefficients. Flow variables are standardized by mean annual daily discharge (MAD) to allow for comparisons among reaches. Data points are survival estimates from reaches with small (GVC-12, MAAC-18, SRC-25; open markers), medium (MWC-44, SRC-55, MWC-88; black-shaded markers), and large (MAAC-112, MAAC-118, MWC-128; gray-shaded markers) catchment areas. Lines indicate mean (solid) and 95% credible interval (dashed) of parameter estimate (see Figure 1 for definition of site codes).

Vineyard land use in the study watersheds had a significant negative association with survival (Figure 5C). Vineyard land use had a mean multiplicative effect of 0.23 (95% CI = 0.13–0.38), indicating that survival was, on average, five times lower in reaches with the highest vineyard use compared with reaches with the lowest levels of vineyard development (Figure 4). There was no support for an adverse effect of either road density or rural residential density; these variables were not evaluated in the final model because their coefficients were not significant and did not improve model fit. Habitat

suitability had a significant positive association with survival. When comparing units of low and high summer habitat rating, there was a predicted mean increase in survival of 31% (mean effect = 1.31; 95% CI = 1.17–1.47). Maximum unit water depth was not significant and did not improve model fit. Initial fish density had a significant negative association with survival rates, while pools had a small but significant positive effect on survival in comparison with riffle habitat units (Table 3).

DISCUSSION

Our results indicate that streamflow, land use, and habitat variables are important for explaining patterns in oversummer survival of juvenile steelhead. First, higher streamflows had a strong positive association with oversummer survival, with evidence of significant effects of both early summer flow and late-summer low-flow conditions. Second, vineyard land cover had a significant negative association with survival, while other land use variables, including road density and rural residential development, did not have a significant effect. Third, the effects of summer habitat suitability and the pool habitat types were positive. Lastly, there was evidence of negative density-dependent effects of early summer fish abundance on oversummer survival.

The low apparent oversummer survival rates suggest that the dry season is an important period of stress for rearing juvenile steelhead in the study region. Long-term population patterns and oversummer survival rates for wild, free-ranging juvenile steelhead in the study area are not known, and such information is likewise unavailable for other ecologically comparable watersheds in the California coast region, but the apparent annual survival of 30% (median = 25%) is lower than rates reported from other Pacific Northwest streams. May and Lee (2004) observed a 59% decline in oversummer juvenile salmonid abundance for intermittent Oregon streams that were dominated by coho salmon *O. kisutch*, while studies conducted by Harvey et al. (2005, 2006) in the temperate-climate region of northern California indicated that the oversummer survival of steelhead in coastal streams was generally greater than 60%.

These findings challenge previous research, which has suggested that winter rearing habitat is the primary limiting factor to juvenile salmon production in Pacific coast streams (Bustard and Narver 1975; Reeves et al. 1989; Nickelson and Lawson 1998). In this study, estimated oversummer survival rates for juvenile steelhead were comparable with reported values of overwinter survival for coho salmon and steelhead from coastal streams in California (Brakensiek and Hankin 2007), Oregon (Solazzi et al. 2000; Ebersole et al. 2006, 2009b), and Washington (Quinn and Peterson 1996). Therefore, evidence suggests that at least in some coastal streams, summer rearing habitat can be as important as winter habitat in limiting juvenile salmon survival. Nevertheless, most studies on dry-season rearing habitat have focused on seasonal growth, size, and condition of fish in the late summer (Harvey et al. 2005, 2006; Ebersole et al. 2009a) because these factors are known to be related to size-dependent

mortality in the winter season (Quinn and Peterson 1996; Biro et al. 2004; Ebersole et al. 2006). The importance of juvenile salmonid mortality during the oversummer rearing period has received less attention, even though it is likely to have carry-over effects on smolt production (Ebersole et al. 2009a).

The movement of fish between sampling events potentially confounds the survival rate estimates, particularly in years with higher summer flows. Although little is known about the movement patterns of juvenile salmonids during the summer in low-flow and intermittent streams of California, there is evidence that movement between stream reaches is common among juvenile salmonids in western Washington streams (Kahler et al. 2001), where hydrological connectivity is presumably higher. However, the assumption that migration between habitat units is restricted in the dry summer months is supported by the fact that fish abundance decreased between the early and late-summer counts in over 90% of the sampled units. Furthermore, because our sampling in each reach targeted units that had deep-water habitat, which is known to be a preferred physical habitat feature for juvenile salmonids in the dry season (Bisson et al. 1988; Lonzarich and Quinn 1995), movement of fish to the sampled units is more likely than emigration from them (Kahler et al. 2001). Thus, the influence of fish movement, if any, would be to increase the late-summer count and result in a more conservative overestimate of apparent juvenile steelhead survival.

