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Hwan, Jason L.

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Fragmentation of an intermittent stream during seasonal drought:
intra- and interannual patterns and ecological consequences

by

Jason Lun Hwan

A dissertation submitted in partial satisfaction of the
requirements for the degree of

Doctor of Philosophy

In

Environmental Science, Policy, and Management

in the

Graduate Division

of the

University of California, Berkeley

Committee in charge:

Professor Stephanie M. Carlson, Chair

Professor Vincent H. Resh

Professor Mary E. Power

Summer 2015

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Jason Lun Hwan

ABSTRACT

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Doctor of Philosophy in Environmental Science, Policy, and Management

University of California, Berkeley

Professor Stephanie M. Carlson, Chair

Intermittent streams lose surface flow for part of the year as shallow riffle habitats dry, leaving behind a series of residual pools that provide habitat for aquatic organisms. Historically, intermittent streams have been understudied when compared to perennial streams but this is changing. For example, there has been growing interest in the importance of intermittent streams for regional species richness, their use by fishes for spawning and rearing, their importance in providing refuge from winter spates, and their importance in nutrient dynamics and in maintaining the integrity of entire river networks. However, other studies have reported that physical conditions in intermittent streams can be harsh during the drying phase, which can result in large mortality events, including local extinctions during extreme drought. I hypothesized that drought intensity, which is driven by antecedent precipitation, plays an important role in determining whether conditions in intermittent streams are relatively benign or harsh. I tested this hypothesis by studying the ecology of a single intermittent stream, the John West Fork, a tributary of Olema Creek in Marin County, California, across four years that differed in drought intensity. Specific goals of my dissertation included examining the influence of antecedent winter precipitation on (1) patterns of stream fragmentation and pool habitat availability, (2) movement and survival of juvenile salmonid fishes, and (3) leaf decomposition, a key ecosystem process providing an important source of carbon in low-order streams.

In Chapter 2, I used long-term rainfall data to determine the drought intensity of each of my study years: two study years were relatively dry (2009 and 2012) and two years were relatively wet (2010 and 2011). I monitored changes in water level, including in both riffles and pools, at weekly intervals in each year. I then quantified the rate of riffle drying (as a measure of stream fragmentation) and the rate of pool drying (as a measure of habitat availability), and compared these rates between wet and dry years. Additionally, I track the movement of individually-marked juvenile steelhead trout (*Oncorhynchus mykiss*), and used a logistic regression to determine factors that influenced their movement among pools. Lastly, I estimated the difference

between biological fragmentation (defined as the date when fish movement ceases) and physical fragmentation (defined as the date when riffles completely dry). I found that riffles dried earlier following dry winters when compared to wet winters, which limited the movement of juvenile steelhead to the early summer following dry winters (but not wet winters). I found that fish movement was positively associated with riffle volume and negatively associated with originating pool depth, riffle length, and day of year. Lastly, I found that biological fragmentation preceded fragmentation by many weeks during each year, suggesting that there is a minimum level of water required for fish to move despite the presence of streamflow.

In Chapter 3, I explored differences in survival of juvenile steelhead trout between wet and dry years using Program MARK. I marked individual trout in the early summer and tracked their fates each week across the summer dry season in each of four years. I found that survival was higher following wetter winters. Moreover, I found that survival was high through the midsummer during all years; however, during dry years, survival was considerably lower during the late summer. These findings suggest that steelhead in the study region are resistant to drying conditions in intermittent streams to an extent. During wet years, steelhead can experience relatively high rates of survival intermittent streams, suggesting that such systems may be important to the overall productivity of the watershed following wet winters. During dry years, however, harsh physical conditions during the late summer result in high rates of mortality. These results highlight the importance of this critical period during the late summer in shaping fish population dynamics in intermittent streams and suggest that monitoring efforts should be focused on late-summer surveys in such systems.

In Chapter 4, I compared differences in leaf decomposition rates among years that differed in drought intensity and across a single season, including the early, middle, and late summer. I used generalized linear mixed-effects models (GLMM) to determine whether abiotic (water level and stream temperature) and/or biotic (shredder density) factors were important in determining leaf decomposition rates. I found that leaf decomposition was fastest during the wettest year and fastest during the early summer, suggesting that breakdown is generally faster when conditions are wetter. I also determined that the density of macroinvertebrate shredders was positively associated with leaf decomposition rates and that shredder decomposition rates were higher following wet winters and during the early summer, suggesting a possible indirect influence of drought intensity on leaf decomposition through its influence on shredder density.

In conclusion, the studies outlined in this dissertation highlight the role of antecedent precipitation in shaping physical conditions during the late summer, which have a strong influence on stream biota and ecosystem processes in an intermittent stream. Climate change is slated to heavily influence hydrologic regimes and will likely result in perennial streams shifting to intermittent flow states. As such, studies contributing to the body of research focused on intermittent streams are becoming increasingly important and findings from such studies can help guide management decisions and help prioritize conservation efforts.

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CHAPTER 1

INTRODUCTION: FRAGMENTATION OF AN INTERMITTENT STREAM DURING SEASONAL DROUGHT: INTRA- AND INTERANNUAL PATTERNS AND ECOLOGICAL CONSEQUENCES

Introduction: Fragmentation of an intermittent stream during seasonal drought: intra- and interannual patterns and ecological consequences

Drought events can have a profound impact on streams, resulting in habitat contraction and potential loss of surface flow (Stanley et al. 1997). However, until recently, the influence of drought on stream ecosystems has been largely understudied (Lake 2000) in part because their unpredictable nature makes drought difficult to study (Matthews and Marsh-Matthews 2003). Seasonal drought, which occurs in regions with distinct wet and dry seasons, is an important exception because seasonal drought is a fairly predictable event. Stream habitats in such systems are dynamic and undergo cycles of expansion and contraction that coincide with wet and dry seasons (von Schiller et al. 2011). Lake (2003) describes seasonal drought as a press disturbance, in which there is an abrupt change in the physical environment followed by an abrupt response by the biota.

Mediterranean-climate streams are a model system for studying seasonal drought because of the predictable patterns of precipitation, with rainfall concentrated during the winter months followed by a long, dry summer drought season (Gasith and Resh 1999). In addition to strong seasonal variability, Mediterranean-climate regions exhibit strong interannual variability, with some winters being much wetter than others (Gasith and Resh 1999). Low-order streams in Mediterranean-climate regions can experience an extreme form of habitat contraction that results in stream intermittency, wherein a portion of the stream dries during the summer drought season (Gasith and Resh 1999, Lake 2011).

Temporary streams (including intermittent and ephemeral streams) are common throughout the world and comprise a large proportion of total stream length (Larned et al. 2010). For example, in the United States (excluding Alaska), intermittent streams comprise approximately 59% of total stream length. Despite this, intermittent streams have been understudied when compared to perennial streams with year-round flow (Datry et al. 2011a). In recent years, there has been a growing interest in intermittent streams, including studies focused on hydrologic connectivity and habitat contraction during the drying phase (e.g., Stanley et al. 1997, von Schiller et al. 2011), their use by stream fishes (e.g., Labbe and Fausch 2000, Wigington et al. 2006, Bêche et al. 2009, Grantham et al. 2010) and macroinvertebrates (e.g., Bêche et al. 2009, Boersma et al. 2014, Bogan et al. 2015), and ecosystem processes and stream metabolism (Acuña et al. 2004, Datry et al. 2011b).

Previous studies have also highlighted that intermittent streams can provide important breeding and rearing habitat for native stream fishes (Erman and Hawthorne 1976, Wigington et al. 2006), including imperiled salmonid fishes (Ebersole et al. 2006). In contrast, other studies have reported that intermittent streams can be extremely harsh environments for stream biota (e.g.,

Tramer 1977, Mundahl 1990, Bogan and Lytle 2011). The varied biotic response to drought is very likely a result of differences in drought intensity, which can vary considerably from year to year (LeRoy et al. 2014).

The aim of my dissertation research was to explore the cascading influence of antecedent winter precipitation on drought intensity, stream physical conditions, ecosystem processes, and stream-dwelling salmonid fishes. Specifically, I explored the influence of seasonal drought on (1) hydrological connectivity and pool habitat contraction, (2) the movement and survival of juvenile steelhead trout (*Oncorhynchus mykiss*) and coho salmon (*O. kisutch*), and (3) leaf decomposition rates among and within years that differed in antecedent precipitation.

Below I provide an introduction to my study site, focal fish species, and an overview of my three chapters.

Study Site

My dissertation research was carried out in the John West Fork, a first-order, Mediterranean-climate stream that has an approximate watershed size of 3.1km² and is located within the Golden Gate National Recreation Area. The John West Fork is a tributary of Olema Creek, which is a tributary of the Lagunitas Creek Watershed in Marin County, California, USA. Generally, precipitation and streamflow are highest between the months of November and April. Beginning in May, streamflow is reduced, resulting in the eventual loss of surface flow and stream fragmentation. Hydrologic connectivity is reestablished with arrival of the first fall rains, typically in October or November; however, the duration of the low-flow period varies depending on the timing and magnitude of fall precipitation. For example, if the first fall rains arrive later than normal and/or are unusually low in magnitude, the low-flow period can be extended into the winter months (Figure 1.1). During the low-flow period, a series of remnant pools persist through the dry season and provide over-summer habitat for juvenile steelhead trout and coho salmon. Despite stream fragmentation and the overall decrease in water level during the summer, stream temperatures remain relatively cool at this site (<16°C) because of the presence of dense canopy cover flanking the stream. The presence of a culvert in the lower John West Fork restricts the upstream movement of stream fishes, with the exception of adult salmonids that are able to ascend the barrier during high flow events.

Focal Species

Two species of salmonids, steelhead trout and coho salmon, occur in the John West Fork. Throughout the state, populations of Pacific salmonids have been in decline over the last several century, with factors driving their decline including but not limited to presence of major dams,

urbanization, agriculture, and invasion by non-native species (Katz et al. 2013). Steelhead populations in Marin County are part of the Central California Coast (CCC) distinct population segment (DPS), which ranges from the Russian River in Sonoma and Mendocino Counties to Aptos Creek in Santa Cruz County (National Marine Fisheries Service 2006). CCC steelhead were listed as federally threatened in 1997 and the listing was reaffirmed in 2006 (National Marine Fisheries Service 2006). Coho salmon in the region are a part of the Central California Coast evolutionary significant unit (CCC ESU), which ranges from Punta Gorda in Humboldt County to the San Lorenzo River in Santa Cruz County, and represents the southern extent of the species range (National Marine Fisheries Service 2005). CCC coho were listed as federally endangered in 2005 (National Marine Fisheries Service 2005). Among the populations of coho salmon within the Central California Coast ESU, the Lagunitas Creek Watershed has been a stronghold for coho salmon, with populations in this watershed faring better than populations in other watersheds within the central coast region (Moyle et al. 2008).

Both steelhead and coho are anadromous, breeding and rearing in freshwater prior to ocean outmigration (Hartman 1965, Groot and Margolis 1991). However, they differ in that steelhead are iteroparous, while coho are semelparous (Quinn 2005). Shapovalov and Taft (1954) conducted a nine-year study (1933-1942) investigating the life histories of both CCC steelhead and coho in nearby Waddell Creek (Santa Cruz County, California, USA). In Waddell Creek, steelhead were documented to spend between one to three years as juveniles within the freshwater environment prior to ocean outmigration. In contrast, almost all coho salmon (>99%) they encountered were found to have spent one year in freshwater prior to ocean outmigration. They reported that most steelhead returned to freshwaters to breed as age-3 or age-4 fish, whereas most coho returned as age-3 fish, with the exception of a small proportion of males that returned as age-2 fish (so called 'jacks'). The life histories of steelhead and coho within the Lagunitas Watershed are very similar to those reported by Shapovalov and Taft (1954), with coho typically smolting after one year in freshwater and steelhead smolting after 1-2 years (Carlisle and Reichmuth 2015). Within the Lagunitas Watershed, peak spawning for steelhead occurs between the months of January and April, while steelhead typically spawn between the months of November and January (Carlisle et al. 2010). As a result, coho tend to have a size advantage when they co-occur in their first year of life in the stream (Hartman 1965, Young 2004).

The diverse life history of steelhead includes overlapping generations that provides some resiliency to interannual variation in the environment. In contrast, the strict three-year life cycle of most coho populations in this region results in less potential for 'dispersal through time' (Buoro and Carlson 2014), and leads to the emergence of 'strong' and 'weak' year classes. For example, in the Olema Creek Watershed, there is one strong year-class of coho salmon compared to two relatively weak year-classes (Carlisle et al. 2010). As a result, steelhead were numerically

dominant in the John West Fork during all four study years (2009-2012) and coho were only present in a sizable number in one year (2011).

CHAPTER OUTLINE

Chapter 2: Fragmentation of an intermittent stream during seasonal drought: Intra-annual and interannual patterns and consequences for fish movement

A major goal of my dissertation research was to understand how among-year differences in antecedent precipitation affect hydrologic connectivity, pool habitat availability, stream temperature, and fish movement during the summer drought season. Previous studies have documented the loss of surface flow and habitat contraction during seasonal drought (e.g., Stanley et al. 1997, Labbe and Fausch 2000); however, studies estimating pool habitat availability across years that differed in antecedent precipitation are rare. Even rarer are studies examining fish behavioral responses to stream drying as the summer drought season progressed (but see Hodges and Magoulick 2011). In chapter 1, I collected fine-scale data on stream fragmentation, pool habitat quantity and quality, and fish movement behavior among and within years that differed in drought intensity.

To determine differences in drought intensity for each year, I used annual precipitation data for the 81-year period from 1931-2012 obtained from a rain gauge in nearby Kentfield (Marin County, CA; National Climatic Data Center Gauge Number 044500-1). The annual precipitation data – including for the four years of my study - were divided into quintiles, which were classified using the following water-year classification: dry, below-normal, normal, above-normal, and wet. Additionally, each week across the summer drought season, I estimated riffle volumes (as a measure of hydrologic connectivity) and pool volumes (as a measure of habitat availability) for a continuous stretch of stream that included 28 pool-riffle hydrologic units. I also tracked the movement of individually-tagged fish within this region. I deployed thermistors in each study pool to monitor water temperature at 10-minute intervals across the summer drought season in each year. Using a Bayesian modeling approach, I estimated the initial water levels (e.g., early summer depths) and the rate of drying for both riffles and pools in my study stream. I used a similar approach to model stream temperature for each study pool. Additionally, I used data on riffle and pool volumes combined with observations of fish movements to explore the factors influencing juvenile steelhead movement among pools. Finally, I compared the difference in timing between biological fragmentation (i.e., date when fish movement ceases) and physical fragmentation (i.e., date when all riffles have dried) among my four study years.

My study encompassed two relatively dry years (2009, 2012) and two relatively wet years (2010, 2011), providing a natural contrast for comparing habitat availability and fish movement.

Hydrographs from nearby Walker Creek illustrate the consequences of interannual variation in rainfall for streamflow (Figure 1.2). I found that the stream fragmented earlier—that is, riffles dried earlier following dry winters when compared to wet winters, and as result, fish movement was highly restricted, both spatially and temporally, during dry years. In contrast, fish were able to move farther distances and later into the summer following wet winters. Once the stream fragments, the fish are concentrated in residual pools, so a second part of my study focused on changes to pool habitat availability. Following dry winters, I found that pools dried at a faster rate and more pools dried completely when compared to wet years. I also determined that fish were less likely to move out of deep pools when compared to shallow pools and were also less likely to move across long riffles when compared to short riffles. Overall, the findings of my first chapter highlight the strong influence of antecedent precipitation on drought intensity and stream physical conditions in an intermittent stream, which in turn heavily influence the movement of juvenile steelhead trout.

Chapter 3: Antecedent precipitation determines the over-summer survival of imperiled salmon and trout in an intermittent stream

Beyond exploring how variation in rainfall influences the timing and extent of stream contraction, I was also interested in understanding how drought intensity influences the summer survival of juvenile salmonids rearing in intermittent streams in coastal California. Past research had emphasized that stream fishes can persist in intermittent streams during the summer dry season (e.g., Labbe and Fausch 2000), but that – under some circumstances – stream fishes rearing in intermittent streams can experience high rates of mortality (e.g., Tramer 1977, Mundahl 1990). Most studies examining fish use of intermittent streams have been single-year studies (but see Bêche et al. 2009 and Grantham et al. 2012), providing little opportunity to explore environmental influences on over-summer survival. Because drought intensity varies among years, I hypothesized that interannual variation in rainfall influences the quantity and quality of the pool habitat available to stream fishes (see chapter 1), which should then influence interannual variation in survival.

In my third chapter, I compared the over-summer survival of juvenile steelhead trout and coho salmon across four summers that differed in antecedent precipitation (see Fig. 2). Using Program MARK, I estimated recapture probability and apparent survival each week across the drought season, examining variation among years (e.g., wet vs. dry years) and across the summer drought season (e.g., early vs. late summer) within each year. Additionally, I explored the influence of body size, age class (for steelhead only, age-0 vs. age-1), and species on summer survival.

I found that juvenile steelhead survived at higher rates following wet winters when compared to dry winters. Moreover, during dry years, I found that survival was relatively high through the midsummer, followed by an abrupt decrease in survival during late summer, suggesting that

juvenile salmonids can withstand drought conditions until pool conditions deteriorate in late summer. Finally, I found little effect of size, age (age-0 vs age-1 steelhead) or species on over-summer survival. My findings highlight that physical conditions during the late summer are critical in determining the fate of juvenile salmonids in intermittent streams in coastal California.

Chapter 4: Drought-mediated effects on leaf decomposition rates and macroinvertebrate shredder density in an intermittent stream

For my fourth chapter, I examined how among-year differences in drought intensity and associated reductions in water level influenced leaf decomposition rates. Leaf-litter is an important source of carbon fueling low-order stream food webs. Here I was especially interested in exploring the influence of abiotic factors (water level and stream water temperature) and biotic factors (the density of macroinvertebrate shredders) on rates of leaf breakdown. Previous research has demonstrated that rates of leaf decomposition tend to be faster in wetter conditions, including faster in perennial streams that remain wetted through the year when compared to intermittent streams (Tate and Gurtz 1986). Within intermittent streams, studies have also demonstrated that leaf decomposition rates are lower following cessation of surface flow when compared to periods after flow has resumed, however no studies have compared how breakdown rates vary as drying progresses during the summer drought season.

I used among- and within-year comparisons to assess the influence of stream drying, water level, stream temperature, and the density of macroinvertebrate shredders on leaf decomposition rates by deploying leaf packs containing red alder (*Alnus rubra*) leaves in the John West Fork in each of three years (2009-2011) and across the summer drought season in one year (2011). Using generalized linear mixed-effects models (GLMM), I tested the influence of year (including wet vs. dry years) and timing within the summer (e.g., early vs. late summer) on breakdown rates. Additionally, using more detailed data collected from a subset of ten pools, I explored the influence of pool water depth, water temperature, and macroinvertebrate shredder density on leaf decomposition rates.

In general, I found that decomposition rates were faster when conditions were wetter, including faster decomposition in the wettest year (2011) compared to the driest year (2009) and faster decomposition in early summer compared to late summer. When I examined pool-specific leaf decomposition rates, I determined that a model including shredder density was the best-supported model, and that models including pool water level and temperature received less support. These findings suggested that the physical effects of drought might have an *indirect* influence on leaf decomposition through the influence of drought on the density of macroinvertebrate shredders. Indeed, shredder density during the summer was higher following wetter winters, and these tended to be years associated with faster leaf decomposition. Overall, I

determined that drought intensity plays an indirect role in influencing leaf decomposition rates, a key ecosystem process in low-order streams.

CONCLUSION

With climate change, drought events are likely to become more frequent and severe (Kundzewicz et al. 2008). Decreases in stream runoff as a result of recent warming trends have already been documented in the Western United States (Saunders and Montgomery 2008) a trend which is likely to continue. Such runoff changes will alter flow regimes and it is likely that many systems will transition from perennial to intermittent flow (Larned et al. 2010, Jaeger et al. 2014). In California, the impacts of climate change are already being manifested in the form of decreased runoff (Moser et al. 2009). Furthermore, recent climate models predict that precipitation is expected to decrease from 15-30% by the year 2100 in California (Hayhoe et al. 2004) and to become more variable in timing, possibly leading to longer dry seasons (Miller et al. 2003). Over the past several years, California has experienced an ongoing, multi-year drought (2012-2015) that has rendered over 97% of the state as experiencing “severe drought” conditions (Simeral 2015), which provides a glimpse into future conditions because these conditions are predicted to be more common with climate change. Decreased precipitation and runoff within the state are likely to take a toll on populations of imperiled salmonids. A recent study indicated that the interactions between the effects of climate change and other drivers of decline (e.g., dams, urbanization, and agriculture) have put 81% of salmonid species at risk of imminent extinction (Katz et al. 2013). In light of recent and impending drought events, understanding the ecological impacts of drought in low-order is becoming increasingly important. My dissertation research contributes to this effort and will hopefully inform management decisions for Pacific salmonid fishes at the southern end of their range.

LITERATURE CITED

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Figure 1.1. Images of the John West Fork during the drought year of 2013-14 showing the dry stream bed in January 2014 (left) and the same site after flow resumption in February 2014 (right).

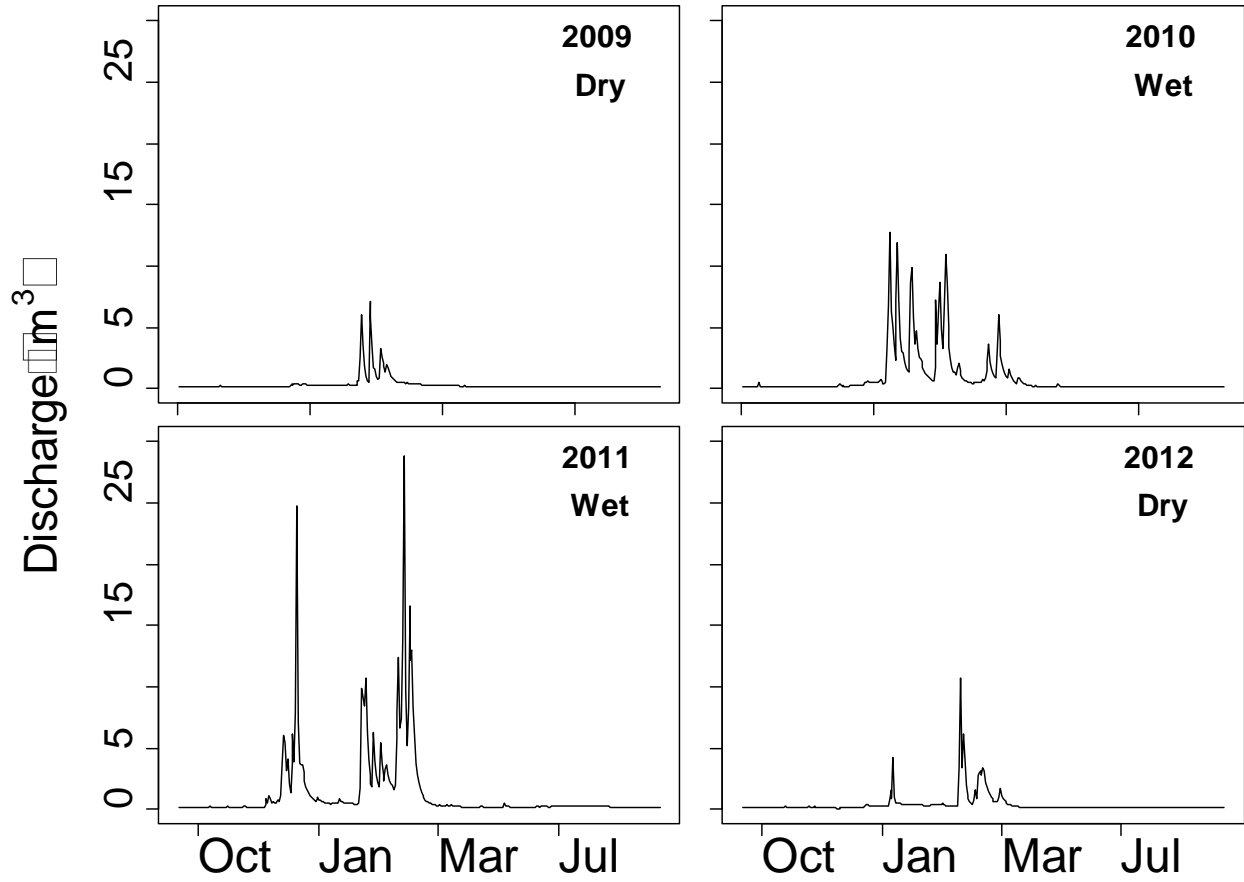


Figure 1.2. Hydrographs from nearby Walker Creek (Marin County; USGS Station 11460750) during four study years (2009-2012).

