# DRY SEASON SURVIVAL OF JUVENILE SALMONIDS IN AN INTERMITTENT COASTAL STREAM

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DRY SEASON SURVIVAL OF JUVENILE SALMONIDS IN AN INTERMITTENT COASTAL STREAM

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Abstract: We estimated dry season survival of imperiled salmonids in an intermittent coastal stream in California across four years (2009-2012). Our study encompassed two dry and two wet winters allowing us to explore patterns of survival across and within dry seasons with different antecedent precipitation. Apparent survival of age-0+ steelhead trout (\textit{Oncorhynchus mykiss}) was higher following wet winters compared to dry winters. Moreover, antecedent precipitation was positively correlated with cumulative survival of age-0+ steelhead. Within years, apparent survival of steelhead varied among weeks with a tendency to decrease in the late summer indicating that fish exhibited some resistance to seasonal drought. Additionally, we found a slight but significant survival advantage for age-0+ coho salmon (\textit{O. kisutch}) compared to equal-aged steelhead. Our results emphasize the influence of antecedent precipitation in driving the
survival of imperiled salmonids and highlight that these fishes are somewhat resistant to seasonal
drought, at least to a point.

**Introduction**

Seasonal and multi-year drought events can result in loss of surface flow and extreme
habitat contraction in lotic ecosystems (Stanley et al. 1997; Hakala and Hartman 2004).
Declining water levels during stream contraction can in turn result in decreased water quality
conditions, including increased stream temperatures and decreased dissolved oxygen levels
(Boulton and Lake 1992; Elliott 2000), particularly in smaller streams (Lake 2011). In regions
that experience seasonal drought, smaller streams are often ‘intermittent’, exhibiting reduced or
zero surface flow during the dry season or dry years (Gasith and Resh 1999; Lake 2011).

Previous studies have demonstrated that intermittent streams, which are common
throughout the world (Larned et al. 2010), can provide important breeding, rearing, and refuge
habitats for stream fishes (e.g., Erman and Hawthorne 1976; Fausch and Bramblett 1991;
Wigington et al. 2006; Magalhães et al. 2007; Arthington et al. 2010; Pires et al. 2010; Lake
2011). Conversely, other studies have demonstrated that intermittent streams can be harsh
environments and sites of high mortality of resident stream fishes (Tramer 1977; Mundahl 1990)
and other vertebrates (e.g., turtles, Leidy et al. 2016). These contradictory results may reflect
differences in drying severity, which can vary considerably through space and time. In fact,
interannual variability in drought severity results in dramatically different physical conditions
from year to year within single streams (Acuña et al. 2005; Boughton et al. 2009; Hwan and
Carlson 2016).

Native biota in intermittent streams can withstand drying events under some
circumstances (Miller and Golladay 1996; Dodds et al. 2004; Arthington and Balcombe 2011).
Lake (2003) characterized the response of biota to press disturbances like seasonal drought as an abrupt transition when a critical threshold is reached in the physical environment, suggesting that biota are resistant to the drying event prior to the realization of a critical threshold, after which there is a negative response. Some macroinvertebrate taxa can exhibit resistance to moderate drought conditions; however, when drying is more severe, their abundance and biomass decreases sharply (Boulton 2003; Boersma et al. 2014). Similarly, a study examining the response of multiple species of fish found that survival rates were high during the initial phases of drying, but decreased sharply when drying was more pronounced (Larimore et al. 1959). This collection of studies highlight the importance of drought severity in structuring communities in intermittent streams.

Beyond the severity of abiotic conditions, biotic conditions can also influence fish performance during the dry season. For example, body size plays a critical role in survival of stream fishes. Territoriality and aggressive behavior are well-documented in many stream fishes (Gerking 1953; Titus 1990; Young 2004), with smaller fish often displaced from optimal habitat by larger conspecifics (Bohlin 1977; Berg et al. 2014) or the presence of large piscivores (Power 1987; Schlosser 1988). Moreover, interspecific competition can regulate habitat use, with larger, dominant species often excluding non-dominant species through aggressive displays (Fausch and White 1986; Sabo and Pauley 1997; Stradmeyer et al. 2008). In particular, density-dependence and self-thinning in salmonids are well-known phenomena that can influence survival and growth (e.g., Jenkins et al. 1999), and density-dependence could be intensified in intermittent streams as drying progresses, habitat contracts, and fish are concentrated in the remaining habitat.
In this study, we tracked the fates of imperiled salmonid fishes in an intermittent coastal stream in California across four dry seasons that differed in antecedent precipitation. Our goal was to estimate over-summer survival of juvenile salmonids and explore among- and within-year variation in survival. Specifically, we estimated apparent survival at the weekly scale as well as cumulative survival across each summer. We hypothesized that survival would be higher (1) following wetter than drier winters, (2) in the early summer compared to late summer (i.e., fish can withstand drought conditions to a point), and (3) for larger species when compared to smaller species because of the ability of large individuals to exclude smaller individuals from preferred habitat.

Methods

Study site

The John West Fork (JWF; 37.99° N, 122.75° W) is a first-order stream located in the Golden Gate National Recreation Area and is a tributary of Olema Creek, which itself is a tributary of Lagunitas Creek (Marin County, California; Figure 1). The JWF is an intermittent stream that is approximately 3 km in length and is situated in one of the world’s Mediterranean-climate regions, which are typified by wet winters and dry summers (Gasith and Resh 1999). As such, the watershed receives most rainfall in the fall and winter months and typically receives little to no rainfall during the summer months (Figure 2). However, the timing, frequency, and magnitude of precipitation events varies within the wet season, with some years experiencing larger storms, more frequent storms, and/or earlier storm events in the wet season. The JWF typically experiences continuous stream flow from November through June. Declining water levels during the summer lead to residual pools that provide refuge habitat for juvenile salmonids.
rearing in the creek (Bogan et al. 2015; Hwan and Carlson 2016). Our study area (approximately 450 m in length) was located in the lower section of the creek, which is characterized by dense vegetation dominated by California Bay Laurel (*Umbellularia californica*), beaked hazelnut (*Corylus cornuta*), bigleaf maple (*Acer macrophyllum*), and poison oak (*Toxicodendron diversilobum*). At the onset of our study in 2009, we included 12 riffle-pool sequences. From 2010-2012, we expanded our study area to include 19 riffle-pool sequences. In a previous study, we explored changes in pool habitat availability and stream temperature across the summer at JWF and those results are described in Hwan and Carlson (2016).

