Title

Resilience of an endangered salmon complex: understanding the relationships between habitat heterogeneity, environmental variability, and population diversity

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Resilience of an endangered salmon complex: understanding the relationships between habitat heterogeneity, environmental variability, and population diversity

By

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Abstract

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Habitat heterogeneity, defined by spatial variation in local environmental conditions, fosters variation in organism traits and life history strategies, which in turn can stabilize populations by buffering against climate fluctuations. In Pacific salmon (*Oncorhynchus spp*.), large watersheds with intact habitats support commercially, ecologically, and culturally important populations by generating a variety of life history strategies that contribute to population stability and resilience. However, habitat loss and modification have homogenized river networks inhabited by salmon, diminishing intraspecific diversity and its stabilizing effects. In systems with highly modified habitats, it is unclear whether the processes that generate intraspecific diversity are still intact. Furthermore, it is yet to be explored what level of population diversity is sufficient to ensure the survival and stability of small, imperiled populations, especially those experiencing increasingly extreme environmental conditions. This dissertation addresses these knowledge gaps by exploring the relationship between habitat diversity and population diversity within modified habitats of an endangered salmon population complex, aiming to understand its resilience amidst increasingly variable environmental conditions. I focus on a population of critically endangered Central California Coast coho salmon (*O. kisutch*) in the Lagunitas Creek watershed in Marin County, California as a case study of an imperiled population in a small watershed at the southern edge of the species' range experiencing effects of climate change. In Chapter 1, I examine how diverse habitats across the watershed differentially filter extreme drought conditions and the consequences for juvenile coho persistence, foraging behavior, and growth opportunities. Building on observed variation in juvenile traits during a summer of drought in Chapter 1, I assess diversity in long-term juvenile subpopulation dynamics across the region and the effects of seasonal flow conditions in Chapter 2. In Chapter 3, I explore trait variation at the adult stage, leveraging monitoring data and isotopic analysis of fish ear stones to characterize spawning distributions in space and time in relationship to winter hydrology. Spawning dispersal data also revealed key habitats that support returning adults. Findings from all three chapters highlight the importance of habitat diversity and connectivity for population persistence amidst environmental variability and disturbance. By better understanding the underlying dynamics of an endangered population, we can better assess vulnerability to extirpation and create targeted restoration actions to enhance population resilience.

In dedication to:

my parents Jane and Rob,
who empower me to wander wherever my curiosity leads me,
with the knowledge that I can always come back home.

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Ayers, you have been such an incredible mentor and friend, and our walks were always the breath of fresh air I needed. Emily Chen, my fishiest friend, I seriously doubt I would have got through this degree without you. Thank you for teaching me what it means to *really* love fish, and for all our adventures across states and countries.

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Introduction

Habitat heterogeneity can generate diversity in traits and dynamics of organisms spread across a landscape. Spatial variation in local environmental conditions creates a range of growth opportunities and abiotic cues that influence behaviour, movement, and ultimately life history traits of organisms (Watters et al. 2003; Harper & Peckarsky 2006; Weybright & Giannico 2018; Cordoleani et al. 2024). For example, differences in temperature between stream reaches lead to variation in emergence of adult mayflies (Everall et al. 2015) and pool conditions determine the size and timing of metamorphosis in tadpoles (Lauck et al. 2005). Additionally, variation in local habitat alters abundance and survival outcomes for organisms inhabiting these patches, where some habitats are more favourable given regional climate conditions (Brennan et al. 2019). Across time, this spatial variation can produce asynchrony in population dynamics, buffering a population complex against climatic variability.

In Pacific salmon (*Oncorhynchus spp.*), habitat diversity across watersheds has been shown to give rise to a diversity of life history strategies that confer stability and resilience to populations (Hilborn et al. 2003; Greene et al. 2010; Schindler et al. 2010; Moore et al. 2014). This in turn supports ecosystems (Schindler et al. 2013), cultures (Nesbitt 2014; Nesbitt & Moore 2016) and economies (Schindler et al. 2010; Des Roches et al. 2021) that rely on these keystone species. However, habitat loss and modification, such as alterations to stream flows for the benefit of human water use, has homogenized river networks (Poff et al. 2007). This has led to a loss of intraspecific diversity and its stabilizing effects (Moore et al. 2010; Carlson & Satterthwaite 2011; Munsch et al. 2022).

Much work documenting the maintenance and decline of diversity within salmon populations has been done in large watersheds and stock complexes that support commercial fisheries. There has been less attention on diversity within and among salmon populations that are imperiled. Populations of conservation concern are often small and isolated, confined to a limited range of habitats and vulnerable to extirpation from disturbance and demographic stochasticity (Lande 1998; Lacy 2000). While the benefits of stability and resilience conferred by diversity are most needed in these precarious populations, it remains unclear to what extent reduced populations in small, modified habitats can express meaningful diversity. Furthermore, with climate change intensifying, there is an urgent need to understand the capacity of isolated and reduced populations to withstand environmental variability. Through my dissertation research, I was interested addressing these knowledge gaps by characterizing diversity within a small, endangered salmon population, the factors that generate diversity, and understanding whether sufficient diversity exists to buffer against environmental variability and disturbance.

California represents the southern end of the range for several species of anadromous (ocean-migrating) Pacific salmon, many of which are imperiled. In fact, 47% of evolutionary significant units (ESU) of salmonids in the state are listed as either Endangered or Threatened under the federal Endangered Species Act (Nehlsen et al. 1991; Katz et al. 2013). Declines are attributed to extensive habitat loss and habitat modification, historical overfishing, water quality issues, and now, climate change (Brown et al. 1994; Herbold et al. 2018; Munsch et al. 2022). Numerous threatened population complexes persist in reduced numbers and restricted habitats that are often further modified by water infrastructure, diversions, and managed flow regimes. Moreover, projections of increased climate volatility across California are starting to be realized (Diffenbaugh et al. 2015; Swain et al. 2016, 2018) and have increased urgency in conservation and recovery initiatives, especially those aimed at helping fish cope with hotter, drier conditions. Persistence and recovery of salmonids in the wake of increasing environmental variability may depend on whether the existing and newly restored network of habitats can generate a variety of life history strategies that build resilience in these vulnerable populations.

Central California Coast (CCC) coho salmon (*O. kisutch*) are the southernmost population of the species. The CCC ESU was listed as endangered in 2005, although their numbers began to plummet decades earlier (in the 1960's) and they have disappeared from many streams in the region (Brown et al. 1994). Populations have failed to recover despite multi-pronged efforts involving habitat restoration, conservation hatcheries, and intensive monitoring (National Marine Fisheries Service 2012). The life cycle of coho salmon at their trailing edge in Central California is tightly tied to the natural flow regime of coastal rivers. The Mediterranean climate of California leads to distinct wet and dry seasons, where most of the precipitation falls in the winter wet season as rain in coastal systems and elevates flow, which then recedes to low base flow levels in the summer dry season (Cid et al. 2017). The upriver migration of adult salmon is constrained by sufficient flows, and the return of winter rains enables entry into rivers and streams to spawn. Eggs incubate in gravel nests and fry emerge 9-10 weeks after spawning (Shapovalov & Berrian 1940), with emergence coinciding with the spring flow recession. The spring-summer period is a critical period where fry rapidly grow and may disperse from natal sites to rear elsewhere in the watershed. CCC coho salmon typically rear for one year in freshwater, including through the summer dry season and continuing to rear and grow during the following wet season, before undergoing physiological transformations and migrating to the ocean as smolts the following spring. The average adult then spends 18 months in the ocean before returning, often to their natal stream, to spawn. The life cycle of southern coho salmon populations is perceived to be more inflexible compared to more northern populations, but there is a growing appreciation of the diversity of life history strategies expressed (Lestelle 2007; Nordholm 2014; Ghrist 2019; Halloran 2020). The ability of fish to pursue alternate life history pathways may be critical to population persistence, especially given increasing climate variability, including intensifying flood and drought disturbance events.

My dissertation used CCC coho salmon in the Lagunitas Creek watershed in Marin County, California as a case study to explore relationships between fine-scale habitat heterogeneity and diversity within a population complex on the brink of extinction. The largest natural-origin population at the southern edge of the species range, the Lagunitas Creek watershed is considered a regional stronghold and maintains variable yet consistent annual returns of coho salmon (Miller 2010). The Lagunitas system is ideal for investigating the importance of fine-scale habitat heterogeneity in generating diversity within an endangered salmon complex for several reasons. First, the basin has a series of dams, which have reduced the available breeding and rearing habitat by 50%, thus confining the fish to a subset of accessible sites. Sites available to salmon are spread across a gradient of streams that can be treated as subpopulations, connected to one another by dispersal, forming a larger watershed metapopulation. Second, the dammed and flow-regulated mainstem Lagunitas Creek provides a contrast to the unregulated tributaries with natural flow regimes. Flow is considered the "master variable" in stream ecology (Poff et al. 1997; Power et al. 2008) and the effects of climate variability on coho salmon are largely experienced through stream flow conditions; however, reservoir releases can alter relationships between climate and flow (Zimmerman et al. 2018; Chalise et al. 2021). Thus, the system offers opportunities to examine the effects of flow regulation on salmon life history and population dynamics for a small, imperiled population complex. Third, the watershed spans two continental plates, resulting in high geologic diversity underlying streams that support salmon. This underlying geologic diversity combined with other aspects of landscape diversity (land use, topography, vegetation) combine to generate a mosaic of habitats within the watershed. Finally, extensive life-cycle monitoring for over 20 years by the municipal agency Marin Water and federal agency National Park Service provide excellent long-term data across life stages, as well as a 10-year otolith (fish ear stone) collection from deceased spawners. I leveraged the habitat heterogeneity and rich monitoring data within this small system to tackle open questions about population diversity in endangered complexes using different approaches in each of my three dissertation chapters.

In Chapter 1, I examined how spatial distribution of heterogenous habitat patches, or the "habitat mosaic", within the watershed was influenced by extreme drought conditions and the consequences for juvenile coho salmon. Stream habitat and prey phenology across a watershed interact to generate differential foraging and growth opportunities for juvenile coho salmon during the spring and summer months following their emergence from the nest (Rossi et al. 2022). The rate at which a fish grows and its movement within a watershed influence their life history trajectory (Hayes et al. 2008). Yet, drought can reduce stream habitats and connectivity, deteriorate habitat quality, and alter macroinvertebrate productivity (Lake 2011), impacting growth potential and potentially leading to mortality of juvenile coho salmon (Woelfle-Erskine et al. 2017; Vander Vorste et al. 2020). While the effects of drought on salmon in individual streams are well studied, a comprehensive picture of how drought affects the entire watershed and variation in juvenile salmon growth opportunities is lacking. The historic drought of 2020-21 provided an opportunity to study how the habitat mosaic in the Lagunitas Creek watershed changed as drought deepened and the response of juvenile coho salmon, measured by their persistence in pool habitats and foraging behaviours. I predicted a gradient of stream sensitivity to drought, with small streams experiencing the most intense streamflow recession and potential disconnection, while the large, flow-regulated mainstem would be largely buffered from drought effects. I hypothesized that a suite of habitat changes associated with streamflow recession and drought (reduced dissolved oxygen, velocity, wetted habitat, riffle crest thalweg depth, increased temperatures), compounded by prey availability and competition, would drive changes in fish foraging behaviour and presence in habitats. The spatiotemporal variation in foraging behaviour and exploitation of different resources could lead to diversity in growth trajectories, with downstream consequences for life history strategies such as timing of outmigration. Ultimately, I sought to characterize the habitat mosaic during extreme drought conditions, document fish behavioural responses to environmental changes, and evaluate the ways in which variation in habitat dynamics support juvenile salmon population trait diversity.

Chapter 2 expanded upon the findings of chapter 1 to investigate whether the variation in juvenile traits and abundance across stream habitats in a single year translates into diversity of juvenile subpopulation dynamics in the longer-term. Extensive research on large salmon complexes from California to Alaska has demonstrated how filtering of regional environmental conditions across vast watersheds results in asynchronous subpopulation dynamics, which can buffer the aggregate population against climate variability and disturbance (Rogers & Schindler 2008; Greene et al. 2010; Schindler et al. 2010; Braun et al. 2016). Yet, it remains an open question whether these same dynamics occur in smaller populations in reduced watersheds. I used an 18-year time series of juvenile density in four streams within the Lagunitas Creek watershed, in addition to data from nearby Redwood Creek, to assess the level of synchrony in juvenile coho salmon subpopulation dynamics in the region and investigate drivers of juvenile population variability across space and time. Specifically, I was interested in how more spawning activity could increase juvenile numbers, while higher flows in winter and spring and lower flows in the summer might suppress juvenile salmon subpopulations similarly during their early life. My expectation was strong synchrony between subpopulations given the small regional system, and I hypothesized that flows during extreme wet or dry years might synchronize the dynamics of subpopulations through large mortality events. Overall, this chapter aimed to uncover diversity in stream subpopulation dynamics to better evaluate the stability of this small, endangered salmon complex.

In my third chapter, I combined the 18-year monitoring data with otolith microchemistry data to assess diversity at the adult stage by characterizing the distribution and drivers of spawning variation in the system. The timing and location of spawning within a watershed can influence the habitat use and life history of juveniles (Foldvik et al. 2010); despite this, surprisingly little is known about how climate variability influences spawn timing and dispersal of southern coho salmon (but see Shapovalov & Taft 1954). Differences in flow regulation and underlying geology between the Lagunitas Creek subbasin and Olema Creek subbasin set up a natural experiment in which to compare spawn timing characteristics between subbasins and flow regimes, especially in wet years and drought years, and to assess natal-origin contributions to the spawning population. I predicted that spawn timing in the smaller, unregulated Olema Creek subbasin would be more variable, dependent on the timing of sustained winter flows driven by precipitation, which vary substantially year-to-year. Alternatively, Lagunitas Creek mainstem is flow-regulated, with consistent, stable flows provided every year to support multiple salmon life stages. Thus, I predicted that regulated flow conditions would decouple spawn timing from precipitation in Lagunitas Creek. I used otolith microchemical analysis to reveal natal origins of a subset of spawners and characterize adult dispersal across the metapopulation (dispersal in space), paired with data on spawner maturity to understand dispersal through time. As a much larger, more stable subpopulation, I hypothesized that Lagunitas Creek subbasin would act as a “source” to the Olema Creek subbasin, where dispersal of Lagunitas-origin spawners would contribute to the Olema spawning population. This supplement of the Olema subpopulation could be more pronounced following years when rearing fish experienced disturbance. In addition, complex age-structure of spawners would support the spawning population and reduce risk of cohort failure. Bringing together characterizations of spawn timing and dispersal, I aimed to understand how habitat diversity gives rise to spawning trait variation and metapopulation stability across climate contexts, contributing to the resilience of an endangered complex.

In summary, the goal of my dissertation was to investigate interactions between habitat, population diversity, and environmental variability to understand the capacity of our most vulnerable populations to persist and withstand environmental change. With population loss occurring at an alarming rate (Hughes et al. 1997) and a precursor to species extinction, focusing on the scale at which habitats and populations can generate diversity that supports resilience and stability is critical to conservation efforts. My work comes at a pivotal moment, when many resources are being allocated to urgent restoration actions, developing strategies to manage competing water needs between humans and aquatic ecosystems, and helping fish adapt to the new climate reality. My dissertation aimed to address knowledge gaps and provide insights to inform some of these management actions. Overall, my work points to the importance of maintaining a diversity of habitats and flow connectivity at the right times to give fish options in the face of environmental variation and change.

Chapter 1

Reduced habitat mosaic supports variation in endangered coho salmon response to extreme drought

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Abstract

Within a watershed, climate and hydrological conditions generate a shifting mosaic of habitats that influence traits and population dynamics of aquatic organisms. For stream-dwelling salmonids, the interactions of stream pool characteristics, prey phenology, and competition can produce spatiotemporal variation in growth opportunities across the mosaic that can be exploited through diverse foraging behaviours and dispersal, potentially supporting different life history trajectories important for population stability and resilience. Yet, disturbance events such as drought can alter the mosaic and reduce connectivity between habitat patches that could suppress juvenile salmonid survival, growth and trait expression. Using a small, coastal California watershed containing an endangered coho salmon complex as a case study, we explored how extreme drought conditions during the spring and summer months of 2021 influenced the watershed habitat mosaic. We then evaluated the response of juvenile salmon within the mosaic, focusing on fish presence and foraging behaviour, and uncovered environmental drivers of variation in juvenile behavioural response. Drought led to the partial collapse of the habitat mosaic, where some disconnected pools became “ecological traps” for juvenile coho salmon. However, many pools remained refuges for salmon and supported variation in fish foraging behaviour and pool occupancy. As drought deepened, the likelihood of fish changing their foraging behaviour or ceasing to forage entirely both increased, but to differing degrees depending on the intensity of streamflow recession, prey decline, and warming in each of the four streams. This led to a range of foraging behaviour observations and growth potential for fish across the mosaic. Overall, extreme drought reduced the capacity of the watershed to produce salmon and restricted the potential life history pathways; however, variation in growth and dispersal opportunities within the existing mosaic suggest a diversity of life history expressions are still possible, despite drought conditions. With drought events in California increasing in frequency and intensity, it is critical to understand the effects of drought on the habitat mosaic and cascading impacts on juvenile salmonid survival and life history.

Introduction

River networks are made up of interconnected, diverse habitat patches, or “mosaics,” that expand and contract with climate and hydrological conditions. Seasonal patterns of stream discharge dictate habitat availability and quality; for example, productive riparian and upland habitats become accessible during the wet season (Bernal et al. 2013), while dry season low flows reduce wetted habitat (Godsey & Kirchner 2014) and may drive deterioration of habitat conditions (Boulton & Lake 1992). Interannual variation in climate (i.e., floods and drought) can alter the intensity of seasonal effects on habitat patches (Power et al. 2008; Lake 2011; Sarremejane et al. 2022). The spatial and temporal dynamics of habitat mosaics influence many aspects of stream ecology, from ecosystem function to habitat use (Stanford et al. 2005; Moidu et al. 2023).

Habitat mosaics can contribute to variation in organism traits and abundance, potentially influencing population dynamics and stability (Brennan et al. 2019). Habitats within a mosaic often vary in hydraulic conditions, temperature, and primary productivity, affecting resource availability for stream-dwelling salmonids across seasons (Nislow et al. 2000; Gowan & Fausch 2002; Woo et al. 2019; Kaylor et al. 2021; Rossi et al. 2021b), as well as between years with different environmental conditions (Armstrong & Schindler 2013; Coleman et al. 2022). Such differences drive variation in key traits, such as growth rate, which in turn supports a diversity of life history strategies in salmonid populations (Thorpe 1977; Metcalfe et al. 1988; Metcalfe 1998; Bacon et al. 2005; Railsback et al. 2014; Cordoleani et al. 2024).

Juvenile salmonid growth is largely determined by the consumption of aquatic and terrestrial invertebrate prey. Juvenile salmonids in streams are considered drift foragers that hold position in the current to intercept invertebrates (Fausch 1984; Puckett & Dill 1985; Nielsen 1992a); however, other foraging behaviours are also utilized such as active-search foraging in the water column (Nielsen 1992) and picking prey from the benthos (Nakano et al. 1992). Fish may alter their behaviour and diet beyond drift foraging in response to competition (Nielsen 1992a; Nakano & Furukawa-Tanaka 1994), reduced streamflow and drift prey (Fausch et al. 1997; Nakano et al. 1999; Caldwell et al. 2018), or to exploit other available resources (Nielsen 1992; Nakano & Furukawa-Tanaka 1994; Gowan & Fausch 2002). Such changes in foraging behavior contribute to variation in growth rates at different times in the season, for example, when the profitability of drift foraging at the head of the pool declines with flow (Fausch 1984; Nielsen 1992a; Rosenfeld & Raeburn 2009; Rossi et al. 2021b). Search and benthic foraging behaviours are considered less bioenergetically favorable than drift foraging (Caldwell et al. 2018), yet there is a growing appreciation for the role of these behaviours when streamflow is reduced, and drift foraging is no longer profitable (Harvey & Railsback 2014; Spaulding 2016). This is especially true for smaller fish that may be excluded from drift foraging positions by larger, dominant individuals (Hwan et al. 2018; Rossi et al. 2022). Overall, spatiotemporal variation in foraging behaviours potentially determine the growth trajectories of juvenile salmonids.

Connectivity between mosaics is another important factor that influences resource availability and growth opportunities for fish. Seasonal tracking of resources and thermal regimes within and between streams has been shown to increase growth and survival of juvenile salmonids (Ebersole et al. 2006) and potentially diversifies growth trajectories (Armstrong et al.

2021; Bellmore et al. 2022). During the spring-summer foraging period, the ability of fish to disperse to non-natal habitats allows them to track shifting high-quality habitat and foraging opportunities nearby and mitigate competition to maximize growth (Nakano 1995; Fausch et al. 1997; Kahler et al. 2001; Gowan & Fausch 2002). Fish that grow rapidly early in the spring season can also disperse to expand the usable habitat mosaic into non-natal stream habitats (Anderson et al. 2008) or the estuary to exploit the resource-rich environment in the summer (Weybright & Giannico 2018). Connectivity between natal and non-natal habitats can also enhance survival of juveniles, especially where favorable spawning habitats become unsuitable for rearing, such as has been observed in intermittent streams (Erman & Hawthorne 1976; Hwan & Carlson 2016).

The movement of fish to access growth opportunities across shifting habitat mosaics likely plays an important role enhancing life history diversity. Yet such movement is often highly dependent on interannual hydrological conditions. While wet years can enhance connectivity between streams and the expanded mosaic (Goertler et al. 2018), drought can limit and homogenize the available habitat (Cline et al. 2020), restrict movement between existing patches (Rossi et al. 2023), and potentially create “ecological traps” if conditions become unsuitable (Vander Vorste et al. 2020). Drought effects are often exacerbated by habitat degradation and human water withdrawals that further disconnect and reduce the mosaic (Rolls et al. 2012). Although the consequences of drought and stream disconnection on juvenile salmonid mortality have been well documented (Woelfle-Erskine et al. 2017; Hwan et al. 2018; Obedzinski et al. 2018; Vander Vorste et al. 2020), less focus has been given to behavioural responses of persisting fish to drought, if and how they access food resources, and consequences for growth, and trait variation across a population.

Here we expand upon previous work by exploring how behaviour of juvenile salmonids shifts within dynamic habitat mosaics. Our study coincided with a historic drought that provided us the opportunity to further investigate how extreme drought influenced the watershed mosaic in its ability to support juvenile salmonids and their foraging behaviour. Focusing on a small, coastal watershed in California, we sought to 1) characterize the habitat mosaic within the watershed during the dry season of an extreme drought year by describing differences in stream habitat, prey phenology and fish growth opportunities; 2) characterize variation in juvenile salmonid response to drought within the mosaic via fish persistence and foraging behaviour; 3) assess aspects of the mosaic that support fish foraging behaviour in drought. We hypothesized that habitat in streams with natural flow regimes would be most sensitive to drought conditions and experience more intense low flow conditions, to varying degrees, while perennial, flow-regulated mainstem habitats would be least impacted given patterns of flow inflation during the dry season (Grantham et al. 2018; Zimmerman et al. 2018; Ayers et al. 2024). In turn, differences in stream response to drought would have cascading effects on resource availability as effects of streamflow recession and temperature changes interact to alter the macroinvertebrate community (Rolls et al. 2012; Herbst et al. 2019). We expected fish to track these differences by shifting to non-drift foraging modes as streamflow receded (Caldwell et al. 2018; Rossi et al. 2021b, 2022), or by ceasing to forage entirely if no longer able to disperse. We speculate that the spatiotemporal diversity of behavioral responses to drought could give rise to various growth trajectories and support diverse life history strategies within the juvenile salmon population, potentially bolstering resilience to climate variability.

Methods

We sampled the Lagunitas Creek watershed in Marin County, California in 2021 amidst the historic drought of 2020-2022 (**Figure 1A**). This small, coastal watershed (270km^2) is a stronghold for natural-origin Central California Coast coho salmon (*Oncorhynchus kisutch*), an endangered Evolutionary Significant Unit at the southern end of the species' range. It also contains a population of threatened Central California Coast steelhead trout (*O. mykiss*). The watershed runs through a mixture of private and public federal (Golden Gate National Recreation Area, Point Reyes National Seashore), state (Samuel P. Taylor State Park) and municipal (Mt. Tamalpais Watershed) land that support residential and recreational use, agriculture, and cattle grazing. The vegetation in the watershed includes redwood-dominated forests, chaparral, scrubland, grassland, and marsh. The watershed lies across two tectonic plates, the Pacific Plate (Olema Creek sub-basin) and the North American Plate (Lagunitas Creek sub-basin), resulting in distinct geological differences. A series of dams on the mainstem Lagunitas Creek and a major tributary, Nicasio Creek, provide water for the county while blocking access to anadromous salmonids to approximately half of the watershed. Yet, high variation in geology, topography, land use, and vegetation across the accessible ~120 km^2 catchment generates a mosaic of rearing habitats ranging from small pools in intermittent streams to large pools in the flow-regulated mainstem.

Like other coastal streams in Mediterranean-climate California, Lagunitas Creek watershed is rainfed and primarily relies on winter precipitation to elevate stream flow, with little to no precipitation in the summer (Lane et al. 2017). The timing, frequency, and magnitude of winter and, to some extent, spring storms dictate the rate of flow recession and aspects of dry season flow conditions (duration, magnitude, etc.). It is during the spring-summer recession that coho salmon and steelhead trout emerge from the nest and begin to feed, grow, and potentially disperse from their natal site. To partially mitigate the impacts of dam construction and river regulation, the municipal operating agency Marin Water is mandated to maintain minimum summer flows in the mainstem of Lagunitas Creek downstream of Peter's Dam, released from the upstream reservoir, at 0.23 cubic metres per second (cms; 8 cubic feet per second (cfs)) or 0.17 cms (6 cfs) during drought years (Marin Municipal Water District 2011). The 2021 water year (October 1, 2020-September 30, 2021) was the second year of drought, with minimal rainfall leading to unregulated streams experiencing early onset of low flows and disconnection (**Figure 1B**).

Our study focused on habitats within the Lagunitas Creek watershed utilized by coho salmon, given the concerns about the impact on drought of this critically endangered ESU. Coho salmon typically spend one year rearing in freshwater before migrating to the ocean and juvenile coho salmon in their first year ("young of year") are particularly vulnerable to drought conditions during the dry season. Juveniles typically prefer deep, slow moving pools for rearing habitat and rely on pool refuges with cooler temperatures and adequate dissolved oxygen (DO) levels.

We selected five sites across four streams that represented a gradient of physical habitat conditions as a sample of the watershed habitat mosaic, including (from largest to smallest stream): mainstem Lagunitas Creek (2 sites), Olema Creek, San Geronimo Creek, and Devil's Gulch (**Figure 1**). In Lagunitas Creek, we chose a site near the most downstream dam (LAG2), as well as a site further downstream where there have been recent restoration efforts (LAG1) to capture within-stream diversity. The four streams selected covered the most consistent coho salmon summer rearing habitat across the watershed on an annual basis and had pools with fish in them in mid-April. We selected sites within a stream based on presence of coho salmon “redds” (nests); 2020-21 was a low spawning year for some streams and we had to target areas adults had accessed and successfully spawned. At each site we chose three pools as replicates that had nearby redds or presence of coho salmon juveniles, totaling 15 pools throughout the watershed. Starting in late April and early May (hereafter “May”), we sampled each pool at three monthly time points (May, June, July) over the course of the dry season. We also sampled physical habitat and coho salmon presence in September and October, the driest period of the year, before precipitation events rewetted the system (***Supplementary Materials***).

Objective 1. Characterizing the mosaic during drought

To characterize the habitat mosaic and how it was influenced by drought, we described stream habitat, prey availability, and growth potential in each pool in May, June, and July. We used descriptive statistics due to lack of data limiting our ability to generate robust models.

1.1 Stream habitat dynamics

To document changes in stream pool habitat throughout the summer due to deepening drought conditions, we repeatedly measured pool dimensions (width and depth), velocity, and water quality. We measured wetted width at 3-4 equally spaced transects across pool, dividing the pool length into sections starting at the very head of the pool. At each width transect, we measured depth at 3-4 points along the thalweg, the deepest continuous path along the stream profile. At each depth measurement, we used a USGS Pygmy Current Meter to measure mean velocity at 0.6 depth. Width, depth and velocity sampling all started at the head of the pool and proceeded downstream. In May, we also identified the downstream riffle-crest-thalweg (RCT), the point at which the thalweg intersects with the riffle crest (Rossi et al. 2021a). The downstream RCT can be used as a metric for flow recession as it is the point in the pool-riffle sequence where flow is the most restricted; as flow recedes, this point becomes increasingly shallow and can restrict fish movement between pools. We measured the depth at this point every two weeks during the summer (May-July) and at sampling periods in September and October, at which times we also measured temperature and dissolved oxygen (DO) using a handheld YSI Pro20 near the head of the pool. Additionally, we deployed Onset HOBO Pendant temperature loggers in each pool, and PME miniDOT loggers for DO in one pool at each site to continuously record temperature and DO every 30 minutes. We collected them at the end of the season in October, or when a pool dried up. Finally, during our first sampling event we also did a one-time assessment of habitat complexity and shelter in each pool (***Supplementary Materials***).

To characterize physical habitat, we used a principal components analysis (PCA) using monthly data collected from each pool (RCT depth, maximum velocity, maximum depth, median width, spot temperature, spot DO), which allowed us to explore patterns in abiotic conditions across sites and through time. We generated a PCA for the May to July sampling period, to match available fish foraging data.