Effects of Summer Low Flows

The positive relationship between survival and the flow metrics indicates that stream discharge is an important mediator of steelhead rearing habitat conditions during the dry season. All of the hydrologic metrics that described the magnitude of early summer flows and severity of late-summer low flows had a significant positive association with oversummer survival. Although it is likely that other short- and long-term streamflow regime characteristics are important for juvenile salmonid populations, the selected hydrologic metrics captured key attributes of the dry-season hydrograph, including the magnitude of early summer flows and the severity of low flows in the late summer. Many studies have documented a strong correlation between discharge and the abundance of salmon in their early life history stages (Jager et al. 1997; Mitro et al. 2003; Lobón-Cerviá 2004; Beecher et al. 2010). There is also evidence that summer streamflows, in particular, can regulate juvenile salmon production. For example, Beecher et al. (2010) documented a strong positive relationship between coho salmon smolt production and increasing summer low flows in Washington streams. They attributed differences in annual smolt production to the availability of and access to quality rearing habitat during the low-flow period the previous summer. Other studies have also documented a positive relationship between summer streamflows and adult salmon returns (Mathews and Olson 1980; Arthaud et al. 2010). Nevertheless, because salmon production is constrained by a variety of environmental and anthropogenic pressures over multiple life history stages, empirical relationships between summer

streamflow and juvenile abundance are generally confounded. Here, the late-summer abundance of juvenile steelhead is modeled as a function of oversummer survival. Thus, the effects of the low-flow period can be directly assessed while controlling for annual variation in early summer recruitment (e.g., driven by differences in adult returns and spawning success).

There are a variety of plausible mechanisms by which increased dry-season flows could improve the fitness and survival of juvenile steelhead. Flows control the velocity, depth, and volume of water in the stream channel and thus directly mediate the size and suitability of habitat (Dewson et al. 2007). Therefore, higher low flows are likely to increase the size and suitability of fish habitat by maintaining riffle connectivity and pool depths, potentially reducing the risk of mortality by predation, competition, and stranding (Chapman 1966; Magoulick and Kobza 2003; May and Lee 2004; Stradmeyer et al. 2008; Irvine et al. 2009). Flow patterns are also tightly coupled with water quality and stream thermal regimes, and increasing the duration or severity of low flows in the warm summer months could elevate stream temperatures above critical thermal maxima for salmonids (Myrick and Cech 2004), concentrate pollutants to toxic levels, and decrease dissolved oxygen concentrations (Nilsson and Renofalt 2008). Finally, flows can have important effects on the production and delivery of food resources for juvenile fish. For example, a reduction in invertebrate drift inputs resulting from decreasing flow is likely to adversely affect the growth, fitness, and survival of fish during the dry season (Harvey et al. 2006; Hayes et al. 2008).

There is some evidence that the effects of flow on fish survival vary across reaches, which suggests that fish responses to streamflow may be conditional on site-specific environmental factors. For example, reaches with larger watersheds (>100 km^2) tended to have lower steelhead survival rates than reaches with small watersheds over the range of observed interannual flow variation (Figure 5A, B). These differences are probably due to longitudinal changes in stream habitat characteristics that occur with increasing drainage areas, including increased stream temperatures, reduced riparian cover, and changes in fish assemblages, all of which could influence oversummer survival rates. Nevertheless, the increasing trend in survival is consistent across all watershed sizes, indicating that the apparent positive influence of flow is not confounded by the position of sampling reaches in the stream network.

Effects of Land Use and Habitat

The model results indicate that vineyard land cover has a negative association with juvenile steelhead survival, which could be related to the impacts that intensive agriculture has on both habitat and streamflows. The direct effects of land use conversion are consistent with previous studies that document impacts to salmonid habitat and populations from the conversion of wild lands to agricultural, managed forest, urban, and exurban uses (e.g., Paulsen and Fisher 2001; Bilby and Mollot 2008). Vineyard and exurban development in the region is associated with increased fine sediment inputs to streams (Lohse et al. 2008) and thus may be indirectly affecting salmonids through habitat degradation. Vineyards could also be indirectly affecting habitat through alterations to streamflow because they often rely on groundwater pumping or direct surface water abstraction to meet their water demands. Although our analysis does not explicitly account for this potential effect of water use on flows, vineyard irrigation can impair streamflows in the late spring for frost protection and summer for heat protection (Deitch et al. 2009). Thus, vineyard water use could affect juvenile salmonids by dewatering streams, reducing habitat availability, and potentially stranding fish on gravel bars (Bradford 1997). The rapid expansion of vineyard and exurban development in the study area (Merenlender 2000; Merenlender et al. 2005; Newburn and Berck 2006) suggests that the adverse effects of land use on freshwater ecosystems are likely to increase in severity and warrant greater attention.