**Study species**

Two species of salmonids occur in the JWF—steelhead trout (*Oncorhynchus mykiss*) and coho salmon (*O. kisutch*). No other species of fish are present within the study area, presumably because of a downstream culvert that restricts the access of non-salmonids. Both steelhead trout and coho salmon are anadromous, using freshwater environments for breeding and rearing, and the ocean for maturing. With the exception of a small proportion of steelhead that spend two years in freshwater, juveniles of both species in many coastal California basins spend one year in freshwater prior to their seaward migration (Shapovalov and Taft 1954). Steelhead in the study region are part of the Central California Coast Distinct Population Segment, which has declined in recent decades and was listed as federally threatened in 1998 (NMFS 2011). Coho salmon in the Central California Coast Evolutionary Significant Unit have also experienced marked declines in recent decades and were listed as federally endangered in 2006 (NMFS 2006).

Coho salmon in the region have a strict three-year life cycle, leading to three distinct cohorts. Currently, there is one strong year class in the study region, which results in higher
abundances of coho every three years (Carlisle and Reichmuth 2015). During our study period (2009-2012), coho salmon were absent or nearly absent from JWF in all but one year (2011) (Table 1), limiting our analysis of coho summer survival to that year. Throughout much of their sympatric range, coho salmon spawn earlier than steelhead (Young 2004), including in our study region (Carlisle et al. 2010). As a result, coho salmon emerge earlier and generally maintain a size advantage over steelhead during their first summer.

Among-year differences in antecedent rainfall and physical conditions

We used precipitation data from a nearby rain gauge (Kentfield, CA, NCDC 044500, period of record = 70 years) to examine daily precipitation totals and the timing and frequency of storm events across all four study years (Figure 2). We also used the long-term precipitation data to determine the water-year type for each of our study years. Specifically, we partitioned the total annual precipitation across the 70 year period of record into quantiles. We then assigned each of our focal years to one of five water-year categories: dry, below normal, normal, above normal, and wet. This analysis revealed that each of the four years was categorized as a different water-year type, with 2009 being a ‘dry’ year; 2010 being a ‘normal’ year; 2011 being an ‘above-normal’ year; and 2012 being a ‘below-normal’ year (Table 2) (Hwan and Carlson 2016). For each study year, we also estimated pool half-life, which represents the number of weeks for pools required to reach half their initial volume (Hwan and Carlson 2016).

We deployed temperature loggers in each pool over the course of each summer. In a previous comparison of pool temperatures, we found that differences in temperature among years and pools were slight (averages across all years and pools were within 1 °C), presumably because of the buffering effect of heavy riparian cover (Hwan and Carlson 2016). Because
summer stream temperatures were generally low and fell within the tolerance zone of juvenile salmonids (average temperature and standard error across all pools and years = 14.31 ± 0.01) and because temperature varied little among pools or across the summer (Hwan and Carlson 2016), we did not explore the influence of temperature on over-summer survival in this study.

Fish survival

Across each of four study years, we used three-pass electrofish depletion to sample fish on two occasions—once during the early summer and once at the end of summer (see Table 1 for details). During these capture events, we anesthetized and identified all captured fish to species, recorded the pool number they were captured in, and measured (fork length, to the nearest mm) and weighed (to the nearest 0.01g) each fish. We implanted a passive integrated transponder (PIT) tag into the peritoneal cavity for all fish that were 60 mm or larger in fork length. Following recovery, we released tagged fish back into their initial pools. Tagged fishes were subsequently re-sighted every week across the summer (with a few exceptions; see below) using a portable PIT antenna (FS2001F-ISO BP, Biomark, Inc., Boise, ID, USA), allowing us to assess their presence, state (i.e., dead or alive), and position (i.e., pool location). We re-sighted fish each week across each summer, although there was one instance where we missed three consecutive weeks (in August 2011). Each time a tag was detected, we gently disturbed the substrate near the tag location to determine their state. If the tag was detected at the same site in successive re-sight attempts, we determined that the fish was dead. An alternative is that the tag had been shed. However, the use of a fin clip as a secondary mark revealed that our tag loss rate was very low (across all years, we recaptured only one fish that had shed its tag), which is consistent with other studies using this same approach (e.g., Ostrand et al. 2011).
During our two ‘wet’ study years (2010 and 2011), there was sufficient riffle connectivity in early summer to allow for movement outside of the pools where our initial capture and tagging occurred (Hwan and Carlson 2016). During wet years, we observed much higher rates of movement [maximum distance/number of pools moved = 240 m/14 pools (2010) and 193 m/12 pools (2011)] when compared to dry years [maximum number of pools moved = 1 (2009 and 2012)]. To account for movement outside of the study area following wet winters, we expanded our study area for re-sighting events to include several pools upstream and downstream of our focal study reach. Specifically, we surveyed pools until we no longer detected tagged fish in three contiguous pools, approximately 140 m upstream and 90 m downstream of our study site.

Note that the weeks in which the initial and final capture events occurred differed among years (Table 1). The timing of the initial capture event and tagging was motivated by fish size (i.e., sampling was delayed until a larger proportion of fish reached the threshold tagging size of 60 mm). For the final capture event, we scheduled our sampling to precede the first substantial rain event of the fall, a point marking the end of the seasonal drought period. Additionally, the resumption of flow would have allowed for fish to move beyond our study system, which would have artificially reduced estimates of survival had we continued our mark-recapture study following flow resumption that connected the formerly isolated pools.

We encountered both age-0+ and age-1+ steelhead, but because there were far fewer age-1+ fish (Table 1), we excluded them from our survival analyses. Ages were determined based on observed bimodality in size distributions in early summer with trout falling into the upper mode (>97 mm) considered to be age-1+, age-0+ otherwise.
Fish abundance and growth rates

For each year, we estimated population size for each pool using data from the early summer capture event to estimate abundance at the pool scale. These abundance estimates were used to explore the influence of fish abundance on fish growth.