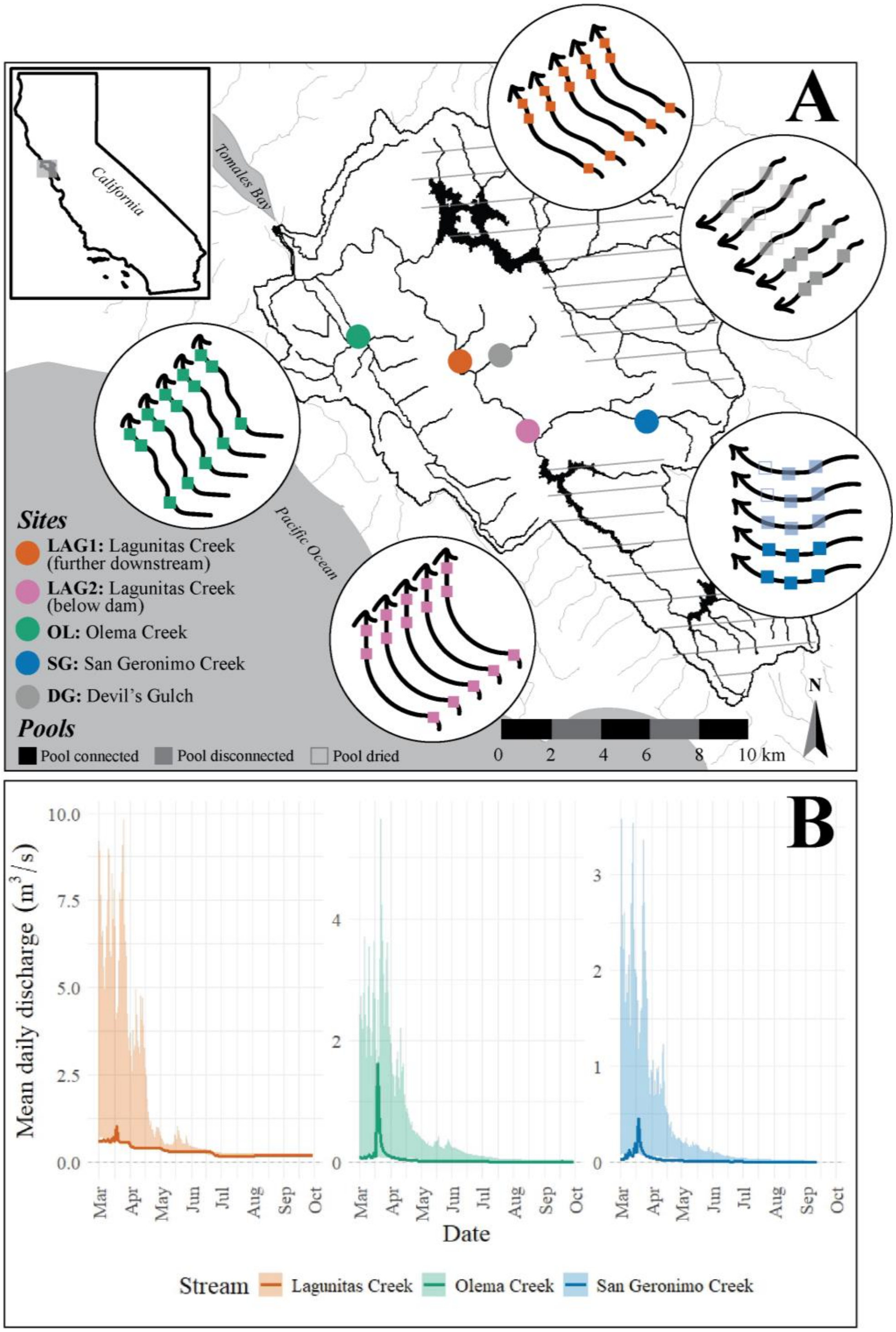


Figure 1 Map of Lagunitas Creek, Marin County, California with study sites and 2021 hydrographs from March to October in three of the four study streams. (**A**) The watershed is highlighted on the inset map of California. Study sites are colour-coded on the map, with inset circles showing the three pools (squares) sampled per site according to streamflow recession and disconnection (shading) at each sampling time point (May, June, July, September, October), where the bottom streamlines represent May sampling conditions. (**B**) Solid lines are discharge recorded by stream gauges during the spring-summer flow recession, colour-coded by site. Shaded areas are the 10th-90th percentile long-term flows.

For visualizing habitat changes at a finer temporal scale, we plotted maximum daily temperature and daily average DO from loggers and biweekly RCT depth to identify where and when stressful conditions occurred. Temperatures > 21°C impede growth and eliminate juvenile coho salmon from a habitat, but there may be impacts to fish at 18-20 °C (Carter 2005).

Dissolved oxygen below 3 mg/L for three continuous days can be lethal for coho salmon (Chapman 1986). The RCT depth at which juvenile coho salmon cannot disperse from a pool depends on fish size, but below an RCT depth of 4.5 cm, young of year salmonids may start to experience impediments to movement (McBain & Trush, Inc. 2012).

1.2 Macroinvertebrate prey phenology

We sampled macroinvertebrate drift to characterize prey phenology within pools because it is the primary source of prey for drift-feeding juvenile salmonids. For each pool at the May, June, July sampling periods, we set one drift net (30 x 30 cm, 500 μm mesh) at the head of the pool where we observed fish foraging. We measured depth at the net placement and velocity at the mouth of the net. We set nets for 1hr (+/- 10min) between 3-7pm to capture the "dusk" hour where there is higher influx and feeding (Culp et al. 1994; Neale et al. 2008). We used a 500 μm sieve to filter invertebrates from the net and transfer into a sample container with 70% ethanol to be stored for lab analysis. In the months of June and August, we also sampled invertebrates in the benthos and from infall to estimate prey availability in the pool from different sources (Nielsen 1992a; Rossi et al. 2022). For benthic sampling, we selected 5 rocks from the bottom of the pool using a random walk and removed all contents from their surface with a squeeze bottle onto a sieve, then transferred to a sample vial with 70% ethanol (Peckarsky 1984). In pools that did not have rocks, we used organic materials that provided a surface for invertebrates such as sticks and bark. Salmonids have been observed to pick prey items off benthic surfaces but cannot access those burrowed (Nakano et al. 1992; Suttle et al. 2004); thus, we only selected benthic materials such as rocks and sticks that would provide available prey to salmon. We measured the dimensions of the rocks and sticks to calculate the exposed surface area. To collect infall samples, we set 3 pan traps of clear plastic Tupperware (34 cm x 21cm) with 2 cm of water and a drop of liquid detergent to prevent anything from crawling out and left them for 24 hours. At the end of the sampling period, we filtered all invertebrates in the water through a sieve and stored all specimens from the pool in a single vial with 70% ethanol.

In the lab, all samples were sorted and macroinvertebrate specimens were identified to family under 10x magnification using a dissecting microscope. Unknown specimens were removed, and terrestrial invertebrates were not classified beyond being terrestrial, unless easily identified to order. We measured the length of each organism to the nearest 0.5 mm then used published length-weight regressions to estimate dry mass and calculate total biomass within each sample (Dumont et al. 1975; Benke et al. 1999; Sabo et al. 2002; Cummins et al. 2022). To assess drift macroinvertebrate availability in a pool, we divided drift biomass by the number of seconds the drift net was set (mg/s), then divided drift flux by the discharge through the drift net (obtained by multiplying velocity, m/s, by drift net area, 0.09 m^2) resulting in drift concentration in mg/m^3. Infall was calculated at biomass per area of the pan traps over time ($mg/m^2/h$), and benthic prey availability was estimated as the biomass per benthic surface area (mg/cm^2). The infall and benthic estimates were not extrapolated to the entire surface area or benthic area of the pool, rather they represent a snapshot of these resources within a pool, standardized by sampling effort, relative to other pools. We plotted invertebrate drift concentration, infall rate, and benthic biomass by site and month (May-July) to visualize patterns in prey availability.

1.3 Fish growth opportunities

Growth opportunities for fish across the mosaic were described by growth potential from drift foraging. Given the endangered status of our focal species, we chose to estimate coho salmon growth in non-invasive ways. For drift-foraging fish at the head of pools, we relied on the drift samples and hydraulic measurements to estimate growth potential (in Joules per second). The approach considers the potential energy gain of an individual fish of a certain size and does not incorporate competition and hierarchical foraging or daily fluctuations in conditions; however, these models can provide insights into the relative energetic benefits of a pool over time and relative to other pools. Bioenergetics models have a long history in the study of drift foraging salmonids (Hughes & Dill 1990; Hayes et al. 2000; Rosenfeld & Taylor 2009; Caldwell et al. 2018), incorporating fish metabolic demands, swimming costs, and capture efficiency to estimate the net rate of energy intake (NREI) based on pool depth, velocity, temperature, and drifting invertebrate prey concentration. We used the software BioenergeticsHSC (Naman et al. 2020) to run a Wisconsin bioenergetics model for coho salmon of median fork length (60 mm) in our system, based on video and snorkel measurements. The inputs for this model include fish size, maximum depth, velocity, temperature, and macroinvertebrate drift separated by size class and family (see ***Supplementary Materials*** for details). We selected the head of the pool only for growth potential estimates as drift recedes moving downstream from the head of the pool (Fausch 1984). In addition, we only calculated growth potential from drift foraging because bioenergetics models for other forms of foraging are yet to be standardized and require many more assumptions (but see Caldwell et al. 2018). To visualize differences in growth potential in space and time, we plotted NREI at the head of the pool for fish of 60 mm in fork length for each site and month (May-July).

Objective 2. Characterizing fish response to drought within the mosaic

Having established the habitat mosaic and how it was affected by drought, we characterized how fish within these habitats responded to drought using descriptive statistics. Responses were characterized in two ways: 1) Whether fish were present in the habitat; 2) If present, how fish were using the habitat (foraging in the drift, active-search or benthic foraging, not foraging at all).

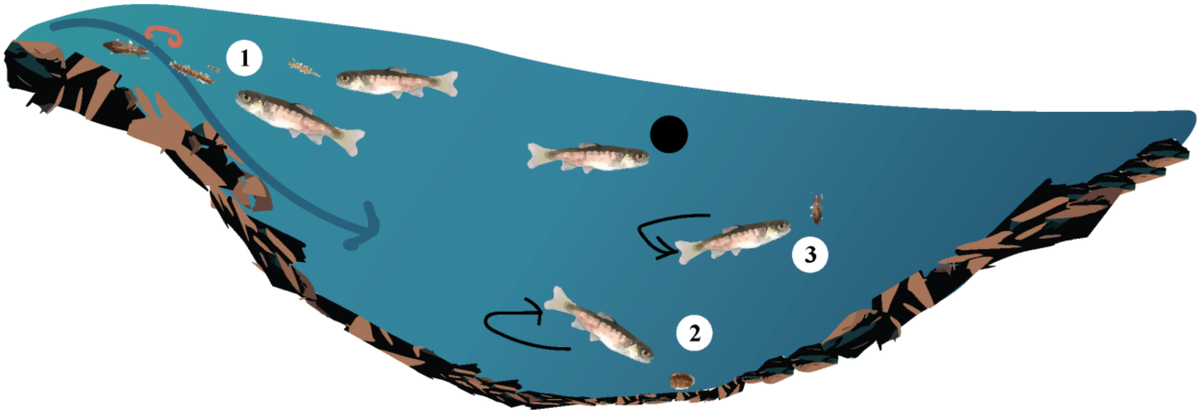
2.1 Fish presence in pools

The first aspect of fish response to drought we considered was the presence of fish in pools across time. We used snorkel surveys to assess abundance and size-structure of salmonids in the pool monthly during the dry season, surveying between 9am-12pm for optimal lighting. These surveys were conducted from May to October to follow up on fish presence into the fall, and thus extend beyond the fish behavioural observations. Two observers moved slowly upstream from the downstream end of the pool, one taking the right bank and the other taking the left bank, scanning ahead and around (see also Georgakakos et al. 2023). We used small rulers marked with different size bins: <40mm, 40-60mm, 60-80mm, >80mm (later collapsed to <40mm, 40-80mm, >80mm for analysis). We counted all coho salmon and steelhead trout and classified each into a size bin when possible. In some cases, pools were shallow enough to warrant only one observer. At one pool in Devil’s Gulch, the pool was so shallow and dense with salmon that instead of snorkeling, the observers performed three repeated visual scans on the bank, covering the whole pool and taking the average of the observer's counts. During all snorkeling sampling events, we did two passes where observers did a first pass, waited at least 15 minutes, then switched sides and did a second pass (three passes were completed in June surveys). We summed the data for each pass across observers, then used the sum for each pass to estimate abundance at each size class using the bounded-count method to get abundance by size class, and total pool abundance (Johnson et al. 2007). We then calculated density of fish within a pool by dividing total pool abundance by pool volume (multiplying length, median width, maximum depth), giving us a conservative estimate of fish per cubic metre. For Devil's Gulch in July pool depth and visibility hindered accurate snorkel estimates; thus, we replaced snorkel estimates for abundance and density with the average number of fish recorded in video subsamples as the cameras captured most of the pool. We assessed how density of fish within a pool changed from May to October by plotting density by site across time.

2.2 Fish foraging behaviour

The second way we characterized fish response to drought was in their behaviour. To observe salmonid behaviour from May to July, we mounted two stereo-paired GoPro Hero7 cameras (1080p resolution, 30 frames per second) onto rebar and placed them at the head and middle of the pool, based on snorkeling observations of fish foraging hotspots. We used two locations to maximize the pool area sampled, as well as to control for foraging differences based on pool position (Nielsen 1992). The "Head" cameras aimed to capture most foraging where the riffle entered the pool and fish were most active, while the "Middle" cameras captured other areas downstream with fish usually where there was complexity and cover. We positioned cameras mid-water column to capture drift foraging but in such a way that we could see also see strikes at the surface or the benthos. Cameras were oriented perpendicular to flow to capture fish in the drift. We let cameras film for 30 minutes at a time between the hours of 3:30pm-7:00pm to maximize lighting and capture pre-dusk foraging activity. After 30 minutes, we removed the cameras and measured the velocity and maximum depth.

We analyzed videos in the lab using a video software VidSync (Neuswanger et al. 2016). This program uses the dual camera set-up to calibrate 3D images, allowing us to measure length of fish, and note their feeding behaviour. For each video, we removed the first and last five minutes to account for human disturbance, then found the most fish-dense 15-minute section where lighting and water quality were sufficient and employed scan sampling. In particular, we watched the first 10 seconds of each minute for a total of 15 samples, scanning for all identifiable salmonids (coho salmon, steelhead trout) and assigning each as displaying foraging (drift, search, benthic) or non-foraging behaviour based on a minimum 4 seconds of continuous observation (**Figure 2**). We counted any foraging attempts, defined as a distinct strike to grab invertebrates, in the drift, benthos, while search foraging, as well as on the surface (adapted from Suttle et al. 2004; Rossi et al. 2021). We also noted conflict events as any instances of aggression (fish chasing or nipping another fish) or submission (a fish fleeing from a chase) within the 10 second interval (adapted from Nielsen 1992) and when possible, we measured fish fork length, repeating measurements 2-3 times to calculate an average length (***Supplementary Materials***). This method of recording behavioural observations (i.e., scan samples) does not account for repeated measurements of an individual fish, thus we focused on the proportion of displays of each foraging mode and the likelihood of each being used in a pool for our visualizations and analysis. Behavioural mode observations were aggregated by site to calculate the proportion of each of the four behaviour modes for each month from May to July. We plotted the proportion of each behaviour, and activity in the number of foraging strikes.



Foraging modes

① **Drift foraging:** Fish holds focal points in the water column and makes short forays to intercept drift

② **Benthic foraging:** Fish primarily cruise over larger areas of stream bed and capture benthic prey by making forceful attacks at the substrate

③ **Search foraging:** Fish undertake continuous undirected swimming, foraging not associated with a focal point

● **Non-foraging:** Fish not continuously swimming, nor holding in the drift (oriented away from drift or no perceived drift); some random movements but slower and more discontinuous than search foraging

Adapted from Rossi et al. 2021, Nielsen 1992, Nakano et al. 1999

Figure 2 Stream pool habitat with the four observed behaviour modes for juvenile coho salmon. The blue arrow indicates the direction of the current coming in at the head of the pool where fish are drift foraging (1). Black arrows indicate active foraging of cruising the benthos (2) or continuous swimming in the water column (3). The fish in the middle of the pool without arrows is not actively swimming or foraging (black circle).

Objective 3. Identifying aspects of the mosaic driving fish foraging during drought

Given variation in the habitat mosaic and fish responses to drought, we developed a model to understand what aspects of the mosaic (habitat, prey, conspecific competition) that changed throughout the summer predicted variation in fish behaviour modes.

We assessed how fish foraging behavior responded to changing conditions in each pool using a multipart model to distinguish non-foraging and foraging fish (model 1), and to distinguish drift foraging from non-drift foraging fish (model 2) (**Figure 3**). Using a Bayesian approach, we developed a conditional logistic mixed regression model to address these two behavioural splits and the drivers of each. We created a custom family function for conditional logistic regression and ran the model in the R package “brms” (Bürkner 2018; R Core Team 2024), which implements Bayesian models using the probabilistic programming language Stan (Stan Development Team 2024). Our response data was the behaviour classification of each fish observation in a pool in May, June, or July. We explored four broad predictor categories using habitat metrics that were not highly correlated ($r < 0.7$): habitat variables associated with streamflow recession (RCT depth, maximum velocity), habitat variables not tightly associated with streamflow recession (temperature, maximum depth), prey availability (drift concentration), competition (fish density). First, the model assessed what factors determined the likelihood of fish not foraging vs foraging given predictor variables; second, given the probability of fish foraging, it estimates the likelihood of fish drift foraging over search/benthic foraging using the same predictors.

The conditional probabilities are expressed as a linear function of predictor variables using the logit link function (***Equation 1***):

$$logit\left(\varphi_{\{NF\}|\{NF,D,SB\}_{ijk}}\right) = \beta_{0,\{NF\}|\{NF,D,SB\}} + \sum \beta_{t,\{NF\}|\{NF,D,SB\}} \cdot X_t + u_{ij} + u_j + b_k$$
$$logit\left(\varphi_{\{D\}|\{D,SB\}_{ijk}}\right) = \beta_{0,\{D\}|\{D,SB\}} + \sum \beta_{t,\{D\}|\{D,SB\}} \cdot X_t + u_{ij} + u_j + b_k$$

where $\varphi_{\{NF\}|\{NF,D,SB\}_{ijk}}$ is the conditional probability of observing non-foraging (NF) behaviour in pool *i*, site *j*, and month *k*, and $\varphi_{\{D\}|\{D,SB\}_{ijk}}$ is the conditional probability, given the likelihood of observing non-foraging behaviour, that fish display drift foraging (D) behaviour. The β_0 is the mean intercept, and β_t represents the coefficients for the X_t predictor variables (see ***Supplementary Materials*** for full equation). We accounted for within-pool and within-site variation with random effect terms for pools nested in sites (u_{ij}) and sites (u_j), and month was included as a crossed random effect (b_k) to control for autocorrelation within pools. It is important to note that the output of conditional logistic regressions coefficients refers only to conditional probabilities of a subset of outcomes rather than estimating the likelihood of a single outcome among all possible outcomes (Kruschke 2014).

We generated hypotheses about the effects of our predictor variables on the likelihood of fish displaying non-foraging behaviour and drift behaviour (**Figure 3**). In brief, we predicted that the likelihood of fish not foraging would increase as streamflow receded, specifically as RCT depth decreased, as maximum depth decreased reducing refuge, and with higher temperatures that create stressful conditions for fish (Carter 2005). Declining RCT depth corresponds to restricted dispersal, decreased pool habitat (width) and decreased DO, potentially leaving fish stranded in small pools with low DO levels (Rossi et al. 2021a). Given fish were foraging, we predicted a higher probability of drift foraging with higher RCT depth (Rossi et al. 2021b) and velocity (Grant & Noakes 1987), pool depth, and prey concentration (Grant & Noakes 1987), but decrease with higher density (Nakano et al. 1999). Temperature effects can be mitigated by increased prey concentration (Lusardi et al. 2020), though given data limitations we did not test this interaction.

In fitting our model, we used weakly informative priors to ensure a robust and unbiased estimation of parameters. The priors for the predictor regression coefficients were set to a normal distribution with a mean of 0 and a standard deviation (SD) of 5. The prior for the first step intercept was a normal distribution with a mean of 0 and an SD of 30 to accommodate low probabilities, while the second intercept was assigned a normal distribution with a mean of 0 and an SD of 20. Additionally, the standard deviation of the random effects was modeled using a Student's t-distribution with 3 degrees of freedom, a mean of 0, and an SD of 2.5. We performed prior predictive checks to ensure our specified priors encompassed the data and potential extreme responses. We ran four Monte Carlo Markov chains using Hamiltonian Monte Carlo sampling and the No-U-Turn sampler with 2000 iterations, each chain with different initial values, and checked for chain convergence and resolution using the potential scale reduction factor and effective sample size. Cross-validation was performed using the leave-one-out (LOO) method (Vehtari et al. 2017). The LOO method allowed us to compare the fit of our full model with a null model that had random effects and no predictors to assess that our predictors improved model fit and predictive ability. Finally, we assessed the posterior distribution to check agreement with input data. Here we report the mean and 95% credible interval posterior estimates for behaviour conditional likelihoods and fixed and random effects.

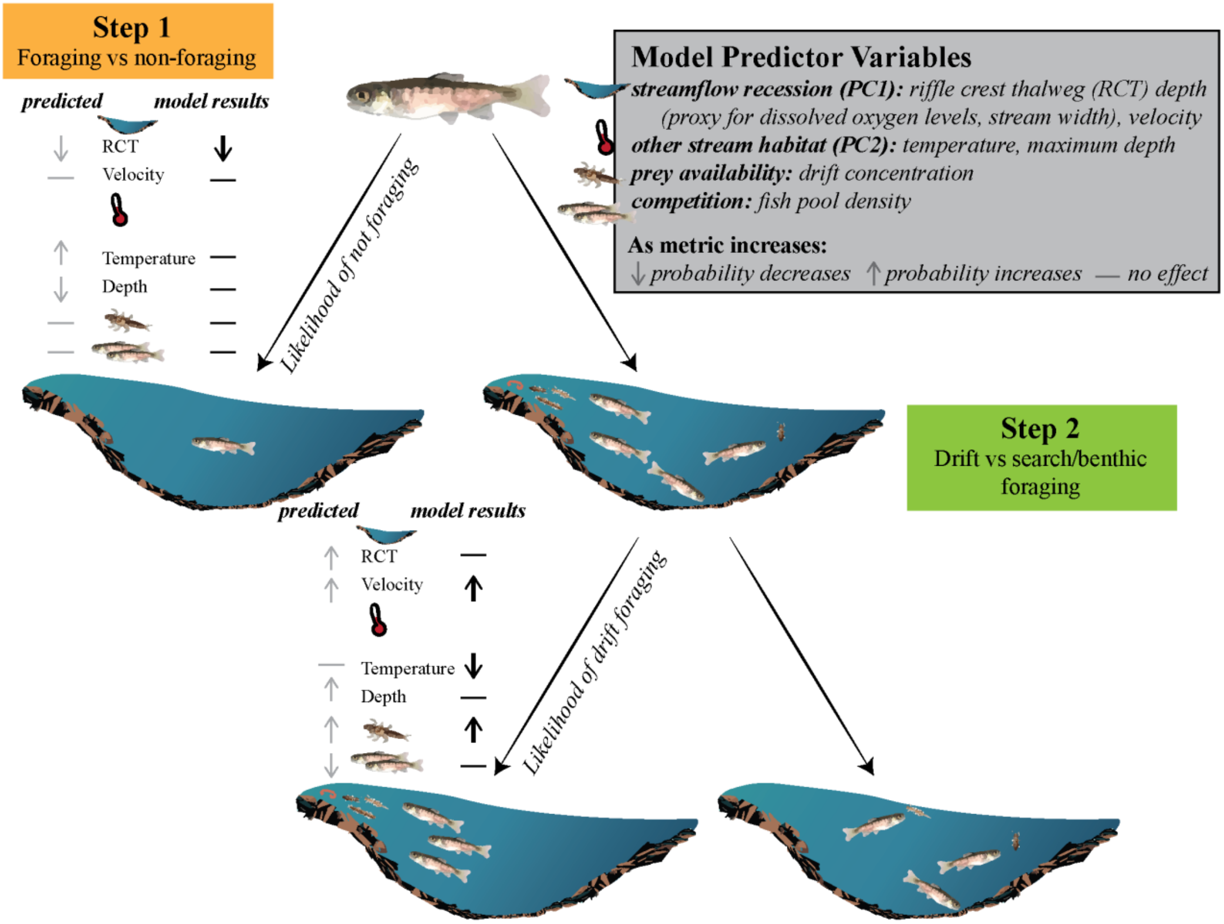


Figure 3 Diagram representing conditional logistic regression two-step behavioural model. The first step is determining the likelihood of fish not foraging at all, as opposed to foraging. The second step, if fish are foraging, is assessing the probability of fish drift foraging, the dominant mode, instead of search/benthic foraging modes. We made predictions (left column, grey) about whether increasing each abiotic or biotic variable would increase, decrease, or have no effect on the likelihood of the behaviour being observed. Black arrows (right column) reveal the model outputs. A black arrow is indicative of the negative or positive central tendency estimate and 95% credible intervals that do not overlap with zero.

Results

1. Habitat mosaic shifts and partial collapse during drought

1.1 Drought reduced useable, connected, high quality stream habitat

We described the habitat mosaic in terms of stream habitat availability and quality and found that part of the mosaic collapsed as a consequence of extreme drought. There were large differences in pool habitats in May, at the start of the dry season, and divergence across sites in terms of how pool habitats changed as drought conditions deepened (**Table 1**). Devil's Gulch and San Geronimo Creek are both small and unregulated tributaries of Lagunitas Creek, and both experienced dramatic declines in pool habitat quantity and quality after stream disconnection left isolated habitat patches. Both streams are typically perennial with year-round flow but became intermittent during the extreme drought conditions of 2021. Devil's Gulch fragmented in late June, and one of our three study pools in Devil's Gulch dried completely by the end of July. San Geronimo Creek remained connected later into the dry season (until mid-July), and one study pool dried by September (**Figure 4A**). Prior to complete pool drying, disconnection in these creeks was associated with sublethal and, ultimately, lethal dissolved oxygen levels (**Figure 4B**). Olema Creek had more variation in pool habitat in response to drought, as one pool became functionally disconnected for fish (RCT depth < 4.5 cm) and experienced lethal DO levels, while other pools maintained higher quality habitat throughout the dry season. Maximum daily temperature increased throughout the summer and peaked in August for most streams, but only briefly hit stressful levels that would impede growth for fish, and these unsuitable conditions were detected in only one pool in San Geronimo Creek (**Figure 4C**). Most pools entered the 18-20 degrees Celsius range during July and August, which can be stressful for fish if food resources are limited.

When plotting pool habitat conditions from May to July in multidimensional space using a PCA, the first two principal components explained 59% and 17% of the variation between pools, respectively (**Figure 5**). The first component (PC1) was characterized by RCT depth, maximum velocity, DO, median width, where each variable was positively associated with PC1. Temperature was most positively associated with PC2, and maximum depth was somewhat negatively associated with PC2. Overall, Lagunitas Creek pools tended to cluster without any clear differences between sites, while pools in the smaller streams were also clustered. Olema Creek clustered closer to the other tributary sites than to the mainstem Lagunitas but was the most intermediate site. As drought progressed, unregulated sites tended to shift more negatively along the x-axis and in the positive direction along the y-axis, indicating streamflow recession led to shallower, warmer habitats with lower DO, lower velocity, decreased wetted widths, and decreased RCT depths. The shift towards lower RCT depths is indicative of reduced connectivity between pools and more restricted dispersal for fish. In contrast, Lagunitas Creek with a regulated (and constant) dry season flow regime, we found that pools shifted little and in a positive direction along the y-axis, becoming slightly warmer and shallower. Overall, we found that drought affected habitat availability and quality in some parts of the watershed but had minimal effects on mainstem habitats.

Table 1 Monthly measurements of habitat and fish abundance and density for all three pools (Seq) within each site. Fish abundance is from snorkel surveys, using the bounded-count method across all passes and sizes (see Methods). Fish density is calculated using fish abundance divided by pool length multiplied by maximum depth and median width. Pools that dried during our study do not have an observation row after drying.