CHAPTER 2

FRAGMENTATION OF AN INTERMITTENT STREAM DURING SEASONAL DROUGHT: INTRA- AND INTERANNUAL PATTERNS AND CONSEQUENCES FOR FISH MOVEMENT

Fragmentation of an intermittent stream during seasonal drought: intra- and interannual patterns and consequences for fish movement

ABSTRACT

Intermittent streams lose surface flow during some portion of the year and can be important breeding and rearing habitats for stream biota. However, habitat contraction and deteriorating water quality across the summer can result in harsh conditions and mortality. We explored patterns of drying in a small intermittent stream across the summer in Mediterranean-climate California, including across four years that differed in antecedent precipitation. Wet-dry mapping revealed earlier stream fragmentation following dry winters and that entire sections of the stream varied in their propensity to dry suggesting an important influence of geomorphology on drying. Within two “slow-drying” reaches, initial riffle volumes were higher following wetter winters, but the rate of riffle drying was higher following wet years, presumably because higher initial volumes resulted in greater drying capacity. Initial pool volumes were similar across years, but the rate of pool drying was faster following dry versus wet winters (pool half-life ranged from 9.7 weeks in the driest year to 26.3 weeks in the wettest year). Stream temperature differed among years, but differences were slight and temperatures rarely exceeded optimal conditions for trout growth. We observed limited movement of trout during drier years and found that movement was negatively associated with pool depth, riffle length, and date, and positively associated with riffle volume and that movement did not occur when minimum depths were below 0.028m. Overall, we found that antecedent rainfall influenced variability in pool drying more than riffle drying; entire sections of the creek varied in their propensity to dry; and that biological fragmentation preceded physical fragmentation by three to seven weeks.

INTRODUCTION

Streams and rivers expand and contract in response to seasonal and interannual variation in patterns of precipitation (Stanley et al. 1997). In small streams, contraction along the longitudinal dimension can result in loss of surface flow, that is, stream “intermittency”. Intermittent streams tend to fragment during dry periods when wetted habitat contracts to a series of residual pools (Lake 2011). Intermittent and ephemeral streams are common in headwaters throughout the world and account for half or more of total stream length in many countries (Larned *et al.*, 2010), including 59% of total stream miles in the US, excluding Alaska (Nadeau and Rains, 2007).

Despite their ubiquity, intermittent streams have been understudied compared to perennial streams (Larned *et al.*, 2010). Habitat contraction and water quality deterioration across the dry season can result in harsh environmental conditions that can lead to shifts in taxonomic composition (Bêche et al. 2006), mass mortality events (Tramer, 1977; Mundahl, 1990), and

even local extinctions (Matthews and Marsh-Matthews, 2007; Bogan and Lytle, 2011). However, intermittent streams can also be important breeding sites for freshwater biota (Erman and Hawthorne 1976, Tatarian 2008). Such streams can also be important fish rearing sites (Wigington et al. 2006, Ebersole et al. 2006), providing refuge from both high flow (Brown and Hartman 1988, Fausch and Bramblett 1991) and predators that may be more common in perennial reaches (Labbe and Fausch, 2000).

Conservation efforts focusing on intermittent streams are limited (Larned et al. 2010), even though these systems support unique taxa with adaptations for withstanding drought (Dodds *et al.*, 2004; Bogan *et al.*, 2013) and provide habitat for many threatened and endangered species (e.g., Labbe and Fausch, 2000; Tatarian, 2008). In Western North America, for example, imperiled salmonid fishes use intermittent streams for breeding and rearing (Boughton *et al.*, 2009; Grantham *et al.*, 2012; Bogan *et al.*, 2015), and threatened coho salmon that moved into an intermittent stream experienced higher survival compared to mainstem reaches in an Oregon watershed (Ebersole *et al.*, 2006; Wigington *et al.*, 2006).

In recent years, studies examining the ecological effects of flow disruption in riverine ecosystems have increased (Pringle, 2003; Fullerton *et al.*, 2010); however, few of these studies have focused on small intermittent streams. Stream fragmentation during seasonal drought isolates residual pools, the primary refuges of stream biota during drought (Matthews and Marsh-Matthews, 2007; Hodges and Magoulick, 2011). In response to stream drying, organisms may initially exhibit high rates of movement as they seek suitable over-summer refuges (Minshall and Winger, 1968; Hodges and Magoulick, 2011). As drying progresses, riffles connecting adjacent pools dry completely and biological fragmentation occurs, that is, the movement of stream organisms between pools ceases (Irvine et al. 2009). What remains unknown is how the timing of biological fragmentation compares to the timing of physical fragmentation in intermittent streams.

The overarching goal of this study was to examine how patterns of habitat availability shifted across the summer drought season in an intermittent stream in Mediterranean-climate California. Streams in Mediterranean-climate regions experience predictable cycles of contraction and expansion during the summer and winter, respectively, and are also characterized by high interannual variability in precipitation and flow (Gasith and Resh 1999). A recent study exploring Mediterranean-climate intermittent streams in California found that the timing of fragmentation was heavily influenced by antecedent rainfall (Boughton et al. 2009). Here, we quantified how the degree of physical fragmentation, habitat quantity, and water temperature changed each week across the summer in each of four years, including two "wet" years and two "dry" years. Additionally, we explored the consequences of variation in the timing and degree of physical fragmentation on biological fragmentation by studying the movements of individually-

marked steelhead trout (*Oncorhynchus mykiss*). We predicted that the stream would fragment earlier and that wetted habitats would contract more rapidly following dry winters. We also predicted that fish would seek out refugial (i.e., deeper) habitats when drying occurred and we explored the difference in timing between biological fragmentation (i.e., cessation of fish movement) and physical fragmentation (i.e., loss of surface flow).

METHODS

Study system

We sampled the John West Fork (JWF; 37.99° N, 122.75° W), a first-order, intermittent stream that is a tributary of Olema Creek within the Lagunitas Creek Watershed and is located within the Golden Gate National Recreational Area (Marin County, CA). The watershed is approximately 3.1km² and the creek itself is ~3km in total length. Much of the creek is flanked by dense vegetation including California Bay Laurel (*Umbellularia californica*), beaked hazelnut (*Corylus cornuta*), bigleaf maple (*Acer macrophyllum*), poison oak (*Toxicodendron diversilobum*), and several species of willow (*Salix* spp.). Uplands are predominantly shrub and grassland. Streamflow is highest from October through April and lowest from May through September.

During the summers of 2009-2013, we studied a 450-meter reach located in the lower JWF (Figure 2.1), where most dry-season habitat is found (Hwan, unpublished). In 2009, we studied 12 riffle-pool sequences, but expanded our study in 2010-2012 to 28 riffle-pool sequences (which encompassed the original 12). In each of the four years, our study focused on the summer low-flow period (Table 2.1).

Steelhead trout (*Oncorhynchus mykiss*) were the most abundant fish in the creek, and so they were the focus of the biological aspects of this study. The only other fish species present, coho salmon (*O. kisutch*), is federally-endangered in this region and was not consistently abundant in the JWF.

Water year classifications

We classified each of our study years into one of five precipitation categories: dry, below-normal, normal, above-normal, and wet (Kiernan *et al.*, 2012). To do so, we used 70 years of rainfall data from nearby Kentfield, CA to calculate the annual precipitation for each water year and then partitioned the data into quintiles. We used United States Geological Survey (USGS) flow data from nearby Walker Creek (approximately 15km from JWF, USGS Station 11460750)

to create hydrographs for each study year to illustrate among-year differences in streamflow (Figure 2.2).

Physical fragmentation

We estimated hydrological connectivity and patterns of stream fragmentation at near-weekly intervals across the summer via (1) wet-dry mapping of the entire study reach and (2) estimating riffle volumes for each study riffle across the summer. This involved measuring riffle length (length of the wetted riffle connecting two pools), average width (based on three width measurements), and average depth (based on 15 measurements, 5 each across three width transects), and then calculating volume as $l \times \bar{w} \times \bar{d}$.

Pool habitat volume

We also monitored the water level (stage) in each study pool at weekly intervals each summer using meter sticks attached to anchored rebar in the deepest point of each pool. To estimate pool volume, we used the observed maximum depth information combined with bathymetric data. We made bathymetric measurements using a total station (Topcon GPT-3205, Topcon Corporation, Tokyo, Japan) to map streambed and water surface elevations of all study pools in May 2012. Using ArcMap (ArcGIS 10.1, ESRI 2012), we used the inverse distance weighted (IDW) interpolation technique to create rasters for the streambed and water surface for each pool. We used the Cut Fill tool to calculate pool volume between the streambed and water surface rasters. By subtracting the maximum depth readings from our weekly stage readings from the maximum depth reading from our total station survey, we were able to use IDW to create water surface rasters at a weekly interval for the summer of 2012.

Total station bathymetric survey data for each pool were not available in 2009-2011, but sediment transport during high flow periods required adjustment of streambed elevations each year using the initial stage readings for each pool. We used an iterative process to determine how to best adjust streambed surfaces based on comparisons of estimated volumes with actual volumes measured in 2009. In early summer 2009, we calculated water volume in each study pool using estimated surface area and an average depth value that incorporated 50 evenly distributed depth measurements. Through an iterative process, we found that the difference between these measured volumes and estimated volumes (i.e., those using the 2012 total station survey data with adjustment for differences in maximum depth between 2009 and 2012) was minimized when we raised the streambed elevation at the deepest point by 10% for pools that aggraded and lowered it by 10% for pools that incised. A paired t-test comparing measured volumes and estimated volumes using this technique revealed no differences ($P > 0.30$, $T=1.09$, $DF=11$), suggesting that our method for estimating pool volume across years was robust.

Statistical approach. We explored patterns of fragmentation and habitat availability each year using a log-linear hierarchical model. For fragmentation, our response variable was log-transformed riffle volume; for habitat availability, our response variable was log-transformed pool volume. While collecting data on pool and riffle volumes in the field, we observed that one section of our study reach went dry much earlier than other sections (hereafter “fast-drying” and “slow-drying” sections, respectively, Figure 2.3), so we incorporated drying regime into our model. We analyzed two sets of linear mixed-effects models – one for riffles and another for pools – that each included drying regime (slow-drying or fast-drying), week, and year as fixed effects and individual habitat unit as a random effect. We compared the deviance information criterion (DIC) values for all candidate models to determine the best-supported model. Visual assessment of diagnostic plots of fitted values and residuals indicated that the assumptions of log-linear decline were not violated (Supplemental Figure S2.1).

We used a Bayesian statistical inference approach because it allows the use of informative priors to constrain parameter estimates to realistic values. Priors for the intercept ranged between the observed minimum and maximum initial values for each habitat type and drying regime. Priors for the slope included only negative values because there was a decrease in habitat volume across all summers. The joint posterior distributions of all the model parameters were obtained by means of Markov Chain Monte Carlo (MCMC) sampling using the R package “rjags”. Convergence of MCMC sampling (number of chains=2 each started at different parameter values, thinning rate=1, number of MCMC samples=10,000) was assessed by means of the Brooks–Gelman–Rubin diagnostic (Brooks and Gelman 1998). We used the posterior predictive distribution for each pairwise year combination to test for differences in intercepts and slopes among years. Specifically, we calculated the difference of the predicted medians for the two years being compared to create a distribution of differences. If the 95% credible interval of this distribution of differences encompassed zero, we concluded there was no difference between the two years being compared (Kruschke 2013). The model code is available in Appendix 2. We also used a generalized linear mixed model to assess riffle and pool drying and the parameter estimates using this approach were very similar to the estimates we obtained using the Bayesian approach. We used package lmerTest in R to run our analyses, which uses Satterthwaite’s approximation to compute p-values when performing F-tests and t-tests (Kuznetsova 2015).

To compare the rate of drying for both pools and riffles among years, we additionally estimated the half-life of pools and riffles each year using intercept and slope estimates from our full model according to the following linear decay equation:

$$t_{1/2} = (N_0/N_{1/2} - N_0)/r$$

where $t_{1/2}$ represents the number of weeks for riffles or pools required to reach half their initial volume, N_0 represents the initial volume (i.e., intercepts from our model), and $N_{1/2}$ represents one half of the initial volume, and r represents the rate of drying (i.e., slopes from our model).

Pool water temperature

To quantify changes in water temperatures across the summer, we deployed temperature loggers (HOBO Pendant UA-002-64, Onset Computer Corporation, Bourne, MA, USA) in each study pool. Loggers were placed 10cm above the streambed in each pool and water temperature (°C) was logged at 10 minute intervals each summer.

Statistical approach. We summarized temperature data (daily average, maximum, and minimum) for each pool. Because we were interested in the dry summer period, we removed all temperature data during and after the first precipitation events of the fall. We used a two-factor ANOVA followed by a post-hoc Tukey procedure to determine whether there were among-year differences as well as differences between fast-drying and slow-drying pools in terms of average of the daily averages, average daily maximum, and average daily temperature range for each pool.

Biological fragmentation

Each year, juvenile steelhead trout were captured in the early summer and all fish longer than 60-mm in fork length were implanted with 12mm passive integrated transponder (PIT) tags (ranged from 38 fish marked in 2009 to 216 in 2010, Table 2.1). We then tracked the location of marked fish each week across the summer (range=9 to 11 weeks) using a portable PIT antenna (FS2001F-ISO BP, Biomark, Inc., Boise, ID, USA) and recorded each individual's location (i.e., pool ID number) to quantify movement between weeks. We delayed fish sampling until early July for three of our study years (2010-2012) to allow fish to reach the threshold size for marking, which limited the amount of detections given that the stream dries rapidly during early summer.

Statistical approach. We analyzed movement data using a mixed effects logistic regression model, where a binary response of '0' ('1') represented fish that were detected in the same (different) pool they occupied the prior week. This analysis assumes movers and non-movers had similar mortality rates, such that associations between movement and predictors are not a spurious effect of differential mortality; and that detection efficiency is similar across different pools and riffles such that differential detection probability and movement probability are not confounded. We used forward stepwise selection to determine the best-supported model. For our full model, individuals were coded as a random effect, while fixed effects included date,

precipitation regime (“wet” or “dry” year), maximum pool depth, pool volume, rate of pool drying, length of the longest adjacent riffle, average and maximum depths of the deepest adjacent riffle, volume of the more voluminous adjacent riffle, and a binary covariate for pool persistence over the summer (“yes” or “no”). For fish that moved, we used physical attributes of the pool that they moved *into* as covariates in the analyses. We also ran a follow-up logistic regression to determine if fish size (length and mass) influenced movement. For this latter analysis, all re-sightings of individual fish were considered and fish that moved during any re-sighting were coded as a “mover” whereas fish that did not move were coded as a “non-mover”.

For all movers, we used a chi-square test to determine whether movement was directional, in other words, whether more fish moved upstream or downstream. Additionally, we used a paired t-test to determine whether fish moved into deeper pools, using depth of the pool that they emigrated from and depth of the pool that they immigrated into as our paired samples. Finally, we estimated the difference in timing between biological fragmentation and physical fragmentation. On rare occasions, we observed late summer movement of fish between adjacent pools connected by a short riffle. To discount these rare movement events, we defined biological fragmentation as the date when 95% of all fish movement had occurred and physical fragmentation as the date when 95% of all riffles had dried.

RESULTS

Water year classification

Each of our study years represented a different water year classification: 2009 was classified as a dry year, 2010 a normal year, 2011 an above-normal year, and 2012 a below-normal year. For simplicity, we discuss 2009 and 2012 as “dry” years and 2010 and 2011 as “wet” years.

Patterns of stream fragmentation

Wet-dry mapping. In early June of 2009, 2010 and 2011, all study riffles and pools were wetted when we began data collection. In contrast, all of the pools in the fast-drying section of the creek (n=9) dried completely by early June in 2012, a below-normal water year (Figure 2.3). Note that we did not survey the fast-drying section of the creek in 2009 (a dry year), but it is likely that this section was also dry by early June. By mid-June, all riffles and pools in the fast-drying section of the creek had dried in 2010, and all but one pool had dried in 2011. In the slow-drying portions of the creek, all riffles but the shortest riffles dried by the end of the summer in 2011. The percentage of pools that dried during the late summer depended on antecedent rainfall. In the slow-drying section, 42-50% of pools went dry in the dry years, but only 11-16% went dry in wet years (Figure 2.3).

Stream fragmentation. We observed increasing stream fragmentation across each summer, measured as reductions in riffle volumes (Figure 2.4, Table 2.1). The best-supported model explaining riffle volumes was the full model (Table 2.2), which included year, week, and drying regime (slow- or fast-drying) as fixed effects and riffle ID number as random effects. For the slow-drying section of stream, our model indicated that initial riffle volumes (represented by the intercept) for the two wet years (2010, 2011) were higher when compared to the dry years (2009, 2012); the second driest year (2012) also had higher initial volumes than the driest year (2009). Riffle volumes in the two wet years were 526% (2010) and 791% (2011) larger than in the driest year (95% credible intervals 229-822% and 328-1253%). In contrast to our expectations, we found that the rate of drying (represented by the slope) was higher during the wet years when compared to the dry years (Table 2.3, Figure 2.5), possibly because the capacity for drying was greater with higher initial volumes. No other differences in initial volumes or rate of drying were detected (i.e., the 95% credible intervals of posterior differences encompassed zero for the remaining comparisons). We estimated the half-life for riffles in the slow-drying section as 6.0, 7.6, 8.2, and 7.0 weeks for 2009 (dry), 2010 (wet), 2011 (wet), and 2012 (dry), respectively.

For the fast-drying section, drying occurred too early in 2009 and 2012 to be included in our analyses because riffles in this section had dried before we started collecting data. Limiting our analyses to the two wet years (2010, 2011), we found that neither initial riffle volumes nor the rate of riffle drying differed significantly between these two years (i.e., 95% credible intervals of posterior differences encompassed zero).

Pool habitat volume

We observed reductions in pool volumes across the summer in all years; however, a rain event in mid-October of 2011 resulted in pool re-wetting and hence a reduction in the number of dry pools (Figure 2.4). The best-supported model explaining differences in pool volume was the full model (Table 2.2), which included year, week, drying regime, and specific pools as random effects. For the slow-drying section of stream, the best-supported model indicated that there were no differences among years in initial pool volumes (i.e., intercepts were similar; 95% credible intervals of posterior differences encompassed zero). However, pools exhibited different *rates* of drying among years (i.e., slopes were different, Table 2.3, Figure 2.6). The rate of pool drying was significantly faster in the driest year (2009) when compared to the two wettest years (2010, 2011). The rate of pool drying was also significantly faster in the second driest year (2012) when compared to the wettest year (2011). No other differences in the rate of pool drying were detected (i.e., the 95% credible intervals of posterior differences encompassed zero). We estimated the half-life for pools in the slow-drying section as 9.7, 18.6, 26.3, and 14.0 weeks for 2009 (dry), 2010 (wet), 2011 (wet), and 2012 (dry), respectively.

For the fast-drying section, pools dried prior to data collection in 2009 and 2012 and hence data were not analyzed for these years. Initial pool volumes were significantly higher in the wettest year (2011) when compared to the second wettest year (2010). The lower initial pool volume in 2010 suggests that fast-drying pools had already started to dry by the time data collection commenced. Moreover, the rate of pool drying was significantly faster in 2011 when compared to 2010 based on a comparison of slopes (Figure 2.6).

Pool water temperature

We found significant differences in daily average temperatures among years (ANOVA, $F=614.58$, $P<0.001$) and between drying regimes (fast- vs. slow-drying) ($F=13.10$, $P<0.001$), as well as a significant interaction between year and drying regime ($F=18.23$, $P<0.001$). All pairwise year combinations differed significantly from each other, but differences among years were slight (averages were typically within 1°C of each other: Figure 2.7). Dry years had slightly lower daily average temperatures than wet years. In general, average daily maximum temperatures were slightly higher in fast-drying pools (15.77°C) than in slow-drying pools (15.45°C) (t-test, $P<0.001$, Figure 2.7).

Fish movement

During the wet years of 2010 and 2011, tagged fish traversed a greater number of pools (maximum number of pools moved=14 (2010) and 12 (2011)) compared to dry years (maximum number of pools moved=1 (2009 and 2012)). One caveat is that we only had 12 study pools in 2009; however, we believe that we would have observed a similar pattern because the subset of riffles that we sampled in all years dried earlier in 2009 when compared to any other year across our study. The number of fish tagged varied among years, as did the number of movers and non-movers, and these details are summarized in Table 2.1. Additionally, a higher percentage of tagged fish moved between pools at least once in wetter years (2010: $52.4\% \pm 3.43$ and 2011: $45.6\% \pm 4.08$) compared to drier years (2009: $26.3\% \pm 7.14$ and 2012: $11.7\% \pm 2.84$). Finally, in the two wet years of 2010 and 2011, movement was also observed later in the summer, with the last observed movements occurring during the fourth week of July (2010) and the fourth week of September (2011) compared to the two dry years, when movement ceased during the second week of July (Table 2.1).

Model selection exploring factors that influence movement in our mixed-effects logistic regression model revealed that the best-supported model included date, precipitation regime, maximum pool depth, riffle length, and riffle volume, which were all significantly associated with fish movement. Movement was negatively associated with date ($P<0.001$), maximum pool depth ($P<0.001$), and longest riffle length ($P<0.01$), and positively associated with drying regime

($P < 0.001$) and riffle volume ($P < 0.05$). Our analysis of the influence of fish size on movement indicated that neither length ($P = 0.71$; length range = 60 to 210mm) nor mass ($P = 0.51$; length range = 2.02 to 97.68g) influenced movement.

Of the fish that moved, a higher proportion moved upstream compared to downstream (upstream=104 fish, downstream 57 fish, $P < 0.001$). Moreover, a higher number of fish moved into deeper pools ($n = 98$ fish) compared to those that moved into shallower pools ($n = 63$ fish). In comparing the depths of pools that fish emigrated from with the depths of pools that fish immigrated into, we found that pools that were emigrated from were shallower (mean depth = $0.40\text{m} \pm 0.13$) when compared to pools that were immigrated into (mean depth = $0.49\text{m} \pm 0.21$; Paired t-test; $P < 0.001$). We also found that fish rarely moved more than once, with only 5% of the 153 movers moving between pools in more than one week.

Fish movement through riffles ceased prior to complete drying of riffles, indicating that biological fragmentation preceded physical fragmentation. However, the magnitude of the effect differed among years. Specifically, biological fragmentation preceded physical fragmentation by three (2012) to six weeks (2009) during dry years and six (2011) to seven (2010) weeks during wet years (Figure 2.8). In most years, the majority of fish movement ceased by late July.

DISCUSSION

Previous work has demonstrated that the onset of fragmentation and rate of contraction are two factors influencing the fitness of biota in intermittent streams (May and Lee, 2004; Deitch *et al.*, 2009). The goal of our study was to examine how these factors differed in years that varied in antecedent rainfall. Wet-dry mapping revealed that a larger percentage of riffles and pools went dry earlier in the summer following dry winters when compared to wet winters. However, regardless of antecedent rainfall, most riffles dried by late summer. Based on our half-life estimates of riffle drying, we found that it took approximately 6-8 weeks for riffles to reach half their initial volume across all years. In contrast, the percentage of pools that dried was heavily dependent on antecedent rainfall, with more refuge pools persisting across the summer following wetter winters. In terms of pool half-life, pools persisted longer following wet winters (half-life ranged from 19-26 weeks and 10-14 weeks, following wet and dry winters, respectively).

Previous studies have reported that riffle drying in intermittent streams is a relatively rapid process, whereas drying of adjacent pools occurs at a slower rate (Stanley *et al.* 1997). Our data support these general patterns, while also highlighting that riffles start to dry sooner - so the stream fragments earlier - following dry winters (see also Boughton *et al.*, 2009). Moreover, we found that riffles dried faster during wet years when compared to dry years, likely because higher initial volumes in wet years resulted in higher capacity for drying. Certain study reaches contained pools that consistently dried early in the summer, whereas other reaches contained

pools that often retained water across the entire summer, highlighting that geomorphology also influences patterns of drying. May and Lee (2004) found that pools in reaches dominated by bedrock contact persisted throughout the summer and experienced relatively low rates of drying, whereas pools in reaches dominated by alluvial deposits decreased at a steady rate. At our study site, there were relatively few pools with visible bedrock, yet many pools in our slow-drying reaches persisted throughout the summer, suggesting that there were other factors that influence drying patterns (e.g., differences in the local water table and local variation in coarse sediment storage in the channel). In contrast, we observed minimal differences in temperature among pools across all years (Figure 2.7) with dry years surprisingly having cooler stream temperatures than wet years. Possible explanations for this pattern is that flow into a pool during dry years occurs *through* riffles as opposed to *over* riffles during wet years or because lateral groundwater inputs comprise a higher proportion of water within the pool.