We estimated specific growth rates for tagged individuals that were captured during both early and late summer as:

\[
Specific\,\,Growth = \frac{\ln M_f - \ln M_i}{t}
\]

Where \(M_f\) is the final mass of the fish, \(M_i\) is the initial mass of the fish, and \(t\) is the growth period in days.

We then tested whether fish growth (based on the subset of tagged fish that were recaptured at the end of the summer) was related to early summer pool abundance using pool volume as a covariate. To do this, we used a generalized linear mixed model (GLMM) with abundance and pool volume as fixed effects and pool ID as a random effect (R Core Team 2016).

Statistical significance of the relationship between growth and abundance was determined using the R package lmerTest (Kuznetsova 2015).

We also examined the size distribution of fish in both early and late summer using length data on all captured fish. To do so, we created kernel density plots to visualize the distribution of steelhead length for early and late summer for each study year and computed mean and median size of steelhead for each period.
Detection probability and apparent survival analyses

We applied multi-event capture-recapture models (Pradel 2005) to our mark-re-sight data (hereafter, MR) to estimate detection probability and apparent survival each week across our four study summers. By explicitly distinguishing the demographic process (i.e., survival) from the observation process (i.e., detection or non-detection) and by incorporating dynamic individual states, the multi-event approach provided us with a robust framework to estimate survival while controlling for heterogeneity in detection (e.g., Pradel and Sanz-Aguilar 2012). Apparent survival is defined as the probability of surviving while remaining available for sampling within the study area (White and Burnham 1999; Cooch and White 2006). Multi-event models are an extension of classical capture-recapture models (i.e., Cormack-Jolly-Seber models, Lebreton et al. 1992) in which field observations (hereafter “events”) are related to a series of underlying biological states, which may not always be recorded in the field, hence making the number of states > number of events. Contrary to classical approaches that consider survival and detection probabilities to be identical among individuals present in the population at the same date, multi-event models allow a relaxation of this assumption by incorporating inter-individual differences not only in survival but also in detection probabilities, thus integrating detection heterogeneities into models (see Pradel and Sanz-Aguilar 2012). In our case, this approach was necessary due to the existence of significant heterogeneity in detection probabilities found during a Goodness-Of-Fit (GOF) test of the MR data prior to the analysis. Indeed GOF tests, performed using U-CARE (Choquet et al. 2009), were all significant, indicating lack of fit of a departure CJS model to each set of data (Table 3). Given that only one cohort of individuals was sampled each year, transient effects could not be tested, so significant GOF results reflected only those of the trap dependence test and pointed to a significant heterogeneity in detection probability
among individuals that violates CJS model assumptions. Consequently, we applied the aware-unaware method described in Pradel and Sanz-Aguilar (2012) to analyze our datasets directly by fitting multi-event models that account for individual heterogeneities in detection.

Multi-event models were constructed in program E-SURGE (Choquet and Nogue 2010). This program allows defining a model pattern to link the events in the data to the corresponding individual states through a series of steps based on transition matrices. MR data were used to construct encounter histories that were summarized in two datasets prior to analyses: one containing data collected across 4 years on age-0+ steelhead and a second dataset containing data collected in one year (2011) on both age-0+ steelhead and coho. Then, we defined the state of fish at each sampling occasion. Event “seen” (coded 1) was directly linked to a state “alive and aware”. Event “not seen” (coded 0) may arise when a fish is alive but not detected (“alive and unaware”) or by true death of the individual (“dead”) (see Appendix A). In our case, both fish that were undetected on a given week and those that were assigned as “dead” in the field were treated as “not seen” and coded as a ‘0’ for analyses. Missing observations were also coded as a ‘0’ in the encounter histories and detection probabilities associated with weeks without surveys were always fixed to zero in the analyses. Once this model pattern was defined, we took advantage of the process-decomposition tool implemented in program E-SURGE to obtain separate estimates for each parameter of interest, i.e., apparent survival ($S$) and detection probabilities ($\psi$) (see Appendix A for further details).

Model selection was based on an information-theoretic approach (Burnham and Anderson 2002) in which we ranked candidate models using Akaike’s Information Criterion corrected for small sample sizes (AICc) to determine which model best fit our data (White and Burnham 1999; Burnham and Anderson 2002). We assessed the among-year survival dynamics of age-0+
steelhead using our capture and weekly re-sighting survey data across our four study years. Because some weekly surveys were not conducted in some years (specifically, 3 weeks were missed in August 2011), detection probabilities ($\psi$) were always modelled as a function of year and week, with $\psi$ parameters fixed to zero for those weeks in which sampling was not conducted. Consequently, for this among-year analysis, modelling was primarily focused on the survival parameter ($S$). In the end, we tested a total of 12 candidate models based on a priori hypotheses that tested combinations of among- and within-year factors and an individual covariate (body size). Among-year factors included a ‘year’ effect in which survival differed among all four study years and a ‘regime’ effect that tested whether survival differed between wet (2010, 2011) and dry years (2009, 2012). A within-year factor of ‘week’ was included, in which survival differed across weeks. Constancy in weekly survival across all years and interactions between among-year and within-year factors (e.g., “regime*week”) were also tested. Furthermore, fish body size at the time of our early summer capture was also included as an individual covariate in our models. Additional models were constructed by adding a length effect to all previously tested structures (Table 4).

For the two-species dataset, we ran an independent analysis to compare survival and detection probabilities of equal-aged steelhead and coho (age-0+). In this analysis, modelling was focused on both survival and detection probabilities and we tested a total number of 12 candidate models based on a priori hypotheses; in particular, we tested a “species” effect in survival/detection probabilities and contrasted it against “week” and “length” effects as well as against constancy in survival/detection parameters. We started modelling $\psi$ departing from a general model with species*week interactions in both $S$ and $\psi$ parameters, and we constructed additional models by removing this interaction from $\psi$ and leaving week or species effects in
place, as well as by removing both species and week effects to test for constancy in $\psi$. At this point, we tested for length effects by adding this individual covariate to the most parsimonious of the previously tested models and retained the best structure for $\psi$ to start modelling survival probabilities (i.e., a consensual model; for a similar approach see Tavecchia et al. 2012).

Survival was modelled following the same procedure and, departing from a model with species*week interaction on $S$, we constructed simpler structures considering week and species effects alone and constancy on survival (three models). Subsequently, we tested for length effects on $S$ by including the length covariate in all previously tested survival models (four additional models) (Table 5).