Site	Seq	Month	Dissolved Oxygen (mg/L)	Stream Temperature (°C)	Max Velocity (m/s)	Riffle Crest Thalweg Depth (cm)	Max Depth (m)	Median Width (m)	Fish Abundance	Fish Density (fish/m^3)
DG	1	May	8.5	13.0	0.00	4.0	0.4	2.6	67	8.75
DG	1	Jun	4.4	13.4	0.00	5.0	0.4	4.4	56	4.60
DG	1	Jul	0.8	14.3	0.00	0.0	0.2	1.9	0	0.00
DG	2	May	7.0	10.8	0.02	2.5	0.8	3.9	4	0.23
DG	2	Jun	4.8	13.2	0.00	2.0	0.8	3.9	2	0.12
DG	2	Jul	1.2	14.4	0.00	0.0	0.6	3.4	2	0.19
DG	3	May	8.7	12.9	0.00	3.0	0.3	2.8	92	20.21
DG	3	Jun	7.2	13.7	0.00	2.0	0.3	2.2	20	5.77
LAG1	1	May	10.6	13.6	0.40	17.0	0.9	7.8	103	0.48
LAG1	1	Jun	9.8	15.2	0.26	15.0	0.8	6.8	49	0.28
LAG1	1	Jul	9.7	17.8	0.22	17.8	0.8	5.0	65	0.55
LAG1	2	May	10.6	13.9	0.31	13.0	0.5	7.2	35	0.52
LAG1	2	Jun	10.0	15.2	0.35	14.0	0.5	6.2	33	0.55
LAG1	2	Jul	9.8	17.7	0.31	17.7	0.6	6.4	40	0.63
LAG1	3	May	10.4	14.1	0.16	21.0	0.7	6.7	140	0.80
LAG1	3	Jun	10.0	15.6	0.14	19.0	0.6	7.1	128	0.84
LAG1	3	Jul	9.9	17.4	0.22	7.6	0.6	6.3	99	0.67
LAG2	1	May	10.8	13.5	0.34	18.0	0.7	7.3	42	0.79
LAG2	1	Jun	10.2	15.2	0.30	9.0	0.7	6.2	60	1.30
LAG2	1	Jul	10.0	16.1	0.26	16.0	0.6	5.7	38	1.08
LAG2	2	May	11.0	12.8	0.17	25.0	0.9	9.2	40	0.14
LAG2	2	Jun	10.2	14.9	0.17	23.0	1.0	8.9	127	0.43
LAG2	2	Jul	9.9	16.7	0.10	20.0	0.9	8.2	173	0.68
LAG2	3	May	11.1	12.6	0.20	24.0	0.6	6.6	10	0.11
LAG2	3	Jun	10.1	14.4	0.19	20.0	0.6	6.5	13	0.16
LAG2	3	Jul	9.8	15.7	0.11	18.5	0.5	6.7	67	0.84
OL	1	May	8.6	16.0	0.06	6.0	0.4	4.7	31	1.36
OL	1	Jun	7.8	17.2	0.00	5.0	0.3	4.8	34	1.64
OL	1	Jul	6.0	15.7	0.00	4.0	0.3	4.5	2	0.11
OL	2	May	8.9	15.4	0.07	7.0	0.7	3.5	38	0.69
OL	2	Jun	8.7	14.2	0.02	7.0	0.7	4.1	32	0.54
OL	2	Jul	6.3	15.5	0.00	9.0	0.7	4.6	2	0.03
OL	3	May	8.7	13.8	0.14	12.0	0.6	4.1	56	1.26
OL	3	Jun	8.0	14.9	0.08	11.0	0.7	3.9	49	1.01
OL	3	Jul	5.3	15.5	0.00	9.0	0.7	3.7	19	0.40
SG	1	May	8.7	12.0	0.07	5.5	0.3	2.9	36	5.08
SG	1	Jun	7.9	14.8	0.02	4.5	0.3	2.9	34	4.75
SG	1	Jul	2.1	15.3	0.00	0.0	0.2	1.9	4	1.20
SG	2	May	8.3	12.0	0.03	8.0	0.7	5.4	153	0.99
SG	2	Jun	4.5	13.8	0.04	6.0	0.7	4.4	116	0.92
SG	2	Jul	1.2	14.3	0.00	0.0	0.7	4.4	44	0.36
SG	3	May	8.6	11.8	0.14	7.0	0.7	3.8	39	0.24
SG	3	Jun	7.2	14.8	0.06	4.5	0.8	4.3	37	0.20
SG	3	Jul	2.6	14.6	0.00	0.0	0.7	3.3	23	0.17

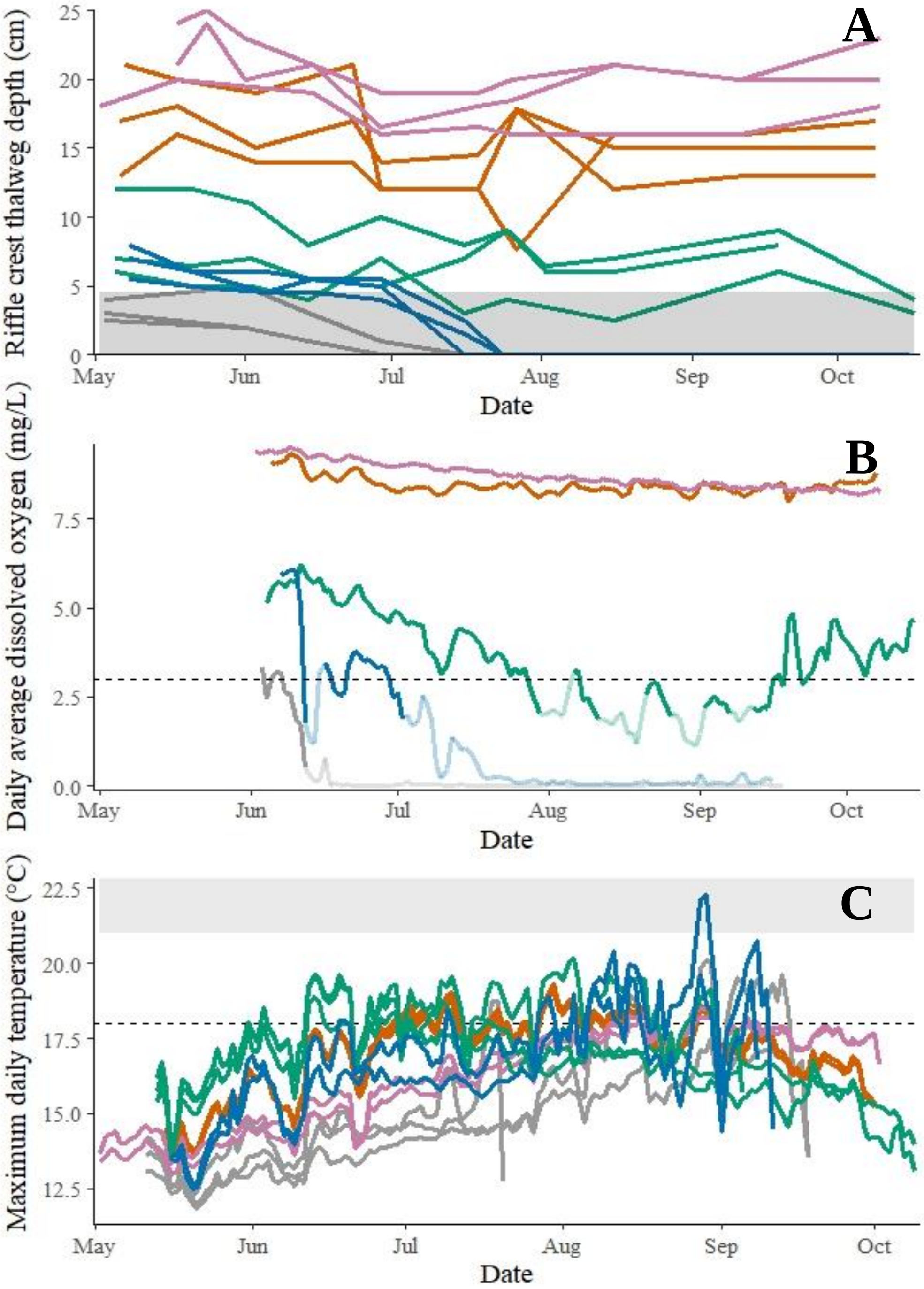


Figure 4 Biweekly measurements of riffle crest thalweg depth for each pool (**A**), daily average dissolved oxygen for one pool at each site (**B**) and maximum daily temperature for each pool (**C**). Colours represent site (orange = Lagunitas 2, pink = Lagunitas 2, green = Olema, blue = San Geronimo, grey = Devil's Gulch). Shaded grey in (**A**) is where juvenile coho salmon dispersal between streams may be restricted. Faded out colours in (**B**) are 3 continuous days of <3 mg/L dissolved oxygen (the dotted line) that can cause mortality in juvenile coho salmon. (**C**) Dotted line is at 18°C, above which fish may experience impediments to growth, and shaded area is where fish may stop growing.

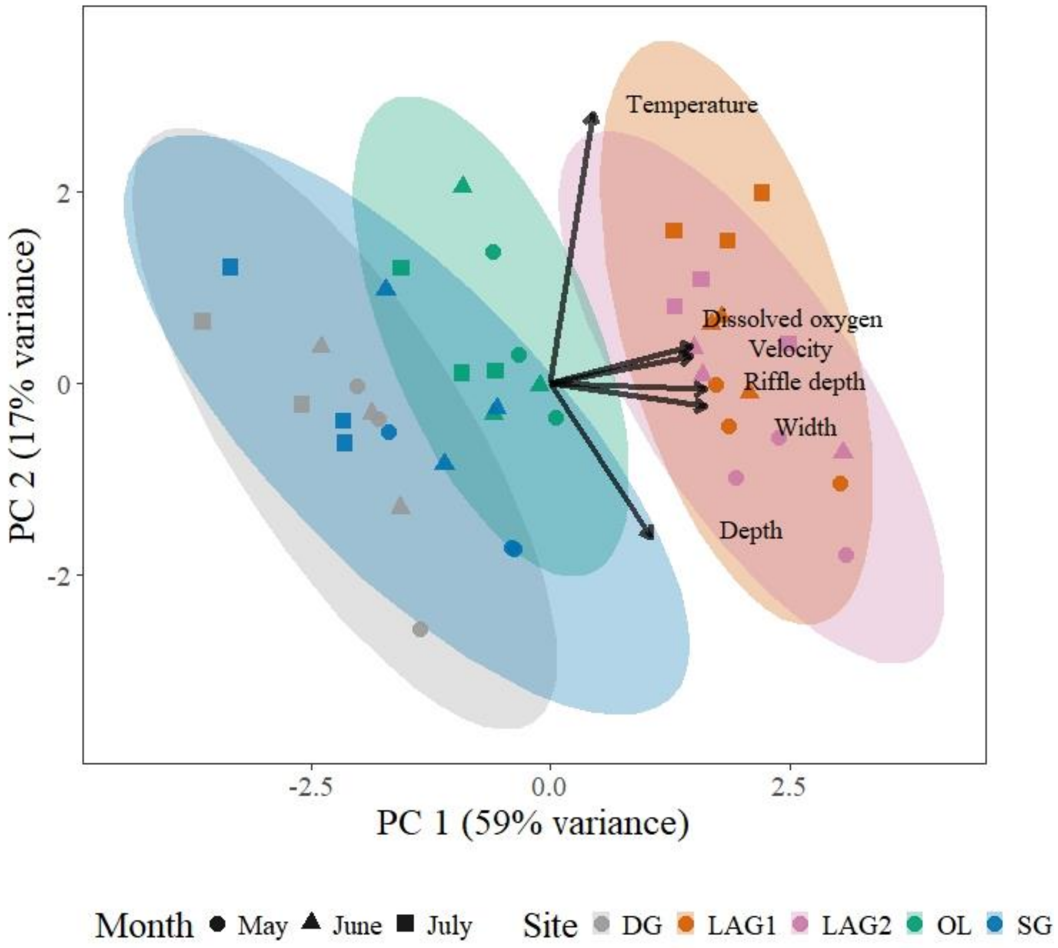


Figure 5 Principal Components Analysis plotted in 2-dimensional space of pools defined by six habitat variables that change with drought. Each point is a pool (colour-coded by site) measured in a month (shape). Black arrows represent weightings of habitat variables for each principal component. Coloured ellipses are the 95% confidence intervals for each site.

1.2 Habitats varied in prey phenology

Prey phenology, described as the timing of peak drift concentration, differed between sites, generating resource pulses across the watershed during drought (**Figure 6A**). Olema Creek and San Geronimo Creek had the highest prey concentration at the head of the pool in May and prey then declined throughout the summer, whereas the Lagunitas Creek sites both peaked in June. One pool in Lagunitas (Lagunitas 1) seems to be an outlier, possibly due to the high concentration of invasive New Zealand mud snails (*Potamopyrgus antipodarum*) that became dislodged from rocks in the riffles and were found in the drift. Devil's Gulch had drift concentrations of approximately zero in all months (flow velocities dropped to very low levels that our meter could not measure). However, in June and August all streams were subsidized by terrestrial prey falling into the pools, and/or had some accessible prey in the benthos (**Figure 6B, 6C**). Benthic invertebrate concentration appeared to be consistent across time, while terrestrial infall declined for Olema Creek and San Geronimo Creek in August and remained steady in other streams. While the three macroinvertebrate sources are not directly comparable, these patterns suggest that even as drift concentration declined, fish had other options in terms of prey resources.

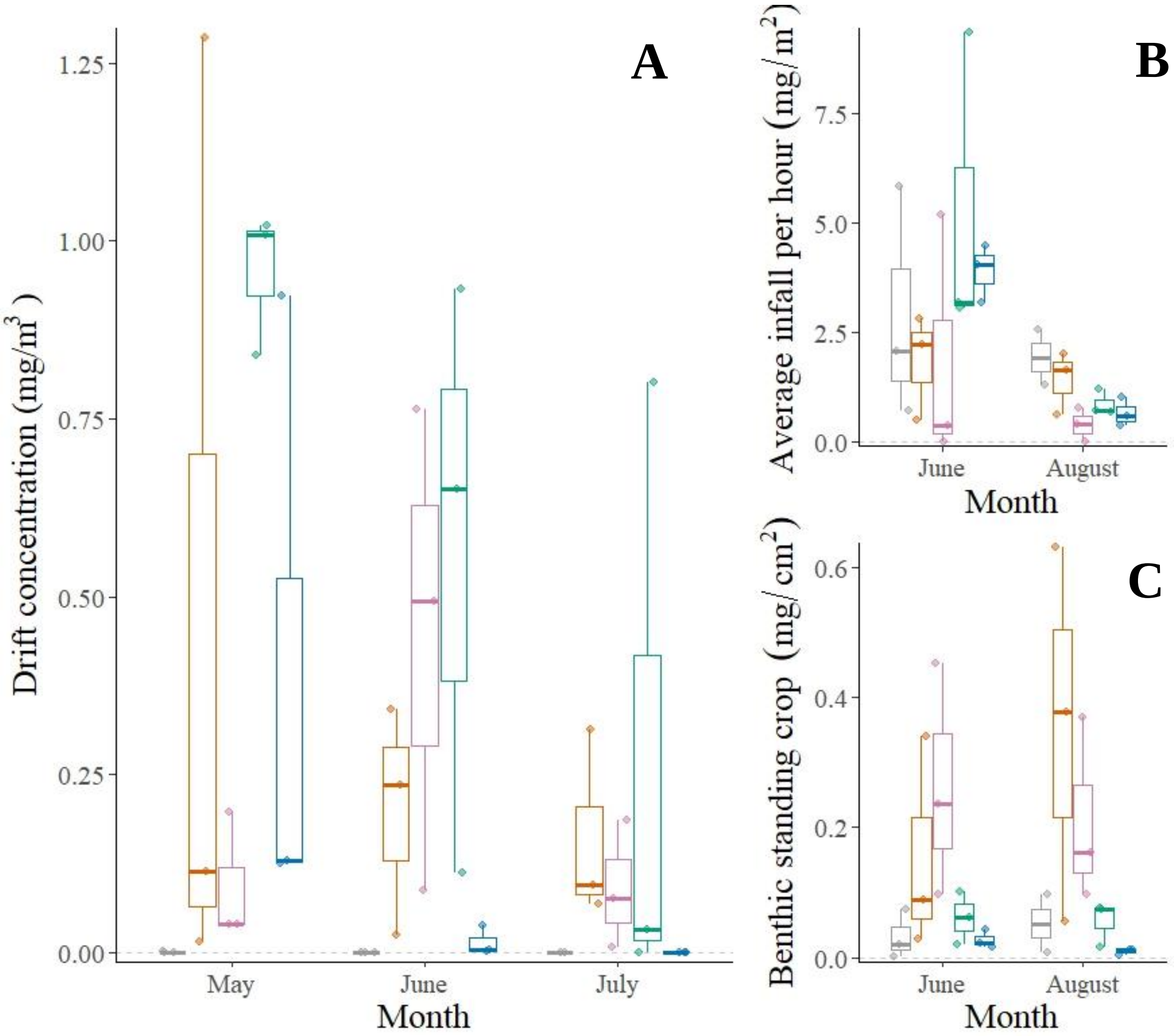


Figure 6 Macroinvertebrate drift concentration (**A**), biomass from infall over time (**B**), biomass on benthic rocks (**C**). Drift was collected in May, June and July while infall and benthic samples were taken in June and August. Colours represent site (orange – Lagunitas 1, pink = Lagunitas 2, green = Olema, blue = San Geronimo, grey = Devil's Gulch).

1.3 Variation in fish growth potential

Using growth potential from foraging in the drift at the head of the pool, growth opportunities during drought were available at different times for some sites, but others did not offer potential for growth from drift foraging. The bioenergetic potential for was highest for Olema Creek in May, but then declined sharply in June and was near zero in July (**Figure 7**). Both sites in Lagunitas Creek were lower in their maximum NREI when compared to Olema Creek, yet remained positive throughout the summer, consistent with the regulated flow regime in Lagunitas Creek. Growth potential peak in one Lagunitas reach (Lagunitas 2) in June before declining to May levels in July, while in the second Lagunitas reach (Lagunitas 1) it was slightly higher in July as compared to June. San Geronimo Creek and Devil's Gulch had zero or negative growth potential the entire summer, likely due to very low velocities in May and flow cessation by July due to extreme drought conditions. In general, growth potential showed similar trends to drift concentration but large differences in magnitude, especially in smaller streams with low velocities, and these two were not highly correlated ($r = 0.13$).

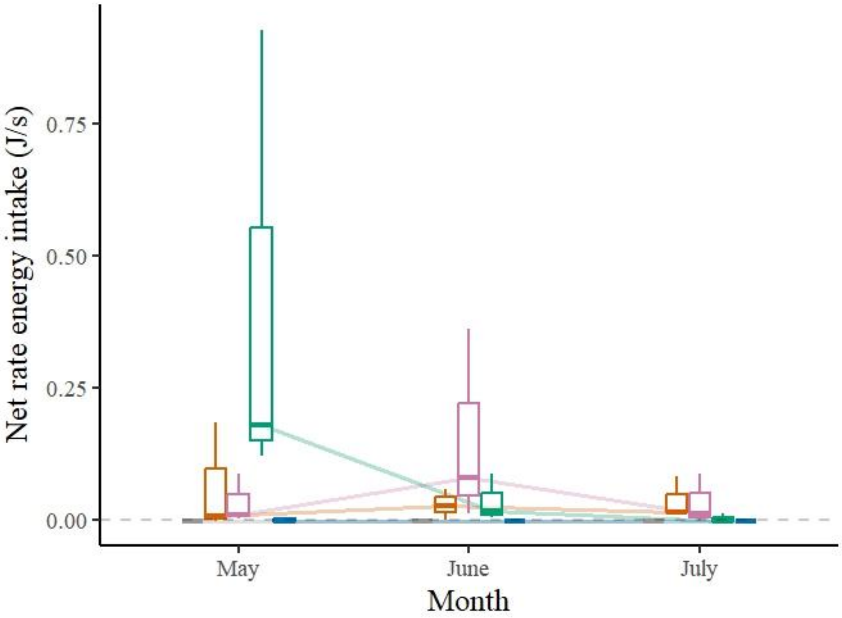


Figure 7 Growth potential, measured as net rate of energy intake, for fish of 60 mm fork length drift foraging at the head of the pool across the spring-summer months. Colours represent site (orange – Lagunitas 1, pink = Lagunitas 2, green = Olema, blue = San Geronimo, grey = Devil's Gulch).

2. *Variety of fish responses to drought within the mosaic*

2.1 Maintenance & decline of fish presence

We assessed fish response to drought and found that following the reduction in connectivity and shifts in where habitat was suitable across the mosaic, fish did not persist in parts of watershed. The results of snorkel surveys revealed a major decline in fish density and abundance in Olema Creek, San Geronimo Creek and Devil's Gulch from May to July (**Figures 8, 9**). In Devil's Gulch, the pool that had the highest density across all sites in May (20 fish/m^3) decreased to a quarter of that density by June and was dry by July (**Table 1**). The other two pools in Devil's Gulch experienced fish declines, and no fish were detected at that site by September even though our other two pools persisted through the summer (**Table S2**). The San Geronimo Creek site also saw steep declines in fish abundance and density, with one pool drying up by September and no fish detected in another by October; however, one pool initially declined in abundance and density before stabilizing despite low DO levels, highlighting pool heterogeneity within a site. While we did not track survival explicitly, low RCT depths in these sites (i.e., little opportunity for dispersal) indicate that fish declines were likely attributed to mortality as fish movement was restricted. In contrast, the Olema Creek site experienced decreases in fish presence but maintained higher RCT depths, thus declines in density may reflect dispersal. Both Lagunitas Creek sites did not show clear trends in abundance and density, but rather remained relatively stable, slightly peaking in June and July, with high RCT depths all summer due to flow regulation, which provided opportunity for dispersal into and out of pools throughout the entire sampling period. Our coarse categorization of fish size suggested fish in the pools were larger by July as compared to May, with most fish in the 40-79 mm range and some >=80 mm by July, except for Devil's Gulch which skewed smaller (**Figure S3**).

2.2 Diversity & shifts in foraging behaviour in response to drought

Drift foraging was the dominant mode of foraging in juvenile coho salmon, but fish foraging behaviour became more varied as drought progressed and the proportion of fish not foraging increased as drought deepened (**Figure 9**). Early in the dry season (June) had the greatest diversity of foraging behaviours across the watershed. Devil's Gulch and San Geronimo Creek pools had a large proportion of fish search foraging in May, with only about a quarter of the observations reflecting drift foraging, but drift foraging was nearly eliminated by June. By July, the few fish remaining were either search foraging or not foraging. Most fish in other sites drift-foraged the entire sampling period, though the proportion of search foraging observations steadily increased across the summer. Larger fish were more likely to feed in the drift, or not forage, and were rarely observed picking the benthos or search foraging (***Supplementary Materials,*** **Figure S4**). Mirroring patterns of foraging mode, the number of foraging attempts in the drift declined over time (**Figure 10**). Strikes at items in the drift were the most common foraging attempt recorded, with surface strikes the second most common method, followed by search foraging and benthic strikes. There were fewer surface strikes overall in July, except for one site in Lagunitas (LAG2), and few benthic and search attempts in all months.

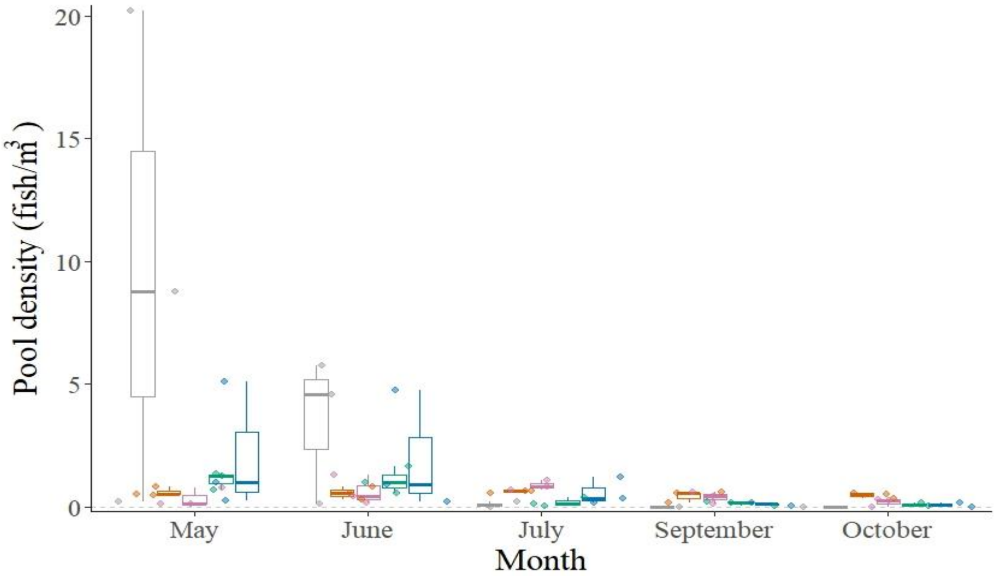


Figure 8 Pool density of juvenile coho salmon from snorkel abundance estimates and pool volume estimates for each sampling time point. Colours represent site (orange – Lagunitas 1, pink = Lagunitas 2, green = Olema, blue = San Geronimo, grey = Devil's Gulch).

In terms of aggression, highest levels of conflict were in May, but the proportion of observations where conflict was recorded did not show a general trend across the summer or by site; some pools where conflict was highest in May declined over time, but other pools with few aggressive events early in the season saw an increase in June and July (**Figure S5A**). Aggressive acts such as chasing or nipping and submissive acts like fleeing did not vary by fish size (**Figure S5B** & ***Supplementary Materials***).

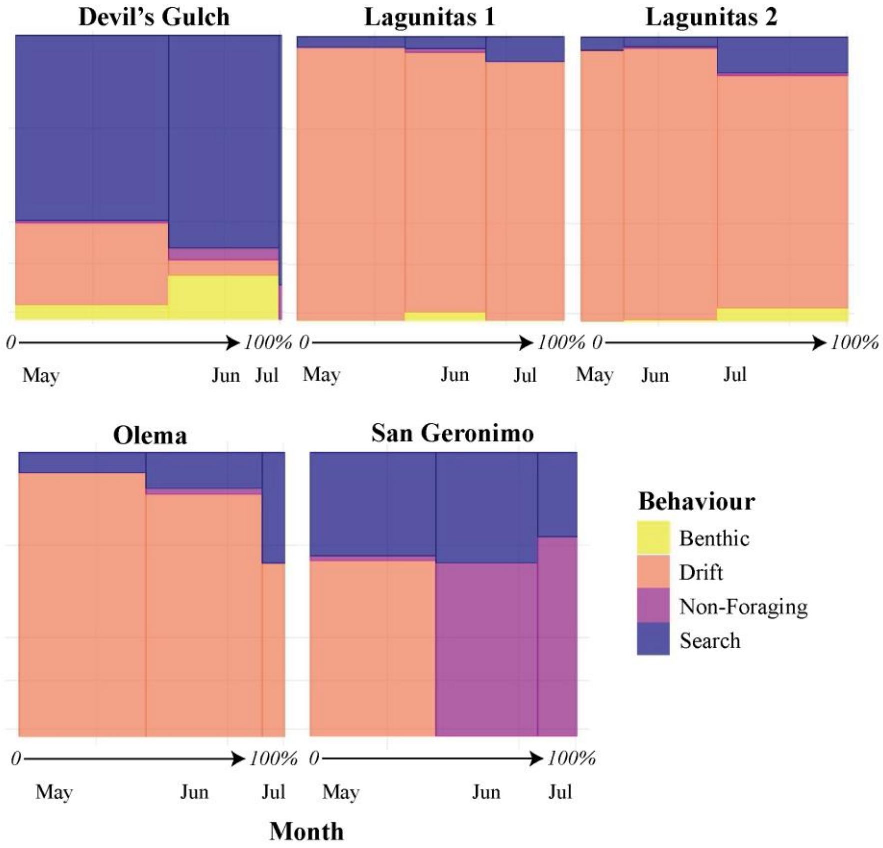


Figure 9 Foraging modes by site (panel) and month (x-axis). Thickness of bars on the x-axis reflects total pool abundance from snorkel surveys in each month. Thickness of each colour on the y-axis is the proportion of fish observations where the behaviour (colours) was displayed.

3. Streamflow recession & prey phenology variation across the mosaic drive fish behaviours

Habitat shifts associated with drought and prey phenology influenced fish in their likelihood to cease foraging or drift forage. When compared to the null model, our full model with predictor variables had a higher expected log predictive density (ELPD = -852.6) and lower leave-one-out information criterion value (LOOIC = 1712.4) resulting in a large increase in model fit and predictive power (ΔELPD = -16.8; ΔSE = 6.6; **Table S1**). In the first decision step, the baseline probability of not foraging was much lower than the probability of foraging (**Table**

2). Increasing RCT depth further decreased the odds of fish not foraging (**Table 2**, **Figure 3**), though no other predictor variables had significant effects on the likelihood of fish not foraging. In the second step, conditional on fish foraging, fish had a high baseline likelihood of drift foraging compared to other foraging types (**Table 2**). The likelihood of drift foraging increased with increasing velocity and drift invertebrate concentration, but decreased with increasing temperature (**Table 2**, **Figure 3**). Density and maximum depth did not significantly influence the likelihood of any behaviour. There was significant variation within all grouping variables (pools, sites, and months), indicating that predictor effects might differ across these groups (**Table 3**). Overall, the model revealed that streamflow recession measured by RCT depth and potentially its associated effects influenced the likelihood of fish to stop foraging, while velocity, temperature, and prey availability influenced the probability of drift foraging vs other foraging behaviours.

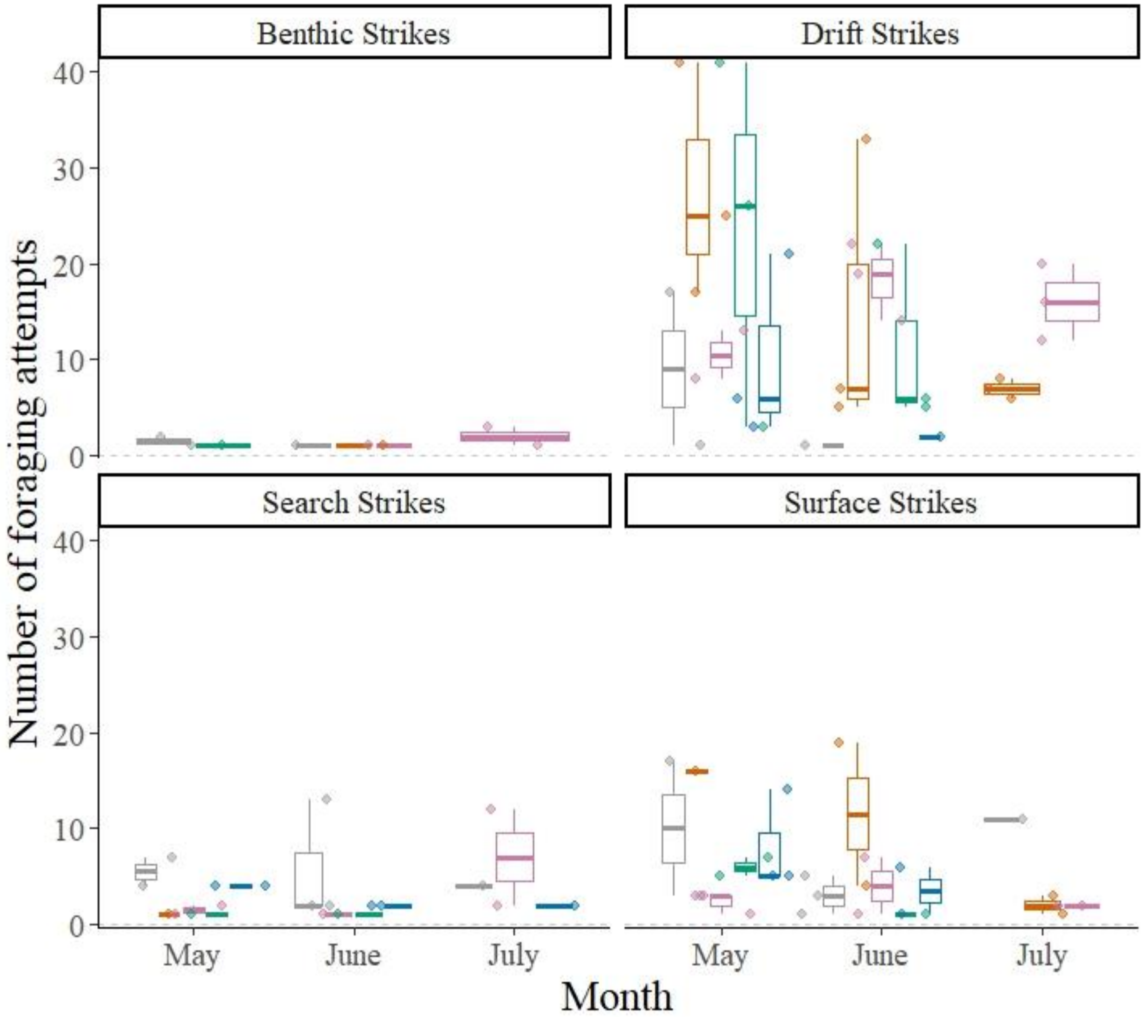


Figure 10 Foraging attempts by type of strike (panel) and month. Strikes were counted as the total number observed across all video samples in a pool. Colours represent site (orange – Lagunitas 1, pink = Lagunitas 2, green = Olema, blue = San Geronimo, grey = Devil’s Gulch).