Not surprisingly, changes in the distribution and temporal duration of aquatic habitats in stream channels have biological consequences. Previous research has suggested that the duration of the low-flow period (Wigington *et al.*, 2006; Grantham *et al.*, 2012) and the rate of pool drying (May and Lee 2004) strongly influence summer survival of fish in intermittent streams. Here we extend these results to explore how stream fragmentation and habitat availability influenced the movement of trout rearing in an intermittent stream. We observed that movement rates were elevated prior to loss of surface flow, possibly because fish were sampling the available refuge pool habitat. In support of this possibility, we found that fish were more likely to move out of shallow pools than deep pools, and there was a higher proportion of fish that moved from shallower pools to deeper pools than vice versa, supporting earlier research suggesting that organisms exhibit high mobility while seeking perennial refuges during the initial phase of stream drying (Minshall and Winger, 1968; Hodges and Magoulick, 2011). Our results suggest that most of the movement typically ceased between three to seven weeks prior to loss of surface flow (Figure 2.8). This result suggests that there is a minimum threshold of water required for fish to move successfully. Of riffles that were traversed during the week preceding biological fragmentation, the average length was 5.1m, the maximum length was 19.6m, the average depth was 0.028m, the depth ranged from 0.019 to 0.244m, and the average volume was 0.458m³, although which of these factors is most important in determining movement through riffles remains an open question.

Although seasonal drying occurs naturally in John West Fork, our results have implications for streams where drying patterns are influenced by water extraction (i.e., “anthropogenic drought”, Cushman, 1985). Indeed, a review of invertebrate responses to low flows found that natural and artificial low-flow conditions have similar effects on invertebrates (Dewson *et al.* 2007). Deitch *et al.* (2009) found that water abstraction for agriculture can accelerate the start of drought conditions by nearly one month. Our results suggest that such acceleration of drought will limit

the movement of stream fishes, and extend the time they are isolated in refuge habitats. Moreover, our results suggest that earlier onset of drought will translate to faster drying of refuge pools, which could lead to reduced survival of biota in those pools.

Studies examining flow intermittency are increasingly important as the effects of climate change are becoming evident. Air temperatures in the western United States are increasing and are very likely to continue rising over the next century (Moser *et al.*, 2009). Warming temperatures will also result in increased aridity and decreased runoff in California streams (Miller *et al.*, 2003). These decreases in stream flow will likely lead to further loss of habitat for salmonids (Kundzewicz *et al.* 2008) and an increase in the number of intermittent streams over the next century (Larned *et al.* 2010). Thus, there is a pressing need to understand the resistance and resilience of stream biota to stream intermittency, including effects of different low-flow magnitudes and durations.

Beginning with the last year of our study (2012) through the present (2015), California has experienced a moderate to extreme multi-year drought due to record low precipitation (Artusa 2012, Heim 2014). Our findings suggest that a better understanding of how imperiled fish populations respond to varying degrees of antecedent rainfall could aid policymakers in setting regulations for water abstractions in stream systems accordingly. Increased aridity coupled with growing human water demand are already resulting in ‘water wars’ that pit human needs against environmental needs (Poff *et al.* 2003). Understanding how patterns of precipitation influence patterns of stream habitat fragmentation, habitat availability and quality, and fish movement and survival will improve our ability to manage and conserve freshwater biodiversity through seasonal and multi-year droughts.

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Table 2.1. Summary of fish tagging events and fish movement for each year.

	2009	2010	2011	2012
Event	Dry	Wet	Wet	Dry
Study Start Date	June 15	May 25	May 27	June 6
Study End Date	Oct 2	Oct 22	Oct 3	Oct 15
Number of pool-riffle units	12	28	28	28
Tagging dates	June 23-25	July 1-4	July 7-11	July 9-13
Number of fish tagged	38	212	149	113
Number of fish that moved	10	110	65	15
Number of non-movers*	25	65	67	95
Number of re-sighting events	10	10	8	11
Average number of re-sightings	6.6	6.2	5.9	5.3
Final movement date	July 13	July 29	August 15	July 9
Date median number of riffles dried	July 21	August 5	August 15	July 9
Date all riffles dried	Sept 11	Sept 13	Sept 28	Sept 4

*For those fish that did not move, we considered only the subset of fish that were re-sighted at least once.

Table 2.2. Model selection results using Bayesian inference of factors that influenced pool and riffle drying.

Model	Week	Year	Drying Regime	Unit	DIC_c	Delta
Full Model	X	X	X	X	-915.3	0
Model 2	X	X	X		3670.2	4585.5
Model 1	X	X			5570.9	6486.2
Null model	X				5614.8	6530.1

Table 2.3. Intercept and slope estimates for riffle and pool habitats in drying models. 95% credible intervals are indicated in parentheses.

Year	Habitat Type	Drying Regime	Intercept	Slope
2009	Riffle	Slow	0.060 (0.005, 0.132)	-0.005 (-0.012, 0)
2010	Riffle	Slow	0.350 (0.250, 0.451)	-0.023 (-0.029, -0.017)
2011	Riffle	Slow	0.524 (0.357, 0.695)	-0.032 (-0.041, -0.023)
2012	Riffle	Slow	0.197 (0.125, 0.267)	-0.014 (-0.019, -0.009)
2009	Pool	Slow	1.811 (1.172, 2.434)	-0.093 (-0.132, -0.053)
2010	Pool	Slow	1.711 (1.364, 2.059)	-0.046 (-0.064, -0.028)
2011	Pool	Slow	1.579 (1.262, 1.900)	-0.030 (-0.046, -0.015)
2012	Pool	Slow	1.599 (1.182, 2.033)	-0.057 (-0.076, -0.039)
2009	Riffle	Fast	N/A	N/A
2010	Riffle	Fast	0.402 (0.228, 0.557)	-0.032 (-0.044, -0.020)
2011	Riffle	Fast	0.411 (0.219, 0.606)	-0.035 (-0.050, -0.019)
2012	Riffle	Fast	N/A	N/A
2009	Pool	Fast	N/A	N/A
2010	Pool	Fast	0.312 (0.146, 0.484)	-0.021 (-0.033, -0.010)
2011	Pool	Fast	1.145 (0.396, 1.930)	-0.082 (-0.139, -0.026)
2012	Pool	Fast	N/A	N/A

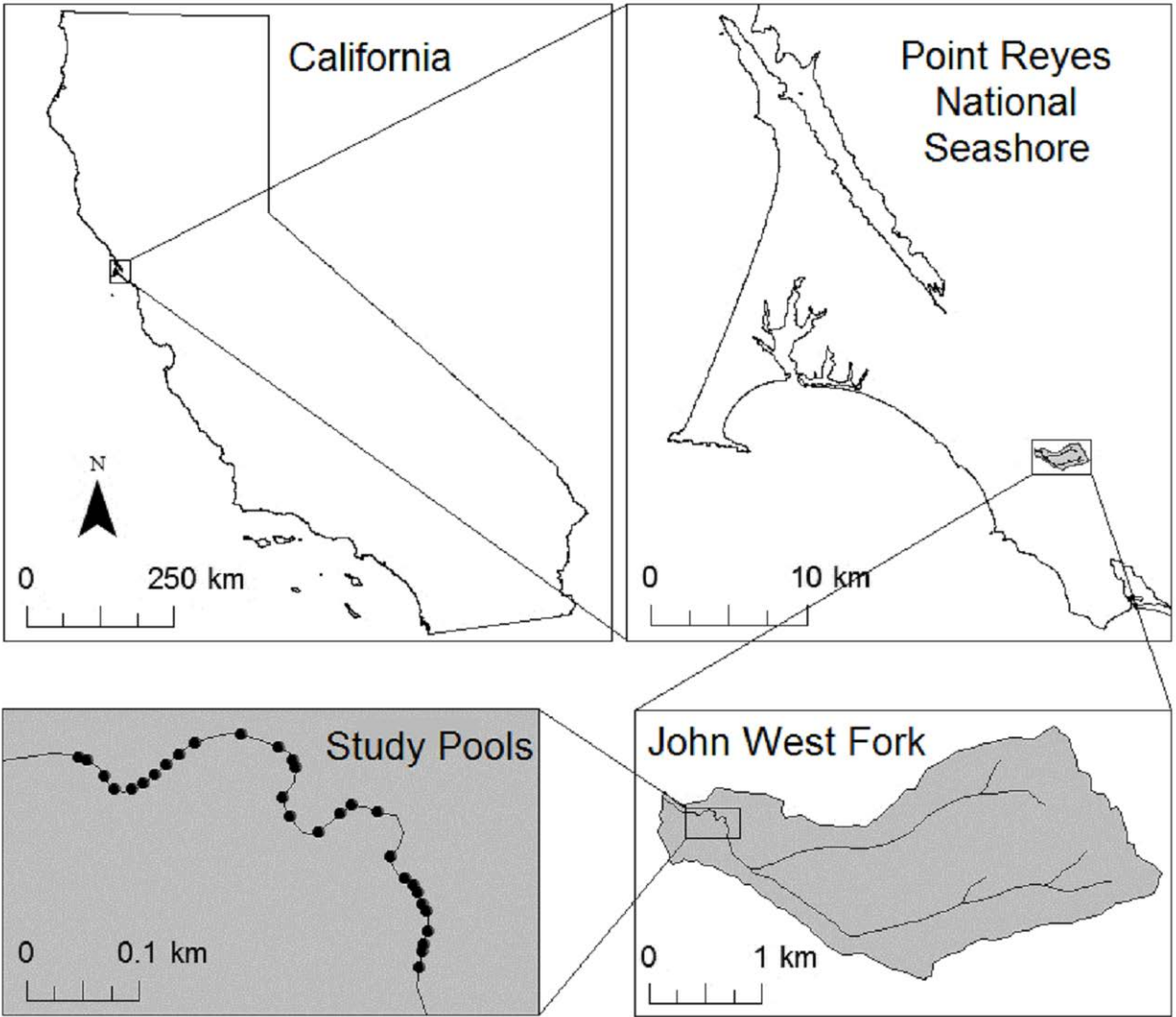


Figure 2.1. Study area within the John West Fork with circles representing study pools.

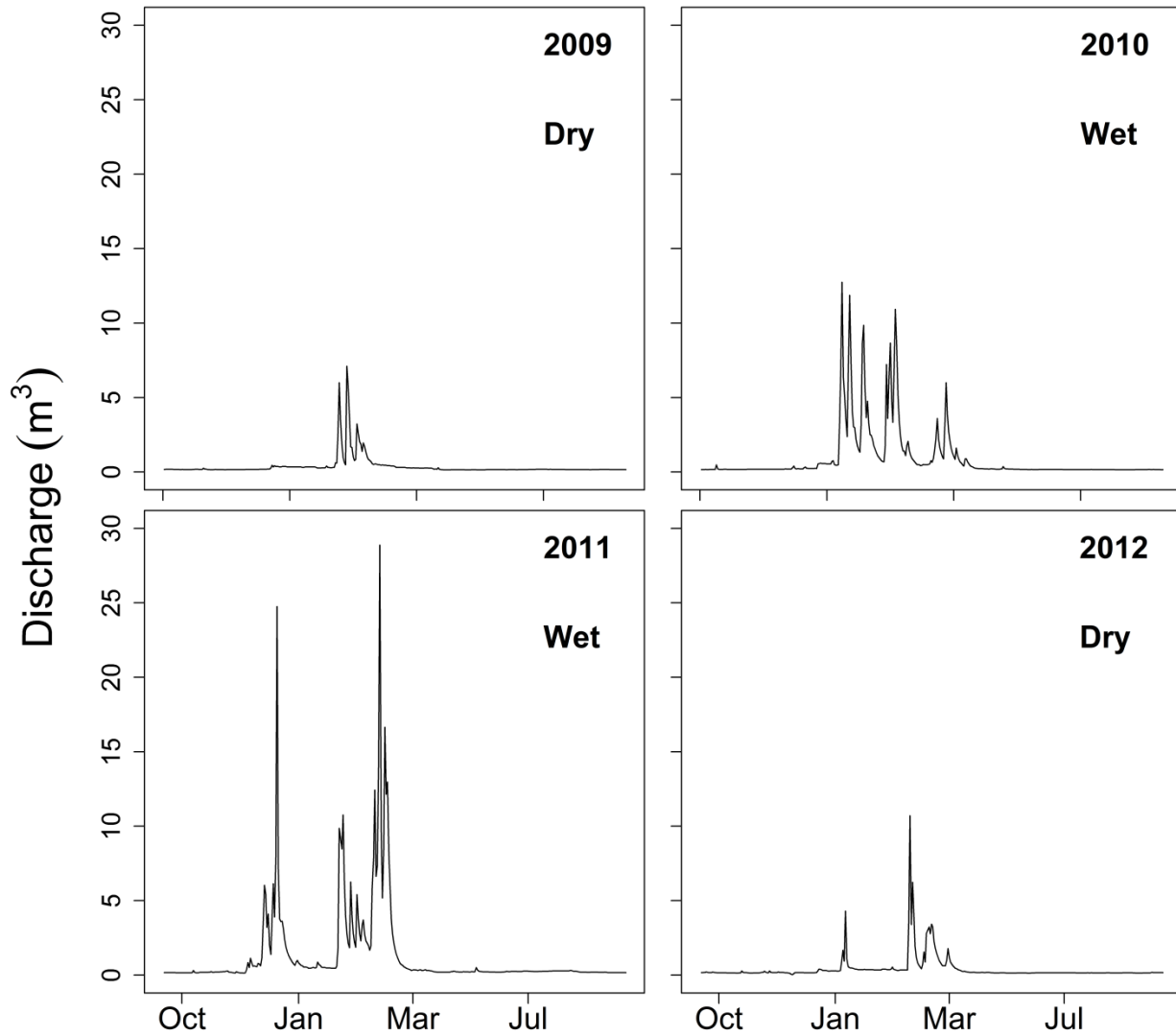


Figure 2.2. Hydrographs shown for each of the four study years using data collected from Walker Creek, a nearby stream with a USGS flow gauge (USGS Station 11460750).

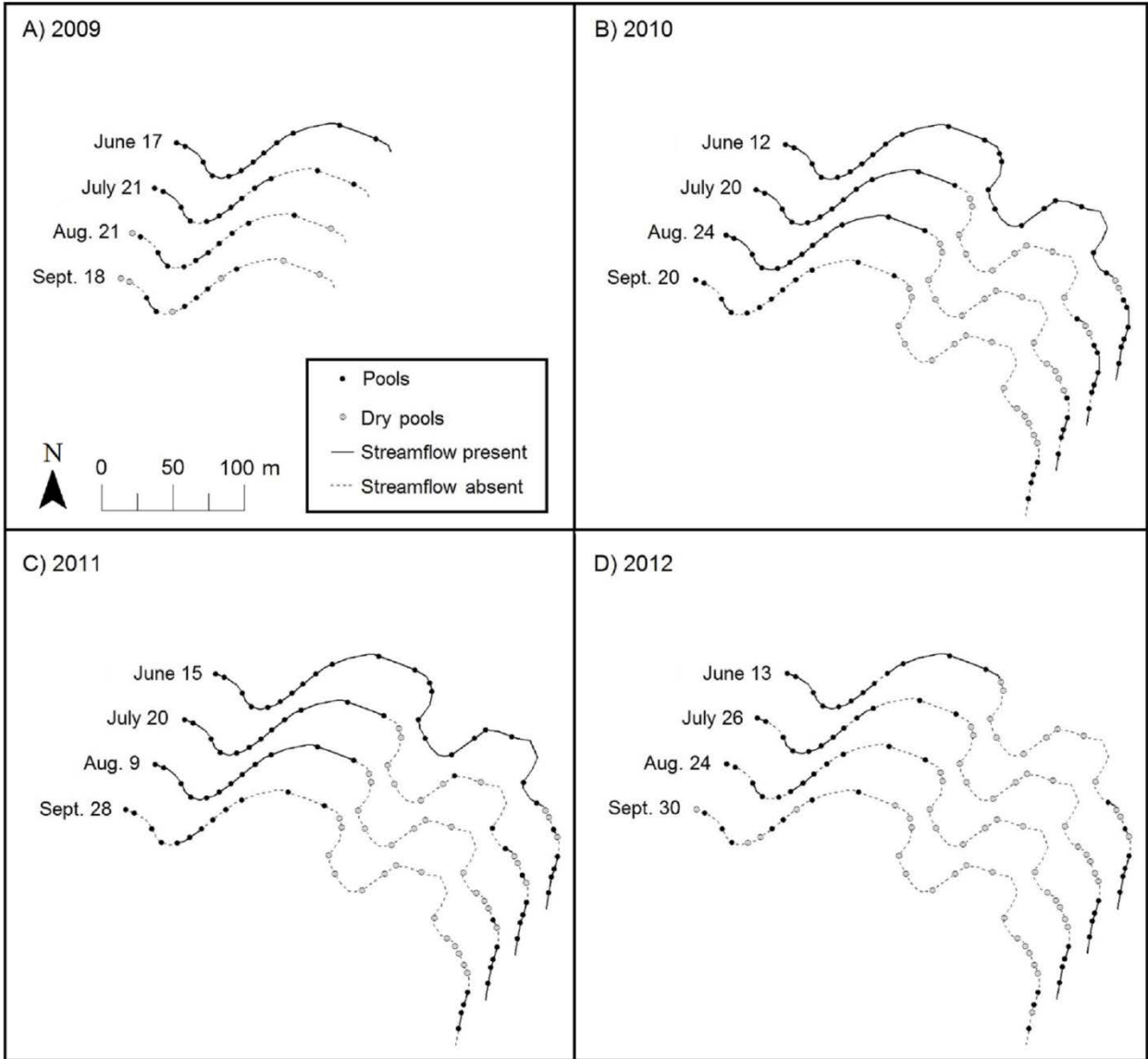


Figure 2.3. Patterns of fragmentation in study area of John West Fork shown for each study year. The filled circles represent wetted pools, open circles represent dry pools, solid lines represent wetted riffles, and dashed lines represent dry riffles.

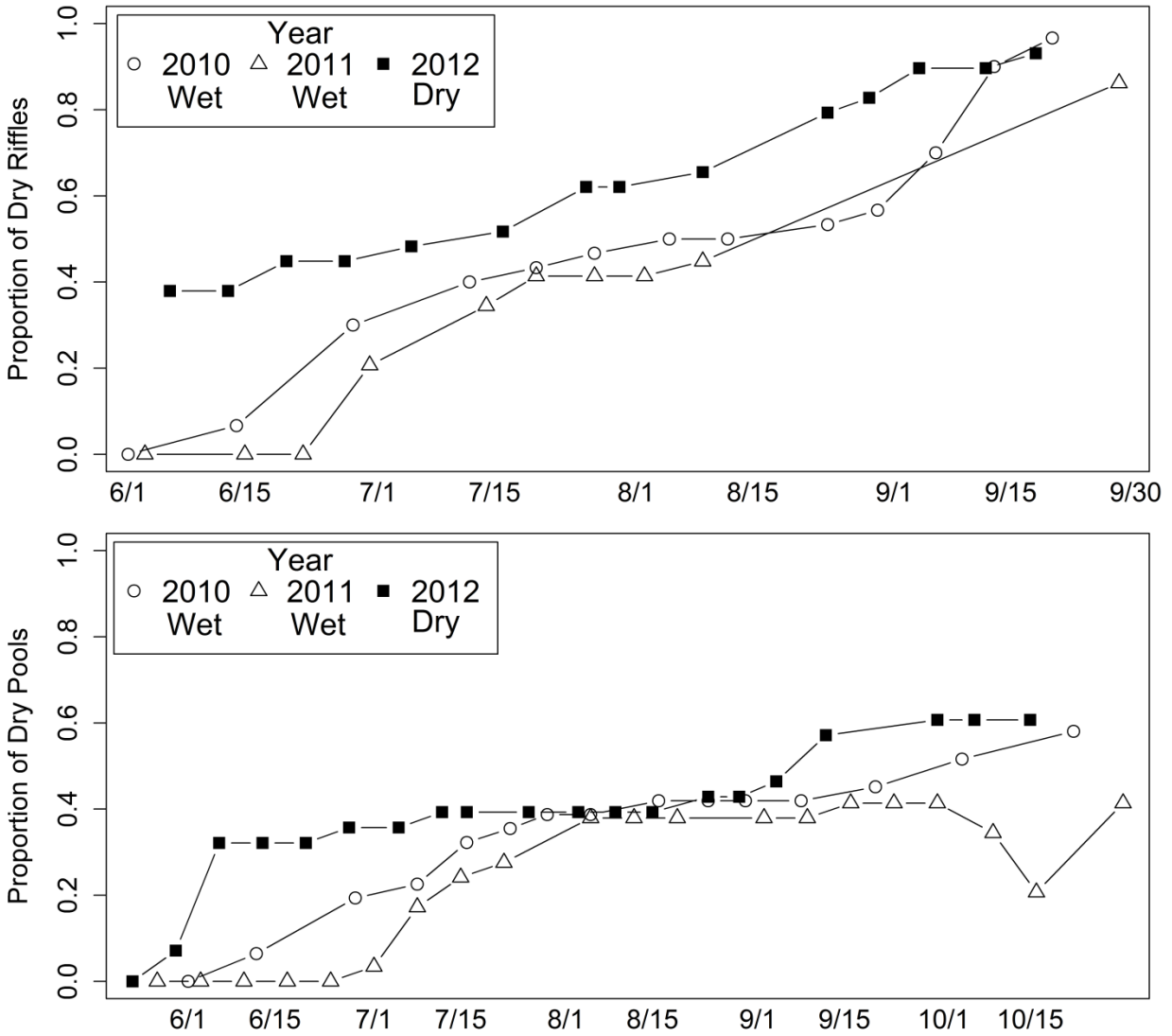


Figure 2.4. Proportion of riffles (top) and pools (bottom) that dry as a function of date shown for each study year. Decrease in proportion of dry pools during the late summer of 2011 was a result of a rain event that caused some dry pools to re-wet.

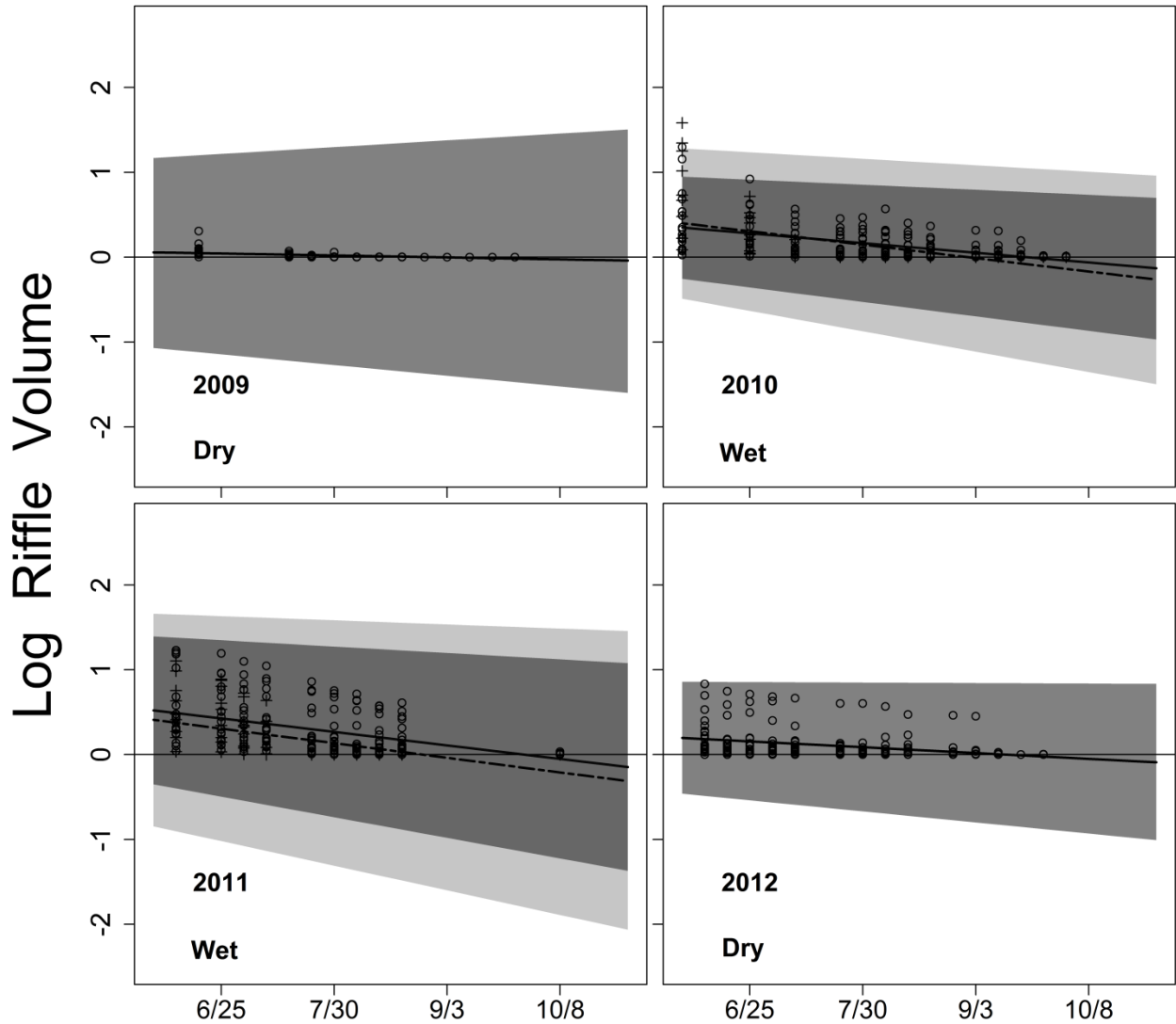


Figure 2.5. Log of riffle volume versus week shown for each study year. Dashed lines represent riffles in section of study area that dried early in the summer ("fast-drying reach") while solid lines represent riffles in section of study area that experienced drying later in the summer ("slow-drying reaches"). Open circles represent observed riffle volumes for riffles in the slow-drying reaches of the stream and crosses represent observed riffle volumes for riffles in the fast-drying reach.