Because the above probabilistic model uses data on live recaptures to estimate survival, fish that migrate out of the system may be treated as dead. Hence, the survival estimates obtained in our model should be considered estimates of ‘apparent’ survival. However, the detection probabilities in our study were much higher than studies in open systems because movement was highly restricted in our system. As such, our estimates of apparent survival are likely to be close to estimates of true survival. For example, during our two ‘dry’ study years (2009, 2012), emigration out of the initial capture area was entirely impossible, while during our two ‘wet’ study years (2010, 2011), emigration out of the initial capture area was limited to the first few weeks of the summer and we attempted to account for it by sampling in our expanded study area.

Although the number of fish that we tagged each year was relatively low, the high detection probabilities along with the use of AICc to correct for small sample sizes suggest that our results should be robust. The mark-recapture data reported in this paper and used to estimate detection and survival are available at datadryad.org (ADD LINK).
In addition to apparent survival, we calculated cumulative survival across the summer as the product of our weekly estimates of apparent survival for all weeks (Kaplan and Meier 1958). We also examined the mortality that was attributed to complete pool drying. To do so, we determined which pools dried by the end of the summer and then, for each of these pools, we took the difference between the number of fish that were initially tagged and the number of fish that emigrated into permanent pools and divided this value by the total number of fish tagged each year. Finally, we explored the influence of antecedent precipitation on cumulative over-summer survival of age-0+ fish through a Pearson correlation analysis focusing on each water year separately.

The above mark-recapture analyses were limited to individuals that were 60 mm or larger in fork length, however, we did capture individuals below this size. To assess over-summer survival of all captured fish, we also estimated survival using early and late summer population size estimates based on three-pass depletion using the maximum weighted likelihood method (Carle and Strub 1978). Over-summer survival for each pool was then calculated as the population size during the late summer sample divided by the population size during the early summer sample. To account for differences in the number of days between early and late summer sampling events among years, we divided our over-summer survival estimates for each by the number of days between early and late summer sampling events and report values averaged across all pools within a given year. We used this method to estimate age-0+ steelhead survival rates across all four study years and coho survival rates for 2011. We then used GLMM to compare survival rates of steelhead among the four years and to compare survival rates of steelhead and coho in 2011. For the among-year and species comparison, year and species were coded as fixed effects, respectively, and pool ID was coded as a random effect. Statistical
differences among years and between species were determined using package lmerTest in R (Kuznetsova 2015).

Results

Among-year differences in antecedent rainfall and physical conditions

Based on data from a rain gauge in nearby Kentfield, California, the total annual precipitation in the study region varied markedly among study years from a low of 173.6 cm in 2009 to a high of 287.2 cm in 2011, with intermediate totals in 2010 (227.0 cm) and 2012 (189.2 cm). Moreover, there were fewer large storm events during dry winters when compared to wet winters. For example, during the dry winters of 2009 and 2012, daily total precipitation exceeded 2.5 cm on only 7 and 12 days, respectively, compared to 16 days in 2010 and 18 days in 2011.

The timing of ‘large’ storm events (defined here as more than 2.5 cm of rain on a given day) also differed among years. During the dry winter of 2009, 5 of the 7 events storm events occurred in late winter, during or after mid-February (Figure 2). In all other years, large storm events occurred as early as October and were more evenly distributed across the wet season from October through April (see Figure 2).

During the drier years of 2009 and 2012, stream fragmentation occurred earlier, with the majority of riffles drying approximately one month earlier than during the wetter years of 2010 and 2011. Additionally, pool half-life was lower in drier years (2009: 9.7 weeks, 2012: 14.0 weeks) compared to wet years (2010: 18.6 weeks, 2011: 26.3 weeks).

We observed complete drying of some study pools in every year, with 50% of pools drying in 2009, 32% drying in 2010, 11% drying in 2011, and 42% drying in 2012. Fish survival
is dependent on remnant pools, and no fish can survive in pools that dry completely. To explore
the influence of complete pool drying on mortality, we determined the mortality rate due to
complete pool drying based on observations of tagged fish (see Methods). This exercise revealed
that when more pools dried, the mortality attributed to complete pool drying was generally
higher. For example, the mortality rate attributed to complete pool drying was highest in 2009
(0.42) when half of the pools dried (6 of 12 pools). Mortality attributed to complete pool drying
was lower in the remaining years when a lower proportion of pools dried: 0.05 in 2010 (when 6
of 19 pools dried), 0.15 in 2011 (when 2 of 19 pools dried), and 0.22 in 2012 (when 7 of 19
pools dried). Although there were fewer pools that dried in 2011 compared to 2010, a higher
proportion of the mortality was attributed to complete pool drying in 2011 due to the large
influence of one pool that dried completely. This pool was the second deepest pool (maximum
depth = 64.8 cm) at the beginning of the summer and a relatively large proportion (0.16) of the
total number of tagged steelhead were in this pool during our early summer capture event.
Although some of these fish moved into nearby perennial pools, 75% (n = 18) of the fish
captured and tagged in that pool remained there, and died as a result.

**Among-year comparison of age-0+ steelhead**

Detection probability estimates from the highest ranking model in our among-year
comparison of age-0+ steelhead confirmed the existence of inter-individual differences on
detectability in the sampled population (Figure B1). In general, fish belonging to the state “alive
and aware” had higher detection probability than fish in the “alive and unaware” state (average
weekly detectability and standard errors: “aware” = 0.88 ± 0.02; “unaware” = 0.60 ± 0.05). Thus,
fish detected alive in a given occasion (“aware”) were more likely to be re-sighted again in the
next occasion, whereas unseen but alive fish ("unaware") were more likely to remain undetected in successive surveys.