Table 2: Model regression estimates for behavioural split 1 (Non-foraging vs Foraging) and split 2 (Drift vs Search/Benthic foraging). Estimate is the central tendency and 95% lower and upper credible interval from posterior distribution. Bolded terms are significant with credible intervals not overlapping with zero.

Parameter	Estimate	Estimated Error	95% CI Lower	95% CI Upper
{NF} | {NF, D, SB}				
Intercept	**-12.87**	**6.39**	**-25.8**	**-0.47**
RCT depth	**-0.46**	**0.17**	**-0.87**	**-0.18**
Max depth	1.09	2.76	-4.28	6.48
Mex velocity	1.52	4.38	-6.74	9.98
Temperature	0.74	0.38	-0.01	1.47
Concentration	-1.55	1.66	-5.38	0.98
Density	-0.01	0.11	-0.25	0.2
{D} | {D, SB}				
Intercept	**7.28**	**3.54**	**0.49**	**14.28**
RCT depth	0.08	0.05	-0.01	0.17
Max depth	-1.93	1.99	-5.63	2.23
Mex velocity	**7.49**	**3.4**	**0.72**	**13.94**
Temperature	**-0.53**	**0.2**	**-0.93**	**-0.14**
Concentration	**2.73**	**0.73**	**1.39**	**4.26**
Density	0.07	0.05	-0.02	0.17

Table 3 Model output for variation within grouping variables Month, Site, and pool (Seq) within Site, for each model step (Non-foraging vs Foraging, Drift vs Search/Benthic foraging). Central tendency estimates and lower and upper 95% credible intervals are taken from the posterior distribution.

Random Effect Grouping	Model Level	Intercept SD Estimate	Estimated Error	95% CI Lower	95% CI Upper
Month	*{NF} | {NF, D, SB}*	2.02	1.28	0.58	5.24
	{D} | {D, SB}	1.12	0.92	0.25	3.48
Site	*{NF} | {NF, D, SB}*	1.69	1.23	0.07	4.67
	{D} | {D, SB}	2.35	1.29	0.39	5.55
Site:Seq	*{NF} | {NF, D, SB}*	2.73	1.13	1.1	5.49
	{D} | {D, SB}	1.61	0.53	0.84	2.91

Discussion

Drought can threaten juvenile salmonids by reducing useable habitat and restricting movement within a stream network (Vander Vorste et al. 2020). Our results from a summer of extreme drought in the Lagunitas Creek watershed revealed a partial collapse of the habitat mosaic, with several typically perennial tributaries disconnecting, and two study pools drying completely. Nevertheless, the persisting habitat provided refuge for juvenile coho salmon and offered different foraging and growth opportunities. Overall, we observed a gradient of habitat responses to drought; the largest, regulated-flow stream was least affected by drought and the smallest tributary streams experienced severe streamflow recession along with decreased dissolved oxygen, wetted pool width, and velocity, including shifts from perennial to intermittent flow at two tributaries. Following flow disconnection, fish could not disperse. Deteriorating conditions across the summer in disconnected pools increased the likelihood of fish ceasing to forage and potentially elevating mortality. Among flowing sites, the timing and magnitude of macroinvertebrate availability in the drift varied, with different pool habitats peaking in May, June and July, emphasizing different food web phenology even during drought conditions. Within and between habitats, fish showed a diversity of behaviours beyond the dominant mode of drift foraging to exploit different resources as streamflow and drift receded and water temperatures increased. The result of these diverse responses to drought was survival for fish in a large part of the watershed. Additionally, multiple life history pathways for fish were still available despite the stressors of drought, with the potential to grow at different rates based on foraging mode, habitat conditions, and dispersal abilities to track resources pulses.

Reduced mosaic and connectivity lead to ecological traps & refuges in drought

Extreme drought collapsed part of the habitat mosaic and led to shifts in the mosaic in where suitable habitat could be found. The discrepancy in stream habitat changes throughout the summer largely stemmed from the regulated-flow mainstem sites and unregulated-flow tributary sites. There were no noticeable habitat changes in Lagunitas Creek habitats besides small shifts towards higher temperatures and lower pool depths, likely because of mandated minimum flows implemented June 16th maintaining suitable over-summer habitats for juvenile coho salmon even during extreme drought.

In contrast, all tributary sites followed a similar pattern of streamflow recession as drought progressed, where a decrease in RCT depth was correlated with declines in DO, pool width, and velocity, but the timing and magnitude of these changes varied by site and even within sites. Fine-scale heterogeneity and geomorphic controls at the reach scale can lead to different drying trajectories (Stoelzle et al. 2014; Moidu et al. 2021), as well as variation in DO levels in isolated pools that determine survival for coho salmon (Woelfle-Erskine et al. 2017; Larsen & Woelfle-Erskine 2018). Indeed, within Devil’s Gulch and San Geronimo Creek sites, sampled pools displayed heterogeneity in effects of disconnection, ranging from pools drying to maintaining adequate habitat for fish the entire sampling period. Additionally, the rate of streamflow recession and timing of disconnection of pools can be critical for fish survival (Hwan et al. 2018; Rossi et al. 2023). For example, when DO started declining in parts of Olema Creek, sustained connectivity between pools meant that fish had the ability to disperse to more suitable habitat, while in Devil’s Gulch dispersal was already restricted in early May shortly after emergence, trapping fish in pools that became unfavourable for foraging and, ultimately, unsuitable. Intermittent habitats can be productive for juvenile salmon (Wigington et al. 2006; Hwan et al. 2018; Rossi et al. 2022), yet in our system, most isolated pools were unable to support salmon during extreme drought. Moreover, the observed early disconnection in the perennial Devil’s Gulch and rarely intermittent San Geronimo Creek (E. Ettlinger, personal communication, August 16, 2021) are in line with the concerning trend of earlier and increased intermittency in free-flowing streams in Mediterranean climates (Carlson et al. 2024).

Reduced mosaic supports variation in foraging opportunities for fish

Despite disconnection and habitat collapse in parts of the watershed, variation in food web phenology (Rossi et al. 2022) across sites led to a variation in growth opportunities from early spring to early summer moving from small to large streams. Prey concentration in the drift at the head of the pool was highest in May and decreased across the summer months in San Geronimo Creek and Olema Creek pools, while drift productivity peaked later (June) in the mainstem Lagunitas Creek. Fish responded to drift prey availability by drift foraging; even at low velocities and prey concentrations, fish continued to drift forage, signally the strong behavioural preference (Fausch 1984). High prey concentration may not relate to high quality though, for example the bulk of the biomass in a pool in Lagunitas (Lagunitas 1) in May was made up of invasive mud snails that have little energetic benefits to fish. This could be a concern if the snails are outcompeting other favourable drift invertebrates. When velocity and prey decreased significantly and temperatures rose, fish were more likely to use other foraging behaviours like search and benthic foraging (Fausch et al. 1997; Nislow et al. 1998; Nakano et al. 1999). Non-drift foraging allowed them to potentially exploit alternative resources bases from infall and the benthos and diversify their diet (Nielsen 1992a; Nakano & Furukawa-Tanaka 1994; Spaulding 2016). Interestingly, competition as measured by fish density in our study did not influence the likelihood of fish to drift forage (Nielsen 1992; Nakano et al. 1999). This could be because in pools where fish could disperse, they may have emigrated to find better foraging opportunities and avoid competition (Fausch et al. 1997) and where density was highest and fish could not leave, prey concentration was already suppressed and velocity was already minimal, decreasing the likelihood of fish drift foraging and thus outweighing any effects of competition (Grant & Noakes 1987).

The interactions between hydraulic habitat changes and prey phenology led to variable growth opportunities across the watershed, as measured by growth potential from foraging in the drift at the head of the pool (see Methods). Growth potential was dependent on stream and location within the stream, showing seasonal pulses within a stream (Kaylor et al. 2021). Growth potential as we measured it is representative of a single point in time in the pool and as such, does not capture the entire range of NREI across the pool. Nevertheless, it can give us a proxy for growth rates for drift foraging fish across the watershed (Kaylor et al. 2021; Rossi et al. 2022). NREI estimates from our sites concur with those found in other coastal California streams for steelhead trout (Rossi et al. 2021b, 2022), and are slightly lower than reported values for large steelhead trout in interior California streams (Caldwell et al. 2018). Sites with lower growth potential in the drift and negative NREI still supported active foraging and growth (as suggested by increasing body length through time), providing some support for growth in disconnected pools – to a point. Thus, while growth potential of salmonids from drift foraging has had much attention, energetic costs of other foraging behaviours should not be overlooked as they can contribute important energy pathways supporting fish growth that may especially important in the dry season with reduced flows and drift (Harvey & Railsback 2014). More work needs to be done to estimate costs of more active swimming and burst swimming associated with bioenergetic costs of non-drift foraging, as well as to account for different resource bases fish are leveraging for growth. Nevertheless, these differential peaks in the timing and magnitude of growth potential suggest that a mosaic of habitats relates to variation in growth trajectories across the watershed.

Potential diversity of life history pathways within reduced mosaic

When considering the spatiotemporal variation in habitat, growth potential, and behaviour together, we hypothesize that the habitat mosaic supports multiple life history outcomes based on variation in connectivity, food web phenology, and growth rates linked to fish foraging behaviour and pool position (Fausch 1984; Puckett & Dill 1985; Nielsen 1992a; Nakano 1995; Rosenfeld & Raeburn 2009). For example, rapid growth in sites with early food web phenology enables fish to reach larger sizes in the spring and potentially emigrate – if connectivity allows – once drift opportunities decline. With early growth, fish are well suited to move elsewhere in the watershed to rear and grow in non-natal habitats such as other streams (e.g., into Lagunitas Creek), downstream wetlands, or the estuary, capitalizing on varying resource pulses (Weybright & Giannico 2018). Other fish will stay in their natal habitat the entire summer, either because conditions are suitable, as we found in Lagunitas Creek, or because of disconnection inhibiting dispersal as in Devil's Gulch and San Geronimo Creek. Differences in behaviour and associated growth rates especially can translate into meaningful life history variation (Metcalfe 1998), influencing emigration time to the ocean (Metcalfe et al. 1988), anadromy in salmonids with flexible life histories (Railsback et al. 2014), and the probability of males returning early from the ocean (Watters et al. 2003; Bacon et al. 2005). Furthermore, behavioural strategies of dispersal into diverse habitats contribute to returning spawners; (Walsworth et al. 2015) found that successful adults used a mosaic of habitats as juveniles, including ones with lower productivity. Therefore, maintaining a wide array of habitats that foster variation in behaviour and growth is critical for promoting life history diversity that supports population stability and resilience (Schindler et al. 2010; Brennan et al. 2019).

Overall, extreme drought limited the growth portfolio through reduced connectivity between habitats and rendering multiple life history trajectories unrealized via mortality events. In wet years when connectivity between streams persists throughout the dry season, there are likely more life history trajectories unlocked as fish move through the network to exploit spatial and temporal variation in productivity (Rossi et al. 2024) and avoid impacts of competition. Yet, drought also presents unique opportunities for observing growth pathways that may present successful strategies for coping with drought (Cordoleani et al. 2021). When fish get trapped in isolated pools that maintain suitable conditions, they may hold over another year and outmigrate a year later than most of the cohort, thus contributing to age complexity and resilience. In fact, we observed 1-year old coho salmon in Devil's Gulch in 2021 outside of our study pools that had survived through the dry season (i.e., through our last sampling event in October; Ryan, unpublished data). However, multi-year droughts may decrease resilience of juvenile salmonids as stressors intensify and habitat remains restricted (Bêche et al. 2009), a cause for concern with increasing drought risk in California (Diffenbaugh et al. 2015).

Conclusion

A reduced habitat mosaic supported population persistence during drought and maintained opportunities for life history diversity that buffer against subsequent environmental challenges at other life stages. We hypothesize that habitats that responded poorly to drought will play large roles in population diversity and returns under non-drought years. Thus, a connected mosaic of habitats for all life stages of salmon is important for resilience to increasing climate variability, including extremes drought and flood years.

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Supplementary Materials

Physical Habitat Sampling

In May we characterized habitat complexity and cover for fish in each pool. We measured canopy cover at the head and mid-point of the pool using the Canopeo app (Patrignani & Ochsner 2015) and averaged these values to find the mean canopy cover over the pool. We used a semi-quantitative assessment of instream shelter that considers large woody debris, undercut banks, boulders, small woody debris as well as a semi-quantitative inventory of large woody debris based on binned size classes (California Salmonid Stream Habitat Restoration Manual 2002). We then combined these metrics with the baseline metrics described in the main text (temperature, riffle depth, dissolved oxygen, pool volume, velocity) to generate a Principal Components Analysis as a method of further describing habitat differences by site and pool. We also created a PCA extending the May-July pool habitat analysis to October, using the same methods as described in the main text and adding in September and October sampling points.

In the May PCA incorporating habitat structure, San Geronimo Creek appears to be more like Olema Creek, highlighting how habitat complexity differed at the beginning of the season, but did not buffer against drought changes (***Figure S1***). Patterns in habitat changes by site hold when extending the PCA with the September and October data with the Devil's Gulch and San Geronimo cluster becoming more pronounced as DO dropped further (***Figure S2***).

Inputs to BioenergeticsHSC

We used the "batch model" mode in the software to input data from each pool for May, June, July (Naman et al. 2020). Fish size was estimated using the most common lengths observed snorkeling and in videos (40-80 mm, binned by 10 mm) and established length-mass relationships (Duffy 2005). Depth and velocity were taken from the camera deployment at the head of the pool. Macroinvertebrate concentration was inputted according to the software manual specifications and examples, where invertebrates were inputted by family or lowest taxonomic classification in 1 mm length bins with drift density, and *a* and *b* values for the length-mass regression equation for that invertebrate. For model presents, we used a fish focal depth of 0.5 with the coho salmon swimming cost model (Trudel & Welch 2005) and the assumptions of steady swimming, prey detection capability of 1 and reaction distance multiplier of 1. We optimized fish diet by dropping energetically wasteful prey types.

Fish fork length and behaviour relationships

We estimated fish length into size classes while snorkeling (***Figure S3***). In addition, we measured fish fork length using the program VidSync, allowing us to assess associations between fish behaviour and size. A caveat to this analysis is that video sampling could not identify individuals, thus there is the potential for pseudoreplication of individual fish of a certain length that may skew associations with behaviour. We ran a one-way analysis of variance (ANOVA) to test if fork length differed by aggressive behaviour (chase, nip, flee) and a second ANOVA to test if length differed between foraging/non-foraging modes (drift, search, benthic, non-foraging). Fish length did not differ between acts of aggression (***Figure S4***; F(2, 25) =

1.479, p = 0.25), but it did significantly differ by foraging mode, where larger fish were more likely to be observed drift foraging or not foraging, and smaller fish were associated with benthic and search foraging (***Figure S5***; F(3,351) = 13.42, p < 0.001).

Conditional logistic regression mixed model

The full model equation for the best model (described in the main text) with all predictor variables:

$$\begin{aligned} logit\left(\varphi_{\{NF\}|\{NF,D,SB\}_{ijk}}\right) &= \beta_{0,\{NF\}|\{NF,D,SB\}} + \beta_{1,\{NF\}|\{NF,D,SB\}} \cdot \text{RCTdepth}_{ijk} + \beta_{2,\{NF\}|\{NF,D,SB\}} \cdot \text{Max velocity}_{ijk} \\ &+ \beta_{3,\{NF\}|\{NF,D,SB\}} \cdot \text{Temperature}_{ijk} + \beta_{4,\{NF\}|\{NF,D,SB\}} \cdot \text{Prey concentration}_{ijk} \\ &+ \beta_{5,\{NF\}|\{NF,D,SB\}} \cdot \text{Pool density}_{ijk} + u_{ij} + u_j + b_k \end{aligned}$$

$$\begin{aligned} logit\left(\varphi_{\{D\}|\{D,SB\}_{ijk}}\right) &= \beta_{0,\{D\}|\{D,SB\}} + \beta_{1,\{D\}|\{D,SB\}} \cdot \text{RCTdepth}_{ijk} + \beta_{2,\{D\}|\{D,SB\}} \cdot \text{Max velocity}_{ijk} \\ &+ \beta_{3,\{D\}|\{D,SB\}} \cdot \text{Temperature}_{ijk} + \beta_{4,\{D\}|\{D,SB\}} \cdot \text{Prey concentration}_{ijk} + \beta_{5,\{D\}|\{D,SB\}} \\ &\cdot \text{Pool density}_{ijk} + u_{ij} + u_j + b_k \end{aligned}$$

We ran multiple, modified versions of the conditional logistic regression mixed model predicting conditional probabilities of fish behaviour that had performance issues. First, in testing our hypotheses about habitat changes, we first tried to account for correlated effects of habitat predictor variables using the scores from our May-July habitat PCA for PC1 (streamflow-recession related) and PC2 (less related to recession) in combination with drift invertebrate concentration and fish density. However, these models had divergence issues and were unreliable (**Table S1**). We also tested how growth potential may drive variation in foraging behaviour using NREI instead of prey concentration for the full habitat variable model presented in the main text, as well as the reduced habitat model using the PCA results, but these models again performed poorly and had convergence issues.

Tables

Table S1 Model comparison of the conditional logistic regression mixed model of conditional behavioural probabilities using different predictors. Model comparison was done using the leave-one-out cross-validation method. ELPD is the expected log predictive density, with higher values indicating better predictive performance, p_loo is the effective number of parameters in the model, LOOIC is the leave-one-out information criterion, with lower values indicating better model performance. The top model as indicated by the lowest LOOIC and highest ELPD (ΔELPD = 0) and correct model fit is bolded. If the difference in ELPD or LOOIC between models is greater than 2 times the standard error difference (ΔSE), then the difference is considered significant. The top model can be compared with the null model to show improvement in model fit and predictive power when incorporating predictor variables.

Model Predictors *Assume random effects structure of (1|Site/Seq) + (1|Month) for all*	**ELPD**	**p_loo**	**LOOIC**	**ΔELPD**	**ΔSE**
RCT depth + max depth + max velocity + temperature + concentration + density	**-856.2**	**37.7**	**1712.4**	**0**	**0**
* PC1 + PC2 + concentration + density	-865.2	36.6	1730.5	-9.0	3.1
* RCT depth + max depth + max velocity + temperature + NREI + density	-865.4	37.1	1730.9	-9.2	5.1
NULL	-873.0	26.2	1746.0	-16.8	6.6
* PC1 + PC2 + NREI + density	-876.8	37.1	1753.5	-20.6	5.8

* Issues with model fit (divergent transitions present), interpret with caution

Table S2 Field data collection from May to October for each Site and pool (Seq), including water quality metrics (dissolved oxygen, temperature), physical habitat structure (velocity, riffle crest depth, depth and width of pool) and fish response (abundance, density). Density was calculated by dividing fish abundance by multiplying maximum depth, median width, and pool length to pool volume.

Site	**Seq**	**Month**	**Dissolved Oxygen (mg/L)**	**Temperature (°C)**	**Maximum Velocity (m/s)**	**Riffle Crest Thalweg Depth (cm)**	**Maximum Depth (m)**	**Median Width (m)**	**Fish Abundance**	**Fish Density (fish/m^3)**
DG	1	May	8.5	13	0	4	0.4	2.6	67	8.75
DG	1	Jun	4.4	13.4	0	5	0.4	4.4	56	4.6
DG	1	Jul	0.8	14.3	0	0	0.2	1.9	0	0
DG	1	Sept	2	14.5	0	0	0.1	2.8	0	0
DG	1	Oct	0.3	11.8	0	0	0.4	1.7	0	0
DG	2	May	7	10.8	0.02	2.5	0.8	3.9	4	0.23
DG	2	Jun	4.8	13.2	0	2	0.8	3.9	2	0.12
DG	2	Jul	1.2	14.4	0	0	0.6	3.4	2	0.19
DG	2	Sept	1.2	14.4	0	0	0.3	2.4	0	0
DG	2	Oct	1.1	12.4	0	0	0.4	2.3	0	0
DG	3	May	8.7	12.9	0	3	0.3	2.8	92	20.21
DG	3	Jun	7.2	13.7	0	2	0.3	2.2	20	5.77
LAG1	1	May	10.6	13.6	0.4	17	0.9	7.8	103	0.48
LAG1	1	Jun	9.8	15.2	0.26	15	0.8	6.8	49	0.28
LAG1	1	Jul	9.7	17.8	0.22	17.8	0.8	5	65	0.55
LAG1	1	Sept	9.7	16.5	0.16	15	0.8	6.7	26	0.16

LAG1	1	Oct	10.2	14.2	0.2	15	0.8	6.5	55	0.36
LAG1	2	May	10.6	13.9	0.31	13	0.5	7.2	35	0.52
LAG1	2	Jun	10	15.2	0.35	14	0.5	6.2	33	0.55
LAG1	2	Jul	9.8	17.7	0.31	17.7	0.6	6.4	40	0.63
LAG1	2	Sept	9.6	16.7	0.3	13	0.5	6.5	39	0.62
LAG1	2	Oct	10.1	14.1	0.26	13	0.5	6.5	34	0.58
LAG1	3	May	10.4	14.1	0.16	21	0.7	6.7	140	0.8
LAG1	3	Jun	10	15.6	0.14	19	0.6	7.1	128	0.84
LAG1	3	Jul	9.9	17.4	0.22	7.6	0.6	6.3	99	0.67
LAG1	3	Sept	9.5	16.7	0.09	16	0.6	7.1	82	0.55
LAG1	3	Oct	10	14.1	0.2	17	0.5	7.3	73	0.52
LAG2	1	May	10.8	13.5	0.34	18	0.7	7.3	42	0.79
LAG2	1	Jun	10.2	15.2	0.3	9	0.7	6.2	60	1.3
LAG2	1	Jul	10	16.1	0.26	16	0.6	5.7	38	1.08
LAG2	1	Sept	9.2	17.9	0.41	16	0.6	7.2	21	0.42
LAG2	1	Oct	9.5	14.8	0.37	18	0.6	6.7	12	0.27
LAG2	2	May	11	12.8	0.17	25	0.9	9.2	40	0.14
LAG2	2	Jun	10.2	14.9	0.17	23	1	8.9	127	0.43
LAG2	2	Jul	9.9	16.7	0.1	20	0.9	8.2	173	0.68
LAG2	2	Sept	9.3	17.7	0.1	20	0.9	9.1	42	0.14
LAG2	2	Oct	9.4	14.9	0.17	23	0.9	8.7	4	0.01
LAG2	3	May	11.1	12.6	0.2	24	0.6	6.6	10	0.11
LAG2	3	Jun	10.1	14.4	0.19	20	0.6	6.5	13	0.16
LAG2	3	Jul	9.8	15.7	0.11	18.5	0.5	6.7	67	0.84
LAG2	3	Sept	8.8	17.6	0.17	20	0.5	6.4	48	0.62
LAG2	3	Oct	9.3	15.5	0.2	20	0.5	6.1	23	0.31
OL	1	May	8.6	16	0.06	6	0.4	4.7	31	1.36
OL	1	Jun	7.8	17.2	0	5	0.3	4.8	34	1.64
OL	1	Jul	6	15.7	0	4	0.3	4.5	2	0.11
OL	1	Sept	6.1	16.1	0	6	0.3	4.6	4	0.19
OL	1	Oct	7.3	10.3	0	3	0.3	4.3	3	0.16
OL	2	May	8.9	15.4	0.07	7	0.7	3.5	38	0.69
OL	2	Jun	8.7	14.2	0.02	7	0.7	4.1	32	0.54
OL	2	Jul	6.3	15.5	0	9	0.7	4.6	2	0.03
OL	2	Sept	6.2	16.3	0	9	0.6	3.6	2	0.04
OL	2	Oct	6.9	10.3	0	4	0.6	3.7	2	0.04
OL	3	May	8.7	13.8	0.14	12	0.6	4.1	56	1.26
OL	3	Jun	8	14.9	0.08	11	0.7	3.9	49	1.01
OL	3	Jul	5.3	15.5	0	9	0.7	3.7	19	0.4
OL	3	Sept	6.1	15.8	0	8	0.7	4.8	11	0.19
SG	1	May	8.7	12	0.07	5.5	0.3	2.9	36	5.08
SG	1	Jun	7.9	14.8	0.02	4.5	0.3	2.9	34	4.75
SG	1	Jul	2.1	15.3	0	0	0.2	1.9	4	1.2
SG	2	May	8.3	12	0.03	8	0.7	5.4	153	0.99

SG	2	Jun	4.5	13.8	0.04	6	0.7	4.4	116	0.92
SG	2	Jul	1.2	14.3	0	0	0.7	4.4	44	0.36
SG	2	Sept	1	14.3	0	0	0.6	4	3	0.03
SG	2	Oct	0.4	9.3	0	0	0.6	4.3	0	0
SG	3	May	8.6	11.8	0.14	7	0.7	3.8	39	0.24
SG	3	Jun	7.2	14.8	0.06	4.5	0.8	4.3	37	0.2
SG	3	Jul	2.6	14.6	0	0	0.7	3.3	23	0.17
SG	3	Sept	2.7	14.4	0	0	0.6	3.9	23	0.18
SG	3	Oct	1.8	10.1	0	0	0.6	4.5	10	0.16

Figures

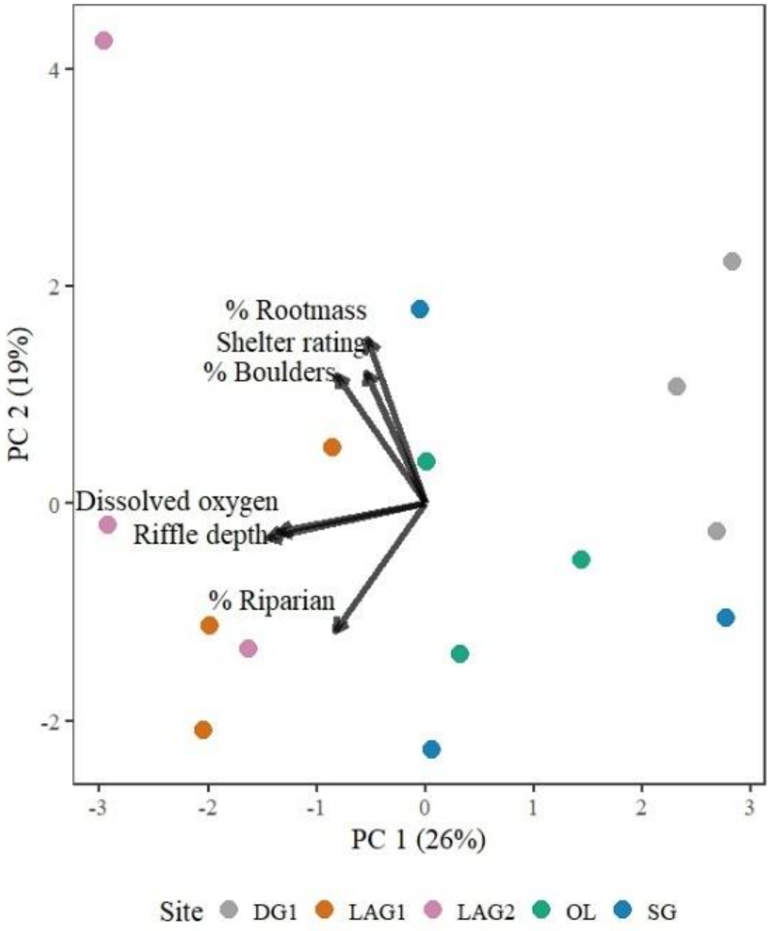

Figure S1 Principal Components Analysis of habitat structure and complexity metrics for each pool at the start of sampling in May. Each point is a pool, colour-coded by site. Arrows show significant habitat complexity metrics that explain variation.

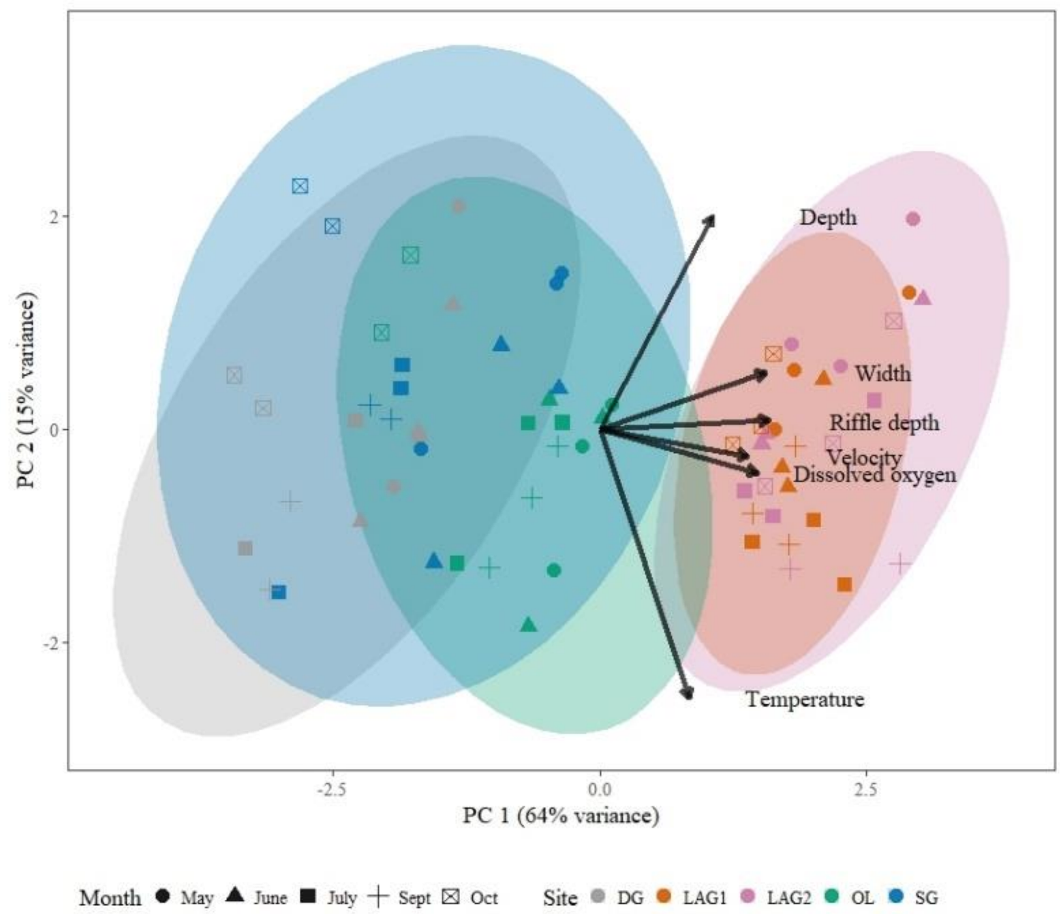

Figure S2 Principal Components Analysis of changing habitat variables in each pool from May to October. Points are pools, colour-coded by site, with 95% ellipses in shaded colours. Point shapes represent different months of sampling. Arrows indicate the weighting of habitat variables on each principal component axis.