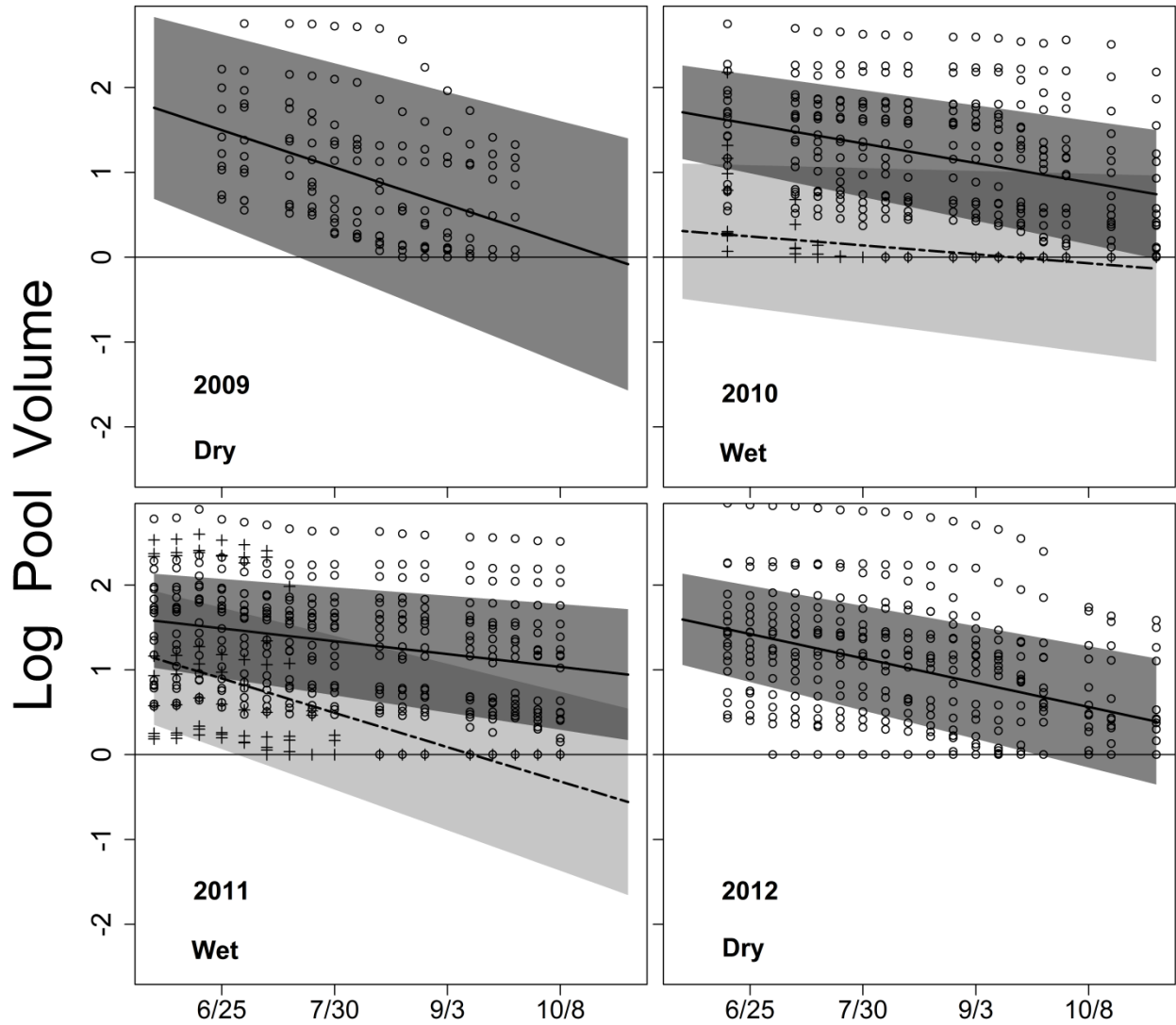


Figure 2.6. Log of pool volume versus week shown for each study year. Dashed lines represent pools in section of study area that dried early in the summer ("fast-drying reach") while solid lines represent pools in section of study area that experienced drying later in the summer ("slow-drying reaches"). Open circles represent observed pool volumes for pools in the slow-drying reaches of the stream and crosses represent observed pool volumes for pools in the fast-drying reach.

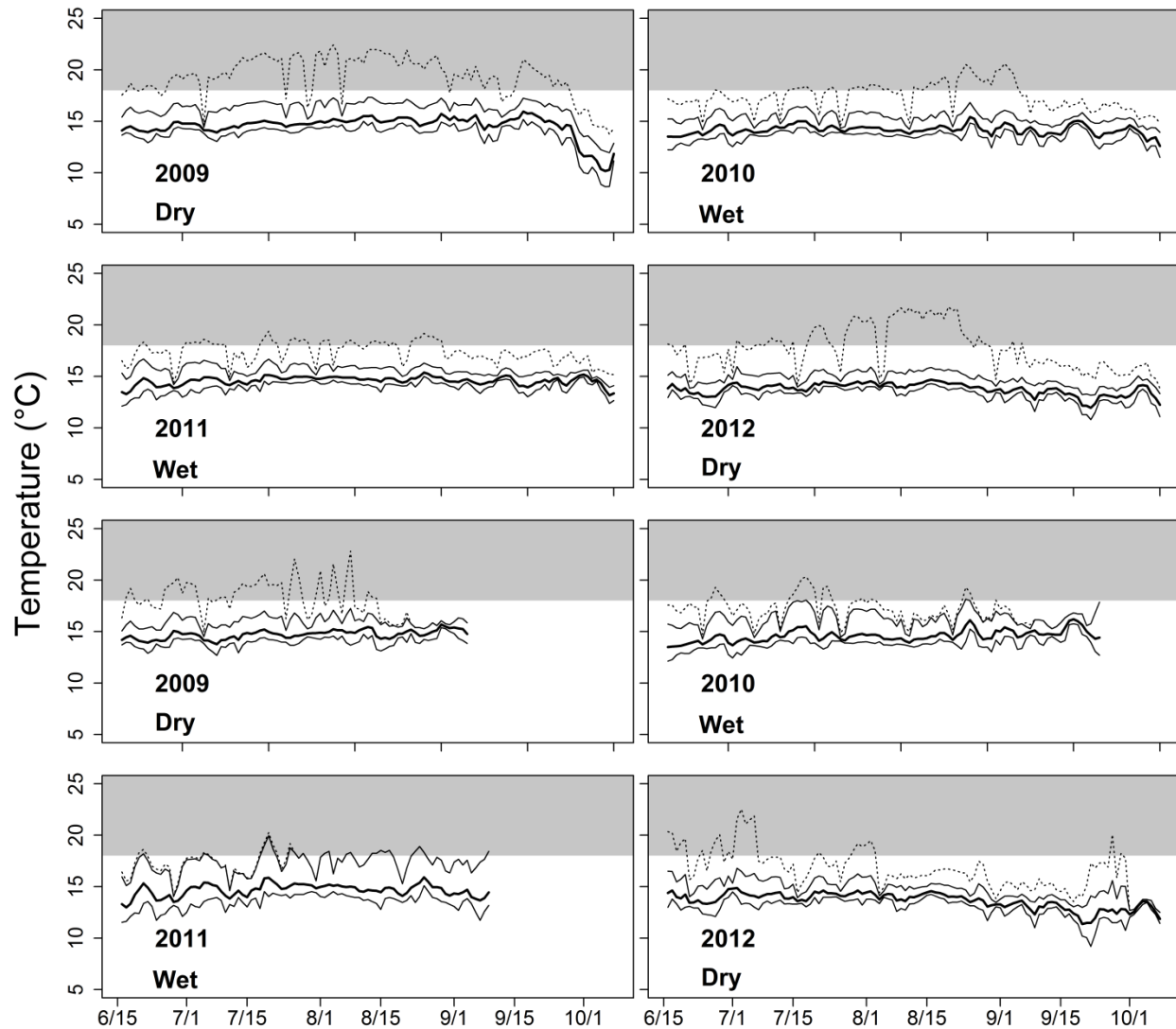


Figure 2.7. Top: Average, daily maximum, and daily minimum temperatures averaged across all pools that remain wetted shown for each study year. Bottom: Average, maximum, and minimum temperatures averaged across all pools that dried shown for each study year. Dotted line represents maximum temperature across all pools. Shaded region represents suboptimal conditions for juvenile *O. mykiss*.

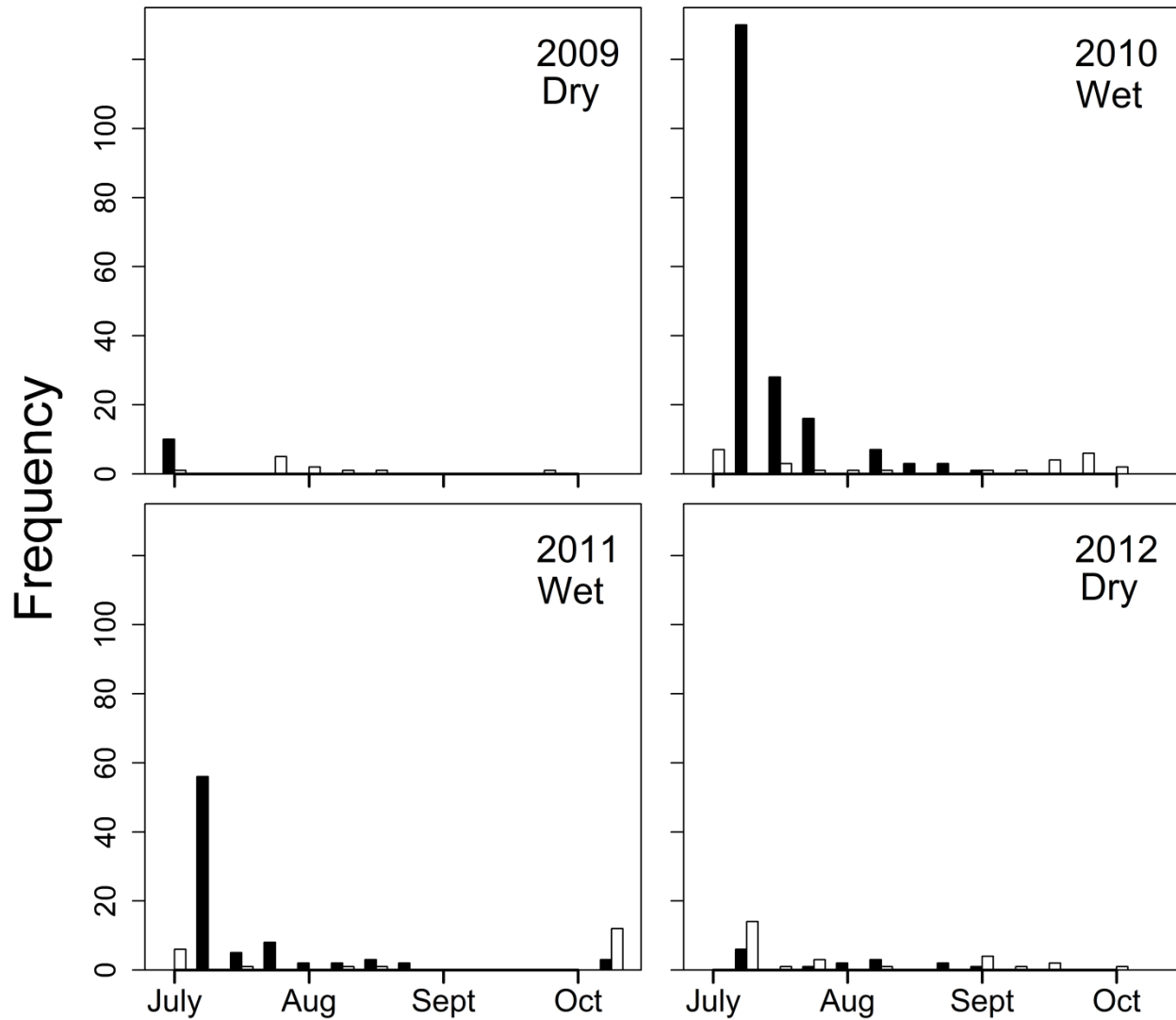


Figure 2.8. The number of steelhead trout that move from one pool to another during a given week (gray bars) and the number of riffles that go dry during the same week (white bars) shown for each study year.

SUPPLEMENTAL FIGURES

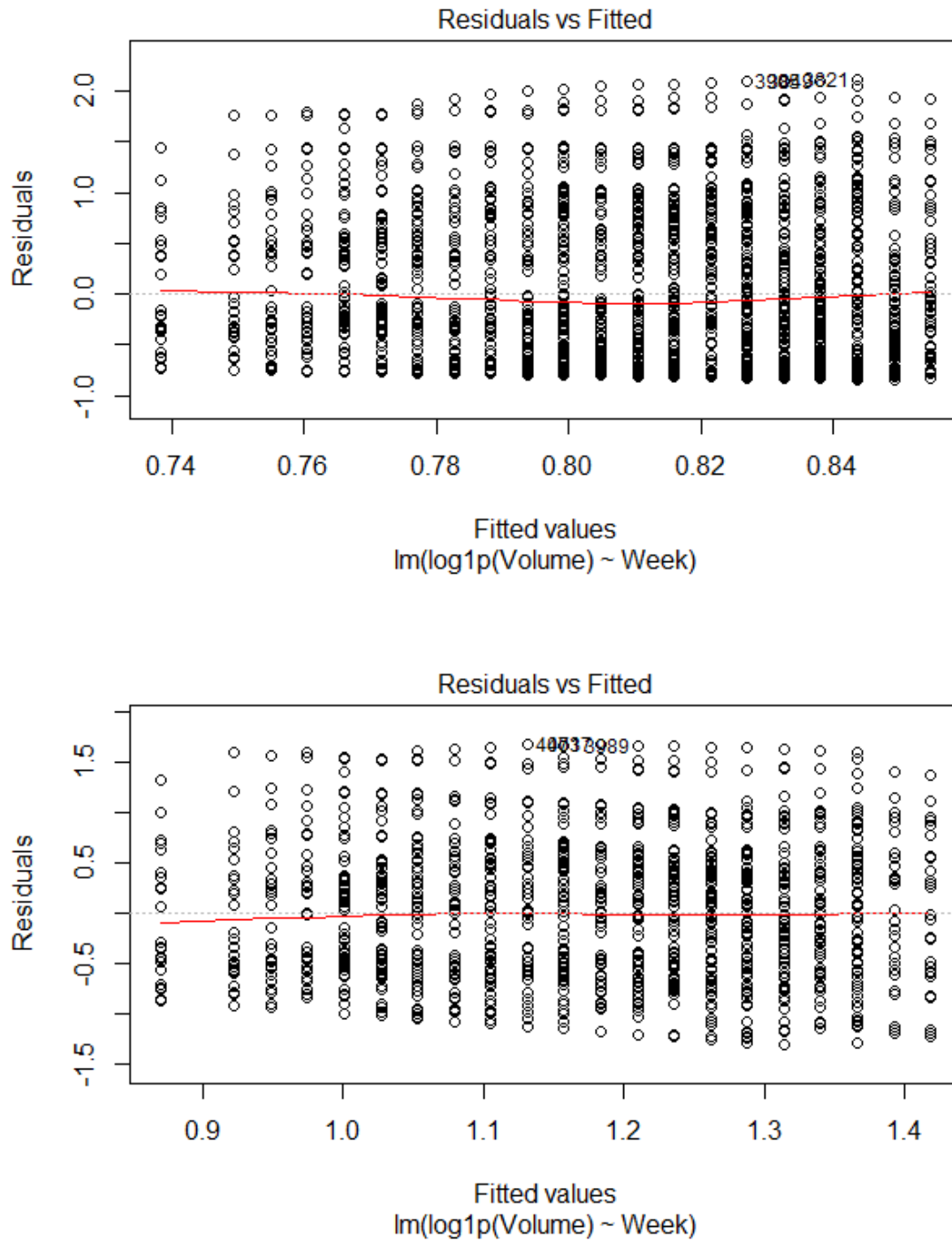


Figure S2.1. Top: Diagnostic residuals vs fitted plots for checking assumptions of log-linear decline for riffles (top) and pools (bottom).

APPENDIX 2

R code for volume estimates using Generalized Linear Mixed Models

```
require(lmerTest)
data<-read.csv("Volumes_all.csv")
sdpools<-subset(data,Pool.Riffle==1)
fdpool<-subset(data,Pool.Riffle==2)
fdpools<-subset(fdpool,Year==2010 | Year==2011)
sdriffles<-subset(data,Pool.Riffle==3)
fdriffle<-subset(data,Pool.Riffle==4)
fdriffles<-subset(fdriffle,Year==2010 | Year==2011)

#Slow-drying pools
spyear<-as.factor(sdpools$Year)
spool<-lmer(log1p(Volume)~I(Week-22)*spyear+(Week|Unit), data=sdpools)
summary(spool)
spyear2 = factor(sdpools$Year, c("2010","2011","2009", "2012"))
spool2<-lmer(log1p(Volume)~I(Week-22)*spyear2+(Week|Unit), data=sdpools)
summary(spool2)
spyear3 = factor(sdpools$Year, c("2011","2010","2009", "2012"))
spool3<-lmer(log1p(Volume)~I(Week-22)*spyear3+(Week|Unit), data=sdpools)
summary(spool3)
spyear4 = factor(sdpools$Year, c("2012","2010","2009", "2011"))
spool4<-lmer(log1p(Volume)~I(Week-22)*spyear4+(Week|Unit), data=sdpools)
summary(spool4)

#Fast-drying pools
fpyear<-as.factor(fdpools$Year)
fpool<-lmer(log1p(Volume)~I(Week-22)*fpyear+(Week|Unit), data=fdpools)
summary(fpool)
fpyear2 = factor(fdpools$Year, c("2011","2010"))
fpool2<-lmer(log1p(Volume)~I(Week-22)*fpyear3+(Week|Unit), data=fdpools)

#Slow-drying riffles
sryear<-as.factor(sdriffles$Year)
sriffle<-lmer(log1p(Volume)~I(Week)*sryear+(Week|Unit), data=sdriffles)
summary(sriffle)
sryear2 = factor(sdriffles$Year, c("2010","2011","2009", "2012"))
sriffle2<-lmer(log1p(Volume)~I(Week-22)*sryear2+(Week|Unit), data=sdriffles)
```



```

summary(sriffle2)
sryear3 = factor(sdriffles$Year, c("2011","2010","2009", "2012"))
sriffle3<-lmer(log1p(Volume)~I(Week-22)*sryear3+(Week|Unit), data=sdriffles)
summary(sriffle3)
sryear4 = factor(sdriffles$Year, c("2012","2010","2009", "2011"))
sriffle4<-lmer(log1p(Volume)~I(Week-22)*sryear4+(Week|Unit), data=sdriffles)
summary(sriffle4)

#Fast-drying riffles
fryear<-as.factor(fdriffles$Year)
friffle<-lmer(log1p(Volume)~I(Week-22)*fryear+(Week|Unit), data=fdriffles)
summary(friffle)
fryear2 = factor(fdriffles$Year, c("2011","2010"))
friffle2<-lmer(log1p(Volume)~I(Week-22)*

```

CHAPTER 3

DRY SEASON SURVIVAL OF JUVENILE SALMONIDS IN AN INTERMITTENT STREAM IN RELATION TO ANTECEDENT PRECIPITATION

Dry season survival of juvenile salmonids in an intermittent stream in relation to antecedent precipitation

ABSTRACT

We estimated dry season survival of imperiled salmonids in an intermittent stream in California across four years (2009-2012). Our study encompassed two dry and two wet winters allowing us to explore patterns across and within dry seasons with different antecedent precipitation. Following wet winters, apparent survival of age-0+ steelhead trout (*Oncorhynchus mykiss*) varied among weeks, but was high overall (weekly average = 0.95 ± 0.07). Following dry winters, apparent survival was high through midsummer (average = 0.96 ± 0.05), followed by a sharp decline in the late summer (average = 0.81 ± 0.01), indicating that fish exhibited resistance to drought until late summer. Cumulative over-summer survival was much higher following wet (0.44) than dry (0.19) winters. Additionally, we found no difference in over-summer survival between co-occurring age-0+ and age-1+ steelhead and similar rates of survival between age-0+ coho salmon (*O. kisutch*) (0.95 ± 0.06) and equal-aged steelhead (0.94 ± 0.08). Our results highlight the influence of antecedent precipitation in driving the survival of imperiled salmonids and emphasizes that these fish are resistant to drought, at least to a point.

INTRODUCTION

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 can in turn result in increased stream temperatures and decreased dissolved oxygen levels (Boulton and Lake 1992, Elliott 2000). Typically, the effects of drought are more pronounced in small low-order streams when compared to larger high-order streams (Lake 2011). In regions that experience seasonal drought, low-order streams are often 'intermittent', losing surface flow for a portion of the year (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 refuge and breeding habitats for fishes (Erman and Hawthorne 1976, Fausch and Bramblett 1991, Wigington et al. 2006). Conversely, other studies have demonstrated that intermittent streams can be harsh environments and sites of high over-summer mortality of resident stream fishes (Tramer 1977, Mundahl 1990). These contradictory results can possibly be attributed to differences in drought intensity, which can vary considerably across space or, at a given site, from year to year. Interannual variability in drought severity can result in dramatically different physical conditions from year to year within a single stream (Boughton et al. 2009, Hwan and Carlson 2015).

Native biota in intermittent streams are often highly resistant to drying events (Miller and Golladay 1996, Dodds et al. 2004, Arthington and Balcombe 2011). Lake (2003) characterizes 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 able to withstand the pressure of the disturbance prior to the realization of the critical threshold, after which there is a negative response. Previous studies have demonstrated that some macroinvertebrate taxa can exhibit resistance to moderate drought conditions; however, when drying is more severe, their abundance and biomass can decrease 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 and decreased sharply when drying was more pronounced (Larimore et al. 1959). These studies highlight the importance of drought severity in structuring lotic communities.

Body size can also play 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 refuge pool habitats by larger conspecifics (Bohlin 1977, Berg et al. 2014) or the presence of large piscivores (Schlosser 1988). Moreover, interspecific competition has been shown to be a factor in regulating habitat use, with larger, more dominant species excluding non-dominant species through aggressive displays of territoriality (Fausch and White 1986, Sabo and Pauley 1997, Stradmeyer et al. 2008). However, large size does not always confer a fitness advantage. Larger individuals of some taxa may have reduced tolerance to hypoxic conditions (Burlerson et al. 2001, Robb and Abrahams 2003) and/or may be more susceptible to predation (Power 1987, Trexler et al. 1994, Lankford et al. 2001), particularly in contracting pools.