The best-supported model for survival probability included an interaction between year and week (Model 1, Table 4). Neither a length effect nor a regime effect (i.e., wet versus dry year) for survival were supported (i.e., lower ranked, Table 4). Based on the top-ranked model that included the year*week interaction, survival tended to be higher following wetter winters compared to drier winters (Figure 3). Based on comparisons of 95% confidence intervals, the mean apparent survival calculated across weeks was significantly higher in the wettest year, 2011 (0.97 ± 0.01), when compared to the two driest years, 2009 (0.92 ± 0.02) and 2012 (0.89 ± 0.04). Mean apparent survival was intermediate in the second wettest year, 2010 (0.94 ± 0.03). Additionally, results from the top-ranked model revealed that mean apparent survival was generally higher during the early summer compared to the late summer. In the driest year (2009), the mean apparent survival was 0.96 ± 0.01 for early period compared to 0.85 ± 0.05 for the late period. We observed a similar pattern in 2010 and 2012, with higher survival in the early period compared to the late period (2010: 0.97 ± 0.02 vs. 0.85 ± 0.12; 2012: 0.98 ± 0.01 vs. 0.81 ± 0.05). In 2011, however, mean apparent survival for the early and late periods were similar (0.97 ± 0.01 vs 0.96 ± 0.01). Estimates of cumulative survival based on results of the top-ranked model revealed that cumulative survival was higher in the two wet years (2010: 0.41, 2011: 0.66) when compared to the two dry years (2009: 0.28, 2012: 0.23). These estimates were calculated across the entire summer; however, movement was possible during the first two weeks of summer during wet years because riffles were still flowing, suggesting that the estimates of cumulative over-summer survival from the two wet years are underestimated.
Over-summer survival estimates based on our three pass depletion estimates tended to mirror results from the mark-recapture analyses. Average survival across all pools was significantly higher in the two wet years (2010: 0.41 ± 0.09, 2011: 0.58 ± 0.09) relative to the two dry years (2009: 0.16 ± 0.11, 2012: 0.11 ± 0.09). No other differences among years were observed.

Size distribution data for the early and late summer capture events indicated that fish were generally larger during the late summer when compared to early summer (Figure 4). However, the size distributions and patterns differed among years. The differences in size between early and late summer were minimal in 2009 (early summer median/mean = 60.5 mm/66.2 mm ± 3.14, late summer median/mean = 66.5 mm/66.6 mm ± 1.41) and 2011 (early summer median/mean = 54 mm/59.7 mm ± 0.96, late summer median/mean = 57 mm/61.9 mm ± 1.08), whereas the size difference was more pronounced in 2010 (early summer median/mean = 69 mm/74.8 mm ±1.51, late summer median/mean = 77.5 mm/84.3 mm ± 2.14) and 2012 (early summer median/mean = 47 mm/53.5 mm ± 0.94, late summer median/mean = 56.5 mm/66.4 mm ± 3.44).

Influence of antecedent precipitation on over-summer survival

Cumulative over-summer survival for age-0+ steelhead was positively correlated with the previous winter’s precipitation (r = 0.97, P = 0.03), indicating that survival tended to be higher when precipitation totals were higher.
Species comparison

During 2011, the only year when coho salmon were abundant at our study site, coho and steelhead co-occurred in all but two of the 19 study pools (coho were absent from these two pools). On average, coho were larger than age-0+ steelhead during the early summer capture event (coho average length and standard error = 74.4 ± 0.71 mm; steelhead average length = 55.1 ± 0.34 mm; P < 0.001, Mann-Whitney U).

When comparing detectability of the two species, we found that the best-supported model for detection included an effect of week and species, indicating that steelhead and coho had different detection rates (Model 1, Table 5). As in previous analyses, weekly detection probability of fish in the state “alive and aware” was, in general, higher than that of “alive and unaware” ones (Figure B2), indicating that detection was not identical among individuals and that re-sighted (“aware”) fish were more likely to be re-sighted again in the next occasion. Length effects on detection probabilities were not well supported (Model 5 vs. Model 1, Table 5).

The highest-ranking model for survival in 2011 included an interaction between week and species (Model 1, Table 5). Models considering constancy or length effects on survival were lower ranked (Table 5). Based on the top-ranking model, average weekly apparent survival was relatively high in this wet year for both species, but slightly higher for coho (0.97 ± 0.01) than steelhead (0.95 ± 0.01, see also Figure 5). The slightly higher average weekly survival for coho translated to higher cumulative survival estimates for coho (0.70) than steelhead (0.57).

Using the GLMM analysis to assess cumulative survival using three-pass depletion data, we found that there was no difference in cumulative survival between the two species (0.55 ± 0.09).
Fish abundance and growth

In addition to exploring patterns of survival among years, we also explored how fish growth varied among years, and whether growth was density-dependent. To do so, we estimated early summer fish abundance for each pool in each year, which revealed that average abundances were highest in the wettest year (2011, average abundance and standard error among pools = 42.05 ± 7.15 fish), and lowest in the driest year (2009, average abundance = 5.7 ± 1.29 fish).

Average fish abundance for 2010, a ‘normal’ precipitation year, was 15.76 ± 3.01 fish, while average abundance in 2012, a ‘below-normal’ year, was 38.06 ± 5.55 fish. Based on body mass change across the summer for the subset of recaptured tagged fish, juvenile steelhead exhibited zero growth during the summers of 2009, 2011, and 2012 (at alpha = 0.05). We observed positive growth in only one summer (2010), when the average specific growth rate was 0.20 ± 0.04 % grams per day. Using data from 2010, a GLMM revealed that there was no relationship between growth and early summer fish abundance when pool volume was included as a covariate (P = 0.24).

Discussion

Seasonal drought and associated stream habitat contraction poses challenges to aquatic organisms in intermittent streams. Our results suggest that ecological responses to seasonal drought are conditional on drought severity, which varies among years. During our four-year study of an intermittent coastal stream in California, two winters were relatively dry and two were relatively wet. Following wetter winters, fewer pools dried completely during the dry season (resulting in less mortality of juvenile salmonids due to pool drying), and average apparent survival rates of threatened trout were higher. Interestingly, estimates of apparent
survival tended to decline during the late summer in most years (with the exception of the wet year, 2011, Figure 3), suggesting that juvenile salmonids show some resistance to seasonal drought and that late summer is a potential bottleneck period for these organisms. Survival was slightly higher for age-0+ coho salmon compared to age-0+ steelhead trout, suggesting that species-specific differences in size or behavior can lead to different survival patterns. Finally, we observed a positive relationship between total cumulative precipitation and cumulative survival of age-0+ steelhead.