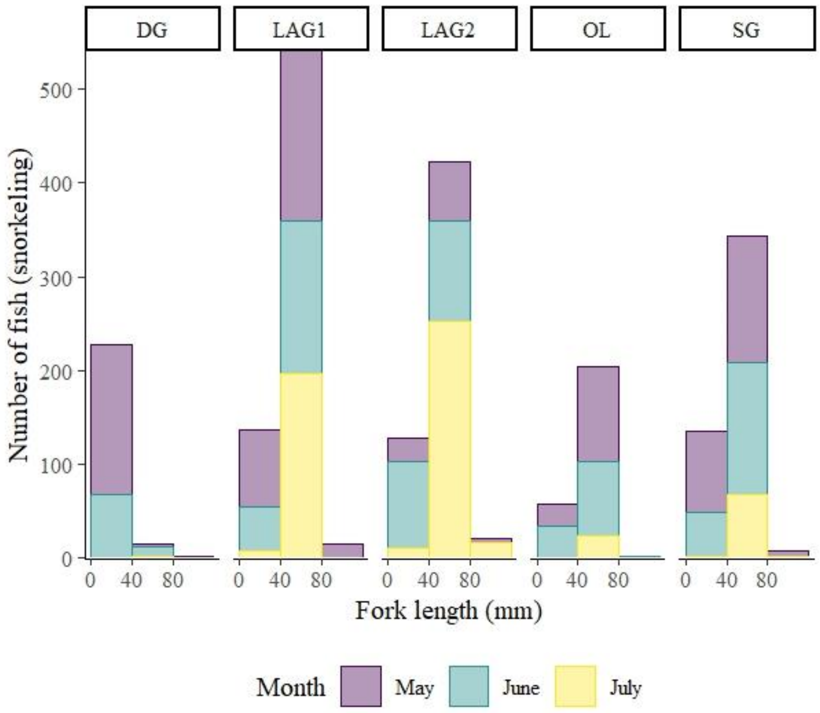

Figure S3 Distribution of coho salmon fork length from snorkel surveys in May, June and July, summed across pools in each site.

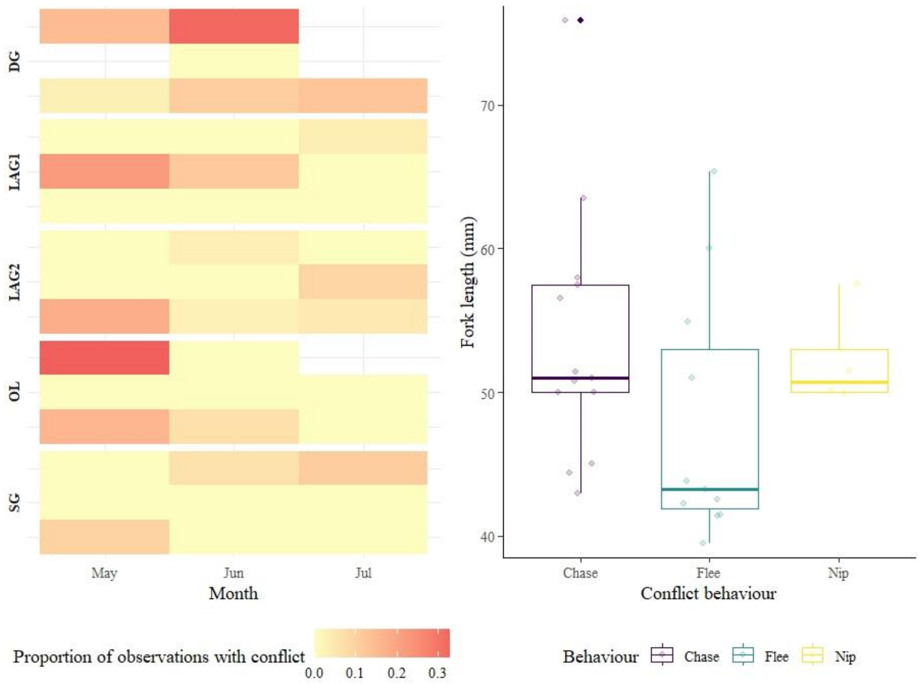

Figure S4 Conflict events recorded by coho salmon in underwater video sampling. *Left panel:* the proportion of all fish observations where conflict was observed in each sampling month, with darker colours indicating a high proportion. *Right panel:* the measured fork length of coho salmon exhibiting one of three recorded conflict behaviours.

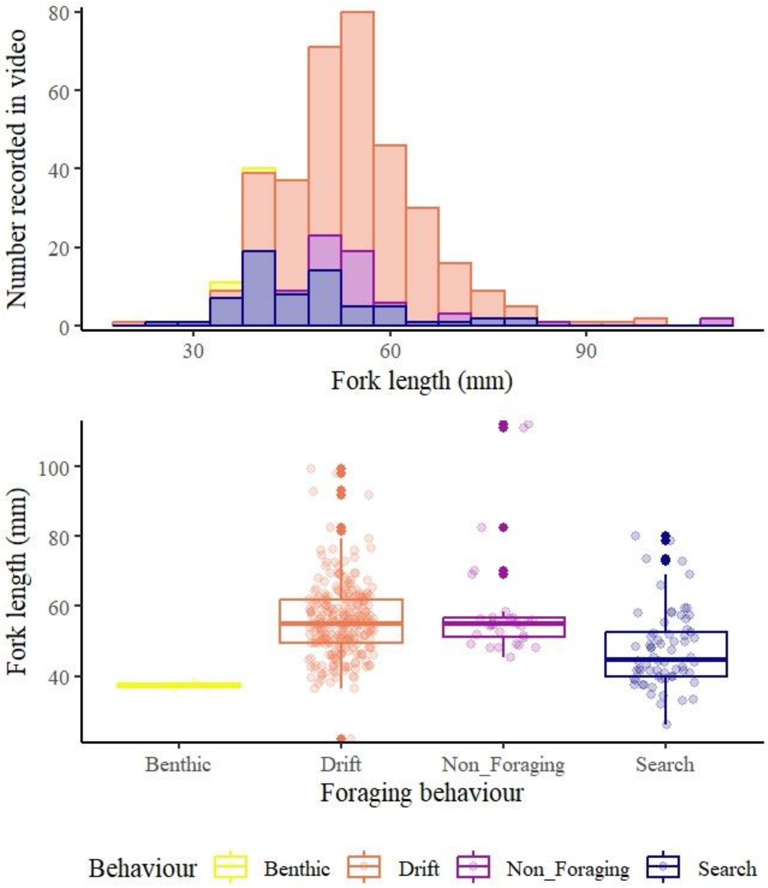

Figure S5 Relationships between coho salmon fork length and foraging behaviour. Top panel: distribution of all fish fork length measurements, colour-coded by foraging behaviour. Bottom panel: box and whisker plot of fork length distributions within each foraging behaviour. The box represents the interquartile range (IQR), which contains the middle 50% of the data. The line inside the box denotes the median value. The "whiskers" extend from the box to the smallest and largest values within 1.5 times the IQR from the lower and upper quartiles, respectively. Points are observed raw data.

Chapter 2

Synchronous juvenile dynamics in an endangered salmon population complex signals vulnerability to extirpation in wake of increasing environmental variation

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Abstract

Asynchrony among fish subpopulations is well known to stabilize, and confer resilience to, large population complexes. However, it is poorly understood if asynchronous dynamics are also important in small populations, which are often highly vulnerable to environmental change and disturbance. Here, we examined time series of juvenile coho salmon in central California to assess variation in juvenile densities across subpopulations and responses to stream flow characteristics. Using 18 years of fish and flow monitoring data across five streams in the region, we found that despite spatial variation in physical watershed characteristics and juvenile densities across streams, subpopulations were highly synchronized over time. Subpopulations in tributary streams were the least stable over time, with high interannual fluctuations in density, while the subpopulation in the largest stream was the most stable. Multivariate autoregressive state-space (MARSS) models revealed that across the metapopulation, adult returns were positively associated with higher juvenile densities, whereas higher flow in the wet, spring, and dry seasons somewhat depressed densities. Adult returns and wet-spring season flow also had slight effects on synchronizing density dynamics across the region. Nevertheless, a substantial portion of the variation remained unexplained, indicating that other biotic and abiotic drivers control population dynamics. The high degree of synchrony in juvenile densities among subpopulations, combined with strong interannual fluctuations, leaves the regional metapopulation vulnerable to collapse due to disturbance, as declines in multiple subpopulations are likely to occur concurrently in response to environmental extremes. Yet, the more stable larger subpopulation may act as a buffer against complete collapse. Our findings underscore the critical need to understand the spatial patterns and drivers of population diversity, even in small, endangered complexes, to anticipate and promote resilience in the face of environmental change.

Introduction

Ensuring the persistence and recovery of endangered species is an urgent conservation challenge, especially in a changing climate. Small, declining populations of endangered species are particularly vulnerable to stochastic environmental disturbance because their higher variability in population dynamics leaves less demographic buffer to withstand large mortality events, thereby reducing recovery capacity and increasing extinction risk (Belovsky et al. 1994; Lande 1998; Lacy 2000). While tools such as population viability analyses predict trajectories of endangered species populations (Menges 1992; Brook et al. 2000; Maschinski et al. 2006; Zambrano et al. 2007), they often overlook elements of population diversity, which can have important effects on extinction risk. Population diversity – the variation in traits and dynamics of subpopulations distributed across a heterogenous landscape – is now recognized as a key ingredient for stability and resilience of large population complexes (Hilborn et al. 2003; Schindler et al. 2010; Des Roches et al. 2021). Metapopulations have been shown to have greater stability on aggregate if subpopulations exhibit asynchronous dynamics in response to environmental variation (Hilborn et al. 2003; Schindler et al. 2015). Yet, the extent to which population diversity is expressed and provides stabilizing effects in small, endangered populations is unclear.

A primary mechanism for generating population diversity is through the filtering of regional climatic forces by heterogeneous habitats across a landscape that produce differences in the local environmental conditions experienced by organisms (Oliver et al. 2010; Brennan et al. 2019). However, significant habitat loss has often restricted endangered species to small, highly fragmented areas (Belovsky et al. 1994; Kerr & Deguise 2004) and it remains an open question whether these critical habitats can support the processes that give rise to population diversity. Some evidence does suggest that even small-scale spatial variation can promote ecological stability by desynchronizing population dynamics, including in heterogeneous meadow patches (Abbott et al. 2017), coral reefs (Srednick et al. 2023), estuaries (Colombano et al. 2022), intertidal zones (Denny et al. 2011) and branching stream networks (Kovach et al. 2018; Terui et al. 2018; Valentine 2023).

Understanding the degree of synchrony within endangered species populations, and the extent to which existing habitat may be suppressing (or enhancing) such dynamics, is important for assessing their extinction risk and informing conservation (Stowe et al. 2020). Analysis of long-term, time series data can help reveal levels of synchrony amongst spatially distinct subpopulations (Ward et al. 2010; Tolimieri et al. 2017; Stowe et al. 2020), as well as uncover how local and regional environmental conditions influence synchrony (Ruhí et al. 2015; Greenville et al. 2016; Ruhi et al. 2018).

Pacific salmon (*Oncorhynchus* spp.) are an ideal model to investigate the relationships between population diversity and stability. Salmon are known to have high levels of intraspecific diversity (Quinn 2018), primarily driven by use of heterogeneous habitats across the landscape (e.g., Lisi et al. 2013; Walsworth et al. 2015; Braun et al. 2016). However, habitat transformation has resulted in the loss of population diversity, thereby increasing the synchrony of subpopulations, and making salmon population complexes more sensitive to environmental stochasticity (Moore et al. 2010; Carlson & Satterthwaite 2011). This is especially pressing at the southern edge of their range in California, where habitat loss and modification have driven the collapse of most Pacific salmon populations (McClure et al. 2008; Munsch et al. 2022), resulting in 14 of 30 species complexes (47%) now listed under the federal or state Endangered Species Act (Katz et al. 2013). The capacity of these imperiled species to withstand future environmental change is not well understood, but likely depends in part on whether the reduced, extant habitats in which these severely depleted salmon populations inhabit can generate aspects of population diversity that bolster resilience.

Stream flow is an important component of environmental variation that structures salmon populations. Salmon are particularly sensitive to flow conditions during their early life stages, from winter incubation and emergence to over-summer rearing. Flows during the early life stages affect the distribution of juvenile salmon across the watershed, promoting or inhibiting dispersal to non-natal habitats (Hartman et al. 1982; Kahler et al. 2001; Zimmerman et al. 2018), as well as their outmigration to the ocean as smolts (Kastl et al. 2022). Extreme high or low flows can also cause significant mortality in juvenile salmon (Montgomery et al. 1996; Greene et al. 2005; Obedzinski et al. 2018; Vander Vorste et al. 2020). Furthermore, extreme hydrologic events, such as droughts and floods, that operate at regional scales can homogenize environmental conditions across a landscape (Cline et al. 2020), thereby synchronizing populations and further undermining their stability (Kovach et al. 2013). Both drought and floods are increasing in frequency in California as a consequence of climate change (Swain et al. 2016, 2018), likely placing small, endangered populations of salmon further at risk .

Given ongoing and future climate challenges for endangered California salmon and the need for resilient populations, we addressed the question of whether diversity can be expressed in the most vulnerable salmon populations. Here, we evaluated the population dynamics of endangered Central California Coast (CCC) coho salmon *(O. kisutch)*, located at the southern end of the species' range, using 18 years (2005-2022) of monitoring data from small coastal watersheds in Marin County, California. Taking advantage of the historical, long-term biomonitoring data than spanned significant annual variation in hydrological conditions and multivariate autoregressive state-space (MARSS) modeling methods, we sought to characterize juvenile salmon subpopulation dynamics within the region and how spatial and temporal variation in juvenile densities was affected by local breeding and hydrologic conditions. Specifically, we 1) characterized population diversity as defined by spatial and temporal patterns in juvenile density amongst streams; 2) examined spatial and temporal patterns in environmental conditions amongst streams, including breeding success and median and extreme (high and low) winter, spring, and dry season flows; 3) quantified how these environmental factors influence density dynamics. In a regional system of small watersheds (<300km^2 total drainage) and a reduced salmon population, our baseline expectation was minimal population diversity, with strong synchrony in juvenile density subpopulation dynamics ("juvenile synchrony"). We assumed this would reflect little evidence of streams filtering regional climate conditions; we predicted breeding success and flow conditions to show synchrony across the region ("environmental synchrony"), especially extreme flows (e.g., peak wet season flows) that further homogenize habitats. Finally, in testing which environmental conditions explain density dynamics, we hypothesized that higher breeding success would increase juvenile densities (via egg production), higher median flows would suppress (via dispersal) or enhance (via survival) densities, and high (wet-spring seasons) or low (dry season) extreme flow conditions would have the largest effects on reducing and further synchronizing densities across streams through large mortality events. While our null hypothesis was to find support for juvenile and environmental synchrony, the region is unique in its high physical diversity (e.g., geologic diversity, flow variation) that could influence subpopulation dynamics, conferring stability to this endangered population.

Methods

Study species

Coho salmon are distributed around the Pacific rim and California represents their southern extent in North America. In coastal California watersheds, adult coho migrate upstream to spawn during the winter season (~November-February, peaking in December and January), when the winter storms act as cues for upstream migration. Females lay eggs in gravel nests (“redds”) and the eggs incubate and hatch over the next 5-7 weeks. Emergence of fry from the gravel occurs 8-10 weeks post-spawning in ~February-April, depending on the timing of spawning and temperatures experienced. Higher flows during the winter months can provide expansive habitat for spawning and for rearing of emerging fry, enhancing survival, but extreme high flow events can scour incubating eggs and displace newly emerged fry (Montgomery et al. 1996; Greene et al. 2005). The emergence period can extend into the spring flow recession, wherein stream flow recedes to summer base flow levels. Though many fish rear in the vicinity of the nests ("natal rearers"), elevated flow in the spring and the spring recession can facilitate movement to "non-natal" habitats and thus redistribute juveniles across the watershed, altering stream densities (Erman & Leidy 1975; Milner 2023). As spring transitions to summer, juveniles continue to grow. Low flows during the dry season can enhance productivity within a stream and thereby increase growth and survival, but extreme low flows can restrict movement and lead to high mortality (Grantham et al. 2012; Hwan et al. 2018; Obedzinski et al. 2018; Vander Vorste et al. 2020). Coho salmon that survive the dry season continue to rear in streams through the fall and winter and migrate to the ocean as smolts the following spring.

Study region

Marin County, California is considered a regional stronghold for CCC coho salmon (National Marine Fisheries Service 2012). In particular, the Lagunitas Creek watershed provides mainstem and tributary habitats that regularly support salmon spawning and juvenile rearing (**Figure 1**). In the last twenty years, the Lagunitas watershed has averaged 184 (SD = 114) coho salmon redds each year, though the number varies depending on the year and cohort. The watershed has a drainage area of 270 km^2 but a series of dams on the mainstem and a major tributary (Nicasio Creek) block access for anadromous salmonids, reducing the available watershed for anadromous fishes by 50%. There are four streams within the watershed that consistently support coho salmon rearing: Lagunitas Creek (below Peters Dam), Olema Creek, Devil’s Gulch, and San Geronimo Creek. Nearby Redwood Creek, south of Lagunitas, also supports coho salmon spawning and rearing and is a much smaller (18 km^2) watershed without dams. Redwood Creek has averaged 22 (SD = 26) redds per year since 2005.

The five focal streams (Lagunitas Creek, San Geronimo Creek, Devil's Gulch, Olema Creek, Redwood Creek) vary in their catchment size, elevation, slope, geology, long-term median seasonal flows, and surrounding land use, potentially generating some degree of environmental filtering and producing diverse local habitat conditions for rearing juvenile salmon (**Table 1**). Lagunitas Creek also has a modified flow regime due to dam regulation, which can disrupt climate-habitat relationships (Grantham et al. 2014). For example, Lagunitas Creek has mandated minimum dry season flow releases from the reservoir, even during drought conditions. Additionally, streams differ in low flow barriers and floodplain access (Marin Municipal Water District 2011), and sediment load (Downs et al. 2018) that may alter mortality risks for juvenile salmon under different flow scenarios. Given these differences across the region, we assumed stream subpopulations were partially independent and assessed variance in juvenile density for each stream.

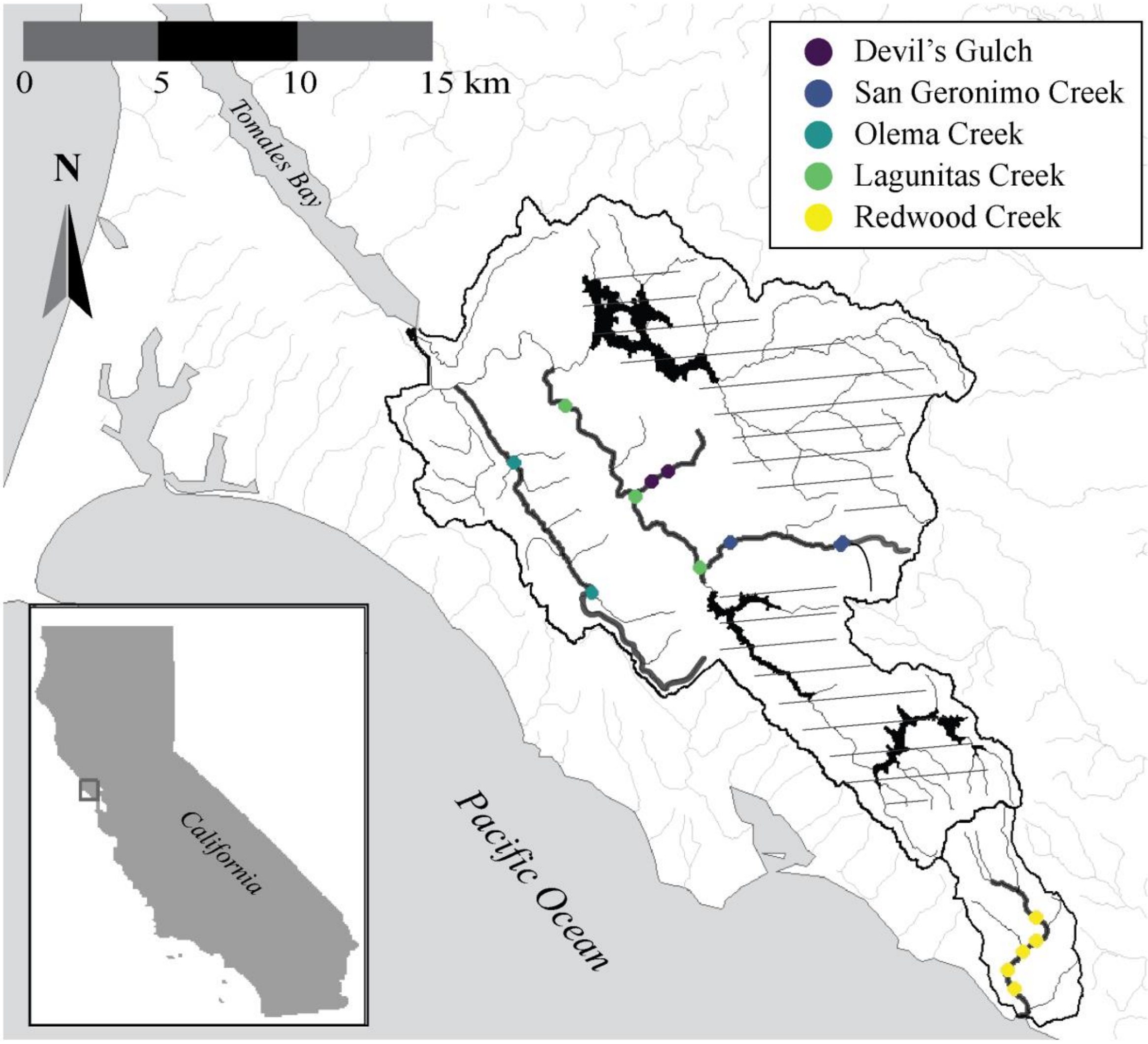

Figure 1 Map of California (inset) with study region in the grey box. Study region is in the larger inset map, with the Lagunitas Creek (top) and Redwood Creek (below) watersheds outlined. Study streams are denoted by thicker black lines and the corresponding colour dots that indicate where juvenile coho salmon sampling occurred.

Juvenile coho salmon density

Coho salmon in our focal streams are monitored throughout the year during their freshwater life stages, which includes spawning, juvenile rearing over the summer, and the spring smolt outmigration. Olema Creek and Redwood Creek salmonids are monitored by the National Park Service (NPS). The three streams in the Lagunitas Creek subbasin (Devil's Gulch, San Geronimo Creek, Lagunitas Creek) are monitored by Marin Water, a municipal water agency. Monitoring at various life stages has occurred since the 1990's, but juvenile monitoring only became consistent and comparable across all streams in summer 2005, thus we use this year as the start date for our time series which runs through 2022, omitting 2020 for NPS-monitored streams due to COVID-19 restrictions.

Juvenile coho salmon sampling is conducted annually during August and September (the end of the summer season) using snorkel surveys and three-pass depletion electrofishing surveys. We identified stream reaches sampled annually and used these units for our analysis. In the Lagunitas subbasin, juvenile surveys focus on 100-300 meter index reaches that have been consistently sampled by Marin Water for over 20 years and encompass a variety of stream habitats. In Olema Creek and Redwood Creek, surveys focus on the stream scale, randomly selecting habitats to electrofish each year; however, the creeks are demarcated by ~100 metre reaches and many of these reaches have a random selection of pools sampled in most survey years (> 12 years), allowing us to generate index reaches comparable to that of the Lagunitas subbasin streams. We removed reaches that were not sampled or had zeroes catches for ⅓ or more of the time series. Thus, our final data set included 2 reaches in Devil's Gulch, 3 reaches in Lagunitas Creek, 3 reaches in San Geronimo Creek, 2 reaches in Olema Creek, and 5 reaches in Redwood Creek, where each reach had 1-4 pools sampled to estimate juvenile densities.

Table 1 Physical habitat features of five focal study streams in Marin County, California. Lagunitas Creek is the stretch of stream from the dam down to the confluence with Nicasio Creek. Dominant geology and adjacent land use are for the underlying streambed and adjacent riparian zones, rather than the entire catchment area.

Physical habitat characteristic	***Study stream***				
	Lagunitas Creek	**Olema Creek**	**San Geronimo Creek**	**Devil's Gulch**	**Redwood Creek**
Catchment size (km^2)[1]	112	38	24	7	23
Stream order[1]	3	2	2	1	2
Median wet baseflow (cms)[2]	0.58	0.09	0.09	0.02	0.07
Median dry baseflow (cms)[2]	0.27	0.024	0.013	0.004	0.015
Average air temperature (deg C)[3]	14.1	13.9	14.5	14.2	14
Average precipitation (mm)[3]	960	935	1120	1028	1020

Streambed slope[1]	0.003	0.01	0.013	0.023	0.017
Dominant streambed geology[4]	Franciscan complex (35% melange, 36% sandstone/shale, 25% greenstone)	52% Franciscan complex sandstone/shale, 14% Monterey Formation, 11% alluvium	Franciscan complex (59% melange, 13% greenstone)	Franciscan complex (48% melange, 41% greenstone)	90% Franciscan complex, melange
Max elevation (m)[1]	55	263	154	118	119
Adjacent land use[5]	Evergreen forest, grassland/herbaceous, shrub/scrub	Evergreen forest, grassland/herbaceous, shrub/scrub	Evergreen forest, developed open space, shrub/scrub	Evergreen forest, shrub/scrub	Evergreen forest, mixed forest, shrub/scrub

[1] National Hydrography Dataset, US Geological Survey
[2] California Environmental Flows Working Group, https://rivers.codefornature.org/
[3] PRISM Climate Group, https://prism.oregonstate.edu/
[4] Geology of Marin County, US Geological Survey
[5] National Land Cover Database, US Department of Agriculture

We focused on data collected from pool habitat via electrofishing surveys. We summed electrofishing counts over all passes (2-5, depending on depletion) from each pool to calculate total number of juvenile coho salmon within a pool. We next calculated abundance within pool habitat using a k-depletion method (Carle & Strub 1978) and the `FSA` package in R (Ogle et al. 2023; R Core Team 2024). To evaluate whether total counts are a good proxy for abundance, we compared counts to abundance estimates using a regression analysis, which showed close to a 1:1 relationship, after removing one outlier (slope = 1.08; $p < 0.05$; $R^2 = 0.98$; ***Figure S1***). Thus, we used total counts for the response variable to better estimate observation error from the model. To calculate density, we divided the total number of juvenile coho salmon across all pools within a reach by the total surface area of sampled pool habitat within a reach (sum of all pool lengths multiplied by the average width). Pool surface area was measured at the time of juvenile sampling. Our final response variable was the number of juvenile fish per metre squared of pool habitat for reaches within each stream (15 reaches across 5 streams) from 2005-2022.

Breeding success

The three-year life cycle of coho salmon has led to three distinct cohorts in the region that potentially have their own trends, but we do not incorporate the cohort effect here given the limited length of our time series. Instead, we control for cohort return trends and account for the influence of egg production on offspring densities by including breeding success within a year as a covariate in our models. Spawning ground surveys are done by NPS and Marin Water in late November until the end of the coho salmon spawning season, typically late January. Surveyors walk sections of the focal streams and other tributaries once a week and record any live adult coho salmon and any new redds. Absent a female adult salmon on the redd, redd characteristics and nearby species are used by Marin Water to assign species (Ettlinger et al. 2023), and a linear regression analysis and known-nearest-neighbour algorithm are employed by NPS to assign species (McNeill et al. 2020). In cases where species was recorded as unknown, we removed these observations from our analyses. We calculated the total number of confirmed coho salmon redds in each stream for the spawning season and used this value as a covariate, recognizing that juvenile densities partly reflect egg production.

Flow variables

We tested the influence of stream flow characteristics at different stages of the early salmon life cycle on juvenile densities (summarized in **Figure 2**, see *Objectives 2 & 3*). Streamflow data from water years 2005-2022 were acquired from gauges on Olema Creek (NPS 2004-2018; USGS # 11460605 from 2018-2022), Lagunitas Creek (USGS # 11460400), Redwood Creek (NPS 2004-2014; USGS # 11460151 from 2014-2022) and San Geronimo Creek (gauge run by Balance Hydrologics). No discharge data was available for Devil's Gulch and we used nearby San Geronimo Creek data as a proxy given their similar size. To assess whether extreme conditions have different impacts across stream populations as compared to moderate conditions within a season, we used two metrics per season representing extremes and median values, except for spring recession where we used three metrics. We obtained stream-specific long-term seasonal start dates and duration from the California Natural Flows Database and selected the median metrics across all years (wet, dry, moderate) to generate an average seasonal window for each stream (California Environmental Flows Working Group 2021). All flow values are presented in cubic metres per second, except spring rate of change which is the median percent daily decrease in discharge.

For the wet season metrics, we calculated the peak flow value and median baseflow. We focused on the portion of the wet season that would have affected early life stages of salmon, especially potential scouring of eggs; thus, for each stream we shifted the start of the wet season according to the date of the first recorded redd and then calculated the maximum mean daily flow from the date the first redd was detected to the end of the wet season. We also calculated the median wet season baseflow, representing general habitat conditions for incubating eggs and emerging fry.

During the spring recession period, defined as the long-term start timing and duration of the spring recession, we extracted the maximum and median mean daily flow to identify the peak and median values during this period of fry emergence and rapid growth, as well as the rate of change, which can be cue for dispersal of fish. Spring rate of change was calculated by taking the magnitude at the beginning of spring, the magnitude of summer baseflow, the number of days between the two flow points, and calculating the percent decrease in flow for each day. We then found the median rate of change across that same period. We started at the long-term average start of the spring recession rather than based on a given year's hydrograph to control for the conditions experienced by fish during the period of emergence, growth, and dispersal of fry.

The dry season start was designated as the long-term season average, but the end date shifted depending on the start date of juvenile sampling within a stream as surveys are done at the end of summer while the dry season can extend well into fall (depending on the timing of the onset of fall rains). Within this modified seasonal window, we calculated the extreme low flow as the 10th percentile mean daily discharge value and median summer baseflow as the median mean daily discharge for each stream.