In this study, we tracked the fates of imperiled salmonid fish species in a Mediterranean-climate stream across four dry seasons that differed in antecedent winter precipitation. Our goal was to estimate survival of juvenile salmonids across each dry season and determine how antecedent precipitation affected salmonid survival through the dry season. Specifically, we estimated apparent weekly survival and cumulative survival across each summer. We hypothesized that (1) survival would be higher following wet winters than dry winters, (2) survival would be higher in the early summer followed by a reduction in survival in late summer (i.e., fish can withstand drought conditions to a point), and (3) larger species and age classes of fish would experience higher rates of survival compared to smaller individuals because of their ability to exclude smaller individuals from optimal 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 (Marin County, California; Figure 3.1) and is a tributary of Olema Creek, which itself is a tributary of Lagunitas Creek. The JWF is an intermittent stream that is approximately 3 km in length and is situated in Mediterranean-climate California. Declining water levels in JWF during the summer dry season lead to residual pools that provide refuge habitat for juvenile salmonids rearing in the creek (Bogan et al. 2015, Hwan and Carlson 2015). Our study area (approximately 450 m in length) was 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, including the 12 that were studied in 2009 (Table 3.1).

Study species

Two species of salmonid fishes are found in JWF—steelhead trout (*Oncorhynchus mykiss*) and coho salmon (*O. kisutch*). Both are anadromous, using freshwater environments for breeding and rearing. 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 a 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). We encountered both age-0+ and age-1+ steelhead at our study site and include both age classes in our analyses. Coho salmon in the Central California Coast region have also seen 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 this region, which results in relatively high abundances of coho every three years (Carlisle and Reichmuth 2015). During our study period (2009-2012), coho salmon were absent or nearly absent in all but one year (2011) from JWF (Table 3.1), limiting our analysis of coho survival data to that year. Throughout much of their sympatric range, coho salmon have been documented to 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 throughout their freshwater rearing stage.

Among-year differences in antecedent rainfall

Under typical conditions, the John West Fork experiences continuous stream flow from November through June. Starting in the early summer, stream flow decreases resulting in stream fragmentation wherein shallow riffle habitats dry, leaving behind remnant pools. In a previous study, we explored changes in pool habitat availability across the summer at JWF (Hwan and Carlson 2015). We observed two ‘wet’ study years (2010 and 2011) and two ‘dry’ study years (2009 and 2012) driven by variation in antecedent winter precipitation. Dry years were associated with earlier stream fragmentation with the majority of riffles drying approximately one month earlier following dry winters. In contrast, pool drying occurred at a slower rate in wet years. The pool half-life, which represents the number of weeks for pools required to reach their initial volume, was higher during wet years (18.6-26.3 weeks) when compared to dry years (9.7-14.0 weeks). Additionally, there was a higher percentage of pools that dried completely during dry years (42-50%) when compared to wet years (11-32%).

Fish Survival

Across each of four study years (2009-2012), we used three-pass electrofish depletion to sample fish on two occasions—once during the early summer (late June/early July) and once at the end of summer (late September/early October; see Table 3.1 for sampling dates). During these capture events, we anesthetized captured fish, identified all captured fish to species, recorded the pool number they were found 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. To re-sight tagged fish, we used a portable PIT antenna (FS2001F-ISO BP, Biomark, Inc., Boise, ID, USA) to detect tagged fish each week across the summer, noting each fish's pool location upon detection.

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 effort occurred (Hwan and Carlson 2015). To account for movement outside of this area, we re-sighted several pools upstream and downstream of our original study area. Specifically, we surveyed until we no longer detected fish in three contiguous pools, approximately 140 m upstream and 90 m downstream of our study site. We continued to re-sight fish within this expanded study area during subsequent re-sighting events.

Data Analysis

We used the Cormack-Jolly-Seber model in program MARK to estimate recapture probability and apparent survival (i.e., the probability that fish are alive and within the survey area) each week across our four study summers (White and Burnham 1999). We used model selection based on an information-theoretic approach (Burnham and Anderson 2002) to compare several candidate models, each representing different a priori hypotheses regarding the influence of a suite of factors on survival and recapture probability. We ranked models using Akaike's Information Criterion corrected for small sample sizes (AIC_c) to determine which model best fit our data (White and Burnham 1999, Burnham and Anderson 2002). Models that were within 2 ΔAIC_c of the top ranking model were considered suitable alternative models and we used model averaging to estimate parameters and standard errors for the subset of high-ranking models (Burnham and Anderson 2002).

Age-0+ steelhead were numerically dominant in the JWF when compared to age-1+ steelhead (n=74 out of 521 total tagged steelhead across all years). As a result, we tested two sets of models, one in which only age-0+ fish were included in our analyses (Table 3.2) and one in which both age-0+ and age-1+ fish were included (Table 3.3). Prior to analyzing survival, we determined the best models for recapture probability for both sets of models.

We tested the influence of among-year and within-year factors on recapture probability (P) and apparent survival (ϕ) for age-0+ fish. Among-year factors included a 'year' effect in which survival/recapture probability differed among all four study years, a 'water year' effect that tested whether survival differed between wet and dry years, and a 'constant year' effect in which survival/recapture probability was constant across all years. Within-year factors included a 'constant week' effect in which survival/recapture probability was constant across weeks, an effect of 'week' in which survival/recapture probability differed across weeks, and a 'resistance' effect in which we postulated that survival would be high early in the summer up until a point, after which it would decline. Fish body size (mass and fork length) at the time of our early summer capture was also included as an individual covariate in our models. We determined that the results for both mass and length were similar in our models; however, models including length consistently received more support (i.e., were associated with lower AIC_c values). For simplicity, we present only models that include length as an individual covariate. Based on a priori hypotheses that tested combinations of among- and within-year factors and the length covariate, we compared seven candidate models for our recapture probability analyses and 11 candidate models for our survival analyses (Table 3.2).

For 2011, which was the only year when a sizable number of coho salmon were present in JWF, we ran a separate analysis to compare survival and recapture probabilities of equal-aged

steelhead and coho (age-0+). This analysis included a ‘species’ effect to test whether survival/recapture probability differed between coho and steelhead, or a ‘constant’ effect in which survival/recapture probability did not differ between species. Additionally, two within-year factors, a ‘week’ effect and a ‘constant week’, were included in these models. We used a priori hypotheses to establish seven candidate models for our recapture analysis and an additional seven models for our survival analysis, which included different combinations of species effects, within-year effects, and a length covariate (Table 3.4).

In addition to apparent survival, we calculated cumulative survival across the summer as the product of our weekly estimates of apparent survival (Kaplan and Meier 1958). We calculated cumulative survival for the grouping factors that were included in the best models for our among-year comparisons (including the models with only age-0+ and models with both age-0+ and age-1+ steelhead) as well as our species comparison in 2011.

The above mark-recapture analysis was 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 fish that were captured, we also estimated survival using early and late summer population size estimates from 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 here. We used this same method to estimate steelhead and coho survival rates for a comparison of the two species in 2011.

RESULTS

Among year comparison of age-0+ steelhead

The best-supported model for recapture probability for our among-year comparison of age-0+ steelhead after setting survival constant included an effect of week and fish length ($AIC_c = 3247.16$, Table 3.2). The second highest-ranking model ($\Delta AIC_c = 0.80$) included an interaction between year and week, in addition to length. Based on model-averaged results from our two highest-ranking models, recapture probabilities were relatively high across all years (average recapture probabilities: 2009 = 0.89 ± 0.04 ; 2010 = 0.87 ± 0.06 ; 2011 = 0.85 ± 0.11 ; 2012 = 0.91 ± 0.06 ; Figure 3.2). In general, smaller fish were more likely to be recaptured than larger fish (Supplemental Figures S3.1-S3.4).

The highest-ranking model for the survival analysis included an effect of water year-type, Moreover, during wet years, survival varied by week, whereas during dry years, we found evidence for a resistance effect ($AIC_c = 3107.29$, Table 3.2). Average apparent survival was higher during wet years (0.95 ± 0.07) when compared to dry years (0.89 ± 0.08) in our highest-ranking model (Figure 3.3). During dry years, we observed relatively high rates of survival through mid-summer (average weekly apparent survival = 0.96 ± 0.05), after which sharp declines in water level during the late summer were associated with a pronounced decrease in survival (average apparent weekly survival = 0.81 ± 0.01). In contrast, during wet years survival varied among weeks but showed no clear trend over the summer and remained relatively high even in the late summer. As a result, cumulative survival was also higher in wet years (0.44) than dry years (0.19). Based on over-summer survival estimates from our three-pass depletion estimates, we observed the same pattern of higher survival during wet years (2010: 0.0050 ± 0.0051 , 2011: 0.0068 ± 0.0051) when compared to dry years (2009: 0.0035 ± 0.0050 , 2012: 0.0015 ± 0.0027).

Among year comparison of age-0+ and age-1+ steelhead

When we examined differences in recapture probability among years with age-1+ steelhead included in the analysis, we found that the highest-ranking model included effects of year, week, and length ($AIC_c = 4014.92$, Table 3.3). This same model was the second highest ranking model in our age-0+ comparison and was considered a plausible model (i.e., it was $< 2 \Delta AIC_c$ units from our top-ranking model). Based on this model, recapture probabilities were generally high across all years (2009 – 0.76 ± 0.20 ; 2010 – 0.77 ± 0.19 ; 2011 – 0.88 ± 0.11 ; 2012 – 0.84 ± 0.15 ; Figure 3.2). This model also suggested that smaller fish were recaptured at a higher rate when compared to larger fish. Average recapture probabilities were slightly lower for this analysis incorporating age-1+ steelhead when compared to our age-0+ analysis (Figure 3.2). In comparing survival across years when all age classes of steelhead were included, we found that the highest-ranking model was one in which there was an interaction between wet years and week and an interaction between dry years and a resistance effect ($AIC_c = 3836.21$, Table 3.3), which was also the highest-ranking model when age-1+ fish were excluded from the analysis. Similar to the age-0+ analysis, average apparent survival was higher during wet years (0.95 ± 0.06) when compared to dry years (0.88 ± 0.09 ; Figure 3.3). We also found that cumulative survival was similar to the age-0+ analysis with higher cumulative survival during wet years (0.46) when compared to dry years (0.16).

Species comparison

During 2011, the only year when coho salmon were abundant at our study site, coho were larger than steelhead during the early summer capture event (coho average length = 74.4mm; steelhead average length = 65.1mm; $P < 0.001$, Mann-Whitney U).

When comparing the recapture probability of the two species, we found that the best-supported model for recapture when survival was held constant included an effect of week and length as an individual covariate, but not an effect of ‘species’ ($AIC_c = 1929.61$, Table 3.4). The second highest-ranking model ($\Delta AIC_c = 0.35$), included species, week, and length. One other model was within two AIC_c units of our highest-ranking model ($\Delta AIC_c = 1.00$), and this model included an effect of week only. Using model-averaged parameter estimates for these three models, we found that recapture probability was generally higher for smaller fish in 2011. Despite this, we found that the average recapture probability was higher for coho (0.90 ± 0.11) when compared to steelhead (0.88 ± 0.12 ; Figure 3.4).

The highest-ranking model for survival in 2011 included an effect of week only ($AIC_c = 1929.61$, Table 3.4). One other model was within 2 ΔAIC_c ($\Delta AIC_c = 0.01$) and included an interaction between species and week. Based on model-averaged results of these two models, apparent survival remained high throughout the summer (average apparent survival: steelhead = 0.94 ± 0.08 , coho = 0.95 ± 0.06 ; Figure 3.4). Based on these results, cumulative survival for both steelhead and (0.51) coho (0.61) were relatively high in wet years. Using three-pass depletion estimate, we found that over-summer survival rates were similar for both steelhead (0.0068 ± 0.0054) and coho (0.0064 ± 0.0053).

DISCUSSION

Seasonal drought and associated stream habitat contraction can pose significant challenges to aquatic organisms, though the intensity of these challenges can vary from year to year. During our four-year study, two winters were relatively dry and two were relatively wet. Average apparent survival was considerably higher during wet years (0.95 ± 0.07) compared to dry years (0.89 ± 0.08), indicating that survival in intermittent streams can vary greatly from year to year depending on drought intensity. Our end of the summer population sizes varies considerably from year to year as well (2009: 0.0035 ± 0.0050 , 2010: 0.0050 ± 0.0051 , 2011: 0.0068 ± 0.0051 , 2012: 0.0015 ± 0.0027), which could reflect a combination of over-summer survival and higher number of adults in wetter winters.

Studies investigating the summer survival of fishes inhabiting intermittent streams have found that fish can persist in isolated pools throughout the summer. For example, in the Big Sandy Creek Watershed (Colorado, USA), Arkansas darters (*Etheostoma cragini*) were able to persist through the summer in isolated pools despite stream temperatures exceeding lethal levels (Labbe and Fausch 2000). Similarly, a study of creek chub (*Semotilus atromaculatus*) in Indian Creek (Arkansas, USA) found relatively high rates of survival throughout the summer in isolated pools during a single summer (Hodges and Magoulick 2011). Conversely, other studies have found that habitat conditions in intermittent streams can be extremely harsh, resulting in reduced

survival. Tramer (1977) described a ‘catastrophic mortality’ event in Tenmile Creek (Ohio, USA), in which many individuals across eight species of fish died as a result of hypoxia prior to the summer drying of isolated pools. Mundahl (1990) also documented a similar phenomenon in Indian Creek (Ohio, USA), with 14 species of fish exhibiting extremely high mortality rates as a result of heat stress during a mid-summer drying event. These were single-year studies that demonstrate that fish survival in intermittent streams can be variable and is likely driven by drought intensity.

In a rare multi-year study, Grantham et al. (2012) found that the survival of juvenile steelhead in the Russian River Watershed (California, USA) was positively associated with the magnitude of summer streamflow, which is mediated by antecedent precipitation and groundwater extraction in that system. Their study encompassed a nine-year period, of which four were relatively dry years and five were relatively wet years (California Department of Water, 2014). Our results provide further support for the influence of antecedent precipitation in driving over-summer mortality of juvenile salmonids rearing in intermittent streams in Mediterranean-climate California.

Past studies have demonstrated that aquatic biota inhabiting intermittent streams are highly resistant to moderate levels of drought, but they can experience sharp decreases in survival and/or biomass during periods of severe drought. 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 (no decrease in water level) and moderate drying treatments and abundance was significantly higher in these treatments when compared to a severe drying treatment. During our study, we observed that steelhead exhibited high resistance to drought and were able to withstand moderate decreases in water level. Indeed, steelhead experienced relatively high rates of survival through the midsummer of all years, regardless of drought intensity. However, during dry years, we observed a precipitous decline in steelhead survival during the late summer when the decrease in water level was most extreme. 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 (mid-September). These parallel results suggest that late summer is a stressful time for stream fishes, and that studies aimed at monitoring the effects of seasonal drought should focus on the late summer, when water levels 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 survival, though it was an important factor for explaining variation in recapture probability (Supplemental Figures S3.1-S3.4). The higher detection rates of smaller fish observed here can possibly be attributed to competitive exclusion, with larger fish excluding

smaller fish from higher quality habitat (e.g., undercut banks and rootwad vegetation), which is more difficult to sample. We also found that modeled survival rates were very similar whether the models included only age-0+ fish or both age-0+ and age-1+ fish. 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 (California, USA). However, this was likely due to the higher rates of emigration by small fish compared to larger fish. In our study, movement was highly limited and we did not observe differences in survival rates between the two age classes.

The last year of our study (2012) marked the beginning of an extreme multi-year drought (2012-2015) in California (Griffin and Anchukaitis, 2014; Simeral, 2015). During the two dry years of our study (2009 and 2012), fish experienced relatively high survival rates through midsummer, followed by a sharp decrease in 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 2014, the percentage of land in California experiencing drought conditions in late September has increased from 69% to 100% (Artusa 2012, Heim 2014). As a result, it is likely that stream habitats across the state, including at our study site, have 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 has been reduced for at least three 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 (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 drought conditions.

Intermittent streams are prevalent throughout the world (Larned et al. 2010), so the findings from our study are relevant to conservation of salmonid and other sensitive fish species around the globe. Balancing human water use with environmental flows for freshwater organisms is becoming increasingly contentious (Poff et al. 2003). Based on our findings, over-summer survival of salmonids in our study stream is largely dependent on drought severity, which in turn is driven by antecedent winter precipitation. Future management efforts can benefit from using antecedent precipitation as a cue to indicate when more active and immediate conservation efforts (e.g., fish rescues) are needed to maintain populations of imperiled fishes in intermittent streams.

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Table 3.1. Summary of fish tagging events for each study year.

	2009	2010	2011	2012
Number of pool-riffle units	12	19	19	19
Dates of initial capture	June 23-25	July 1-4	July 7-11	July 9-13
Date of final capture	Sept 18	Sept 24-25	Sept 30-Oct 3	Oct 20-21
Number of steelhead captured	56	249	529	544
Number of steelhead tagged	38	216	149	118
Number of coho captured	0	4	154	0
Number of coho tagged	0	4	129	0
Number of re-sighting events	10	10	8	11
Average number of re-sightings	6.6	6.2	5.9	5.3

Table 3.2. Model selection results for analysis of recapture probability (P) and apparent survival (ϕ) for age-0+ steelhead.

Model	Length		Delta	
	Covariate	k	AIC _c	AICc
P(Week)	Yes	31	3247.16	0.0
P(Year * Week)	Yes	76	3247.96	0.80
P(Year * Week)	No	61	3265.76	18.60
P(Year)	Yes	11	3269.51	22.35
P(Year)	No	5	3295.06	47.90
P(Week)	No	16	3306.14	58.97
P(Constant survival)	No	2	3368.59	121.43
ϕ (Regime: Wet years * Week, Dry years * Resistance)	No	48	3107.29	0.00
ϕ (Year * Resistance)	No	42	3126.49	19.19
ϕ (Regime: Wet years * Week, Dry years * Resistance)	Yes	63	3127.61	20.32
ϕ (Regime * Resistance)	No	36	3141.43	34.13
ϕ (Regime * Week)	No	60	3152.02	44.73
ϕ (Year * Week)	No	90	3152.82	45.52
ϕ (Week)	No	45	3177.85	70.55
ϕ (Resistance)	No	33	3227.01	119.71
ϕ (Regime)	No	33	3237.01	129.72
ϕ (Year)	No	34	3238.64	131.34
ϕ (Constant survival)	No	31	3247.16	139.87

Table 3.3. Model selection results for analysis recapture probability (P) and apparent survival (ϕ) for steelhead of all age classes.

Model	Length		Delta	
	Covariate	k	AIC_c	AICc
P(Year * Week)	Yes	76	4014.92	0.0
P(Week)	Yes	31	4059.86	44.94
P(Year)	Yes	11	4065.80	50.88
P(Year * Week)	No	61	4077.80	62.88
P(Week)	No	16	4127.22	112.29
P(Year)	No	5	4136.14	121.22
P(Constant survival)	No	2	4206.64	191.72
ϕ (Regime: Wet years * Week, Dry years * Resistance)	No	93	3836.21	0.00
ϕ (Year * Resistance)	No	87	3859.44	23.23
ϕ (Regime * Resistance)	No	81	3867.71	31.49
ϕ (Regime: Wet years * Week, Dry years * Resistance)	Yes	108	3869.04	32.82
ϕ (Year * Week)	No	135	3884.05	47.84
ϕ (Regime * Week)	No	91	3908.26	72.04
ϕ (Week)	No	90	3935.95	99.74
ϕ (Resistance)	No	78	3984.00	147.79
ϕ (Regime)	No	77	3994.88	158.67
ϕ (Year)	No	79	3997.09	160.88
ϕ (Constant survival)	No	76	4014.92	178.71

Table 3.4. Model selection results for analysis recapture probability (P) and apparent survival (ϕ) for steelhead and coho in 2011.

Model	Length		Delta	
	Covariate	k	AIC_c	AICc
P(Week)	No	33	1929.61	0.00
P(Species * Week)	No	44	1929.62	0.01
P(Week)	Yes	55	1947.79	18.17
P(Species * Week)	Yes	44	1998.26	68.65
P(Species)	No	24	2137.51	207.89
P(Species)	Yes	24	2137.68	208.07
P(Constant survival)	No	23	2147.18	217.56
ϕ (Week)	Yes	23	2147.18	0.00
ϕ (Species * Week)	Yes	34	2147.53	0.35
ϕ (Week)	No	12	2148.17	1.00
ϕ (Species * Week)	No	23	2152.08	4.90
ϕ (Species)	Yes	7	2325.44	178.27
ϕ (Species)	No	4	2326.67	179.50
ϕ (Constant survival)	No	3	2330.62	183.45

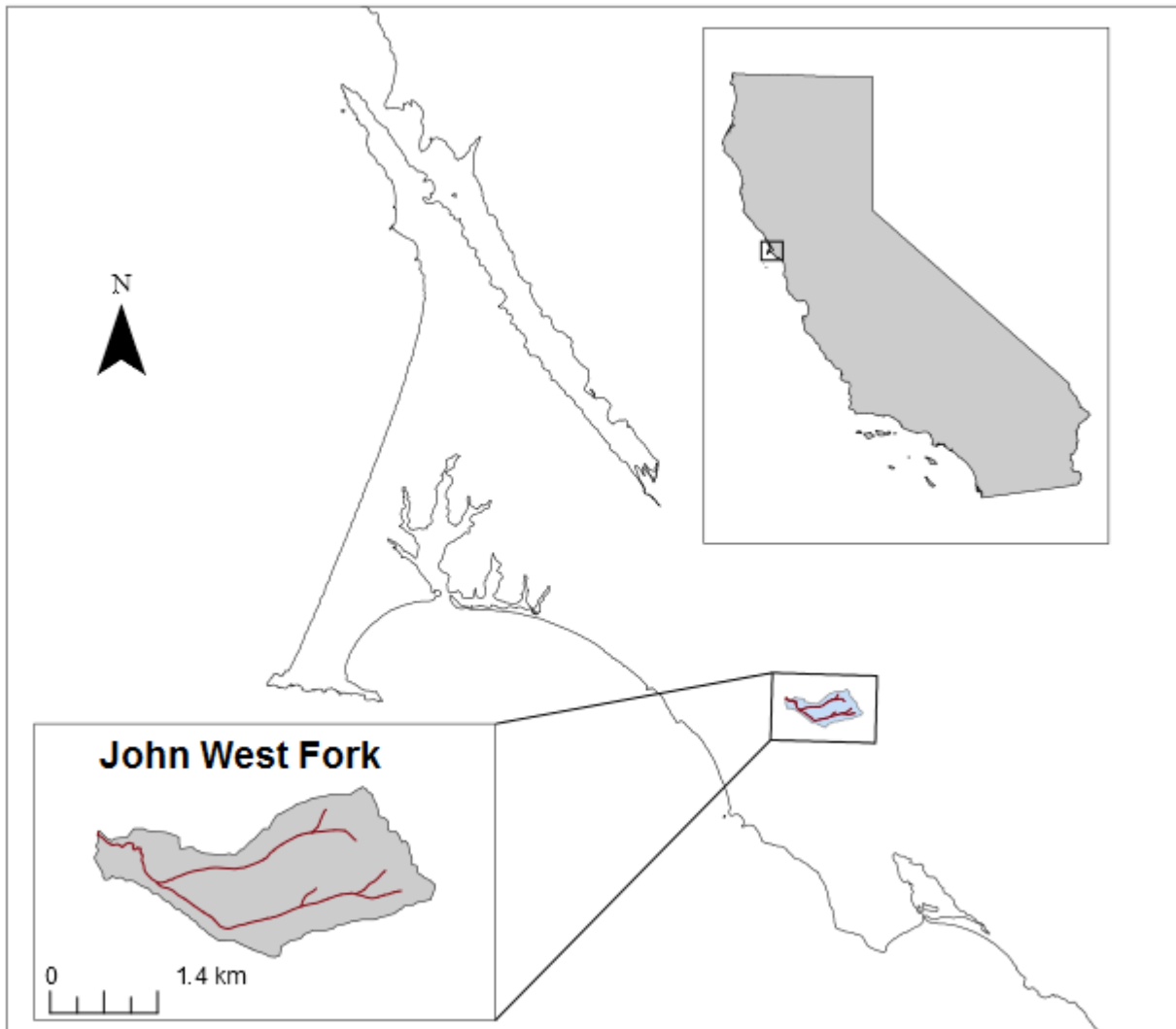


Figure 3.1. Map showing the John West Fork within the Point Reyes National Seashore, California.