Previous research investigating the summer survival of fishes in intermittent streams have reported that survival rates can be high (e.g., Hodges and Magoullick 2011), while other studies have found that harsh summer conditions can result in low rates of survival (e.g., Tramer 1977; Mundahl 1990). However, many previous studies focused on a single year and did not assess how interannual variation in physical conditions affected variation in summer survival rates. In a rare multi-year study, Grantham et al. (2012) found that the survival of juvenile steelhead across nine years in the Russian River Watershed (Sonoma County, California, USA) was positively associated with the magnitude of summer streamflow, which was mediated by antecedent precipitation and groundwater extraction. Although our study was short in duration (n = 4 years), there was a significant positive correlation between antecedent precipitation and cumulative survival for age-0+ steelhead in the John West Fork \( r = 0.97, P = 0.03 \). Our study also explored survival dynamics of juvenile steelhead at finer temporal scales (weekly) than Grantham et al. (2012) (yearly), which revealed that survival tended to be higher during the early summer when compared to the late summer when conditions become more stressful. Overall, our results point to the positive influence of antecedent precipitation on over-summer survival of juvenile
salmonids rearing in intermittent streams and emphasize the importance of late summer/early fall storm events in “rescuing” fish from stressful summer conditions.

There is growing appreciation that aquatic biota inhabiting intermittent streams can be resistant to moderate levels of stream drying, only experiencing sharp declines during periods of severe water contraction. For example, Boersma et al. (2014) used a mesocosm experiment to simulate intermittent stream conditions and found that the abundance of aquatic invertebrates was similar between control treatments (i.e., no decrease in water level) and moderate drying treatments, but significantly lower in a severe drying treatment. Similarly, our results suggest that juvenile salmonids inhabiting intermittent streams show some resistance to seasonal stream drying. Juvenile steelhead experienced relatively high rates of survival during the early summer regardless of antecedent precipitation, but survival declined during late summer, particularly following dry winters (Figure 3). This late summer decline in survival coincided with a period of extreme water level decline (data not shown). During a multi-year drought, Larimore et al. (1959) also documented that fishes of several species in an intermittent stream in Illinois exhibited high rates of survival into the late summer (early September), but survival decreased considerably when drought conditions became more severe in mid-September. In a study assessing the influence of pool persistence of fish assemblages, Capone and Kushlan (1991) observed fish kills only when pools dried completely. These parallel results suggest that late summer is a stressful time for stream fishes in intermittent streams, and that studies aimed at monitoring the effects of seasonal drought on intermittent stream fishes should focus on the late summer, when water levels and quality are at their lowest.

Although we expected fish size to play an important role in influencing survival, we found that size had little effect on steelhead survival, though it was an important factor for
explaining variation in recapture probability. The higher detection rates of smaller steelhead observed in our study might be a result of competitive exclusion, with larger steelhead excluding smaller steelhead from higher quality habitat (e.g., areas with undercut banks, greater depth, and/or rootwad vegetation), which is more difficult to sample. In contrast, Sogard et al. (2009) reported that larger steelhead experienced higher apparent survival rates compared to smaller steelhead in the perennial Soquel Creek Watershed (Santa Cruz County, California, USA), but attributed this result to the higher emigration rates by smaller compared to larger fish. In contrast, in our study, movement was highly limited due to stream fragmentation and size did not influence survival rates. Interestingly, our best-supported model when comparing survival rates between coho and steelhead included a species effect but not a size effect, with larger coho surviving at a higher rate than steelhead. However, the difference in apparent survival rates were slight (0.97 ± 01 for coho vs. 0.95 ± 01 for steelhead), and survival estimates from our three-pass depletion data did not support a species effect.

Stream intermittency and habitat contraction have the potential to influence several aspects of fish performance beyond survival. Habitat contraction can aggregate organisms, potentially intensifying biotic interactions including competition and predation, which could influence their growth. We observed differences in initial fish size among years, with fish being larger in 2009 (median = 60.5 mm) and 2010 (median = 69 mm) when compared to 2011 (54 mm) and 2012 (47 mm). Such differences could be explained by the higher observed densities in 2011 and 2012 (i.e., increased competition) and/or differences in timing of adult spawning leading to differences in emergence timing, a factor we did not explore. While we observed a general increase in the size over the summer when considering all captured fish (Figure 4), PIT-tagged fish grew little, suggesting that smaller individuals that we were initially unable to tag
may have grown to larger sizes or that capture efficiencies of larger individuals increased as pool size decreased. Regardless, negligible growth of tagged steelhead across the summer in three of four years limited our ability to test for density-dependent growth. In 2010, the one summer with positive trout growth, we observed that there was no relationship between growth and early summer fish abundance (measured at the pool scale) \( (P = 0.24) \). This result contrasts other studies that have found trout growth to be negatively density-dependent \( (e.g., \) Jenkins et al. 1999; Bohlin et al. 2002; Rosenfeld et al. 2005; Teichert et al. 2010), likely because we explored this relationship during stressful summer conditions when growth was minimal. While we observed little or no growth during the summer, we did observe large differences in abundance among years that may be related to the timing of large storm events. For example, in 2009, most of the large storm events occurred after mid-February (Figure 2), while in recent years, the peak spawning period for steelhead in the Lagunitas watershed has been early to mid-February (Ettlinger et al. 2010). Presumably as a result, the density of juvenile trout in 2009 was much lower when compared to other years. Woelfle-Erskine et al. (2017) also highlight the importance of large storm events for the recruitment of salmonids in small intermittent streams in the Salmon Creek Watershed (Sonoma County, California, USA).

While the findings of our study highlight the influence of antecedent precipitation on fish survival in an intermittent stream, we did not assess the mechanisms that influenced survival rates beyond complete pool drying. Although we measured the temperature of each of our study pools, we did not include temperature as a factor because we observed minimal variation in temperature across years and pools, presumably because of the dense riparian cover within the study area. We also did not measure dissolved oxygen regularly, but spot measurements taken during the late summer of 2012 indicate large differences in dissolved oxygen among pools.
(average = 2.69 ± 0.32, range = 0.06 to 6.26 ppm), hinting that variation in dissolved oxygen among pools could be a driving factor influencing fish survival. Reduced levels of dissolved oxygen have been shown to increase mortality rates of fishes inhabiting intermittent streams during the drying phase (Tramer 1977; Woelfle-Erskine et al. 2017). With an accumulating body of research suggesting that over-summer survival varies among years that differ in precipitation patterns (e.g., Grantham et al. 2012; this study), future studies should assess the mechanisms of mortality, including abiotic conditions such as temperature and dissolved oxygen, as well as biotic conditions including density and predation pressure (Magalhães et al. 2002).