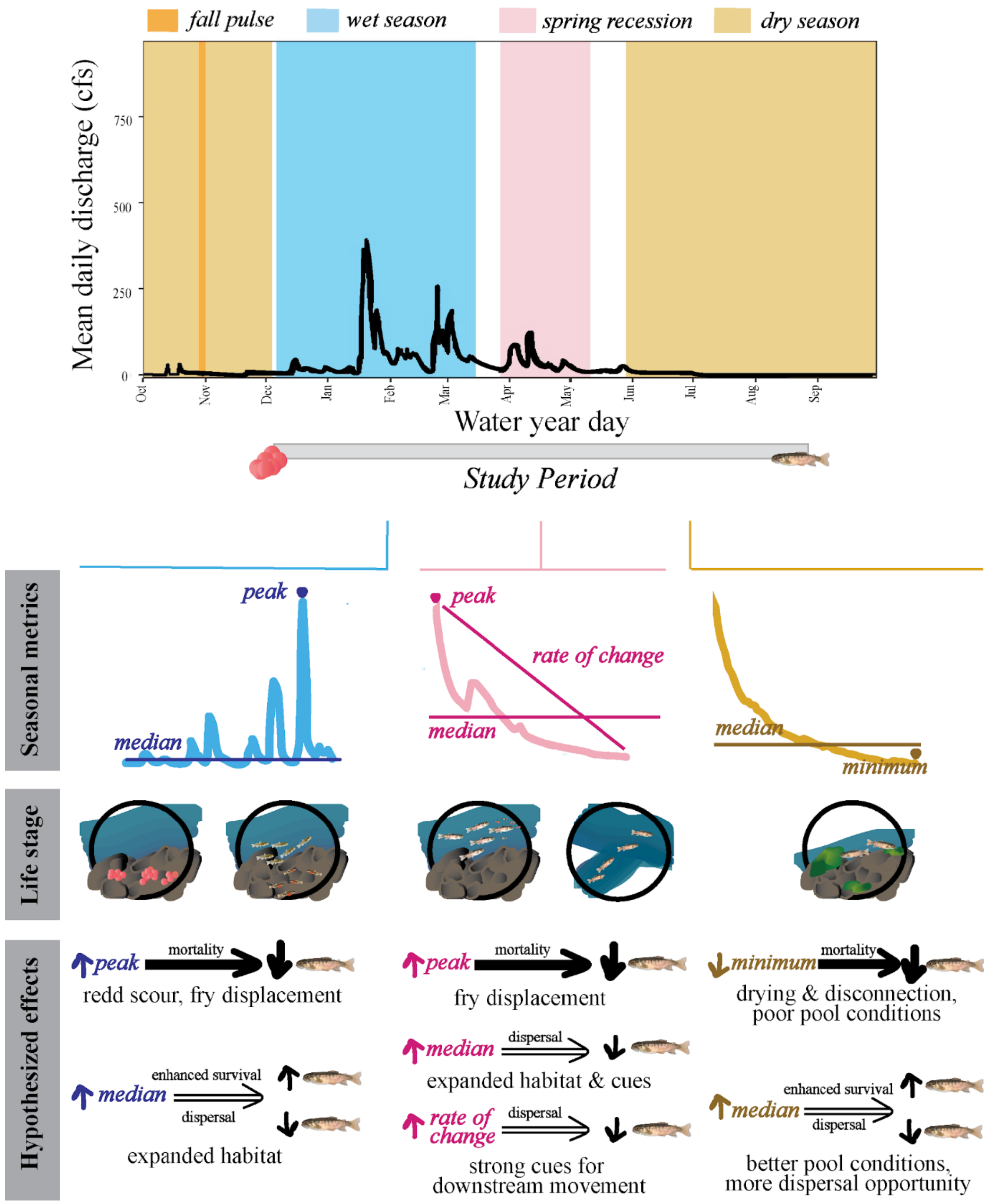

Figure 2 Effects of seasonal flow metrics on juvenile coho salmon life stages. The top graph shows seasonal windows for Olema Creek long-term hydrograph, starting from the beginning of the water year (October 1). Coloured blocks indicate the season, black lines are actual flow values from the Olema Creek hydrograph for the 2010 water year as an example. The gray bar below the graph represents the study period, from egg incubation to juvenile summer sampling. Seasonal metrics are the flow metrics calculated within a season for each year, the "extreme" and "moderate" values, and life stage is early life stage of coho salmon that flow within each season may impact. During the wet season, salmon eggs are incubating in the gravel and fry are emerging from the gravel into the water column. During the spring recession, fry continue to emerge from the gravel and start to feed and grow in the stream, as well as start to disperse to different habitats. The dry season is where fish continue to feed and grow, while combatting higher temperatures and may need to disperse from unsuitable habitats, depending on stream connectivity. For each seasonal flow metric, we hypothesize the effect that higher or lower flows will have on juvenile densities in the region, either through mortality, enhanced survival, or dispersal of fry downstream. Upwards arrows beside juveniles indicate a predicted positive effect on densities, and downward arrows predict a negative effect, and thicker arrows predict strength of the effects. Horizontal arrow thickness symbolizes predictions of strong synchronizing effects.

Model specification

We used multivariate autoregressive state-space (MARSS) models using the MARSS R package (Holmes et al. 2024) to investigate population dynamics and drivers of these dynamics. Building on the capability of multivariate autoregressive (MAR) models to estimate biotic and abiotic effects on ecological time series data, MARSS models additionally partition variation into observation error (i.e., error arising from electrofishing sampling) and process error (i.e., real, stochastic variation in the data) for subpopulations (Ward et al. 2010; Colombano et al. 2022). The MARSS model structure consists of a process model (Equation 1) and observation model (Equation 2):

$$x_t = x_{t-1} + u + \mathbf{C}c_t + w_t, \text{ where } w_t \sim \text{MVN}(0, \mathbf{Q}) \qquad (1)$$

$$y_t = \mathbf{Z}x_t + v_t, \text{ where } v_t \sim \text{MVN}(0, \mathbf{R}) \qquad (2)$$

with the biological response data (log-transformed juvenile density data) entering the observation model as the y_t, a matrix with *n* number of observations or rows (15 reaches) by 18 time steps, (*t*, each year from 2005 to 2022). Different reaches from the same stream informed the same state ($m = 5$) via the *Z* matrix, which connects reach-level observations to stream-level states. In turn, v_t captures observation error, from a multivariate normal distribution (MVN) with mean 0 and covariance *R*. We set the *R* matrix to “diagonal and equal” to estimate a single observation error across the region with no covariance, as testing for alternative *R* structures resulted in this configuration fitting the data best.

By estimating observation error, we can characterize the “true” state of the subpopulations—something advantageous when analyzing long-term data because uncertainty in the data can change inferences about the underlying drivers, specifically in detecting trends and dynamics in threatened salmon populations (Shea & Mangel 2001; Knape & de Valpine 2010). In our case, the process model (Eqn. 1) partitioned the sources of variance in the states (x_t), including covariate effects and ‘unexplained’ variance within (and covariance among) subpopulations. Specifically, our covariate data was environmental (redd counts, flow metrics) data at the yearly time step, which enter the model as c_t. The effects of these covariates on each stream were captured by the *C* matrix, where we estimated a single, region-wide effect. We tested for alternative covariate effect structures, but ultimately region-wide effects made the most sense for our data. The process error remaining, or unexplained variance, is a matrix w_t, drawn from a MVN with mean 0 and covariance matrix *Q*. To evaluate variation within each stream subpopulation and covariance between streams, we used the *Q* matrix (set as “unconstrained”). In this configuration of the *Q* matrix, the variance estimate is unique for each stream but not entirely independent. The model calculates an estimate of variance from each stream (diagonal in the matrix, *Q*), then an estimate for covariance (off-diagonal in the matrix, Q_{cov}) between each stream pair.

We ensured each model converged and inspected the model residuals, then obtained maximum likelihood estimates and 95% confidence intervals for all parameters from 1000 bootstrapped samples (Holmes et al. 2012). We used the MARSS model to address our objectives, described below.

Objective 1: Characterizing spatial and temporal variation in regional population dynamics

Our null hypothesis was that streams would vary similarly in time and space, with highly synchronized density dynamics. We sought to test this hypothesis by characterizing population diversity across the regional metapopulation. We defined population diversity as evidence of distinct subpopulation dynamics, where subpopulations uniquely vary in space (variance) and time (covariance). Correlation considers variance for each stream subpopulation as well as the covariance between streams to illustrate how stream subpopulations fluctuate similarly through time. Synchrony is defined as high correlation between subpopulations. We converted variance and covariance estimates from the MARSS model into correlation between streams to assess synchrony amongst subpopulations, where 1 is entirely positively correlated, 0 is no correlation, and -1 is entirely negatively correlated (Ward et al. 2010).

To characterize population diversity, we created a base (null) model to evaluate the population dynamics of the system without considering biotic and abiotic factors. We extracted variance estimates, mean and maximum densities from the stream states, and stream-pair correlations, and calculated the coefficient of variation (CV, standard deviation divided by the mean) for each stream time series to compare long-term variability controlling for the mean. Additionally, we tested stream states for consistent trends in juvenile densities across our time series by calculating the Theil-Sen estimator slopes in the “mblm” package in R (Komsta 2019).

Objective 2: Characterizing spatial and temporal variation in regional environment conditions

We predicted that the small regional system would show strong environmental synchrony as a null hypothesis, with greatest synchrony in extreme flow metrics. To test this, we calculated the Pearson’s correlation coefficient between each stream pair for all 8 environmental covariates: breeding success, wet season flows (peak and median), spring recession flows (peak, median, rate of change), dry season flows (minimum flow and median). We interpreted a correlation close to 1 as evidence of strong synchrony in breeding success or seasonal flow. Comparisons between Devil’s Gulch and San Geronimo Creek flows were calculated but not considered, as we used the same gauge data for both creeks.

Objective 3: Identifying environmental drivers of population dynamics

We hypothesized that environmental factors such as breeding success and median and extreme flows across the wet, spring, and dry seasons explained variation in juvenile density across streams. While we predicted breeding success to positively impact juvenile density, we were most interested in the effects of high and low flows on juvenile density as these are influenced by the regional climate. As such, we developed hypotheses for each seasonal flow metric and how it might drive variation and synchrony in end of summer densities via mortality events or dispersal opportunities during the early life stage of salmon (**Figure 2**). In general, we predicted extreme flow effects to have the strongest effects on stream density and synchrony in juvenile density due to extreme events causing mortality.

We tested these hypotheses and compared effects of environmental variables in multiple steps. First, we included each environmental factor as a covariate, building on the base MARSS model, starting with redd counts. Next, to control for the effect of the spawning adult returns on juvenile densities in all subsequent models, we built upon the redd count model by adding in flow metrics. We added each flow metric individually to the model to its capture effect, then ran two full models with all extreme flow metrics and moderate flow metrics, respectively, to assess whether variation was best explained by the combination of flow metrics. For the combined flow metric models, we used spring peak and median flows and did not include spring rate of change to stay consistent with the other flow metrics. We calculated the Pearson's correlation coefficient between redd counts and extreme and median flow metrics in each stream, only including those together in models who correlation coefficient was <0.6 to avoid collinearity in covariates (***Figure S2***). All covariates were z-scored for equivalent comparisons (mean = 0, std = 1). To assess impacts of flow on densities, we extracted covariate effect estimates from each model. We determined an effect significant if the estimate confidence intervals did not overlap with zero. In total, we ran 11 models and compared the model residuals and the Akaike Information Criterion, adjusted for small sample sizes (AIC_c) to find the model that had the best support. We selected the one with the lowest AIC_c as the best model, with models $\Delta AIC_c < 2$ from the top model interpreted to have similar support.

We further evaluated how variance and correlation estimates increased or decreased when incorporating covariates to the base model to investigate to what degree each covariate explained subpopulation variation and synchrony (Ruhi et al. 2018), with special attention to comparing moderate and extreme conditions within a season. We calculated Δ Q and Δ correlation between the base model and redds only model (i.e., base model – redds model); this allowed us to assess how the addition of redd counts explained variation and synchrony. We then examined the additional impact of flow by calculating Δ Q and Δ correlation for the moderate and extreme flow models within each season as compared to the best redds model (i.e., redds – flow). We interpreted positive Δ Q as a covariate explaining more variation in a stream as compared to the base (or redds only) model. A positive Δ correlation for a stream subpopulation pair indicated a decrease in synchrony when adding the covariate, meaning the covariate was a "synchronizing agent".

Results

Spatial and temporal variation in regional population dynamics

Evidence for population diversity across in the region was mixed, partially supporting the null hypothesis that the system would not support population diversity in juvenile density dynamics; while subpopulation densities and variance in densities differed, overall density dynamics were highly synchronized (**Figure 3**). When comparing bootstrapped parameter estimates from the designated base model, stream subpopulations differed in the unexplained variance, or the amount that densities fluctuated year-to-year after incorporating observation error. Lagunitas Creek subpopulation was the most stable, with the lowest unexplained variance ($Q = 0.009$) and Devil's Gulch was the most variable ($Q = 0.281$), and in general the tributaries to Lagunitas Creek (Devil's Gulch, San Geronimo Creek, Olema Creek) showed greater variance as compared to the stable, regulated-flow mainstem (**Table 2**). Redwood Creek was relatively less variable than the other unregulated streams. Devil’s Gulch, the smallest stream, had the highest mean and maximum densities (mean = 0.76; max = 3.37) and Lagunitas and Redwood Creeks had the lowest mean and maximum densities (mean = 0.15, 0.12; max = 0.39, 0.37). The CV calculations, another measure of variability that considers the mean and standard deviation of each subpopulation time series, showed similar long-term variability in densities in all unregulated streams (CV > 100%), while Lagunitas Creek was relatively stable (CV = 54%). When we factored in stream variance and stream pair covariance to calculate correlation, all stream subpopulations were highly correlated (~ 1), indicating an extremely synchronized regional population. Devil’s Gulch and Redwood Creek had the lowest correlation (0.95), Devil’s Gulch, San Geronimo Creek, and Lagunitas Creek all had the highest correlation (0.99). The only significant trends in densities across the 18 years detected by the Thiel-Sens (TS) estimator was a small, positive trend in San Geronimo Creek (TS = 0.02; p<0.05) and a negative trend in Redwood Creek that neared zero (TS = -.006; p<0.05).

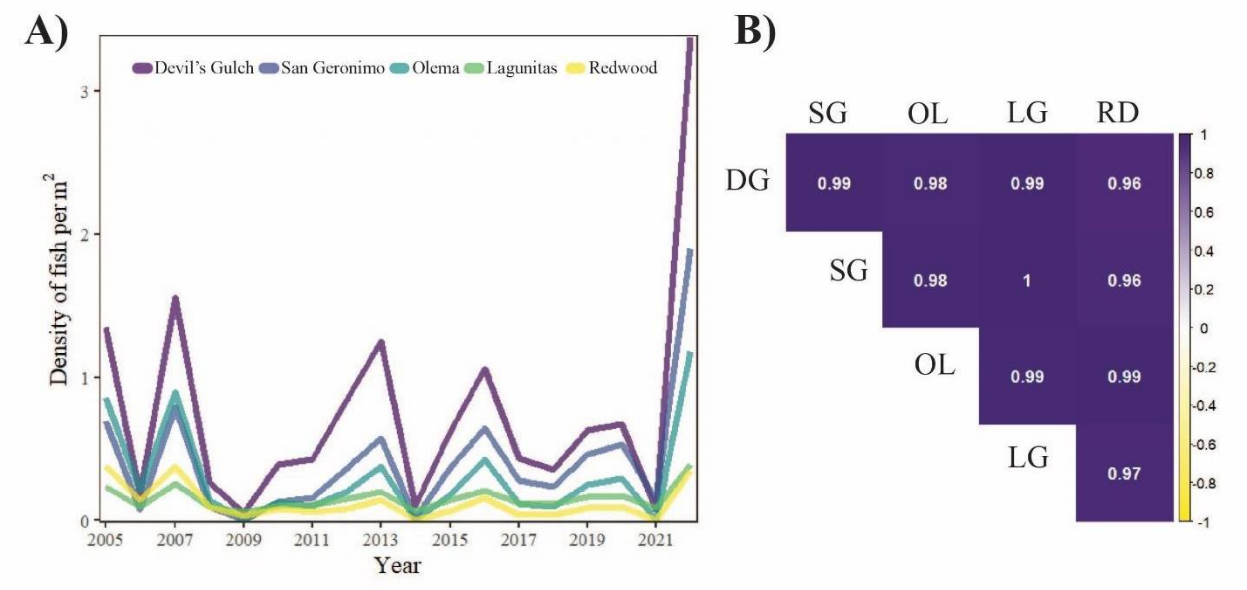

Figure 3 Juvenile density states of each subpopulation and correlation between subpopulations using state estimates from the base (null) MARSS model. **A)** Density of fish per metre squared of pool habitat as estimated by the model, colour-coded by stream. **B)** Pearson correlation values of stream-pair comparisons using estimated density states. A value of 1 is perfect positive correlation; 0 is no correlation between subpopulations; -1 is perfect negative correlation.

Spatial and temporal variation in regional environmental conditions

We tested the null hypothesis that the regional watershed would be synchronized in environmental conditions and found that environmental synchrony was strongest between tributaries of Lagunitas Creek, but weaker between tributaries and the mainstem Lagunitas and Redwood Creeks, providing some evidence of environmental filtering. In terms of absolute values of breeding success and flows, as the largest stream Lagunitas Creek predictably had the most redds and highest magnitude of flows across the time series; all other streams had similar magnitudes in redds and flow metrics (**Figure 4A**). Flow was more variable across time in the streams with natural flow regimes than in Lagunitas Creek, especially in dry season flows where signals of flow regulation were present (***Table S1***).

Table 2 Stream subpopulation variability and trends calculated from the base (null) MARSS model. The *Q* values are parameter estimates of unexplained variance, or process error, in log-space. The TS value is the slope calculated by the Theil-Sen estimator for each subpopulation. Bolded values indicate statistically significant ($p < 0.05$) positive or negative trends in the subpopulation states. Density is the mean and maximum number of juvenile fish per metre squared of pool habitat within a stream across all years.

Stream	Q	TS	CV (%)	Mean density (fish/m^2)	Max density (fish/m^2)
Devil's Gulch	0.281	0.018	105	0.76	3.37
San Geronimo Creek	0.125	**0.020**	108	0.41	1.90
Olema Creek	0.100	-0.003	115	0.30	1.18
Lagunitas Creek	0.009	0.003	54	0.15	0.39
Redwood Creek	0.018	**-0.006**	104	0.12	0.37

When evaluating synchrony in breeding success, the three tributaries of Lagunitas Creek were highly synchronized in the number of redds (r>0.8), but less synchronized with Lagunitas Creek mainstem and Redwood Creek (r<0.5) (**Figure 4B**). Lagunitas Creek and Redwood Creek were uncorrelated in their redd numbers, indicating asynchrony in redd dynamics (r=0). The degree of environmental synchrony across the region in regard to flow varied depending on the season and the metric. Median wet and spring season flows showed the strongest synchrony across all streams (r>0.8), while peak wet and spring flows showed moderate synchrony (0.8>r>0.4), contrary to predictions that extreme flows would further homogenize stream habitats. Both dry season metrics showed the least region-wide spatial synchrony, particularly between Lagunitas Creek and all other streams, suggesting asynchronous dry season conditions (r<0.3). Taken together, we found evidence of strong environmental synchrony in spawning and flow conditions within Lagunitas tributaries, but weak to moderate synchrony at the watershed and regional scales.

Environmental drivers of population dynamics

We evaluated and compared the influence of the eight environmental variables on juvenile density. Overall, we found little evidence to support our general hypothesis that extreme flow metrics, such as higher peak wet and spring season flows and lower minimum dry season flows, have the largest negative effects on juvenile density and act to further synchronize juvenile density dynamics across the region.

Six models had similar support (ΔAIC_c <2) for best explaining spatiotemporal variation in juvenile density in our population complex: redds + wet season peak, redds only, redds + dry season minimum, redds + dry season median, redds + wet season median, redds + spring median (**Table 3**). While 5 of the best supported models included hydrologic drivers, no one model appeared as a clear best model for explaining variation. Models were therefore inconclusive in distinguishing the hydrologic drivers of variation in juvenile density dynamics, though all

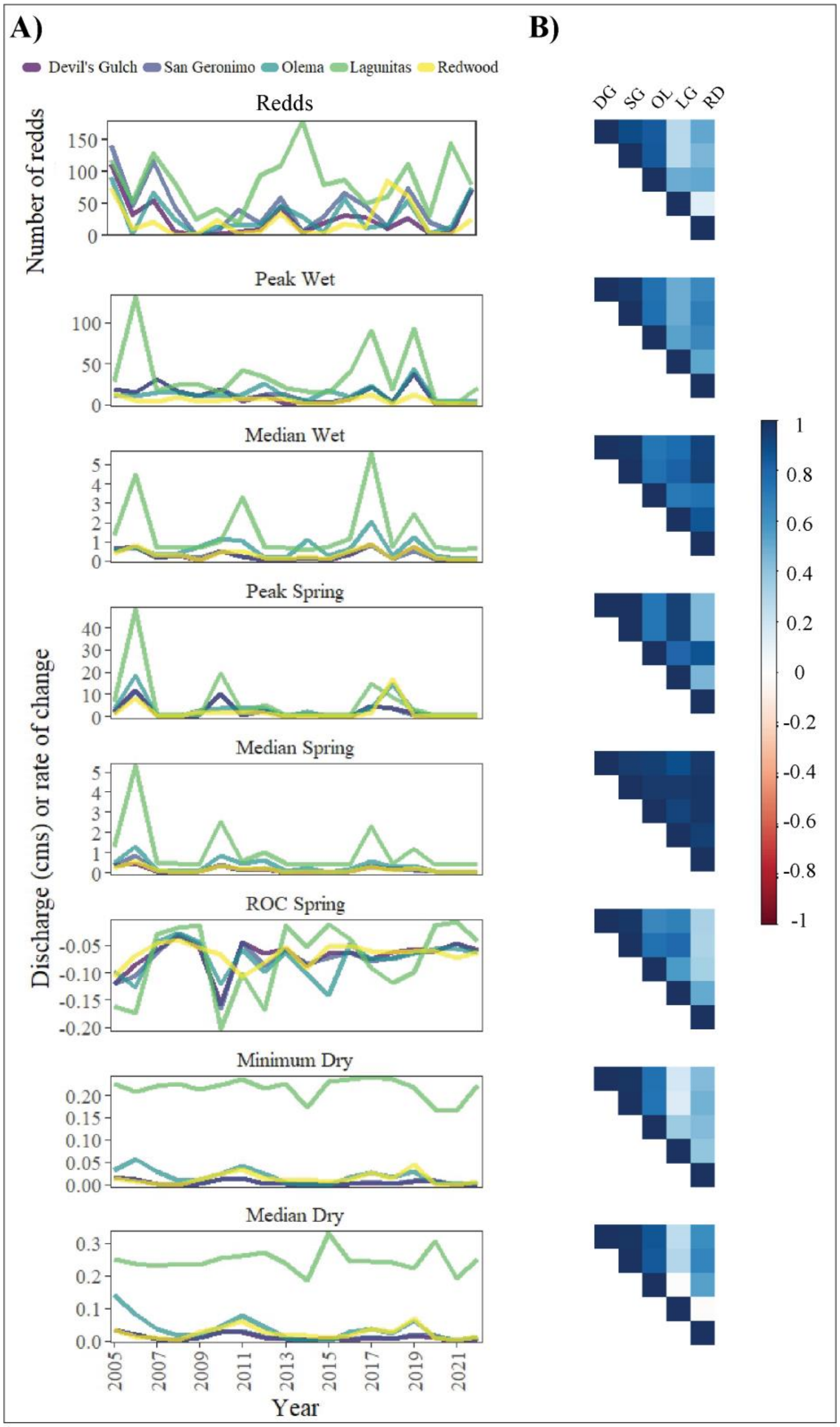

Figure 4 Model covariate inputs for each stream over the length of the time series. **A)** Stream-specific redd numbers and season flow metrics. Excluding spring rate of change, all flow metrics are discharge in cubic metres per second. Spring rate of change is expressed as median percentage of flow decrease. **B)** Correlation matrices for each covariate, representing the Pearson correlation coefficient between each stream pair, where dark blue is perfect positive correlation and white is no correlation.

improved upon the base model. In evaluating hypotheses of environmental impacts on density, covariate effect estimates revealed that the number of redds had a significantly positive effect on juvenile densities in all covariate models, in line with predictions. Flow metrics had a negative effect on juvenile densities for all single-flow models (redds + one flow metric) except for the positive effect of spring rate of change, though none of the effects were significant. Negative effects of flow partially supported hypotheses for effects of wet and spring season flows and median dry season flows but did not support hypotheses for the effects of spring rate of change and minimum dry season flow. The combined flow models had weaker support overall when compared to the single factor models, thus we did not consider them further.

Table 3 Comparison of model support for each redd-flow combination MARSS model, in relationship to one another and the base model (no covariates). The best model could not be determined ($\Delta AIC_c < 2$), thus models were shaded in grey to indicate equal support. Black and bolded terms in the effects columns indicate a significant positive or negative effect on juvenile density, determined by whether confidence intervals overlapped with zero, while grey terms represent a non-significant effect.

Model Group	Redds Effect	Flow Effect	AICc	ΔAICc	RelLik	Model weight
Base			-108.709	5.511	0.064	0.005
Redds + Wet Season (Peak Flow)	**+**	-	-114.22	0	1	0.082
Redds only	**+**		-114.211	0.009	0.995	0.082
Redds + Dry Season (10th Percentile Flow)	**+**	-	-113.851	0.369	0.831	0.068
Redds + Dry Season (Median Flow)	**+**	-	-113.735	0.485	0.785	0.064
Redds + Wet Season (Median Flow)	**+**	-	-113.706	0.514	0.773	0.063
Redds + Spring Season (Median Flow)	**+**	-	-112.514	1.707	0.426	0.035
Redds + Spring Recession (Rate of Change)	**+**	+	-111.926	2.294	0.318	0.026
Redds + Spring Recession (Peak Flow)	**+**	-	-111.816	2.404	0.301	0.025
Redds + All Extreme Flow Covariates	**+**	- wet, - dry, + spring	-110.58	3.64	0.162	0.013
Redds + All Moderate Flow Covariates	**+**	- wet, - dry, - spring	-110.149	4.071	0.131	0.011

After examining covariate effects region-wide, we went a step further and found there were smaller between-stream differences in the degree of variation in juvenile densities explained by the addition of the covariates, as measured by ΔQ (**Figure 5A**). For example, including the number of redds into the model reduced unexplained variance in density ($\Delta Q > 0$) in all streams as compared to the base model to varying degrees. The relative decrease in unexplained variance in density was 5% in Devil’s Gulch, 8% in San Geronimo Creek, 10% in Lagunitas Creek, 15% in Olema Creek, and 27% in Redwood Creek. Thus, breeding success was most important in explaining relative changes in density in Redwood Creek. Beyond the variance explained by redds, median wet and spring season flows had the largest effects in reducing unexplained variance in juvenile densities to some extent in all stream subpopulations, with decreases in variance of 1% (median spring, Devil’s Gulch) to 15% (median wet, Redwood Creek). Dry season low flow was also important in explaining variance in density in Olema Creek (6% decrease), and wet season peak flow substantially reduced unexplained variance in both Lagunitas and Redwood Creeks (18%, 10% decrease).

We also assessed how much covariates explained correlation, or synchrony, in juvenile densities between streams and found environmental conditions did not have strong effects on juvenile synchrony in the region. There were extremely small changes in unexplained correlation between stream juvenile densities on the scale of .01, providing little evidence of synchronizing effects of the environment; however, we can assess changes in correlation relative to one another. For example, the addition of redds as a covariate to the base model explained the most correlation in juvenile density dynamics between Lagunitas Creek and all other streams ($\Delta corr > 0$) (**Figure 5B**). This suggests that even low synchrony in breeding success in these streams can further increase synchrony in juvenile densities. Building on the effects of redds, the addition of flow metrics in general did not show a clear signal of synchronizing or desynchronizing juvenile dynamics. The most pronounced differences were in low flow metrics. Extreme low flow in the dry season tended to further synchronize juvenile density dynamics between Lagunitas Creek and all other stream subpopulations ($\Delta corr > 0$), while median flows in the dry season had slightly desynchronizing, or “buffering”, effects on juvenile dynamics across most streams ($\Delta corr < 0$).

Discussion

We investigated population diversity in juvenile density dynamics and the influence of breeding and hydrology across five streams that support endangered CCC coho salmon at the southern edge of the range. The small streams in the region continue to support spawning by coho salmon, though the number of spawners is generally low and variable. MARSS models revealed that streams could support a range of juvenile densities (0-3.4 fish/m^2) and stability in density long-term (variance of 0.009-0.281), but year-to-year fluctuation in densities was highly synchronized across the region (>0.95 correlation), providing limited evidence for population diversity in juvenile dynamics. Environmental conditions in the wet to spring seasons were spatially synchronized across the region; however, spatial asynchrony in the dry season between the flow-regulated Lagunitas Creek and other streams suggested some degree of environmental filtering. While no single driver of density dynamics emerged, fluctuations in stream juvenile densities were partially explained by the positive influence of spawning success and negative impacts of high stream flows during the early stages of salmon development, with no differences in the effects of median and extreme seasonal flow metrics. Our results suggest that in general, synchronized fluctuations in juvenile densities signal potential vulnerability of the population to years of low adult returns and/or high juvenile mortality from wetter conditions during the incubation and emergence periods of juvenile salmon development. Yet, the limited diversity in the regional metapopulation, particularly in the differences between Lagunitas Creek subpopulation and other streams, may still provide some benefits for stability of the complex and buffer against poor conditions in the dry season.