Vineyard and other land use variables overlap in geographic extent for reaches nested in the same watershed, which introduces spatial autocorrelation within the data. Furthermore, the position of a reach within the stream network is probably correlated with spatial trends in habitat and watershed attributes, which could confound the apparent influence of landscape variables. This is a common problem for watershed-scale studies and can make it difficult to interpret the results of regression models (King et al. 2005). In our analysis, the potential influence of reach position was reduced by sampling from four separate watersheds and by selecting variables that were not strongly correlated. Furthermore, the habitat variable used in the model captured some of the between-reach differences in habitat quality associated with watershed size, in addition to within-reach variation among individual habitat units. Finally, the incorporation of random effects in the model provided robust estimates of SE for regression coefficients that accounted for the influence of unobserved covariates operating at the reach scale that may also be related to the nested, spatial structure of the data.

Despite limitations in the available habitat data, the positive association of habitat quality with the survival of rearing steelhead conforms with previous studies documenting the important role of habitat features in influencing juvenile salmonid growth and survival (e.g., Lonzarich and Quinn 1995; Harvey et al. 2005; Johnson et al. 2005). Notably, the lack of water temperature data and detailed information on physical habitat conditions during the study period makes it difficult to ascertain how different habitat components (e.g., riparian cover, instream shelter, embeddedness, and depths) affect the abundance and survival of juvenile steelhead. Furthermore, because physical habitat information was not recorded during each year of sampling, interactions between flow patterns and habitat features over time cannot be investigated. However, the model makes efficient use of the available data by accounting for the important influence of local habitat features on fish survival relative to other relevant environmental factors.

Our findings underscore the importance of long-term survey data for assessing ecological responses to environmental and anthropogenic change. In climatic regions marked by high inter-annual variability and dynamic flow regimes, multiyear data are particularly important for distinguishing the effects of multiple natural and anthropogenic stressors on freshwater ecosystems (Osenberg et al. 1994; Bêche et al. 2009). However, long-term data necessary to investigate ecological–hydrological relationships are rare and remain a major obstacle to effective freshwater ecosystem conservation and river management (Vaughan and Ormerod 2010). There are likely to be additional sources of natural variability that could not be accounted for in this study. Consequently, the strength of model effects may change with the incorporation of additional explanatory variables that are currently unavailable. Additional research is needed to quantify the potential effects of other variables and identify the underlying mechanisms by which flow and other factors influence juvenile salmonid survival. Nevertheless, opportunistic analyses of available data are important first steps for detecting and quantifying significant relationships between environmental variability and the spatial and temporal patterning of juvenile salmon populations.

Conclusions

The findings of this study have implications for instream flow management in coastal California streams. The increasing trend in survival with incremental increases in flow over the complete range of observed summer flows suggests that low flows are limiting juvenile steelhead in the study watersheds (Figure 5). The findings do not support the identification of a minimum flow that protects the upper range of juvenile salmon survival. Rather, any reduction in summer low flows, either from natural drought or water withdrawals, is likely to reduce juvenile fish survival. Conversely, changes in water management practices that improve summer flow conditions are likely to benefit rearing juvenile salmonids. There are opportunities for restoring summer flows. For example, vineyard landowners could potentially increase the capacity for onsite water storage and for collection of water during high winter flows to limit the water diversions required during the summer growing season (Merenlender et al. 2008; Grantham et al. 2010; Newburn et al. 2011). Projected climate change and population growth in California will unquestionably increase pressures on water resources and intensify impacts to Pacific salmonid populations that are already in severe decline (Moyle 2002). Salmon and other coldwater fishes will be particularly susceptible to climatically mediated changes in dry-season discharge and temperatures (Clews et al. 2011). Therefore, the reduction of water diversions combined with the identification and protection of environmental flows for salmon and other freshwater biota should be a top priority for managers and conservation scientists.

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