The John West Fork is a relatively unimpaired stream with no known diversions in the watershed. Our findings highlight that the late summer period can be a critical period even in unimpaired systems, but also that survival can be very high in intermittent streams following wet winters (e.g., see Figure 3). With water becoming an increasingly valuable resource, stream diversions and groundwater pumping are common activities in arid and semi-arid regions (Poff et al. 2003; Falke et al. 2011). The loss of water in such cases may magnify the effects of late summer drought conditions, especially during drier years (Grantham et al. 2012). Hence, studies such as ours may help guide management decisions for agencies tasked with regulating water diversions and pumping by examining the type of water year that is being managed and whether it is necessary to cease or curtail water deliveries.

The last year of our study (2012) marked the beginning of an extreme multi-year drought (2012-2016) in California (Griffin and Anchukaitis 2014; US Drought Monitor 2016). During the two dry years of our study (2009 and 2012), fish experienced relatively high survival rates through midsummer, followed by decreased survival in late summer. This pattern indicates that late summer (i.e., September) water levels are critical in determining survival of juvenile
steelhead. Between 2012 and 2016, the percentage of land in California experiencing drought conditions in late September has increased from 69% to 84% (US Drought Monitor 2016). As a result, it is likely that stream habitats across the State, including at our study site, contracted to an even greater degree during this recent multi-year drought when compared to the two driest years of our study. Hence, it is likely that salmonid survival in California streams was reduced for at least five consecutive years. Furthermore, climate projections estimate that there will be a 5-10% reduction in runoff in the western United States and this will likely lead to loss of habitat for salmonids by 2100 (Kundzewicz et al. 2008). Reductions in runoff will also result in an increase in the number of intermittent streams over the next century (Larned et al. 2010). In light of these predictions, management of fish populations in intermittent streams will have to adapt new strategies to cope with more severe seasonal and multi-year drought conditions.

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Table Captions

Table 1. Summary of fish tagging events for each study year for steelhead (ST) and coho.

Table 2. Water-year type designations for each of the four study years (October 1, 2008 – September 30, 2012) based on 70 years of precipitation data from the Kentfield, CA weather station (NCDC 044500).

Table 3. Results of the Goodness-of-fit (GOF) test performed in program U-CARE. For each dataset, degrees of freedom (df), chi-square ($\chi^2$) and p-values ($P$) obtained from the global test are shown.

Table 4. Model selection results for the analysis of survival (S) and detection probabilities ($\Psi$) for age-0+ steelhead. Number of parameters (Np), Deviance and AICc for each model are given. $\Delta$AICc is the difference in AICc between the current model and the top ranked one. The best model in the set is shown in bold. Note that detection probabilities are split into their 2 components, reflecting transitions between states ($\Psi_{\text{aware} \rightarrow \text{aware}} = $ detect. prob. of aware individuals vs. $\Psi_{\text{unaware} \rightarrow \text{aware}} = $ detect. prob. of unaware individuals; see also Appendix A).

Table 5. Model selection results for the analysis of survival (S) and detection probabilities ($\Psi$) for the age-0+ steelhead and coho in 2011. Number of parameters (Np), Deviance and AICc for each model are given. $\Delta$AICc is the difference in AICc between the current model and the top
ranked one. The best model in the set is shown in **bold**. Note that detection probabilities are split into their 2 components, reflecting transitions between states ($\Psi_{\text{aware} \rightarrow \text{aware}} = \text{detect. prob. of aware individuals vs. } \Psi_{\text{unaware} \rightarrow \text{aware}} = \text{detect. prob. of unaware individuals};$ see also Appendix A).
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Figure Captions

Figure 1. Map showing the John West Fork within Marin County, California. Gray lines represent streams within the Lagunitas Creek Watershed. Dark lines in the John West Fork inset represent the study reach.

Figure 2. Hydrograph (black line) for nearby Walker Creek (USGS 11460750) and daily precipitation totals (grey bars) for nearby Kentfield, CA (NCDC 044500) and daily precipitation totals for each water year of the study (i.e., October 1, 2008 – September 30, 2012).

Figure 3. Weekly apparent survival probabilities of age-0+ steelhead for each year of the study. Estimates come from the top-ranked model of the set (Table 4). Error bars represent standard error estimates.

Figure 4. Kernel density plots displaying the distribution of steelhead length for early and late summer for each year of the study.

Figure 5. Weekly survival estimates for age-0+ steelhead trout (black circles) and coho salmon (gray squares) for study year 2011 (a wet year), when both species were present. Estimates are based on the top model of the set (Table 5). Error bars represent standard error estimates. Note: x-axis values are offset to avoid overlapping values and y-axis ranges from 0.8 to 1.0.
Figures

Figure 1

Marin County

John West Fork

0 1 km
Figure 2
Figure 3
Figure 4
Age-0+ Steelhead and Coho

Apparent Survival

Jul      Aug      Sept     Oct

Figure 5
Appendix A

Implementation of multi-event models to estimate survival and detection probabilities incorporating detection heterogeneity.

The probability of encountering an animal may differ among individuals (detection heterogeneity) when the biology or behaviour of the animal interacts with the sampling protocol, leading to individuals aware of the sampling process and individuals unaware of it. Such individual states may change in successive occasions, with individuals either becoming aware or unaware depending on whether they were seen or not in a given sampling occasion. In this context, detection becomes equivalent to a transition probability between two individual states (Pradel and Sanz-Aguilar 2012).