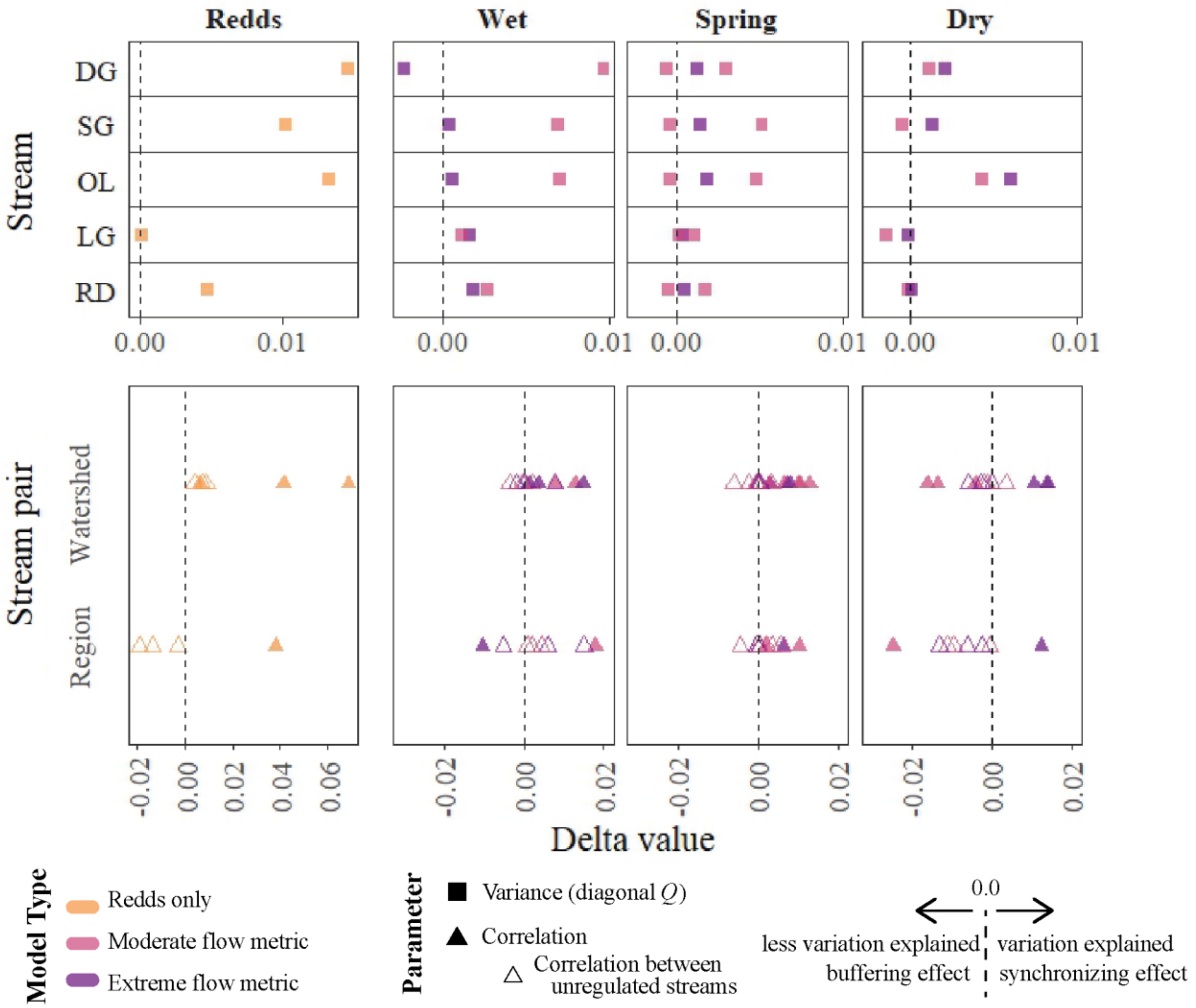

Figure 5 Change in variance and correlation parameter estimates from base model. The far-left column titled "Redds" is the difference between the base model and best model where redds were the only covariate (base – best redds). The other three columns show differences between the parameter estimates from flow covariate models and the estimates for the redds only model (redds – flow) to isolate for effects of flow. Columns are titled for the season, and with colour indicating whether the delta value is from an extreme or moderate flow metric. Squares represent differences in stream variance (process error) *Q* estimates (top panel). Positive values indicate the covariate explains additional variation as compared to the base model or the redds only model, while negative values indicate that adding the covariate increases the amount of unexplained variation. Triangles are differences in correlation from the MARSS models for each pairing of streams in the regional system, where open triangles are comparisons between unregulated streams and closed triangles are comparisons between Lagunitas Creek and other streams, sorted by watershed (bottom panel). Positive values indicate that correlation has decreased as compared to the base or best redds model and has an additional synchronizing effect between the two stream subpopulations. Negative values indicate more unexplained correlation, potentially indicating that the addition of the covariate has a slight buffering effect against synchrony between the two subpopulations.

Limited population diversity and environmental filtering in small regional system

We explored the limits of the relationship between habitat heterogeneity and population diversity in subpopulation dynamics in this small regional system and found some signals of environmental filtering, but strong synchrony in juvenile density dynamics. In the Lagunitas Creek watershed where 50% of the watershed is inaccessible to salmon due to dams and the remaining habitat in the region encompasses a small drainage area of ~200km^2, the regional climate that dictates wet and dry years tends to synchronize flow conditions across streams. Physical habitat diversity across the five streams did not lead to differential filtering of overarching climate conditions in the wet-spring seasons, yet there was evidence of asynchrony in flow conditions in the dry season between the mainstem Lagunitas Creek and other streams. This supports observations of variable responses to extreme drought within the Lagunitas watershed throughout the dry season (Chapter 1), and differences in low flow conditions across other California coastal watersheds driven by variation in stream lithology and geomorphology (Moidu et al. 2021; Dralle et al. 2023). Flow regulation in Lagunitas Creek is likely playing a large role as well in buffering against drought conditions especially. Given that habitat loss and homogenization can reduce the diversity of responses to environmental variability (Anderson et al. 2015) and increase synchrony of salmon population complexes (Moore et al. 2010; Carlson & Satterthwaite 2011), strongly synchronized juvenile subpopulation dynamics in this depleted regional system aligned with expectations. Still, asynchrony in population dynamics has been documented at such fine spatial scales as 1km stream reaches in salmon (Quinn et al. 2012) and 1m^2 plots in plants (Abbott et al. 2017), suggesting that habitat diversity smaller than the stream scale could have hidden benefits to population diversity we did not capture.

Potential mechanisms underlying regional density dynamics

In general, juvenile densities increased with the stream spawning population but decreased with higher flows during the incubation to summer rearing phase, presumably through juvenile mortality or dispersal. High breeding success within a stream resulted in higher juvenile end-of-summer density, supporting our expectation that egg production corresponds to juvenile production (Beland 1996; Knapp et al. 1998). The number of redds only explained a small percentage of variance in density though, indicating this relationship at the stream level was likely mediated by other factors, such as spatial distribution of redds within a stream (Anderson et al. 2008; Einum et al. 2008; Foldvik et al. 2010; Teichert et al. 2011) and flow-induced mortality during the early life stage (Lobón-Cerviá 2004) or dispersal of fry downstream or upstream (Anderson et al. 2013). We found evidence that higher median and extreme flows in the wet and dry seasons, as well as median spring recession flows, decreased the end-of-summer juvenile densities expected from that year's redd counts. We inferred that more extreme high flow events depressed densities in the wet season, and to some extent the spring season, via mortality due to scouring of eggs, entombment of eggs and alevins in the gravel, and washing out of newly emerged fry (Montgomery et al. 1996; DeVries 1997; Jensen & Johnsen 1999; Lapointe et al. 2000). These findings supported our hypotheses of increased wet-spring season flows having negative effects on juvenile density; however, evidence that higher 10th percentile low flows reduced juvenile density did not support hypotheses and did not align with studies in coastal California streams which found high summer base flows increased juvenile survival. Previous studies have shown that extremely low flows during drought can lead to high temperatures, low dissolved oxygen, resource limitations, and potentially lethal conditions if pools become functionally disconnected (Hwan & Carlson 2016; Woelfle-Erskine et al. 2017; Hwan et al. 2018; Obedzinski et al. 2018; Vander Vorste et al. 2020). One explanation for our observed negative effects of higher flows in the dry season on fish densities could be the enhanced habitat connectivity within streams that enable fish to disperse upstream or downstream (Kahler et al. 2001; Winkowski & Zimmerman 2018), particularly out of poor habitats (Rossi et al. 2023), or colonize new habitats throughout the summer (Anderson et al. 2008, 2013), lowering densities overall. In fact, higher median flows across all seasons could have contributed to decreased juvenile density due to enhanced connectivity across the watersheds, allowing dispersal to other habitats such as the mainstem, floodplain, and/or the estuary (Hartman et al. 1982; Kahler et al. 2001; Weybright & Giannico 2018). Seining in the estuary by the National Park Service has revealed the presence of coho fry in the estuary during at least some years (M. Reichmuth, personal communication). Unfortunately, it was not possible to distinguish the effects of flow-induced mortality on juvenile densities from dispersal with our dataset.

We predicted that juvenile synchrony would reflect environmental synchrony, with extreme flows having particularly strong synchronizing effects on juvenile density dynamics across the region. Indeed, other studies on larger regional salmonid complexes have found that high or low flows during critical life stages synchronize population dynamics, even in heterogeneous watersheds (Cattanéo et al. 2003; Lobón-Cerviá 2004; Bouchard et al. 2022). Unlike these previous studies, none of our environmental variables emerged as large synchronizing agents, though the small changes in juvenile synchrony we detected did map onto patterns of environmental synchrony. For example, median and extreme wet and spring season flows had small synchronizing effects. In wetter years, juvenile densities across streams may be synchronized by flow events at emergence that cause mortality (Jensen & Johnsen 1999; Cattanéo et al. 2003) or similar opportunities to disperse throughout the watershed. Small desynchronizing effects of dry season flows on juvenile density dynamics also mirrored variation in regional dry season conditions. Low flows in the summer have been identified as synchronizing agents in streams, an example of the ‘Moran effect’ (Sarremejane et al. 2021; Bouchard et al. 2022). Here, variation in stream connectivity and low flow barriers in tributaries inhibiting watershed-wide dispersal may generate diverse juvenile responses in the dry season. Contrasting these patterns in environmental and juvenile synchrony, the degree of synchrony in breeding success did not correspond to juvenile density synchrony, likely due to mediating effects of local stream biotic and abiotic conditions. In lieu of evidence for strong synchronizing effects of spawning and flow, population dynamics instead may be synchronized by multiple aspects of the hydrograph, other environmental factors such as temperature (Gallagher et al. 2012), or stochastic variation.

Interestingly, we found no evidence of extreme flow metrics having greater effects on density and increasing environmental and juvenile synchrony as compared to median flows. In fact, the strongest environmental synchrony was in median wet-spring flows. It is possible that median seasonal metrics captured aspects of peak and minimum flows as these were correlated, making them indistinguishable. Additionally, rather than major mortality events, median flows more adequately represent “wet” and “dry” years as they are products of sustained precipitation and temperature conditions across the season and as such, may better represent instream conditions.

Overall, our findings show that the effects of regional flow patterns on juvenile salmon densities are complex. Given the high interannual variation in the natural flow regime during our 18-year time series, differences in magnitude, timing, duration, rate of change and frequency of seasonal flow components may be affecting the early life stages of salmon each to differing degrees each year (Beechie et al. 2013), perhaps interacting with the distribution of spawners (and hence juvenile production) across years. In fact, a study on the Lagunitas Creek system from 1997-2006 found that the relationship between number of redds and estimated fall juvenile abundance was inconsistent, varying considerably across years (Stillwater Sciences 2008). Alternatively, weak effects of flow across the region may be a result of juvenile fish density responding to flow at a much finer spatial scale than at the stream level. For example, within a stream, geomorphic controls on drying and water quality during the summer can vary such that streams are not uniformly affected by dry season conditions, leading to differences in fish persistence and survival between pools (Grantham et al. 2012; Hwan & Carlson 2016; Hwan et al. 2018; Vander Vorste et al. 2020; Moidu et al. 2021). Finally, density-dependent effects not captured by our study, such as dispersal (Chapman 1962; Erman & Leidy 1975) and intraspecific competition for limited resources (Jenkins Jr. et al. 1999; Finstad et al. 2009; Pess et al. 2011; Walters et al. 2013), could also be reducing stream-wide densities. Thus, each year juvenile coho salmon could be affected by one or more flow regime components, by fine-scale stream habitat heterogeneity filtering environmental conditions, density-dependent dynamics, or different combinations of all these effects.

Implications for regional metapopulation stability

We found little potential for buffering against disturbance events and environmental stochasticity, in contrast to findings in larger populations (Greene et al. 2010; Schindler et al. 2010). Synchrony between subpopulations matters because it undermines stability of the complex, making it more vulnerable to collapse as densities in multiple streams approach zero simultaneously. For example, the population in Redwood Creek has required intensive hatchery spawning, rearing and releases of the natural origin fish to rescue the subpopulation from near extirpation following a dire drought year in 2014 (Carlisle et al. 2016); our results suggest a high probability of a similar events affecting multiple sub-populations in a single year. However, consistent spawning and juvenile rearing in mainstem Lagunitas with regulated summer baseflows, does provide some stability to the regional metapopulation by serving as potential source for other declining subpopulations (Fullerton et al. 2011; Lin et al. 2011; Bradford & Braun 2021). Stable, non-zero densities in Lagunitas Creek likely correspond to its much larger drainage area (e.g., 230 km^2 vs 38 km^2 for the next largest sub-basin, Olema Creek) and from dam operations that stabilize aspects of the hydrograph by altering spring recession rates and artificially increasing summer baseflows. Furthermore, low to moderate levels of environmental filtering of spawning and climate conditions may explain how in some years the region supported a large range of stream densities. Maintaining different juvenile densities across the region at one time can lead to different growth rates and facilitate dispersal into other habitats (e.g., Everest 1973), influencing life history strategies such as outmigration timing and ultimately supporting the persistence of the population complex (Greene & Beechie 2004; Johnston & Post 2009; Zimmerman et al. 2015; Bourret et al. 2016; Winkowski & Zimmerman 2018). Yet, even with a more stable subpopulation in Lagunitas Creek and some spatial variation in densities, the high unexplained synchrony between streams, enhanced by winter-spring flows, indicates the metapopulation is highly vulnerable to simultaneous collapse.

Conclusion

We present one of the first studies of synchrony in subpopulations in a small regional salmon metapopulation complex. The results of our study highlight the vulnerability of this regional population to simultaneous collapse. Predictions of wetter, shorter wet seasons, sharper recessions and more intense and prolonged dry seasons (Sawaske & Freyberg 2014; Swain et al. 2016; Luković et al. 2021) may cause steep, synchronous decreases in juvenile densities across the region as salmon struggle to adapt to a shifting flow regime (Beechie et al. 2013; Ward et al. 2015; Crozier et al. 2019; Carlson et al. 2024). There is little evidence in our study for substantial population diversity in juvenile dynamics among streams in the system, yet a larger subpopulation and regulated flow regime in Lagunitas Creek could help dampen variation in regional population dynamics and support persistence. Understanding dynamics of each component of a population complex is critical to anticipating its resilience, especially for populations on the edge of a species' range with adaptations to more extreme and variable environments (Hampe & Petit 2005). We urge greater research attention to population diversity within small, endangered populations to better assess their vulnerability to extinction and consider management and restoration options for recovering population diversity.

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Supplementary Materials

Tables

Table S1 Long-term summary statistics for stream biotic and abiotic covariates (“Metric”). The mean, standard deviation (“Std”) and coefficient of variation (“CV”, std/mean) are calculated for the entire time series, 2005-2022.

Stream	Metric	Mean	Std	CV
Devil's Gulch	Redds	26	30	1.14
San Geronimo Creek	Redds	45	38	0.85
Olema Creek	Redds	30	28	0.91
Lagunitas Creek	Redds	83	43	0.52
Redwood Creek	Redds	22	26	1.18
Devil's Gulch	Wet - Peak	404	387	0.96
San Geronimo Creek	Wet - Peak	436	369	0.85
Olema Creek	Wet - Peak	462	344	0.74
Lagunitas Creek	Wet - Peak	1244	1214	0.98
Redwood Creek	Wet - Peak	196	143	0.73
Devil's Gulch	Wet - Median	11	10	0.90
San Geronimo Creek	Wet - Median	10	9	0.85
Olema Creek	Wet - Median	22	18	0.81
Lagunitas Creek	Wet - Median	53	52	0.98
Redwood Creek	Wet - Median	12	9	0.80
Devil's Gulch	Spring - Peak	81	121	1.49
San Geronimo Creek	Spring - Peak	78	122	1.55
Olema Creek	Spring - Peak	118	178	1.50
Lagunitas Creek	Spring - Peak	226	415	1.84
Redwood Creek	Spring - Peak	74	145	1.96
Devil's Gulch	Spring - Median	5	5	0.94
San Geronimo Creek	Spring - Median	6	7	1.17

Olema Creek	Spring - Median	12	12	1.04
Lagunitas Creek	Spring - Median	37	44	1.17
Redwood Creek	Spring - Median	5	5	0.93
Devil's Gulch	Spring - ROC	-0.070	0.029	0.42
San Geronimo Creek	Spring - ROC	-0.074	0.031	0.42
Olema Creek	Spring - ROC	-0.076	0.031	0.41
Lagunitas Creek	Spring - ROC	-0.076	0.066	0.87
Redwood Creek	Spring - ROC	-0.067	0.019	0.28
Devil's Gulch	Dry - Minimum	0.17	0.19	1.08
San Geronimo Creek	Dry - Minimum	0.19	0.19	1.00
Olema Creek	Dry - Minimum	0.66	0.55	0.84
Lagunitas Creek	Dry - Minimum	7.60	0.82	0.11
Redwood Creek	Dry - Minimum	0.49	0.44	0.89
Devil's Gulch	Dry - Median	0.40	0.34	0.86
San Geronimo Creek	Dry - Median	0.44	0.35	0.79
Olema Creek	Dry - Median	1.27	1.26	0.99
Lagunitas Creek	Dry - Median	8.70	1.19	0.14
Redwood Creek	Dry - Median	0.82	0.66	0.81

Figures

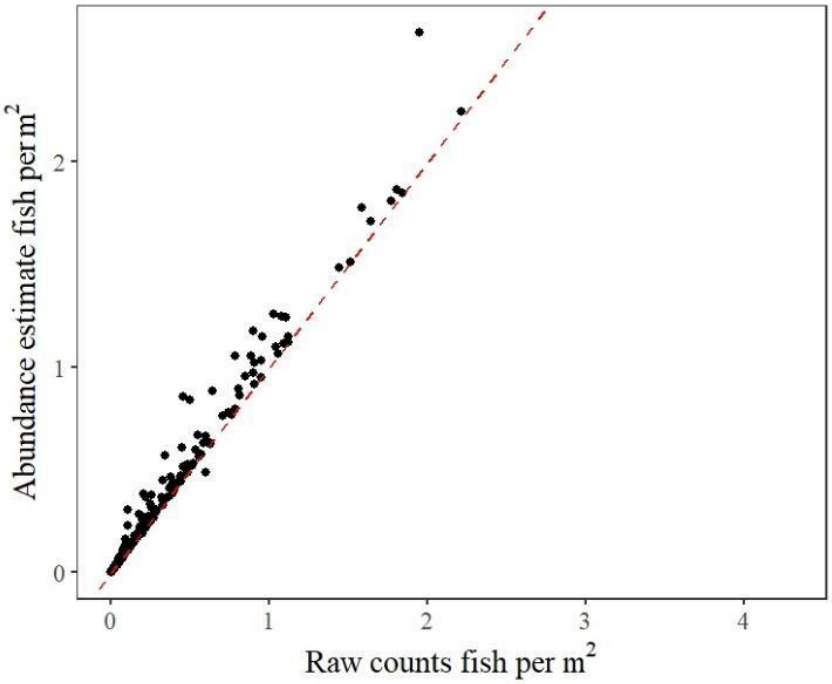
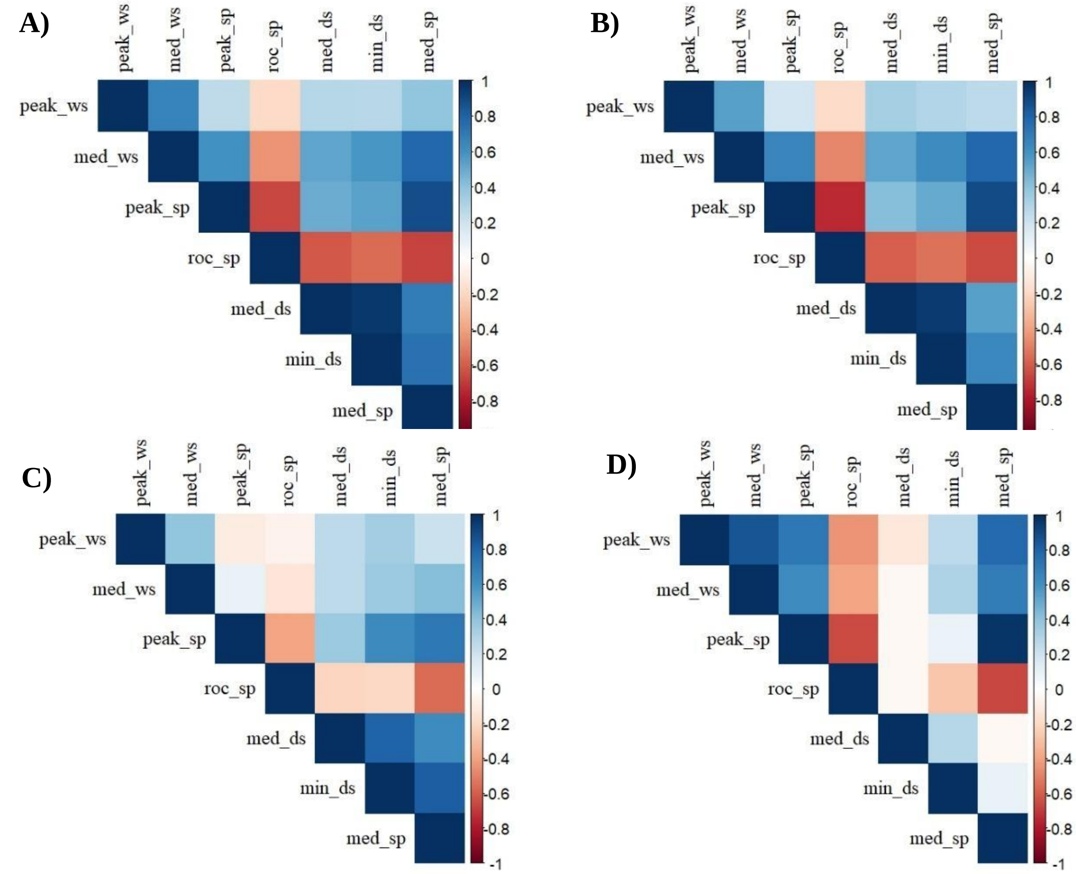


Figure S1 Regression of total juvenile fish counted in a pool by electrofishing, across all passes, and estimated abundance in a pool using electrofishing passes. The dotted red line is 1:1 regression line to show the expected relationship if juvenile counts perfectly corresponded to abundance. The linear regression model produced an estimated slope of 1.08, and an R-squared value of 0.98.



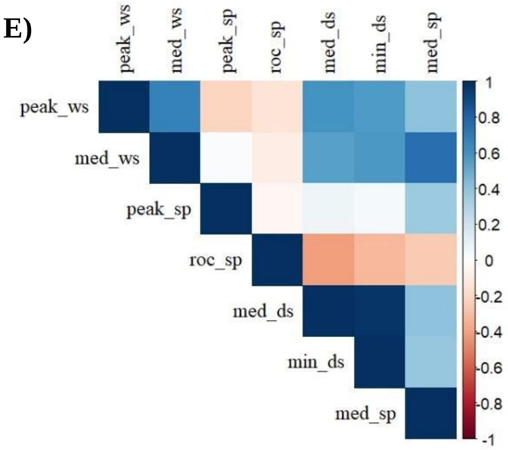


Figure S2 Pearson correlation heat maps, showing correlation between flow metrics across the time series (2005-2022) within each stream. Correlation coefficient is on a scale of -1 to 1, where -1 is perfectly negatively correlated and 1 is perfectly positively correlated. Plots for each stream are as follows: (A) Devil's Gulch, (B) San Geronimo Creek, (C) Olema Creek, (D) Lagunitas Creek, (E) Redwood Creek.

Chapter 3

Spawning distributions through space and time: a case study of an endangered coho salmon population complex in a coastal California watershed

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Abstract

When salmon breed across a watershed, their progeny are also distributed, which exposes juvenile salmon to different environmental conditions, promotes trait variation in offspring, and buffers the population against disturbance. Yet, the factors that control variation in the spatial distribution of spawning are poorly understood. We hypothesize that spawning distributions of Pacific salmon near their southern edge are constrained by rainfall patterns, which influence when flows are sufficient for upriver migration. We test this hypothesis by exploring how spawn timing and location varied across an 18-year time series in an endangered coho salmon population complex in relationship to hydrological variability. Specifically, we compared the onset, peak, and window length of spawning between two sub-basin populations, one with a regulated flow regime and one with a natural flow regime, and the effects of wet season flow timing, variability, and magnitude. Additionally, we used otoliths collected from spawners across 10 years to investigate dispersal patterns of returning adults within and outside of the watershed, giving us insight into the structure of the meta-population of the region. Our results show that in the larger, regulated sub-basin (Lagunitas Basin), the tails of the spawn timing distribution were stable across time and buffered against precipitation variability by regulated flow releases, while the smaller, unregulated sub-basin (Olema Basin) was characterized by highly variable spawn timing, largely driven by variability in wet season flows. Interestingly, the central tendencies of spawning were conserved between the two basins, suggesting that the timing of winter precipitation events – and not simply flow – is an important cue for initiating spawning. Otolith analysis and spawner age structure records revealed that the Olema Basin spawning population was supported by dispersal of fish from Lagunitas Basin, as well as from dispersal of individuals from outside of the watershed and fish from other age classes. Drought severely impacted spawn timing and spawner origins in the Olema Basin, where spawn timing was delayed and restricted and some cohorts were "rescued" by dispersing fish from elsewhere. Our findings show that climate variability can negatively impact spawning salmon, yet diverse stream habitats can buffer the metapopulation against by giving rise to spawning trait diversity and supporting colonization/recolonization of smaller subpopulations, contributing to resilience and the persistence of endangered salmon complexes.

Introduction

Pacific salmon *(Oncorhynchus* spp.*)*, keystone species of significant cultural, economic, and ecological importance, have faced widespread declines across their range (Nehlsen et al. 1991; Huntington et al. 1996; Nehlsen 1997). Steep reductions in many populations have been linked to habitat loss and degradation, extensive dam construction and loss of access to historic spawning and rearing areas, as well as intensive human exploitation and the resulting hatchery supplementation (Brown et al. 1994; Yoshiyama et al. 1998; Lichatowich et al. 1999; Lackey 2003). Despite restoration efforts and regulations to support salmon recovery, decreases in abundance and diversity have continued, which has pushed some populations to the brink of extinction (Katz et al. 2013; Munsch et al. 2022; Atlas et al. 2023). Climate change is an added stressor on declining populations, especially (but not exclusively) at the southern end of their range (Katz et al. 2013; Herbold et al. 2018; Crozier et al. 2019).

Contemporary salmon conservation science has revealed that resilient salmon populations are often comprised of distinct subpopulations distributed across the landscape. Such diversity can buffer the overall population complex to environmental variation and, over time, promote stability and resilience (e.g., Hilborn et al. 2003, Schindler et al. 2010). Spawning plays a particularly important role in preserving the structure of population complexes by influencing the temporal and spatial distribution of juveniles, and hence, the heterogeneity of landscapes that give rise to diverse habitats, diverse life histories, and, ultimately, population diversity (Waples et al. 2009; Schindler et al. 2010). Variation in spawn timing within a year, for example, moderates the risk from disturbance during egg incubation and emergence (Beer & Anderson 2001; McGlauflin et al. 2011; Sparks et al. 2019). Spawning that is distributed across a watershed can also mitigate risk from disturbance, as well as expose juveniles to distinct habitats and growth opportunities (Rossi et al. 2024).

Metapopulations link these distinct subpopulations of salmon together through dispersal (Schtickzelle & Quinn 2007). Dispersal in space, for example spawning adults dispersing into non-natal streams, is thus critical for metapopulation persistence, demographic subsidies to small populations (Bett et al. 2017), and for colonizing non-natal habitats made available following restoration or disturbance events (Anderson & Quinn 2007; Pess 2009; Quinn 2018). Dispersal can also occur through time, such as through age-complexity (Buoro & Carlson 2014). For instance, some salmon spend only one year in the ocean and mature earlier than others in their cohort. These early returns, called jacks, alleviate risk of cohort failure from their brood year, and contribute to the spawning population (Keefer & Caudill 2014; King et al. 2023).

Taken together, this body of work emphasizes that variation in spawning traits underpins the persistence and resilience of salmon populations (Greene et al. 2010). Yet, few studies have characterized variation in spawning through space and time or identified the environmental drivers that contribute to such variation (Kovach et al. 2015; LovellFord et al. 2020; Butler et al. 2021; Austin et al. 2023), especially in populations vulnerable to extinction. In coastal Mediterranean-climate California, the strong seasonality and high interannual variability in precipitation has been shown to strongly affect many life stages of salmon. For example, in wet years, high flows in the winter and spring inundate floodplains and provide juvenile salmon with access to highly productive habitats that improve their growth and survival (Sommer et al. 2001;

Goertler et al. 2018), while in drought years, lows flows can limit the extent of juvenile rearing habitat (Obedzinski et al. 2018) and constrict the timing of outmigration to the ocean (Kastl et al. 2022). The influence of precipitation variability on adult spawning traits is less well understood. However, given the potential for low flows to limit stream connectivity until the onset of the wet season (Moidu et al. 2021), precipitation (and stream flow) patterns likely influence when adult salmon can access breeding sites and their ability to disperse throughout the river network. Given projections of increased precipitation variability and warmer temperatures with climate change, the timing and distribution of spawning could be further restricted (Flitcroft et al. 2019; Tillotson et al. 2021) and there is some indication these predictions are already being realized (Carlson et al. *in prep*). Moreover, human water uses could be expected to further limit water available in California's salmon-bearing streams (Gasith & Resh 1999), although there is also potential for dams to be operated for ecological benefits by providing environmental flows (Kiernan et al. 2012; Yarnell et al. 2015, 2020), including for salmon migration, spawning, and rearing.

Lagunitas Creek in Marin County, California is an ideal system in which to explore the impacts of variability in precipitation and stream flow on salmon spawn locations and timing - and how flow modifications alter these relationships. The watershed supports a small, yet persistent, population of natural-origin Central California Coast Coho Salmon at their southernmost limit (Miller 2010). The Lagunitas mainstem is regulated by dams but its largest tributary, Olema Creek, is not, providing an opportunity to contrast how climate variation - in a regulated vs. natural flow regime context - influences the timing of spawning. Moreover, the diverse underlying geology of the two major stream subbasins also offers the ability to identify provenance and dispersal of returning adults using variation in otolith microchemistry, building on methods employed in California's Central Valley and elsewhere (Barnett-Johnson et al. 2008, 2010; Johnson et al. 2012).