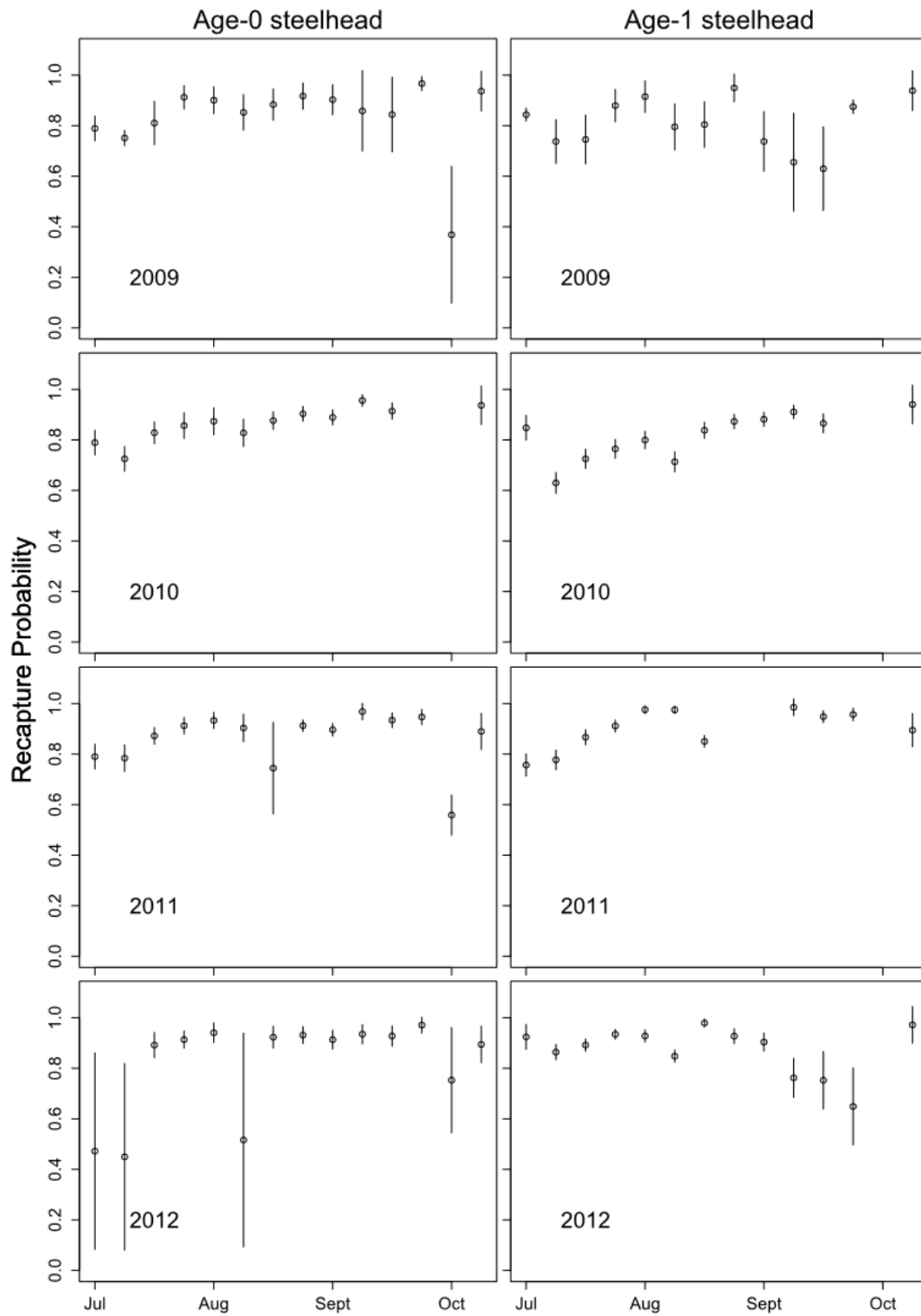


Figure 3.2. Weekly recapture probabilities for age-0+ (left) and age-1+ steelhead(right) based on top-ranking models for each of four study years. Error bars represent standard error estimates.

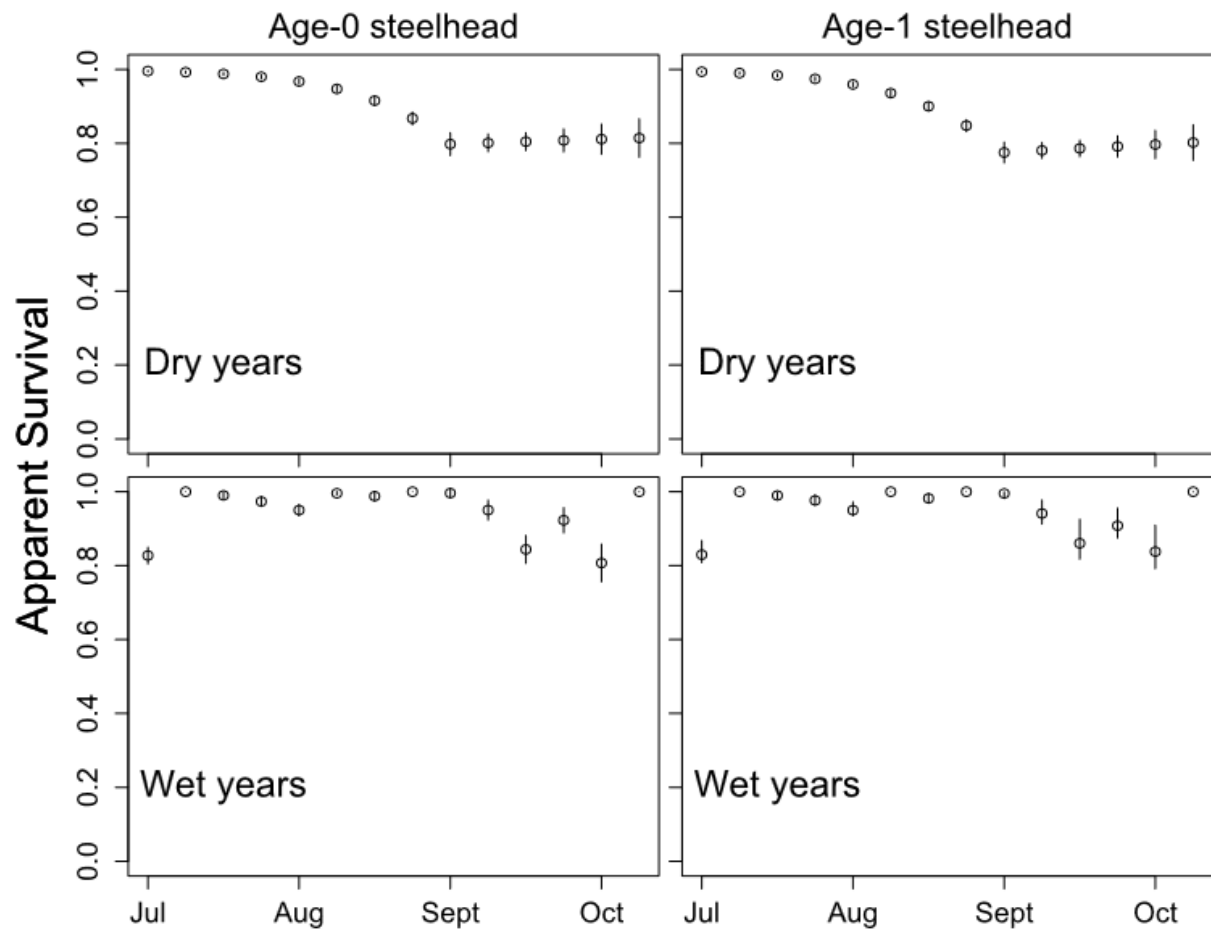


Figure 3.3. Weekly apparent survival estimates for age-0+ (left) and age-1+ steelhead (right) during dry years (top) and wet years (bottom) based on top-ranking models. Error bars represent standard error estimates.

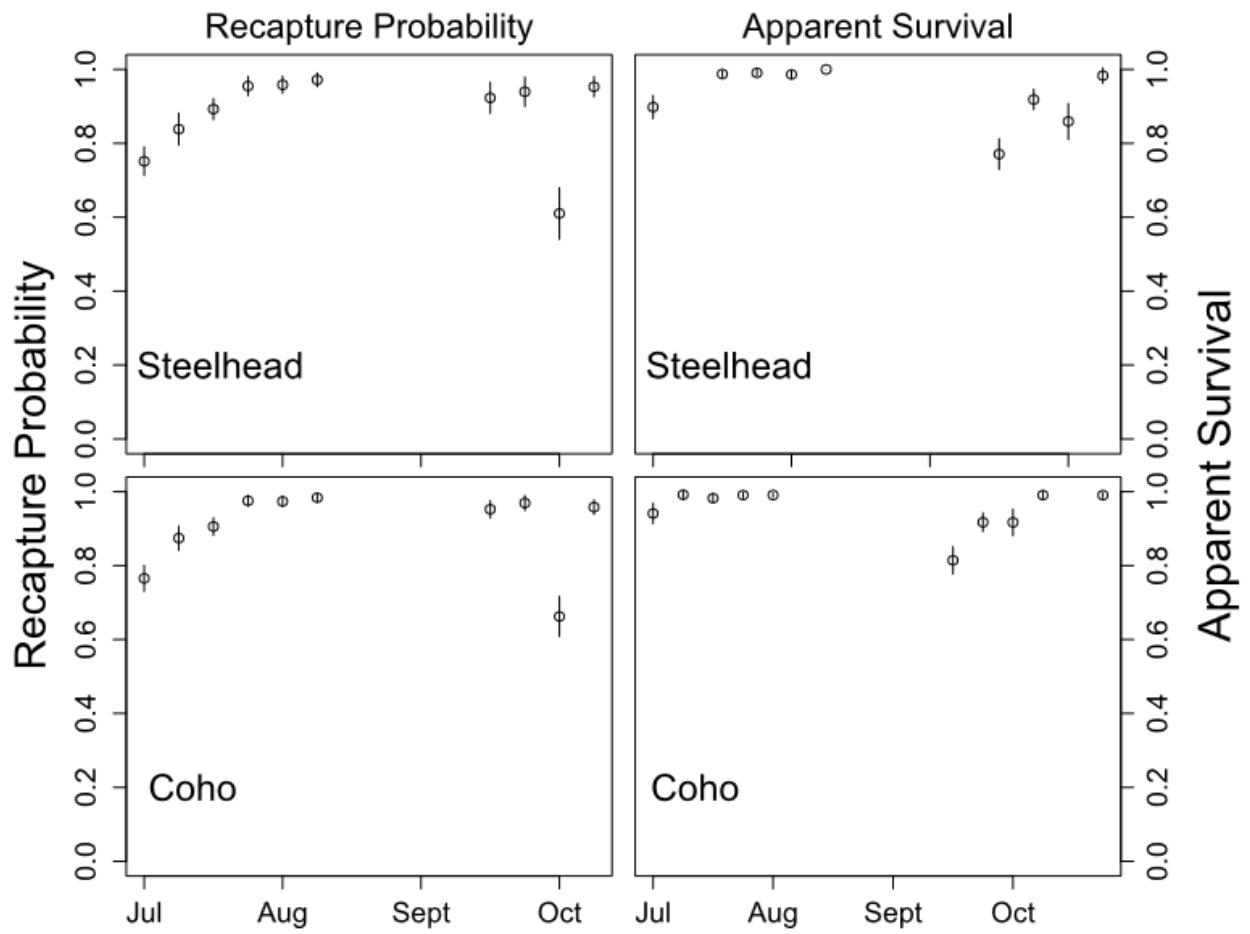


Figure 3.4. Weekly recapture probabilities (left) and apparent survival estimates (right) for steelhead (top) and coho (bottom) in 2011 based on top-ranking models. Error bars represent standard error estimates.

SUPPLEMENTAL FIGURES

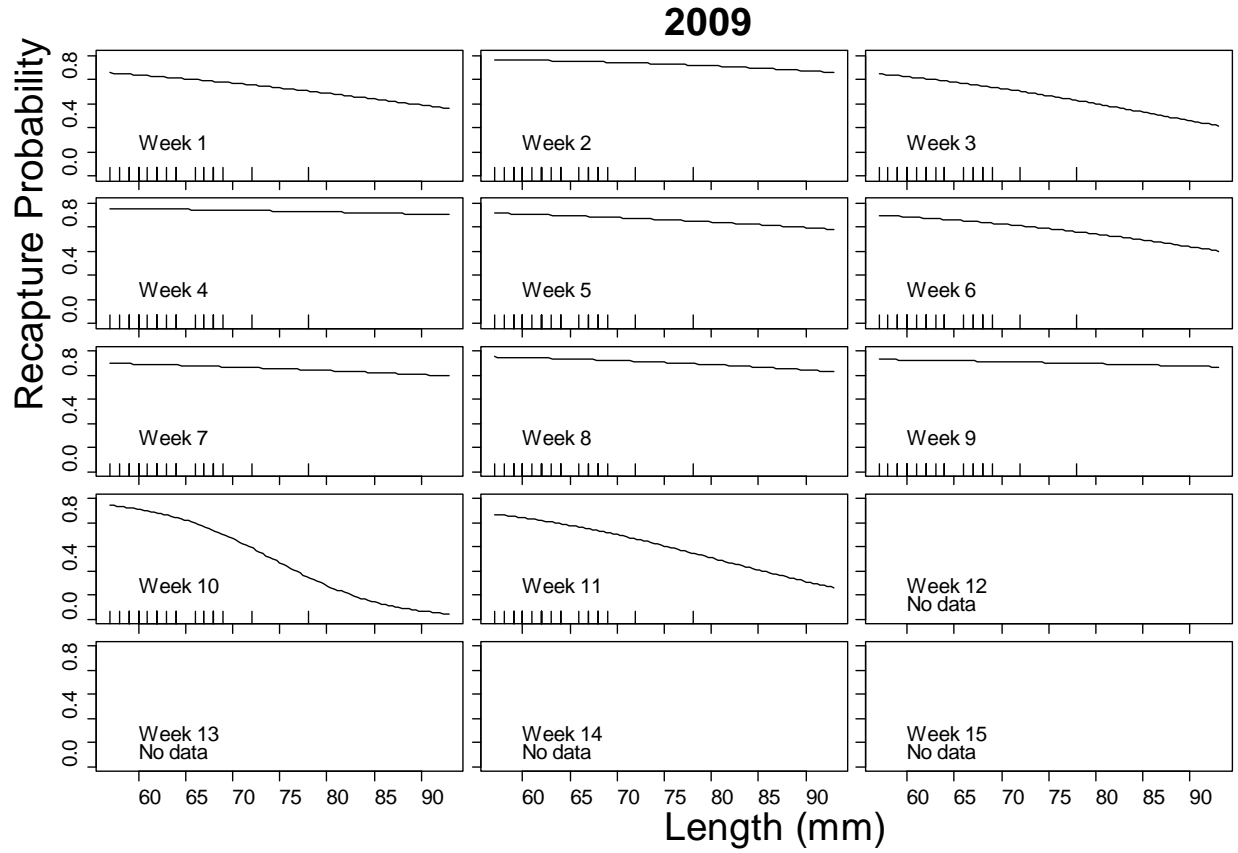


Figure S3.1. Recapture probability as a function of length for each re-sighting event for study year 2009. Estimates are from modeled values obtained from Program MARK. Tick marks above x-axis represent actual length values observed.

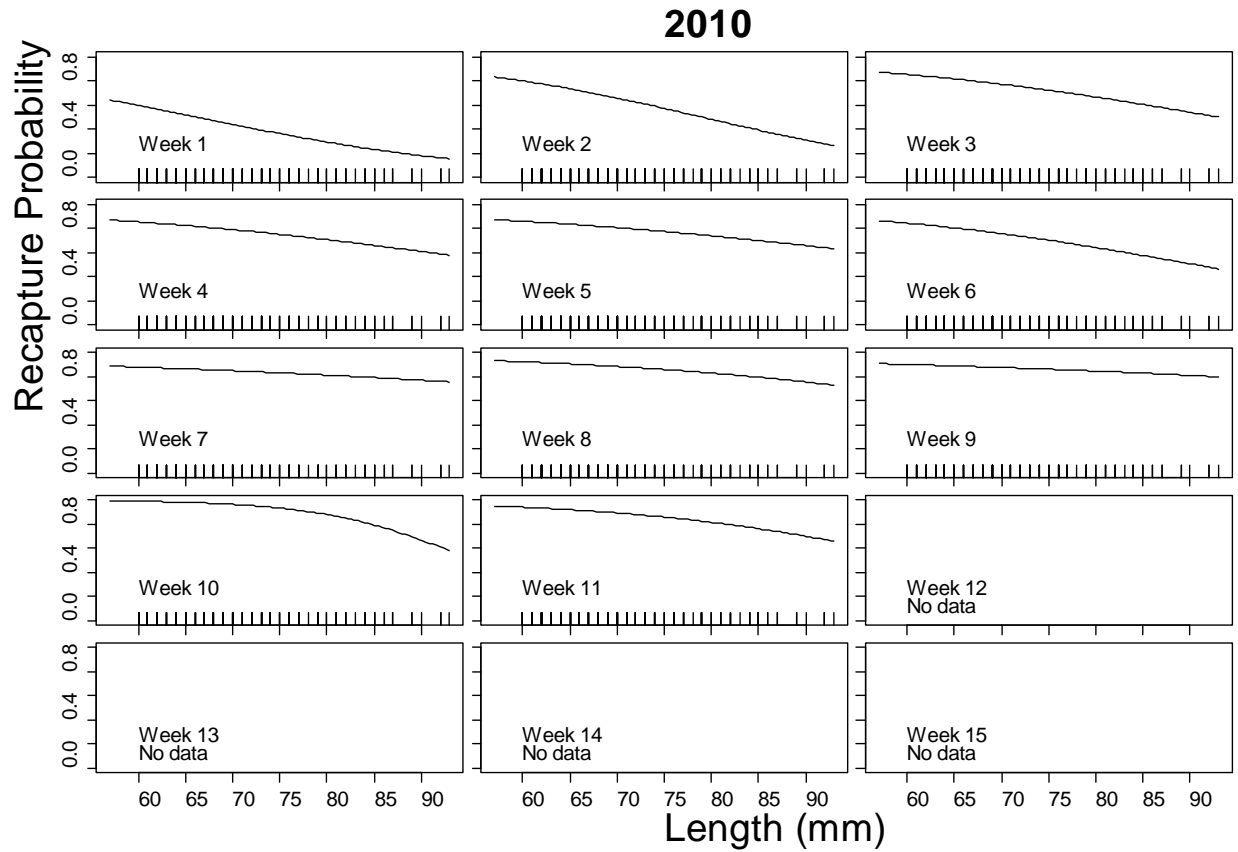


Figure S3.2. Recapture probability as a function of length for each re-sighting event for study year 2010. Estimates are from modeled values obtained from Program MARK. Tick marks above x-axis represent actual length values observed.

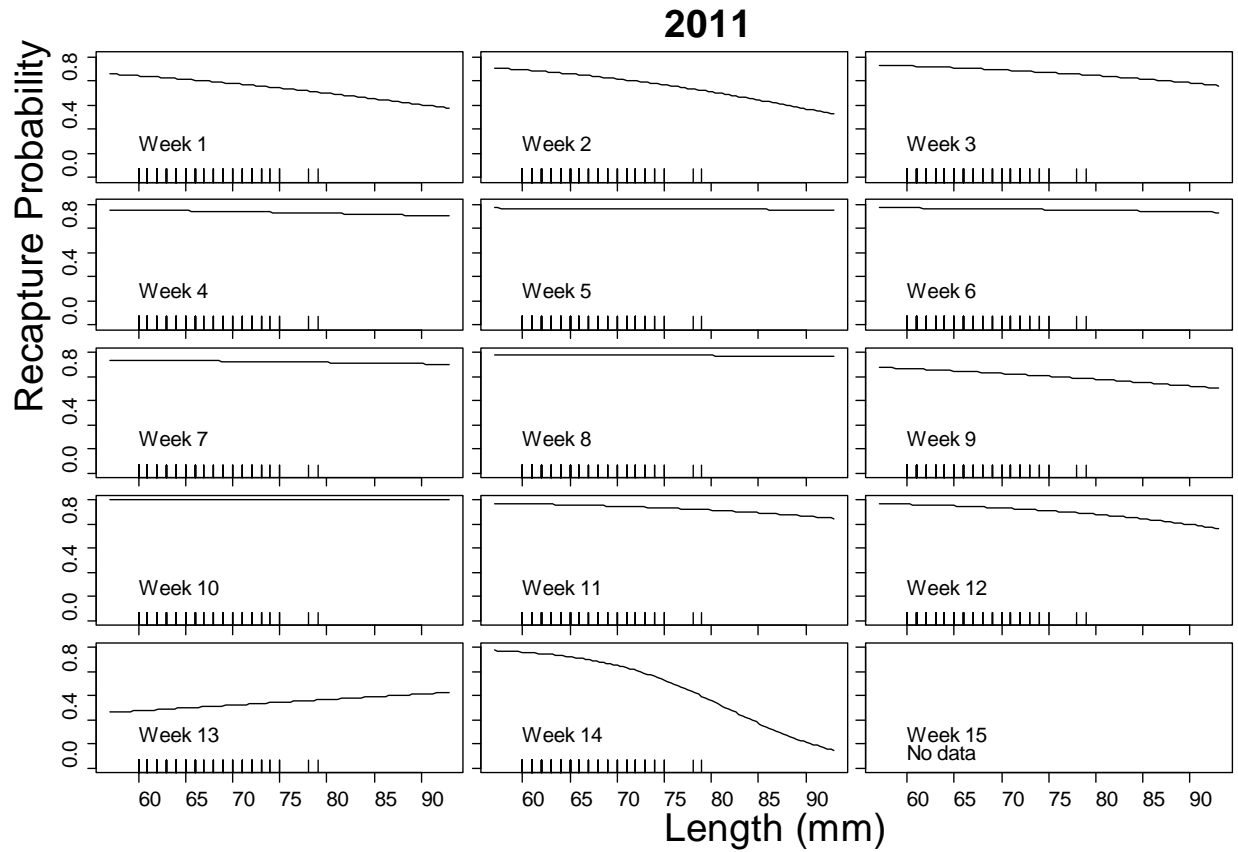


Figure S3.3. Recapture probability as a function of length for each re-sighting event for study year 2011. Estimates are from modeled values obtained from Program MARK. Tick marks above x-axis represent actual length values observed.

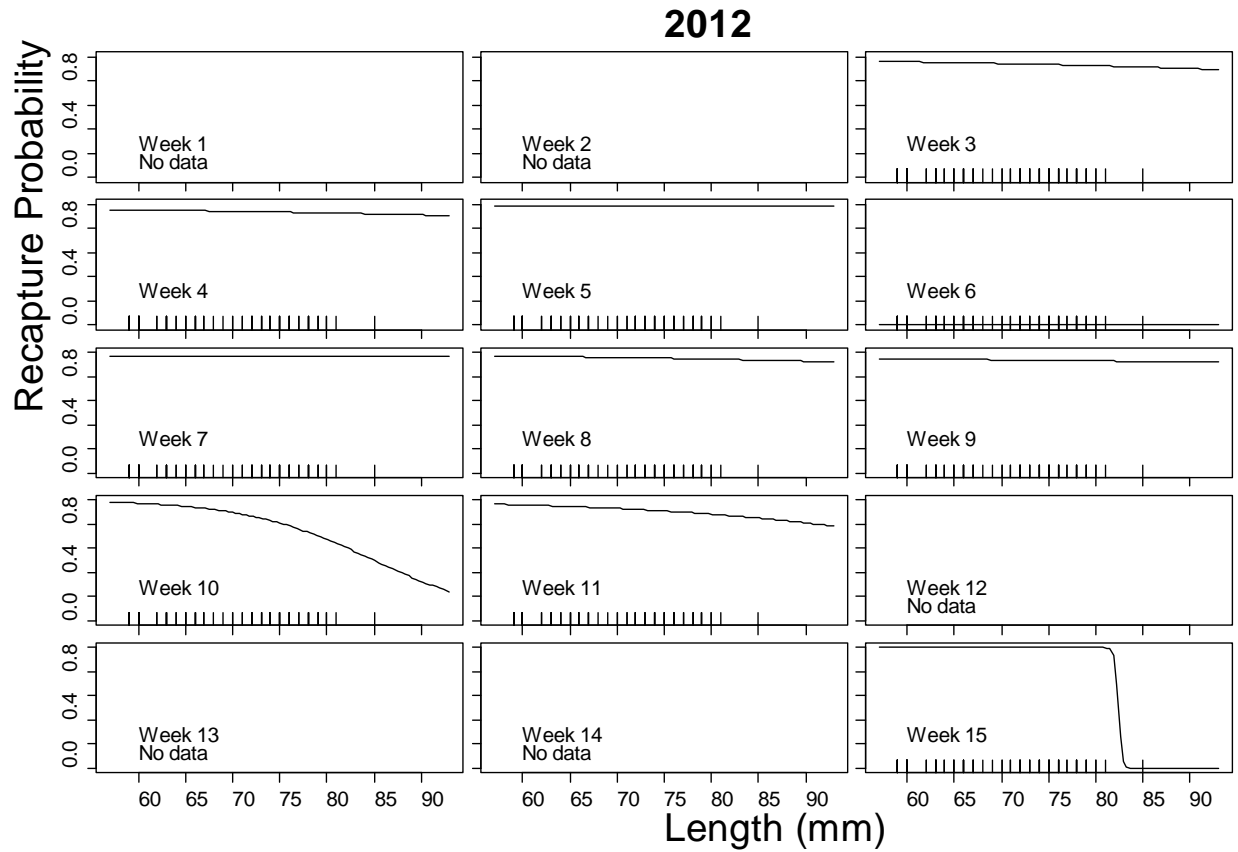


Figure S3.4. Recapture probability as a function of length for each re-sighting event for study year 2012. Estimates are from modeled values obtained from Program MARK. Tick marks above x-axis represent actual length values observed.