By allowing individuals to move within a finite set of states between sampling occasion $t$ and occasion $t+1$, multi-event models allow the estimation of three types of parameters: apparent survival ($S$), state transitions ($\Psi$), and event probabilities ($E$) (Lebreton and Pradel 2002). In our case, only $S$ and $\Psi$ probabilities were explicitly estimated. Transition probabilities are conditional on survival, and in order to obtain separate estimates for each parameter, we took advantage of the process-decomposition tool implemented in program E-SURGE (Choquet and Nogue 2010). In our case, transition probabilities reflect changes in aware/unaware states, and given that only aware individuals are observable (i.e., linked to event “1”), transitions from aware/unaware states to the aware state are equivalent to detection probabilities. More specifically, we estimated two types of detection probabilities: detection probabilities of aware individuals ($\Psi_{\text{aware} \to \text{aware}}$), and detection probabilities of unaware individuals ($\Psi_{\text{unaware} \to \text{aware}}$). Given that detectability was always estimated as a transition probability towards an observable (aware) state, event probabilities were not
estimated in our analyses and those associated with the aware state were structurally defined as equal to 1 (see below).

Specification of the multievent modelling approach in program E-SURGE

Multievent models are built in several stages using program E-SURGE (Choquet and Nogue 2010). Each step represents one type of the different parameters to estimate. This is done by means of row-stochastic matrices, i.e., each row corresponds to a multinomial. Consequently, the total of cell probabilities in the same row is 1. Because of this constraint, one and only one cell probability in each row will be calculated as the complement to 1 of the others. This particular cell is denoted with a ‘*’ symbol. Inactive cells, i.e., cells whose associated probability is structurally 0 are denoted with a ‘-’ symbol. An active cell receives an arbitrary letter. Note that the same letter in two cells does not mean that the two values should be equal.

Model pattern matrices to estimate survival and detection probabilities with E-SURGE

The individual states considered are:

A, “aware”

U, “unaware”

D, dead
The possible events are:

0, not seen

1, seen or resighted

The symbols for parameters are:

\( S \), survival probability

\( \Psi \), transition (detection) probability

With two components:

\[ \Psi_{\text{aware} \rightarrow \text{aware}} \]

\[ \Psi_{\text{unaware} \rightarrow \text{aware}} \]

**Initial State probabilities**

This is an initial step, necessary to start the sequence of transition matrices to estimate survival and detection probabilities. Here the dead state (D) is not represented; this is because dead states cannot be initial states in the individual encounter history. The initial state corresponds to the first tagging of the fish, so it must be an aware state (probability of \( A = 1 \), denoted with symbol ‘\(*\)’).

**States**

<table>
<thead>
<tr>
<th>A</th>
<th>U</th>
</tr>
</thead>
<tbody>
<tr>
<td>*</td>
<td>-</td>
</tr>
</tbody>
</table>

https://mc06.manuscriptcentral.com/cjfas-pubs
Transition probabilities, step 1: Survival

This step allows calculation of survival probabilities (S). The complementary cell denoted with symbol “*” represents total mortality (1-S). Note that two survival probabilities can be estimated at this step, one for each state (A and U); in our case, both probabilities were considered identical and no state effects were tested in the modelling of the mark-resight data.

<table>
<thead>
<tr>
<th>From/to</th>
<th>$A_{t+1}$</th>
<th>$U_{t+1}$</th>
<th>$D_{t+1}$</th>
</tr>
</thead>
<tbody>
<tr>
<td>$A_t$</td>
<td>S</td>
<td>-</td>
<td>*</td>
</tr>
<tr>
<td>$U_t$</td>
<td>-</td>
<td>S</td>
<td>*</td>
</tr>
<tr>
<td>$D_t$</td>
<td>-</td>
<td>-</td>
<td>*</td>
</tr>
</tbody>
</table>
Transition probabilities, step 2: Changes in detectability state (detection process)

This step allows calculation of transition probabilities between detectability states and is the key step for the estimation of detection probabilities in our case. Cells corresponding to transitions towards an aware state (i.e., detection transitions) contain a corresponding probability parameter (ψ) whereas transitions towards an unaware state are treated as the complement to detection transitions (1-ψ) and the cell is filled with the ‘*’ symbol.

<table>
<thead>
<tr>
<th>From/to</th>
<th>$A_{t+1}$</th>
<th>$U_{t+1}$</th>
<th>$D_{t+1}$</th>
</tr>
</thead>
<tbody>
<tr>
<td>$A_{t+1}$</td>
<td>$\Psi_{\text{aware} \rightarrow \text{aware}}$</td>
<td>*</td>
<td>-</td>
</tr>
<tr>
<td>$U_{t+1}$</td>
<td>$\Psi_{\text{unaware} \rightarrow \text{aware}}$</td>
<td>*</td>
<td>-</td>
</tr>
<tr>
<td>$D_{t+1}$</td>
<td>-</td>
<td>-</td>
<td>*</td>
</tr>
</tbody>
</table>
Event probabilities:

This step allows the calculation of event probabilities, which usually corresponds to the recapture probabilities in classical capture-recapture models. However, in our case, we use transition probabilities to estimate detection, so this last step does not estimate any probability parameter. By definition, individuals in state aware (A) are always seen, so they are linked to event 1. Unaware individuals (U) are not seen by definition, so they can only be linked to event 0. The same applies to dead individuals (D). Event probabilities of aware individuals (A) are equal to 1, whereas for the other states (U and D), the corresponding event probabilities are zero.

\[
\begin{array}{c|cc}
\text{From/to} & 0 & 1 \\
\hline
A_t & - & \ast \\
U_t & \ast & - \\
D_t & \ast & - \\
\end{array}
\]
References


Appendix B

This appendix includes our estimates of weekly detection probability associated with the fish survival analyses performed in E-SURGE and presented in the main body of the manuscript. The detection probabilities presented in Appendix B Figure B1 correspond with the survival rates presented in main body Figure 3, while the detection probabilities presented in Appendix B Figure B2 correspond with the survival estimates presented in main body Figure 5.
Figure Captions

Figure B1. Weekly detection probabilities for age-0+ steelhead trout, including for trap-aware (black circle) and trap-unaware (grey square) individuals. Estimates are based on the top-ranked model of the set (Table 3). Error bars represent standard error estimates.

Figure B2. Weekly detection probabilities for age-0+ steelhead trout and coho salmon, including for trap-aware (black circle) and trap-unaware (grey square) individuals for study year 2011. Estimates are based on the top-ranked model of the set (Table 5). Error bars represent standard error estimates.
Figure B1
Figure B2

Age-0+ Steelhead and Coho

Detection Probability