CHAPTER 4

DIRECT AND INDIRECT EFFECTS OF DROUGHT ON LEAF LITTER

BREAKDOWN IN AN INTERMITTENT STREAM

Direct and indirect effects of drought on leaf litter breakdown in an intermittent stream

ABSTRACT

Leaf litter decomposition is a key ecosystem process in headwater streams, where leaf litter is an important source of carbon fueling stream food webs. Leaf decomposition rates are generally reduced when conditions are drier and can be affected by both abiotic (e.g., duration of immersion and stream temperature) and biotic processes (e.g., macroinvertebrate shredder activity and microbial activity). We used a leaf pack experiment to compare decomposition rates across three years (2009-2011) that differed in drought intensity in a coastal, intermittent stream in California, USA. We also compared decomposition rates among early, middle, and late summer periods within a single year (2011). We compared a model that examined the number of days that leaf packs were submerged (k) and a model that integrated temperature using degree days (k') to explore the influence of stream temperature on decomposition rates. Aquatic macroinvertebrates were collected from retrieved leaf packs and we estimated the density of macroinvertebrate shredders on each leaf pack. At the pool-scale, we investigated whether water level and/or shredder density had an influence on leaf decomposition rates. We found that a model using days of exposure (k) had better support than a model using degree days (k'). Leaf decomposition rates were significantly higher during the wet year when compared to the dry year, and higher during the early summer compared to the late summer. At the pool-scale, shredder density was positively associated with k ; however, there was no association between pool depth and k . Pool depths were generally similar across years and across deployments in 2011; however, shredder densities were generally higher during wet years when compared to dry years and during early summer when compared to late summer. This suggests that drought intensity has an indirect effect on leaf decomposition rates through its influence on shredder density. Future studies investigating leaf decomposition rates in intermittent streams should examine bottom-up effects on macroinvertebrate and fish communities. With climate change, drought intensity is likely to increase in many regions of the world and understanding the influence of drought on ecosystem processes is becoming increasingly important.

INTRODUCTION

Drought severity and frequency are predicted to increase with climate change in many regions (Cayan et al. 2010, Jaeger et al. 2014), fueling growing interest in understanding the impacts of drought on stream ecosystems (Lake 2011). Drought leads to stream habitat contraction along longitudinal, lateral, and vertical dimensions (Stanley et al. 1997). Intermittent streams represent an extreme case of habitat contraction, wherein surface flow is lost for a portion of the year (Larned et al. 2010). As a result, leaf litter and other forms of benthic organic matter, which are transported downstream via flow, concentrate in remnant pools when surface flow is lost

(Boulton and Lake 1992). Leaf litter is an important food source in low-order streams that have a high amount of riparian cover (Minshall et al. 1985), and the decomposition of leaf litter is a key ecosystem process in these streams (Lake 2003).

Previous research has emphasized the influence of physical factors on the rate of leaf decomposition and has revealed that decomposition rates are generally faster when conditions are wetter including when flow is more permanent (e.g., Datry et al. 2011) or when the duration of high flow periods is longer (e.g., Langhans and Tockner 2006). Consistent with this pattern, previous studies comparing leaf decomposition rates in intermittent versus perennial streams have found that rates of leaf decomposition tend to be lower in intermittent streams (Tate and Gurtz 1986, Hill et al. 1988). Another approach for examining the influence of water level, and drought specifically, on leaf breakdown is to compare breakdown rates across years that differ in antecedent precipitation, but such studies are rare. Recently, LeRoy et al. (2014) examined interannual differences in leaf decomposition rates in an intermittent stream between two years that differed in antecedent precipitation and found that during the early stages of leaf breakdown, decomposition rates were faster when conditions were drier and suggested that differences were attributed to differences in leaf chemistry the two years.

Beyond the influence of stream flow, stream temperature is also an important driver of leaf breakdown. In general, leaf breakdown is faster when temperatures are warmer (Menéndez et al. 2012, Martínez et al. 2014). However, warmer stream temperatures are also associated with drought conditions, which as previously mentioned, are typically associated with reduced rates of leaf decomposition. Schlieff & Mutz (2011) compared leaf decomposition rates between the dry season and early stages of flow resumption and determined that temperature was a controlling factor. This finding suggests that the positive association between temperature and decomposition rates might override the negative association between drought conditions and decomposition rates.

Drought conditions may have an indirect influence on leaf decomposition rates, suggesting that factors other than drought intensity may be directly influencing decomposition rates (LeRoy et al. 2014). Indeed, biological processes are also important drivers of leaf decomposition, including the shredding activities of some macroinvertebrates (Schlieff and Mutz 2011) or microbial activity (Gaudes et al. 2009). However, findings have differed among studies, and as a result, the causal mechanisms of leaf decomposition remain poorly understood, possibly because of complex interactions among direct and indirect effects, drought severity, and varying study systems. For example, during a field experiment, Datry et al. (2011) found that shredder density was positively associated with decomposition rates, whereas Leberfinger et al. (2010) used a controlled lab experiment and found that decomposition rates were reduced in drought compared to control treatments, despite a high abundance of shredders in both treatments.

In this study, our aim was to assess the influence of drought and drought-mediated changes in water volume and shredder density on leaf breakdown rates during stream drying. Specifically, our objectives were to (1) investigate how leaf litter decomposition rates differed in an intermittent stream among years that varied in antecedent precipitation, (2) investigate how leaf decomposition rates differed within a year as drying progressed and water volume decreased, and (3) examine the relative influence of biotic (shredder density) and abiotic factors (water level and stream temperature) on the rate of leaf decomposition. We hypothesized that decomposition rates would be faster during wet years when compared to dry years and during the early summer when compared to late summer. We also hypothesized that decomposition rates would be positively associated with water level, stream temperature, and shredder density.

METHODS

Study site

The John West Fork (JWF; 37.99° N, 122.75° W, Figure 4.1), is a first-order, Mediterranean-climate stream that is approximately 3 kilometers in length with a watershed size of approximately 3.1 km². JWF is located in the Golden Gate National Recreation Area (California, USA) and is a tributary of Olema Creek in the Lagunitas Creek basin. During the summer, declining water levels lead to residual pools that support at least four species of vertebrates and 160 invertebrate taxa (Bogan et al. 2015). The JWF possesses dense canopy throughout most of its length, with lower sections of the creek dominated by California Bay Laurel (*Umbellularia californica*), red alder (*Alnus rubra*), beaked hazelnut (*Corylus cornuta*), bigleaf maple (*Acer macrophyllum*), poison oak (*Toxicodendron diversilobum*), and several species of willow (*Salix* spp.). Our study area was confined to a 200-m section in the lower portion of JWF, which contained a contiguous sequence of 12 riffle-pool units.

Patterns of fragmentation and pool volume

In a previous paper, we explored changes in pool volume across each summer (Hwan and Carlson, 2015). We analyzed antecedent precipitation and categorized years according to water-year classifications (e.g., Kiernan et al. 2012): 2009 was classified as a dry year, 2010 was classified as a normal year, and 2011 was classified as an above-normal year. We observed that each year exhibited different patterns of drying, with fragmentation and contraction occurring earlier and at a more rapid pace in 2009 when compared to 2010 and 2011.

Water level and stream temperature

In each study pool, we attached a meter stick to rebar that was anchored in the streambed in the deepest portion of the pool. At weekly intervals, we recorded stage measurements to monitor the

decrease in water level across each summer. We also monitored stream temperatures (°C) in each of our study pools with temperature loggers (HOBO Pendant UA-002-64, Onset Computer Corporation, Bourne, MA, USA). Loggers were positioned approximately 10cm above the deepest point in each pool. Temperatures were logged every ten minutes for the entirety of each summer. Degree days were calculated as the sum of the mean daily water temperature over the period of exposure (Irons et al. 1994).

Leaf decomposition

To examine leaf breakdown rates, we used leaf litter packs constructed of bird netting (1.6cm mesh size) that contained red alder (*Alnus rubra*) leaves collected from JWF and downstream Olema Creek. We collected alder leaves in early June of each study year and we allowed them to air dry. Once dry, we placed a pre-measured quantity (approximately ~2.5g) of leaf material into a 15cmx15cm mesh bag.

We explored among-year differences in early summer leaf breakdown rates by deploying 12 leaf litter packs in each of our 12 study pools in mid-June of each year, and retrieved 3 packs weekly from each study pool across four weeks. In 2009 and 2010, we deployed the leaf packs by randomly placing them within the pool. There were a small number of leaf packs that were lost using this method, likely removed by terrestrial animals, so we tethered each bag to a rebar in 2011.

We also explored differences in breakdown rates across the summer dry season in 2011. To accomplish this, we deployed two additional set of 12 leaf packs—one in mid-July and another in early September and retrieved three packs per week for four weeks. This allowed us to compare within-year differences in leaf decomposition rates by comparing the three deployments (early, middle, and late summer) of 2011.

Once leaf packs were retrieved, we placed them in a freezer to prevent further decomposition until we could process them. To process leaf packs, we washed the leaf packs to remove foreign debris and macroinvertebrates, which we retained for additional analyses (see next section). After washing the leaf packs, leaves were removed and placed in a drying oven (at 55°C) until constant mass was achieved. Leaves were then removed and re-weighed (to the nearest 0.01g).

Macroinvertebrates

Due to the large number of samples we collected, we only identified macroinvertebrates from a subset of pools. Specifically, we selected ten pools to study across each of the three years (for the among-year comparison) and each of the three deployments in 2011 (for the within-year comparison). We

sorted and identified macroinvertebrates to the lowest taxonomic level possible (usually genus). We assigned each taxon to a functional feeding group (shredder, scraper, collector-gather, filter, piercer, predator) based on Merritt et al. (2008). We estimated shredder density for each leaf pack as the abundance of shredders divided by the mass of the remaining leaf matter. A list of macroinvertebrates known to occur in the John West Fork can be found in Bogan et al. (2015).

Data analysis

Influence of broad-scale factors on leaf decomposition. To explore factors that influenced leaf decomposition rates, we used a two-step approach. First, we used generalized linear mixed-effects models (GLMM) with log-transformed $[\ln(x+1)]$ values for the proportion of leaf mass remaining as a function of year (or deployment), days of exposure, degree days, or combinations of these factors (Boulton and Boon 1991). Our simplest models included days of exposure or degree days as a covariate and no effect of year or deployment, which were included in our more complex models testing whether relationships between leaf mass remaining and the covariates differed among or within years, respectively. Because the proportion of leaf mass remaining at the initial deployment was equal to 1 in all cases, we used the same fixed intercept for all models, but we allowed slopes to vary across years (or deployments). We compared two sets of models—one for our among-year comparison examining differences in early summer leaf breakdown across years (2009-11; Table 4.1) and one for our within-year comparison, in which we assessed differences in leaf breakdown during the early, middle, and late summer of 2011 (Table 4.2). For our among-year comparison during the early summer, year was coded as a fixed effect and pool ID as a random effect in our models (Table 4.1). For the within-year comparison, deployment (early, middle, and late summer) was coded as a fixed effect and pool ID as a random effect in our models (Table 4.2). We used a model selection approach, using Akaike's Information Criterion corrected for small sample sizes (AIC_c), to compare competing models (Burnham and Anderson 2002). In cases where among- or within-year differences were detected, we assessed pairwise differences in proportion of leaf mass remaining across years (or deployments). To assess pairwise differences here and analyses outlined below, we used package "lmerTest" in R, which uses Satterthwaite's approximation to compute p-values when performing F-tests and t-tests (Kuznetsova 2015).

Second, we used the best-supported model from step one to calculate leaf decomposition rates. When days of exposure was included as a covariate in our best-supported model, we estimated decomposition rates (k) as the slope of the relationship between log-transformed values for proportion of leaf mass remaining as a function of days of exposure. When degree days was included as a covariate in our best-supported model, we instead estimated decomposition rates (k') as the slope of the relationship between log-transformed values for the proportion of leaf mass remaining as a function of degree days. When year (or deployment) were included in our

best-supported model, this indicated that the rate of leaf breakdown differed among years (deployments), so leaf breakdown rates were calculated separately for each year (deployment).

Influence of pool-specific factors on leaf decomposition. After we estimated decomposition rates from our among- and within-year comparisons, we estimated decomposition rates for each pool based on the best-supported model from each of our among- and within-year comparisons. In other words, for each pool, decomposition rates were calculated as the slope of a linear regression with log-transformed $[\ln(1+x)]$ values for the proportion of leaf mass remaining as a function of days of exposure (k) or degree days (k'), depending on which covariate was included in the best-supported model. This allowed us to explore the local, pool-specific physical and biotic factors that influenced leaf decomposition rates in an approach similar to Datry *et al.* (2011). To do so, we used the subset of 10 pools from which we sampled macroinvertebrates, and we tested whether pool-specific leaf decomposition rates were influenced by water level, stream temperature, and/or shredder density using GLMM via package “lmerTest” in R to determine whether any observed relationships were significant. Here, we used all possible pool-specific decomposition rates in a single analysis with pool ID included as a random effect in our analyses. Using our weekly stage data, we estimated water level in each pool as the average pool depth over the four-week period of deployment. To incorporate temperature, we used degree days (i.e., the sum of mean daily temperatures) during the four-week period of each deployment as a factor. Because leaf decomposition rates were relatively rapid in our system and the amount of leaf matter remaining grew progressively smaller each week, we used shredder densities that were estimated during the first retrieval of each deployment. Shredder densities were averaged for the first retrieval for each pool-deployment combination (i.e., from 3 leaf packs) and log-transformed prior to analyses. Both shredder density and pool depth were coded as fixed effects and pool ID was coded as a random effect in analyses. We tested different hypotheses regarding the importance of water level, temperature, and shredder density on leaf breakdown within pools (Table 4.3).

RESULTS

Influence of broad-scale factors on leaf decomposition

Streamflow was continuous throughout the entire study reach on the days when leaf packs were first deployed in early summer. During 2010 and 2011, which were relatively wet years, streamflow persisted through mid-July, with none of the riffles drying prior to the retrieval of all leaf packs. In contrast, in the relatively dry year of 2009, eight out of 12 riffles dried prior to the retrieval of the last set of leaf packs during the early summer. From pairwise comparisons, we found that during the early summer, average initial pool depths were similar across years (Table 4.4). When we examined temperature, we found that temperatures were similar between 2010

and 2011, two relatively wet years, both of which had significantly higher temperatures than 2009, a dry year (Table 4.4).

For our among-year comparison of leaf decomposition rates in the early summer, the best-supported model include days of exposure as a covariate and year as a factor (Table 4.1, Figure 4.2). Using this model to guide our calculation of decomposition rates, we found that leaf decomposition rates were significantly faster during the above-normal water year (2011, $k = 0.024$) when compared to the dry year (2009, $k = 0.020$) ($P=0.0076$). Decomposition rates for the normal year (2010, $k = 0.022$), did not differ significantly from the dry year (2009, $P = 0.16$) or the above-normal year (2011, $P=0.21$).

In 2011, the only year in which there were multiple deployments across the summer drought season, loss of surface flow was initially gradual but accelerated as the summer progressed. During the start of the midsummer (mi-July) deployment, none of the 12 riffles leading into the study pools were dry; however, one riffle dried by the end of the deployment. At the start of the late summer (September) deployment, one of the 12 riffles was dry and an additional nine riffles dried prior to the retrieval of the last leaf pack. Using pairwise comparisons, we found that pool depths averaged across the four-week deployment period were similar between early and midsummer, both of which had significantly higher pool depths when compared to the late summer (Table 4.4). In terms of temperature, we found that all pairwise deployment combinations differed from each other, with the lowest temperatures observed during the early summer, intermediate temperatures during the late summer, and the highest temperatures during the midsummer (Table 4.4).

For our within-year comparison in which we examined differences in leaf decomposition rates as the summer dry season progressed, our best-supported model included days of exposure as a covariate and deployment (early, middle, and late summer) as a factor (Table 4.2, Figure 4.3). Using this model to guide our calculation of decomposition rates, we found that decomposition rates were significantly faster during the early summer ($k = 0.024$) when compared to the late summer ($k = 0.020$) ($P=0.0058$). Decomposition rates for the midsummer ($k = 0.022$), did not differ significantly between the early summer ($P = 0.19$) or the late summer ($P=0.15$).

Influence of pool-specific factors on leaf decomposition

Using the subset of ten pools for which we estimated macroinvertebrate shredder densities, from our pairwise comparisons, we found similar among-year patterns in water level and stream temperature when compared to our analysis including all study pools. That is, there were no among-year differences in average pool depth and stream temperatures during the two wet years were significantly higher when compared to the dry year (Table 4.5). For our within-year

comparison, we found that patterns using the subset of ten pools were similar for both pool depth and stream temperature. Specifically, we found that average pool depths were similar between early and midsummer, both of which were higher than late summer depths (Table 4.5). For our within-year assessment of temperature, all pairwise deployment combinations differed from each other, with the lowest temperatures observed during the early summer, intermediate temperatures during the late summer, and the highest temperatures during the midsummer (Table 4.5).

Across all years and deployments, we collected approximately 27,900 shredders among 12 different taxa. The most abundant shredder was the caddisfly *Lepidostoma* (relative abundance = 58%; present in 383/600 leaf packs sampled). The second most abundant shredder was the midge *Polypedilum* (relative abundance = 19%; present in 223/600 leaf packs sampled). Using pairwise comparisons, we compared differences in shredder density among-years and found that during the early summer, average log-transformed shredder densities were similar in 2010 and 2011, but considerably lower in the dry year of 2009 (Table 4.5). In 2011, average log-transformed shredder densities were similar between the early and midsummer deployment and significantly lower during the late summer deployment (Table 4.5).

In assessing whether water level, stream temperature, and/or shredder density influenced decomposition rates, we found that only shredder density was included in our best-supported model (Table 4.3) and that there was a significant positive relationship between leaf decomposition rates and shredder density (slope = 0.0013, $P=0.0033$, Figure 4.4), indicating that higher shredder density was associated with more rapid leaf breakdown.

DISCUSSION

The impacts of drought on stream ecosystem processes can vary across spatial and temporal scales (Lake 2003). Our three-year study encompassed periods of dry, normal, and above-normal precipitation, resulting in differences in physical conditions among years (Hwan and Carlson 2015). We found that leaf decomposition rates differed both among years and across the summer dry season, with increasing rates of decomposition when conditions were wetter. This pattern is similar to those observed in other studies that have examined leaf decomposition rates across different spatial (Gurtz and Tate 1988, Hill et al. 1988) and temporal (Langhans and Tockner 2006, Datry et al. 2011) gradients of drying.

When we analyzed our data at the pool-scale, however, we found that water level (measured as maximum pool depth) did not influence decomposition rates. Because water levels were generally similar across years and deployments, it appears that drought intensity had an indirect influence on leaf decomposition rates, perhaps through the effect of drought on biochemical conditions, microbial activity, or shredder density. LeRoy *et al.* (2014) investigated differences

in leaf decomposition rates between a normal year and a dry year and found that drought conditions indirectly influenced decomposition rates by inducing changes in leaf chemistry. They found that alder leaves during a drought year had significantly higher tannin concentrations, which are used for plant defense and prevent herbivory, resulting in lower rates of decomposition during the drought year. Schlieff & Mutz (2011) reported that microbial activity was reduced when the stream was fragmented when compared to after reestablishment of flow, which resulted in decreased decomposition rates. In our study, we found that the density of macroinvertebrate shredders was higher following wetter winters, and that this was associated with higher rates of leaf decomposition. Similarly, Datry *et al.* (2011) determined that there was a strong positive association between shredder density and leaf decomposition rates across a temporal gradient of drying (i.e., during fragmentation and after flow resumption).

In contrast to studies that have reported that increased leaf decomposition with increased temperatures (e.g., Schlieff & Mutz 2011), we did not find an effect of temperature (i.e., degree days was not included in top-ranking models). This discrepancy could likely be attributed to differences in temporal variation in temperature among studies. Differences in mean daily temperatures across years and deployments were very low ($<1^{\circ}\text{C}$) in our study, limiting the role temperature could play in our system.. Additionally, we found that yearly differences in temperature were not driven by drought intensity (Hwan and Carlson 2015). For example, average daily temperatures were cooler during the dry year of 2009 ($13.9\pm 1.7^{\circ}\text{C}$) when compared to the wetter years of 2010 ($14.0\pm 0.8^{\circ}\text{C}$) and 2011 ($14.5\pm 0.7^{\circ}\text{C}$), possibly because of a strong influence of groundwater compared to surface water in dry versus wet years. Similarly, Benstead & Huryn (2011) reported that temperature was not a mediating factor in controlling rates of leaf decomposition rates in an arctic stream in Alaska where stream temperatures are relatively stable. In contrast, Schlieff & Mutz (2011) reported that mean daily water temperatures were over 11°C higher in pools during the fragmented state when compared to a period after flow had resumed, and that leaf decomposition rates were higher after flow resumption.

Based on our findings that intense drought conditions can limit leaf decomposition rates, a key ecosystem process, further research examining the bottom-up effects of reduced leaf decomposition rates on macroinvertebrate and fish communities is needed. For example, it remains unclear how reduced leaf decomposition rates might affect the biomass and abundance of other macroinvertebrate functional feeding groups, or the growth and survival of stream fishes that utilize macroinvertebrates as a food source. Covich, Palmer & Crowl (2007) postulated that shredders play a key role in structuring macroinvertebrate communities by “providing” food to suspension feeders. Additionally, benthic shredders may be an important food source for stream-dwelling fishes that preferentially feed on benthic fauna, including the dominant fish at our study site, steelhead trout (*Oncorhynchus mykiss*) (Johnson and Ringler 1980). Furthermore, previous studies have demonstrated that severe drought conditions can result in reduced abundance of

macroinvertebrate fauna (Boulton 2003, Boersma et al. 2014)(Bogan and Lytle 2011)(Bogan and Lytle 2011)(Bogan and Lytle 2011)(Bogan and Lytle 2011)(Bogan & Lytle 2011)(Bogan & Lytle 2011). With increasing drought intensity in many regions of the world as a result of climate change (Jaeger et al. 2014), understanding how changes in leaf litter decomposition will affect bottom-up processes will be critical to predict changes in stream community and ecosystem dynamics.

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Table 4.1. Model selection results for the among-year comparison of leaf decomposition rates during the early summer. Factors include days of exposure (number of days the leaf packs were in the stream prior to retrieval), degree days (sum of mean daily temperature over period leaf packs were in stream), and year (2009-2011).

Model	Effects	AIC_c	Delta AIC_c
Model 1	Days of exposure * Year	-545.43	0.00
Model 2	Degree days	-523.42	22.01
Model 3	Degree days * Year	-510.22	35.20
Model 4	Days of exposure	-505.26	40.17

Table 4.2. Model selection results for the within-year comparison of leaf decomposition rates across three deployment events in 2011. Factors include days of exposure (number of days the leaf packs were in the stream prior to retrieval), degree days (sum of mean daily temperature over period leaf packs were in stream), and deployment (early, middle, and late summer).

Model	Effects	AIC_c	Delta AIC_c
Model 1	Days of exposure * Deployment	-604.06	0.00
Model 2	Degree days * Deployment	-531.78	72.28
Model 3	Days of exposure * Deployment	-509.41	94.65
Model 4	Degree days	-431.17	172.89

Table 4.3. Model selection results examining factors that influence leaf decomposition rates. Factors include pool depth (average pool depth over four-week period of deployment), degree days (sum of mean daily temperature over four-week period of deployment), shredder density (average of log-transformed shredder density values during first retrieval).

Model	Effects	AIC_c	Delta AIC_c
Model 1	Shredder density	-386.81	0.00
Model 2	Pool depth	-370.97	15.84
Model 3	Shredder density + Pool depth	-364.47	22.34
Model 4	Degree days	-345.13	41.68
Model 5	Shredder density * Pool depth	-338.81	48.00
Model 6	Shredder density + Degree days	-338.09	48.72
Model 8	Shredder density * Degree days	-317.76	69.05

Table 4.4. Pool depths (average across four-week deployment) and degree days (sum of mean daily temperature over four-week deployment) for all 12 study pools that we assessed across three years (2009-2011) and three deployments in 2011 (early, middle, and late summer).

Deployment	Pool Depth	Degree Days
2009 Early Summer	0.368m \pm 0.167	408°C \pm 11.6
2010 Early Summer	0.363m \pm 0.123	422°C \pm 6.72
2011 Early Summer	0.369m \pm 0.114	417°C \pm 3.41
2011 Midsummer	0.352m \pm 0.114	432°C \pm 5.82
2011 Late Summer	0.316m \pm 0.119	425°C \pm 9.05

Table 4.5. Pool depths (average across four-week deployment), degree days (sum of mean daily temperature over four-week deployment), and average shredder densities (number of shredders per gram of remaining leaf material averaged across all leaf packs within a pool during the first retrieval) for the subset of 10 pools we sampled for macroinvertebrates across three years (2009-2011) and three deployments in 2011 (early, middle, and late summer).

Deployment	Pool Depth	Degree Days	Shredder Density
2009 Early Summer	0.336m \pm 0.163	409°C \pm 12.8	25.4g ⁻¹ \pm 21.7
2010 Early Summer	0.330m \pm 0.122	422°C \pm 7.13	72.3g-1 \pm 96.4
2011 Early Summer	0.372m \pm 0.145	418°C \pm 3.73	70.3g-1 \pm 30.2
2011 Midsummer	0.347m \pm 0.130	433°C \pm 5.30	53.4g-1 \pm 47.4
2011 Late Summer	0.289m \pm 0.121	426°C \pm 9.83	20.6g-1 \pm 17.8

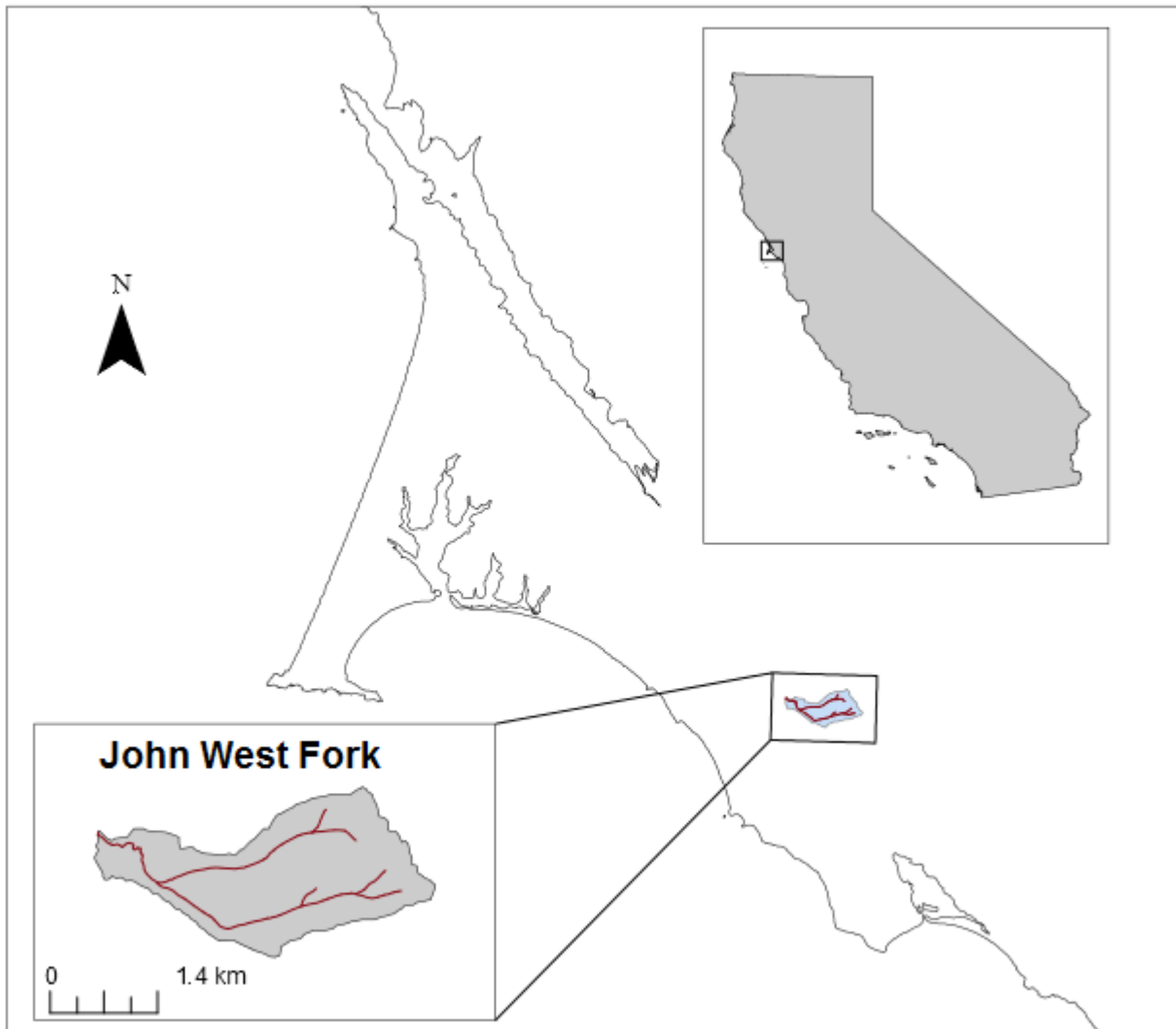


Figure 4.1. Map showing the location of the John West Fork within the Golden Gate National Recreation Area.

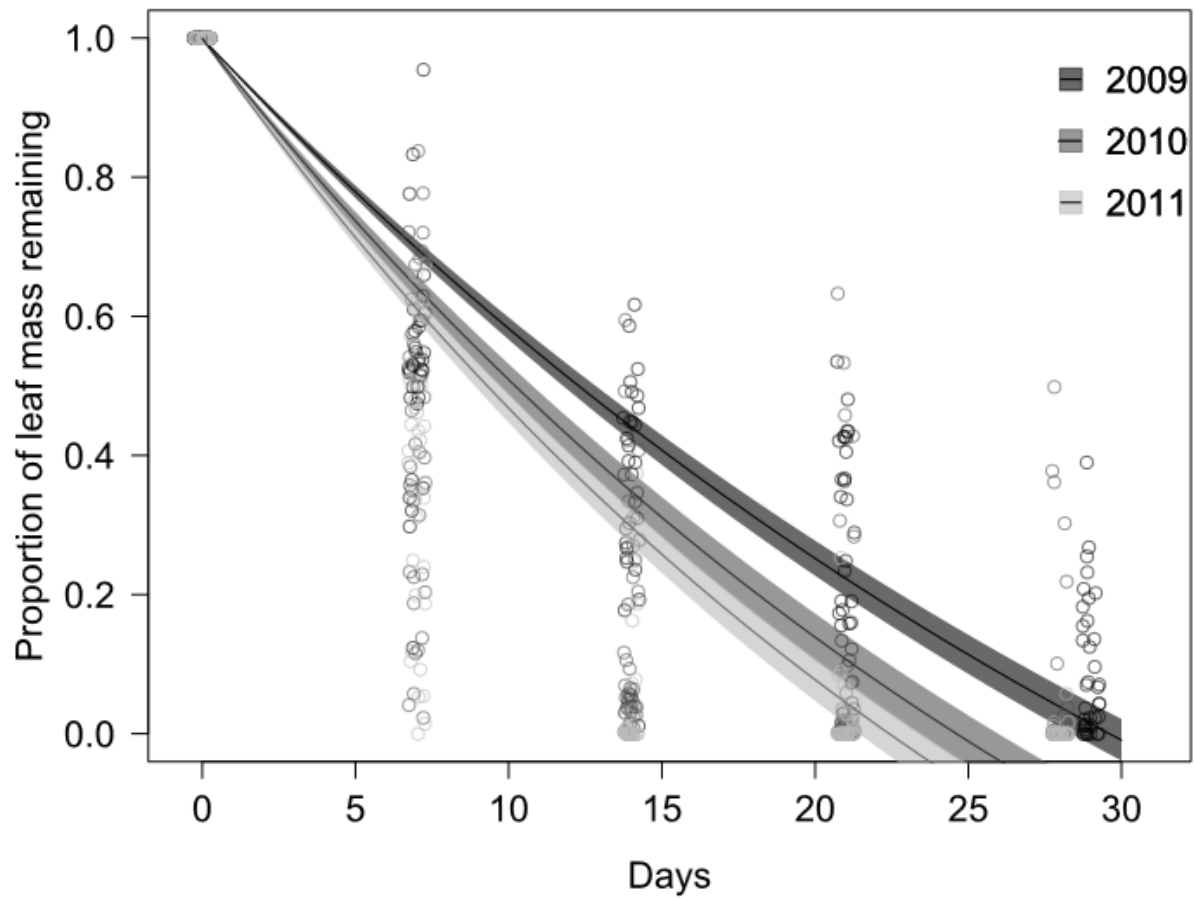


Figure 4.2. Proportion of leaf mass remaining (untransformed) as a function of degree days for the early summer deployment across all four years. Points represent individual leaf packs and are jittered along the x-axis to distinguish superimposed values.

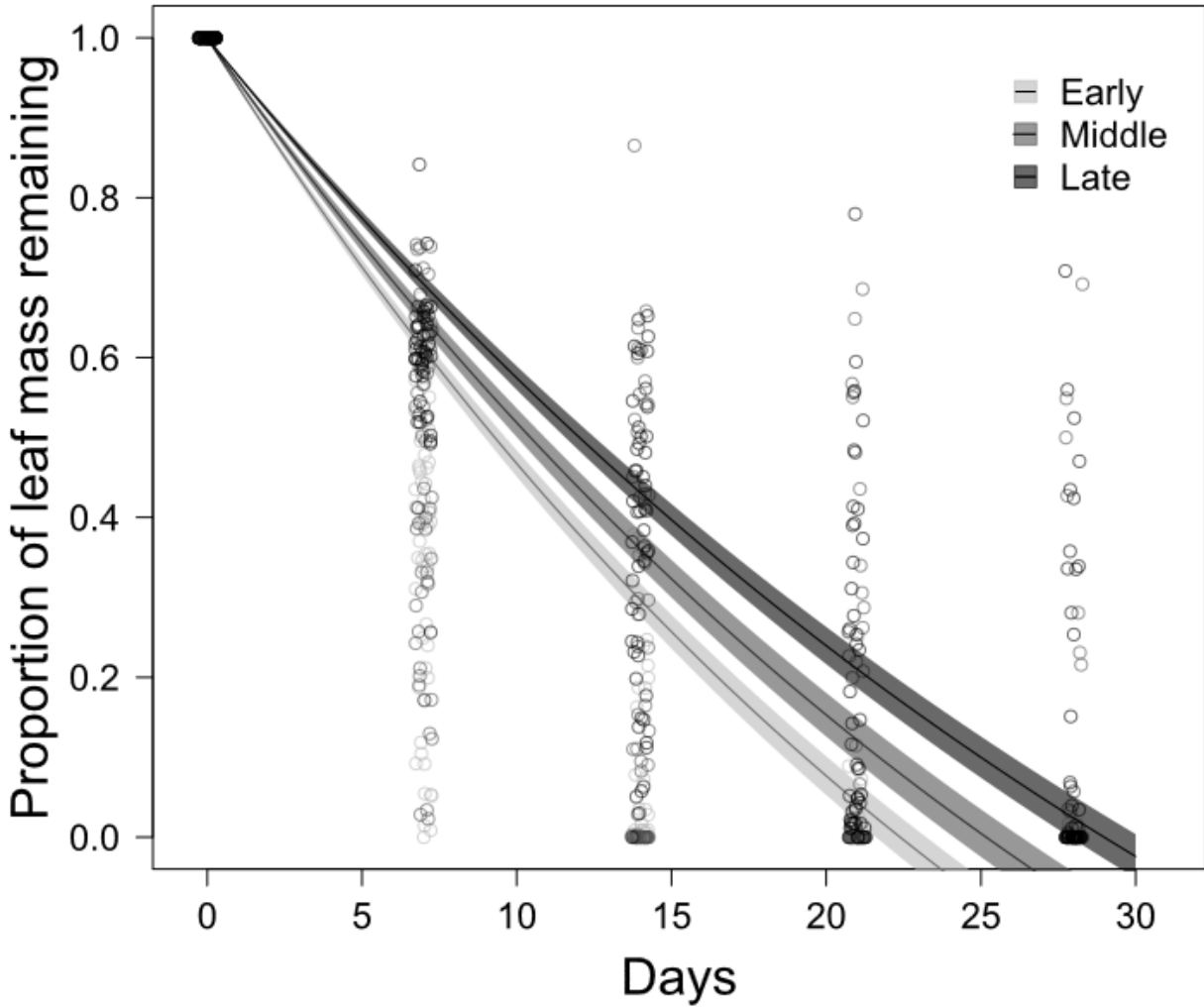


Figure 4.3. Proportion of leaf mass remaining (untransformed) as a function of days for early, middle, and late summer deployments in 2011. Points represent individual leaf packs and are jittered along the x-axis to distinguish superimposed values.

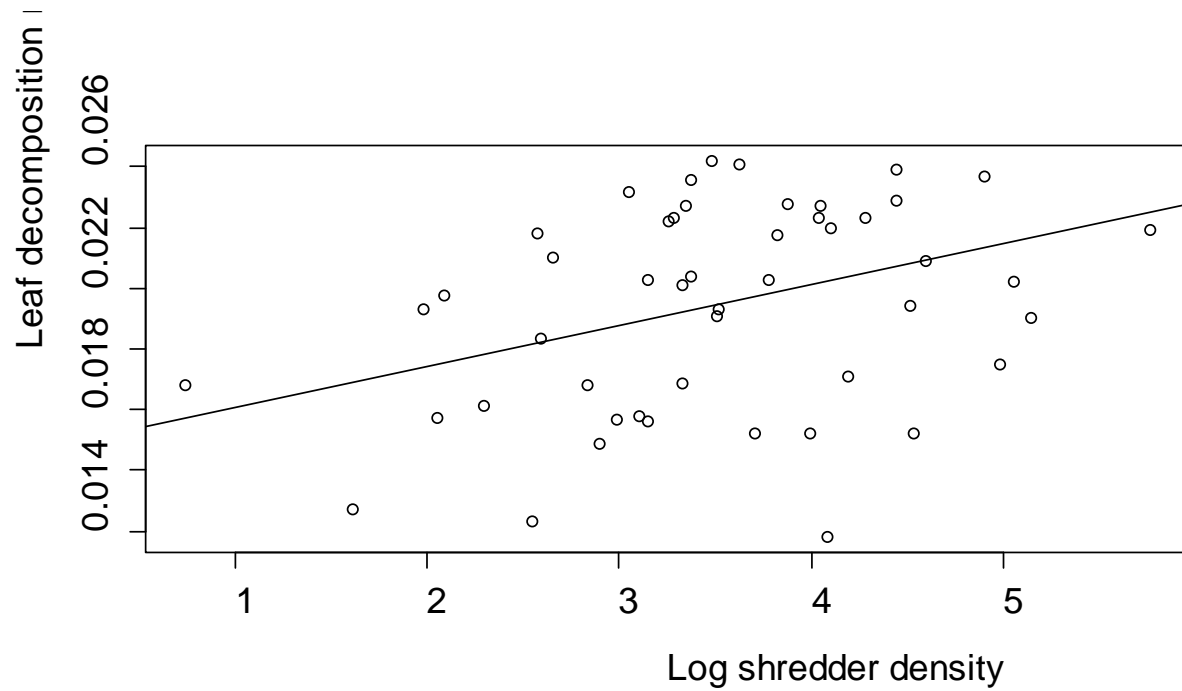


Figure 4.4. Leaf decomposition rates based on days of exposure (k) as a function of log-transformed shredder densities during the first week of deployment. Points represent pool-specific decay rates and shredder density values.

CHAPTER 5
CONCLUSIONS AND FUTURE RESEARCH

Conclusions and future research

In this dissertation, I explored direct and indirect effects of antecedent winter precipitation on physical and biological processes in an intermittent stream in coastal California. A major thrust of my research was a desire to understand the importance of intermittent streams, which comprise the vast majority of stream length around the globe, for imperiled salmon and trout at the southern end of their range in California. I employed a variety of approaches in my research, including stream habitat surveys to measure and monitor the progression of stream fragmentation and contraction during the drought season, mark-recapture methods to study the movement and survival of imperiled juvenile salmonids among and within years that differed in drought intensity, and an experimental study to determine factors controlling leaf breakdown, which provides an important source of carbon fueling food webs in low-order streams with dense riparian cover. Overall, I learned that physical conditions within a single intermittent stream varied considerably among years; the stream fragmented earlier and contracted to a greater degree following dry winters. Variation among and within years in physical conditions had consequences for fish movement, fish over-summer survival, and rates of leaf breakdown.

In Chapter 2, which has now been published in *River Research and Applications* (Hwan and Carlson 2015), I assessed the influence of antecedent winter precipitation on drought intensity and stream physical conditions, and how these in turn influenced the movement of juvenile salmonid fishes during stream drying. During an extensive literature review, I was unable to find any studies that documented fine-scale (i.e., weekly scale) relationships between changes in the physical habitat and fish movement during the drying phase in an intermittent stream, which provided a motivation for this first chapter. Fortunately, my study encompassed two relatively dry years (2009 and 2012) and two relatively wet years (2010 and 2011). I used a combination of transect measurements and total station data to assess weekly changes in riffle and pool volumes to document patterns of fragmentation and pool contraction. Additionally, I tracked the movement of individually-tagged juvenile salmonids each week across the summer drought season. During dry years, riffles dried earlier in the season when compared to wet years. Additionally, following dry winters, pools dried at a faster rate and more pools dried completely when compared to wet winters. Indeed, pool half-life, which represents the number of weeks required for pools to reach half of their initial volumes, was lower during dry years (9.7-14.0 weeks) when compared to wet years (18.6-26.3 weeks). Mean daily stream temperatures averaged across all pools were similar among years ($14.6^{\circ}\text{C} \pm 0.75$) and were generally well below stressful temperature limits for salmonids ($>18^{\circ}\text{C}$) (Hines and Ambrose 2000, Moyle 2002). Fish moved more in the early summer following wet winters when compared to dry years, and movement did not cease until late in the summer during wet year, possibly because stream fragmentation was delayed following wet winters allowing for movement across riffles later in the summer. Movement was positively associated with riffle volume and negatively associated with original pool depth, riffle length, and day of year. I also found that biological fragmentation

(i.e., the date when fish movement ceases) preceded physical fragmentation (i.e., the date when all riffles dried) by three to seven weeks. My findings highlight the influence of antecedent winter precipitation on drought intensity and physical conditions in an intermittent stream, which has consequences for habitat availability and the movement of stream fishes.

In Chapter 3, I investigated the over-summer survival of juvenile salmonids using mark-recapture methods to determine how drought intensity influenced over-summer survival rates. Multi-year studies assessing the summer survival of stream fishes in intermittent streams are exceedingly rare and the few that do exist (e.g., Grantham et al. 2012) tend to estimate survival via comparisons of early and late summer counts, an approach that does not allow pinpointing periods of high mortality during the summer. My research - following the fates of tagged fish each week across the drought season - was designed to address this knowledge gap. In each of four summers, I tagged individual trout and salmon with PIT tags in the early summer. I then used a hand-held antenna to "re-sight" tagged fish each week across the dry season, which allowed me to ask how survival varied among years that differed in rainfall and among weeks across the dry season. I determined that survival was higher following wet winters when compared to dry winters. Moreover, in all years, survival was high through the midsummer, but during dry years, survival decreased considerably during the late summer when conditions tend to deteriorate. These results suggest that native salmonids can withstand drought conditions to an extent - but that these limits are tested following drier winters. This result highlights how critical the late summer period - and not just antecedent precipitation, but also the timing of the fall rains in determining the survival of imperiled salmonids rearing in intermittent streams

In Chapter 4, I used a leaf pack experiment to assess how drought intensity influenced leaf decomposition rates, a key ecosystem process in low-order streams. Building on my earlier efforts to understand the ecological consequences of interannual variation in precipitation, I compared leaf decomposition rates across three summers (2009-2011) that differed in drought intensity and among the early, middle, and late summer during summer 2011 to explore the influence of water level on breakdown rates. Additionally, I collected information on other environmental covariates including stream temperature and macroinvertebrate shredder density to explore the factors that might influence leaf decomposition rates among and within years. My results suggested that leaf decomposition rates were faster when conditions were wetter, including following wet winters in comparison to dry winters, and in the early summer - when water levels were higher - in comparison to late summer. Moreover, I found that shredder density was positively associated with decomposition rates and shredder densities were higher when conditions were wetter. These findings suggest that antecedent precipitation and drought intensity have an *indirect* influence on leaf decomposition rates by influencing the density of shredders. Additionally, benthic invertebrates, such as many shredder taxa, are important prey items for juvenile steelhead trout, the focal fish species investigated in chapters 2 and 3.

Overall, the results of my dissertation research highlight the large variation in physical conditions within a single intermittent stream among years that differed in winter precipitation, which had consequences at the individual (fish movement), population (fish survival), and ecosystem (leaf breakdown) levels. My ongoing collaborative work in this system (with Carlson Lab members) is further exploring the consequences of drought and stream drying on aquatic invertebrates and the larger stream food web.

One important result that emerged from this body of research was the realization that late summer physical conditions differed more among years than did early summer conditions, and this had large consequences for steelhead survival through the summer drought season. Previous studies have documented the importance of intermittent streams for the production of juvenile salmonids (Wigington et al. 2006, Boughton et al. 2009), and my research extends this work by emphasizing that over-summer survival is greater following wetter winters. This result suggests that management agencies tasked with monitoring juvenile salmonids in this region may want to focus limited resources during this critical period during the late summer. However, an important caveat is that my study examined only a single intermittent stream. Along the Pacific coast of North America, there are many intermittent streams that vary in the degree of intermittency (Price et al. 2003, Bogan et al. 2015) and expanding research efforts to include streams across a gradient of intermittency would greatly enhance our understanding of how drought intensity shapes physical conditions and biological communities in these systems. Indeed, the goal of the Intermittent Rivers Biodiversity Analysis and Synthesis project (IRBAS; www.irbas.fr) is to investigate intermittent streams worldwide to improve our understanding of the hydrology and ecology of intermittent streams (Datry et al. 2014).

Beginning in the final year of my study (2012), California has been experiencing a historic multi-year drought (Simeral 2015) that continues to the time of this writing (August 2015). Climate change is poised to severely alter hydrologic conditions in California (Miller et al. 2003, Pierce et al. 2012, Ficklin et al. 2013), and many models suggest that droughts will become more frequent and of longer duration (Kundzewicz et al. 2008). Based on climate models, precipitation within the state is estimated to decrease between 15-30% by 2100 (Hayhoe et al. 2004), resulting in decreased streamflow (Moser et al. 2009). As a result, there is a high likelihood that many streams that are currently perennial will transition to an intermittent flow state (Larned et al. 2010, Jaeger et al. 2014), which further underscores the importance of studies exploring biotic responses to drought and stream intermittency in this region, particularly given the declining state of many of our native salmonids (Katz et al. 2013). Although there has been a growing interest in intermittent streams over the past several decades (Lake 2003, Leigh et al. 2015), researchers agree that intermittent streams are still poorly understood, which has impeded their management (Larned et al. 2010). Additionally, because many temporary rivers (including intermittent and ephemeral streams) are headwater streams and have a large influence on downstream rivers, protection of intermittent streams are critical in maintaining the integrity of

entire river networks (Acuña et al. 2014, Datry et al. 2014). The studies outlined in my dissertation have contributed to this growing body of research and emphasizes that the biodiversity value of intermittent streams can be conditional upon antecedent precipitation, particularly for salmonid fishes at the southern end of their range.

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