In this study, we used an 18-year data set on spawner distributions of coho salmon in the Lagunitas Watershed in California to (1) characterize adult spawn timing and location within the watershed and (2) explore the influence of hydrology on timing and location. Additionally, we used otoliths collected from adult spawners to (3) reconstruct natal origin and characterize adult dispersal patterns. We focused on the two major subbasins: Olema Creek basin (hereafter "Olema Basin") and Lagunitas Creek mainstem basin (hereafter "Lagunitas Basin"), identified as the basin upstream of the confluence with Olema Creek. We hypothesized that different aspects of spawning phenology (start, end, peak of spawning) are driven by key components of the hydrograph that capture the onset, variability, and intensity of the wet season. We predicted more stable spawn timing across years in the Lagunitas Basin given it is a larger, regulated stream system with managed flows that are somewhat buffered against precipitation variability. In contrast, we hypothesized that spawn timing would be more variable in the smaller Olema Basin, reflecting greater flow variability. Finally, given the much larger size of the Lagunitas Basin (230 km^2) versus the Olema Basin (38 km^2), and the larger size of adult coho salmon breeding in the Lagunitas Basin (avg. redds across years: 154, SD: 89) compared to Olema Basin (avg. across years: 38, SD: 39), we hypothesized that Lagunitas Creek would act as a "source population", potentially subsidizing smaller subpopulations, such as Olema Creek. Through our investigation of spawn timing and dispersal in the greater Lagunitas watershed, we ultimately sought to understand how adult spawning traits vary with wet season conditions and flow regulation and thus gain insight into coho salmon resilience in an increasingly variable climate.

Methods

Study system

The Lagunitas Creek watershed is a small (270 km^2), coastal watershed in Marin County, California, whose seasonal hydrology is largely driven by winter rainstorms consistent with other rivers in the region (Lane et al. 2017). It is home to a small but persistent wild population of coho salmon, which are part of the Central California Coast (CCC) Coho Salmon Evolutionarily Significant Unit (ESU). This ESU is listed as endangered and is the southernmost conservation unit for this species. Much of the historic habitat of coho salmon within this ESU has been restricted by dams or heavily modified by logging and other anthropogenic uses (Brown et al. 1994). In the Lagunitas Basin a series of dams on the mainstem and a major tributary (Nicasio Creek) have blocked access by migratory fishes including salmonids to approximately 50% of the watershed (149 km^2). The habitat available to salmonids within the Lagunitas Creek watershed spans the two major subbasins: Lagunitas Basin encompasses the mainstem creek and its tributaries (San Geronimo Creek, Devil's Gulch, Cheda Creek) on the eastern side of the watershed, and Olema Basin contains Olema Creek and its tributaries (including John West Fork) on the western side **(Figure 1)**. The confluence of Olema Creek with Lagunitas Creek is near the head of Tomales Bay, a perennially open estuary.

Beyond differences in their size and underlying geology, the two basins also differ in their contemporary flow regimes. Olema Creek maintains a natural flow regime, whereas the mainstem Lagunitas Creek has a regulated flow regime. Notably, Marin Water, as the public agency operating the four reservoirs on Lagunitas Creek, is mandated to conserve key parts of the hydrograph that are important for salmon life history such as elevated summer baseflows for rearing juveniles, fall pulse flows to attract spawning salmon, and raised winter baseflows to provide spawning access and habitat (Marin Municipal Water District 2011). Specifically, in the spawning season there is an instream flow requirement of 0.57 cubic metres per second (cms) starting November 15th in the absence of winter storms, which is increased to 0.71 cms in January if needed (Ettlinger et al. 2023). In years with little precipitation, there are mandated flow pulses released from the Kent Lake reservoir (impounded by Peters Dam) into Lagunitas Creek to provide cues intended to initiate coho salmon upstream migration, starting November 15th and occurring again on December 1st and January 1st (Ettlinger et al. 2023). Spawning access and cues are presumed to be somewhat independent of one another between basins given the streams are connected low in the system, enabling us to compare the conditions that support spawning in the two basins, including the distribution of spawners across basins as well as the timing of spawning.

Spawner surveys & otolith collection

Adult coho salmon in central California coastal streams typically move upstream starting in mid-November and spawn quickly afterwards, with spawning typically lasting until mid-January (Weitkamp et al. 1995). Spawner surveys for coho salmon and steelhead trout are conducted annually in the Lagunitas Basin by staff at Marin Water with support from California Department of Fish and Wildlife and the Salmon Protection and Watershed Network, and in the Olema Basin by National Park Service staff. Surveyors walk sections of a stream once a week from the beginning to the end of spawning season (roughly November to April), recording the location and counts of live fish, carcasses, and redds (for detailed methods see McNeill et al. 2020; Ettlinger et al. 2023). Starting in the 2009-2010 spawning season, the monitoring programs began collecting sagittal otoliths from salmonid carcasses. When surveyors encounter a carcass, they extract both otoliths if possible and note the species, sex, maturity, fork length, location of the carcass, and date of collection. From 2009-2019, 322 otoliths from 251 coho salmon adults across the watershed were collected and transferred to the University of California Berkeley.

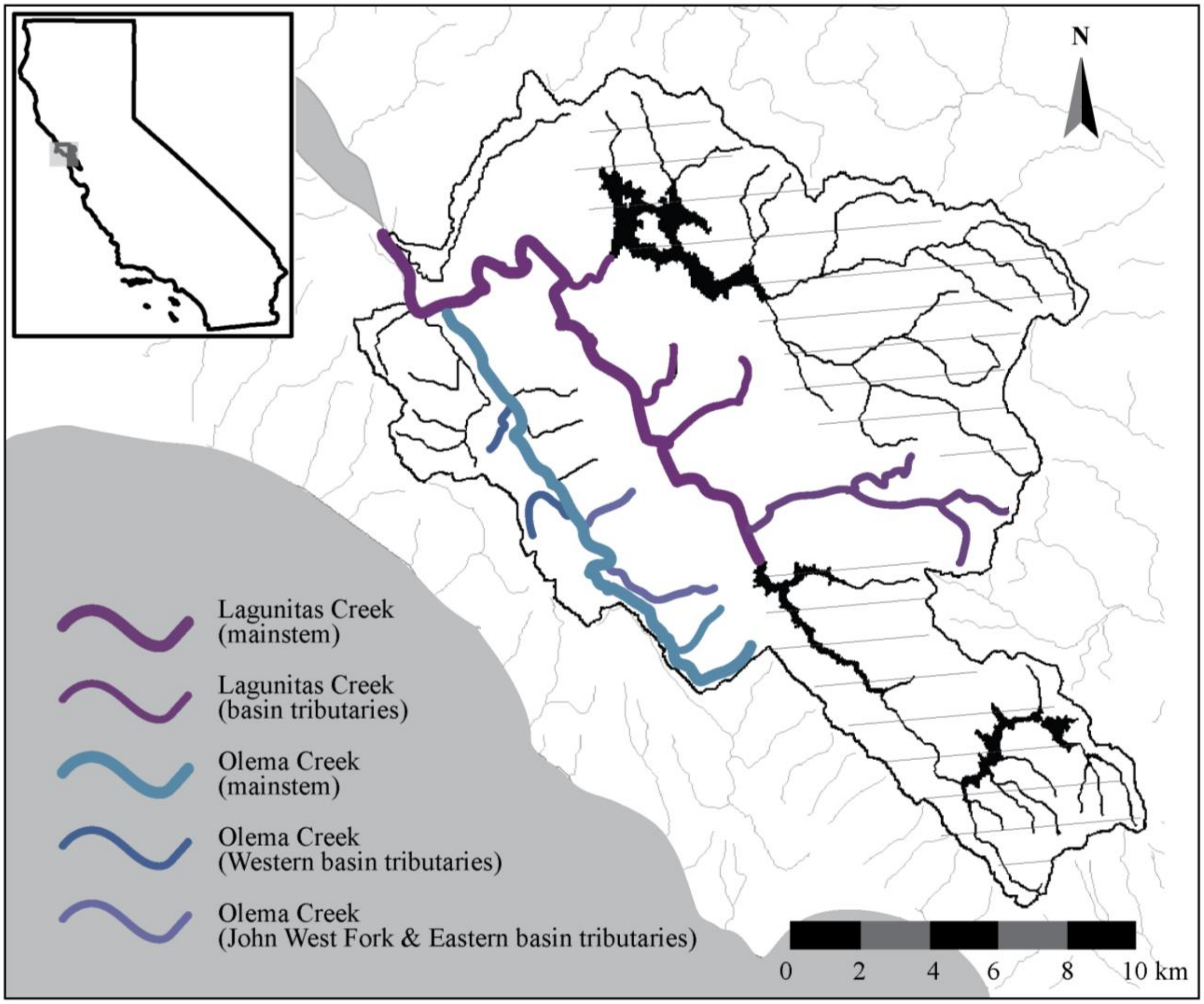


Figure 1 Map of study system. Lagunitas Creek watershed region highlighted on the California map (inset). The entire Lagunitas Creek watershed is outlined in black, with grey lines indicating the area of the watershed inaccessible to anadromous salmonids. Purple lines indicate all streams within the Lagunitas Creek subbasin included in spawn timing and dispersal analysis. Blue lines indicate streams within the Olema Creek subbasin, with tributaries shaded by the part of the subbasin they drain to account for differences in underlying geology, including the notable intermittent tributary John West Fork. Line thickness corresponds to stream size; thicker lines are the mainstems in the subbasin, while thinner lines are tributaries. Note that Olema Creek is a tributary of Lagunitas Creek.

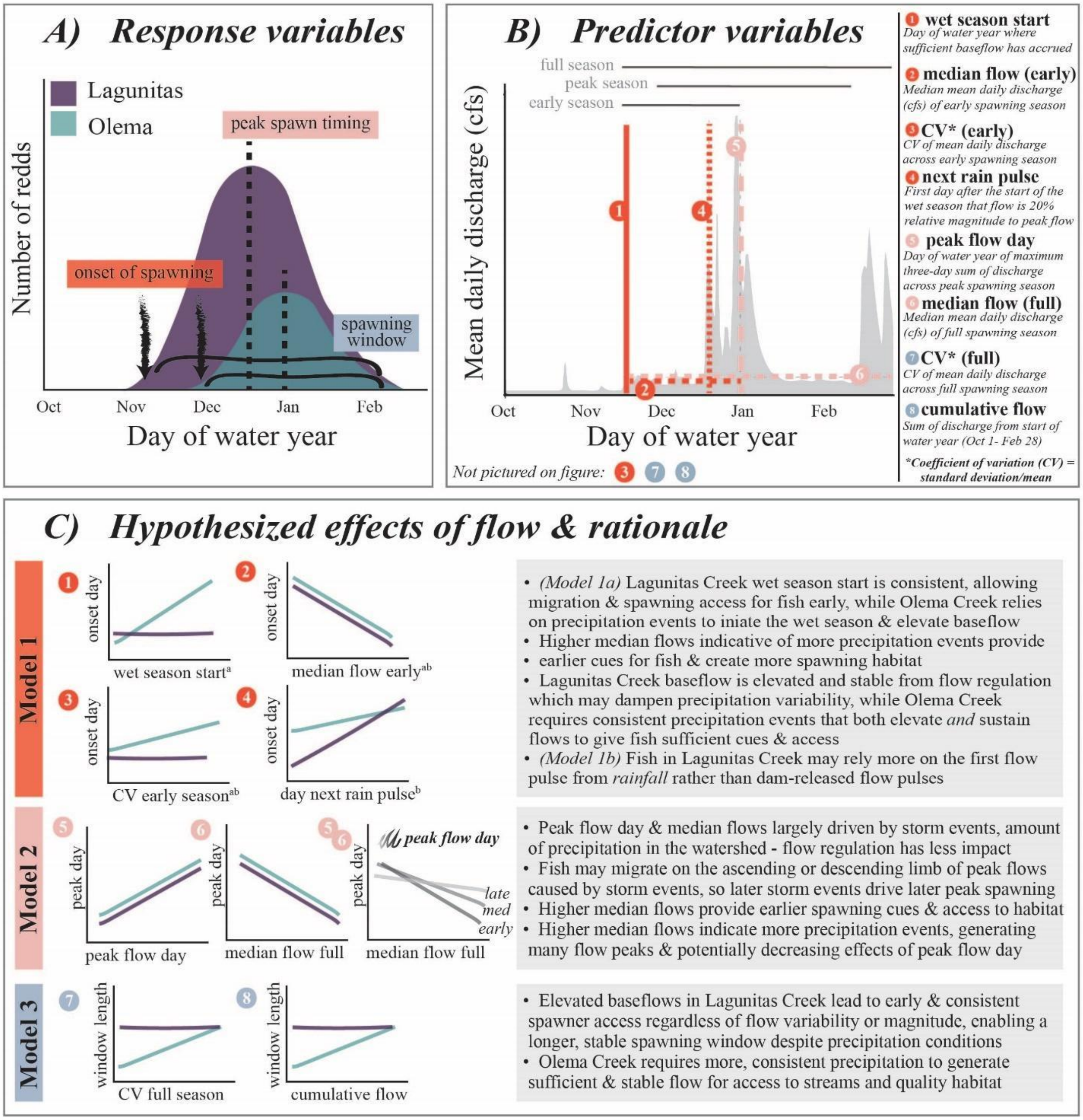
Characterizing spawn timing

We characterized spawn timing for the Lagunitas Basin and Olema Basin across water years 2005-2022. Redd counts were summarized by week for each California water year (i.e., starting October 1st of the previous year). We calculated three spawn timing metrics for each year and basin: date of onset of spawning, date of peak spawning, and length of the spawning window (**Figure 2A**). We selected these metrics to capture different mechanisms by which aspects of flow, including flow modification, might influence spawning phenology. For example, regulated flow could lead to an earlier onset of spawning as compared to an unregulated stream and could shift the entire spawning window earlier, including the peak spawn timing, while conserving the length of the spawning window. Alternatively, the timing of the majority of spawning may be conserved between streams if cues fish are responding to are not entirely captured by flow releases, and the spawning window may be more plastic, extended by later precipitation events. The discrepancies between the onset of spawning, peak spawn timing, and length of the spawning window have implications for the spatial distribution of offspring across the watershed, as well as the offspring emergence patterns suggesting a need to explore all three aspects of spawn timing.

The onset of spawn timing was defined as the week at which the fifth percentile of cumulative redds for the year was reached, representing the timing for the main portion of the spawning run (Flitcroft et al. 2019). Peak spawn date was defined as the week where the maximum number of redds was recorded. The spawning window was calculated as the number of days between the first day of the week where the fifth percentile was recorded and the last day of week where the ninety-fifth percentile of redds was reached. We summarized the mean, minimum, maximum, and coefficient of variation (CV, standard deviation/mean) of the spawn timing metrics across the time series to assess long-term variability of spawn timing. Yearly spawn timing metrics were used in models with hydrological variables to assess drivers of spawn timing variability, as described below.

Hydrological variation & impacts on spawn timing

To characterize hydrological variability and alteration and test how hydrology influences spawn timing, we calculated 8 flow metrics for Lagunitas Creek and Olema Creek, focusing on the fall-winter transition and winter season that encompass the coho salmon spawning window **(Figure 2B)**. Using evidence from the literature on spawn timing (Shapovalov & Taft 1954; Alabaster 1970; van den Berghe & Gross 1989; Tetzlaff et al. 2008; LovellFord et al. 2020; Butler et al. 2021) and ecological functional flows (Yarnell et al. 2015, 2020), we selected flow metrics that represent the timing, intensity, and variability of wet season flows. We obtained mean daily discharge (flow) data, in cubic metres per second, from stream gauges on Lagunitas Creek (USGS 11460400) and Olema Creek (USGS 11460605 [2017-2022], National Park Service [2005-2017]). We divided the spawning season into the early season (November 15-December 31), mid-season (November 30-February 12), and full season (November 15-February 28/29) based on long-term spawn timing across the watershed. The early season was defined as one week before the earliest date of spawning onset (5th percentile of redds recorded) for the entire watershed until one week after the latest date of spawning onset. The mid-season encompasses one week before the earliest date at which the 50th percentile of cumulative redds across the watershed was reached until one week after the latest date. The full spawning period was defined as the week before the earliest onset date and one week after the latest date where the 95th percentile of redds was reached across the watershed. Seven flow metrics were calculated directly from the gauge data, while the start timing of the wet season was estimated using functional flow metric algorithms (Patterson et al. 2020). We summarized long-term average and variability in hydrological conditions by calculating the mean and CV of each flow metric across the study period.



1 wet season start Day of water year where sufficient baseflow has accrued

2 median flow (early) Median mean daily discharge (cfs) of early spawning season

3 CV* (early) CV of mean daily discharge across early spawning season

4 next rain pulse First day after the start of the wet season that flow is 20% relative magnitude to peak flow

5 peak flow day Day of water year of maximum three-day sum of discharge across peak spawning season

6 median flow (full) Median mean daily discharge (cfs) of full spawning season

7 CV* (full) CV of mean daily discharge across full spawning season

8 cumulative flow Sum of discharge from start of water year (Oct 1- Feb 28)

***Coefficient of variation (CV) = standard deviation/mean**

- *(Model 1a)* Lagunitas Creek wet season start is consistent, allowing migration & spawning access for fish early, while Olema Creek relies on precipitation events to iniate the wet season & elevate baseflow
- Higher median flows indicative of more precipitation events provide
- earlier cues for fish & create more spawning habitat
- Lagunitas Creek baseflow is elevated and stable from flow regulation which may dampen precipitation variability, while Olema Creek requires consistent precipitation events that both elevate *and* sustain flows to give fish sufficient cues & access
- *(Model 1b)* Fish in Lagunitas Creek may rely more on the first flow pulse from *rainfall* rather than dam-released flow pulses

- Peak flow day & median flows largely driven by storm events, amount of precipitation in the watershed - flow regulation has less impact
- Fish may migrate on the ascending or descending limb of peak flows caused by storm events, so later storm events drive later peak spawning
- Higher median flows provide earlier spawning cues & access to habitat
- Higher median flows indicate more precipitation events, generating many flow peaks & potentially decreasing effects of peak flow day

- Elevated baseflows in Lagunitas Creek lead to early & consistent spawner access regardless of flow variability or magnitude, enabling a longer, stable spawning window despite precipitation conditions
- Olema Creek requires more, consistent precipitation to generate sufficient & stable flow for access to streams and quality habitat

Figure 2 Spawning traits, hydrological predictors, and model hypotheses. A) We developed three generalized linear models where the response variables were one of three spawning traits: onset day of spawning, peak day of spawning, length of the spawning window. Response variables are colour-coded according to the model. The spawning traits are depicted on hypothetical distributions for Lagunitas Basin (purple) and Olema Basin (blue). B) An example hydrograph from Lagunitas Creek in 2011 with flow metrics used as predictor variables in models overlaid, colour-coded according to the model they are used in. Flow metrics were calculated for both Lagunitas Creek and Olema Creek. Grey horizontal bars indicate the long-term average length of the early, peak, and full spawning seasons across the watershed. Numbers on the right correspond to hydrograph components (3, 7, 8 are not pictured), with names and brief descriptions in the right-hand column. C) Hypothesized effects of flow metrics on spawn timing response variables for Lagunitas (purple) and Olema (blue) Basins and rationale.

To evaluate whether variation in spawn timing was explained by hydrological conditions, we developed a model for each spawning metric. We used generalized linear models with a log link function, where the family depended on the shape of the response data. In each model, we tested the effect of basin in addition to carefully selected flow metrics corresponding to hypotheses for our system (**Figure 2C**). Where we expected the effects of flow metrics to vary by basin because of flow modification in Lagunitas Creek, we included an interaction effect. We explored preliminary relationships between the spawning metric and discharge metrics to assess shape of the curve and determined whether to adjust for a non-linear relationship (e.g., logarithmic curve). We tested that all predictors in a model did not exhibit significant collinearity using Pearson correlations ($r > 0.7$), selecting the most ecologically relevant predictor of a pairing for inclusion in the model if the threshold was exceeded. All model residuals were assessed to ensure proper model fit and we compared the Akaike Information Criterion (AIC) between "base" models with only the basin as a predictor and full models to verify that our discharge metrics explained more variation than basin when considered alone. Analyses were conducted in R Statistical language (version 4.3.2; R Core Team, 2024). Specifics for each spawning metric model and their accompanying hypotheses are described in **Figure 2C** and below.

i) Model 1(a,b): Onset of spawning model

We modeled the day of the onset of spawning for each basin using a gamma distribution as the data was positively skewed. The flow metrics used as predictors were the day of the wet season start, the CV of the early spawning period, and the median flow of the early spawning period **(Equation 1)**:

$$Day\ onset = exp\ (\beta_0 + \ \beta_1 * Basin + \beta_2 * flow + \beta_3 * CV + \beta_4 * wet\ start\ + \beta_5 * Basin * CV + \beta_6 * Basin * wet\ start)$$

Given the modification of the first major flow pulse in Lagunitas Creek, we also tested a version of the model where wet season start was replaced with the date of the first peak of 20% relative flow *after* the start of the wet season. We compared the AIC of the models and beta estimates of the wet season start (Model 1a) versus first pulse post-wet season (Model 1b) to test the hypothesis that the first pulse flow after base flows had been elevated is the main cue for spawning fish in Lagunitas Creek, rather than the onset of the wet season as indicated by the elevation of baseflow levels.

ii) Model 2: Peak day of spawning model

We modeled the peak day of spawning for each basin again using a gamma distribution. The flow metrics used as predictors were the day of peak flow within the middle spawning period and the median flow for the entire spawning season, log transformed as we expected a logarithmic relationship **(Equation 2)**:

$$Day\ peak = exp\ (\beta_0 + \ \beta_1 * Basin + \beta_2 * peak\ day + \beta_3 * log\ log\ (flow)\ + \beta_4 * peak\ day * log\ log\ (flow))$$

iii) Model 3: Length of spawning window model

Length of spawning window for each basin was modeled using a gaussian distribution and the flow metrics used as predictors included cumulative flow from the start of the water year through to the end of the spawning season, log transformed, and the CV across the spawning season **(Equation 3)**:

$$Window\ length = exp\ (\beta_0 + \ \beta_1 * Basin + \beta_2 *log\ log\ (flow)\ \ + \beta_3 * CV + \beta_4 * Basin * CV + \beta_6 * Basin * log\ log\ (flow))$$

Characterizing natal origin of adult returns

To characterize natal origins of returning adult coho salmon based on their otoliths, we first developed an "iscoscape", building on the approach employed in assessments of California's Central Valley chinook salmon populations (Barnett-Johnson et al. 2008). In short, we created an isoscape of stream ^{87}Sr/^{86}Sr values in the Lagunitas Creek watershed (see ***Supplemental Materials*** for detailed methods). We then used laser ablation inductively coupled plasma mass spectrometry (LA-ICPMS) along transects on polished otoliths to produce ^{87}Sr/^{86}Sr profiles from otolith core to ocean entry (Barnett-Johnson et al. 2008). From the resulting profiles, we isolated the point where fry began feeding exogenously, when ^{87}Sr/^{86}Sr values no longer contain maternal signature and instead reflect the natal stream isotopic makeup. We matched the ^{87}Sr/^{86}Sr otolith signature at the natal region to our established ^{87}Sr/^{86}Sr values within the watershed using a linear discriminant function analysis to assign natal origin of the fish (***Supplemental Materials*** for detailed methods).

Samples within the watershed revealed distinct ^{87}Sr/^{86}Sr value differences between Lagunitas Basin (avg. 0.706415, 4.11E-04 SD) and Olema Creek mainstem (avg. 0.707528, 1.22E-04 SD) that we could leverage to distinguish basin origin of returning fish. In addition, eastern intermittent tributaries of Olema Creek, including the notable salmon-bearing stream John West Fork (JWF), had an Sr isotopic value (avg. 0.706585, 1.47E-04 SD) similar to Lagunitas Creek mainstem (**Table S1, Figure S1b-c**). While the Lagunitas Basin and JWF signatures overlapped, we assumed fish with this natal signature but returned to Lagunitas Basin were of Lagunitas-origin given the much larger size of the Lagunitas Basin spawning population. We assumed fish that had the overlapping signature but shifted to the Olema Creek signature shortly after emergence were more likely JWF-origin, given that JWF is a tributary of Olema Creek. When fish with this natal signature did not have the Olema Creek signature in their freshwater profile but returned to spawn in the Olema Basin, we used multiple lines of evidence to assign natal origin (see ***Supplemental Materials*** and **Table S2**). This suite of approaches allowed us to determine natal origin on a finer scale within the Olema Creek watershed.

Fish that returned to basins within the watershed that differed from their natal origin were labeled "interbasin" strays. In some cases, the otolith signature did not match any watershed Sr isotopic values from within the system, so we assumed it originated from outside of the watershed and classified it as an "out-of-watershed" stray. We sampled streams from outside the basin to determine provenance for these fish but were unsuccessful in finding the source population or identifying between possible source populations (full list of Sr values are included in **Table S1**, see also **Figure S1a-c**). Consequently, we include four possible natal origins (Lagunitas Basin, Olema Creek, JWF, out-of-watershed) and two possible stray types (interbasin strays and out-of-watershed strays) in our final analyses.

Field data collected with carcasses indicated whether a spawner was a three-year old adult or a two-year old "jack", a precocial male that only spent one year in the ocean before returning to spawn. Where age was not indicated, we assigned fish that were <51cm in fork length as jacks, based on the range of fork lengths of recorded jacks in the system (34-47cm) and documented lengths of full adult (Moyle 2002). We plotted the natal origin data by return water year to visualize the contributions of each natal origin (dispersal in space) and maturity type (dispersal in time) to the adult returns to the Lagunitas Basin and Olema Basin across the study period.

Because of the much larger size of the Lagunitas Basin relative to the Olema Basin (230 km^2 versus 38 km^2, respectively) as well as the larger number of adult spawners in the Lagunitas Basin relative to Oleman (avg. across years 154 redds vs 38 redds, respectively), we hypothesized that Lagunitas is a "source" population contributing a demographic subsidy to nearby, smaller populations (including Olema). The importance of this subsidy may be most pronounced in years with low Olema-origin returns, or very high Lagunitas-origin returns. Furthermore, we hypothesized that in years where discrepancies in fall-winter flow between basins were most pronounced, the propensity of Lagunitas-origin fish to stray into the Olema Basin (i.e., the interbasin stray rate of Lagunitas-origin fish) would decrease because of greater access to Lagunitas Basin. Specifically, different flow conditions in Olema Basin reflecting the natural flow regime such as later onset of the wet season, lower discharge, and higher variability in the early fall-winter months might decrease the Lagunitas-origin interbasin stray rate.

To examine these patterns, we first assessed the proportion of Lagunitas-origin fish that comprised the Olema Basin spawning population to understand Lagunitas contributions to Olema Basin productivity (defined as the number of redds). We then looked at the proportion of Olema Basin that was made up of all strays (from Lagunitas and outside of the watershed). The stray rate of Lagunitas-origin fish into Olema Basin was calculated as the number of redds of Lagunitas-origin found in the Olema Basin divided by the sum of the total number of redds attributed to Lagunitas-origin across the watershed within a year. We adjusted the otolith return numbers to number of redds by multiplying the proportion of returns of each natal origin by the total number of redds recorded in each basin, allowing us to account for differences in recovery rate of carcasses across the watershed. We assumed that the subset of returning fish from which otoliths had been extracted was approximately representative of the whole spawning population of each basin (see also Cordoleani et al. 2024). Given the short time series of our straying data (9 years), we were unable to develop robust models with demographic and environmental predictors to test hypotheses. However, we ran Pearson correlation tests to explore correlations between (1) the proportion of Lagunitas-origin strays making up the Olema Basin spawning population and two demographic variables (total number of Lagunitas-origin returns, Olema-origin returns, adjusted for number of redds recorded) and (2) the stray rates of Lagunitas-origin fish and eight Olema Creek flow variables (onset of wet season, CV of discharge in the early and entire spawning season, early and full season median flow, cumulative discharge since Oct 1st at the end of October, November, December). These tests are included as an exploratory analysis of factors that might be important to consider in future studies of dispersal within the Lagunitas Creek watershed coho complex.

Results

Interannual and interbasin variability in spawn timing

Over the 18 spawning seasons from 2005-2022, the Lagunitas Basin on average had an earlier onset of spawning (18 days earlier), earlier peak time of spawning (8 days earlier), a longer window of spawning (24 days longer), and four times as many redds (154 redds) as compared to Olema Basin (38 redds) **(Table 1)**. Moreover, the date of onset of spawning, window of spawning, and total number of redds varied less among years in the Lagunitas Basin than the Olema Basin. Differences in spawn timing and spawning window length were most pronounced in 2012, 2014, 2018, 2021, though peak spawn timing was similar between basins (the exception being 2021) **(Figure 3)**. In the Lagunitas Basin, the onset of spawning was between November 19th and December 17th, and the window of spawning was 3-12 weeks. In contrast, the onset of spawning in the Olema Basin was between November 26th and February 11th, with the window of spawning ranging from 0 (all fish spawned within one week, such that final week minus initial week is zero) to 9 weeks. Additional visualizations of interannual variability in spawning and redd accumulation over the spawning season can be found in the ***Supplementary Materials*** **(Figure S3)**.

Table 1 Mean, minimum, maximum, and coefficient of variation (CV) of spawn timing metrics and total number of redds for Olema Basin and Lagunitas Basin across the sampling period 2005-2022. Values for mean, minimum and maximum for spawn timing metrics are in water year days (starting October 1st).

	Lagunitas Basin				Olema Basin			
Spawning metric	**Mean**	**Minimum**	**Maximum**	**CV**	**Mean**	**Minimum**	**Maximum**	**CV**
Onset	62	50	78	0.13	80	57	134	0.25
Peak	82	64	127	0.21	90	71	134	0.2
Window	54	21	84	0.34	28	0	63	0.53
Total basin redds	154	26	370	0.58	38	0	138	1.01

Hydrological variation & impacts on spawn timing

There was considerable hydrological variability across our study period, which encompassed the multi-year droughts in 2007-2009, 2012-2016, and 2020-2021, as well as a significant wet year in 2017. Lagunitas Creek had higher discharge and was less variable in most flow metrics compared to Olema Creek. Exceptions to this pattern include cumulative February discharge, where the Lagunitas pattern was slightly more variable, and day of peak flow, which was similar between basins **(Table 2)**. Several metrics varied little in Lagunitas across years, including wet season timing and early season median flow, highlighting the effects of flow regulation in providing minimum summer baseflows (0.17-0.23 cms) and elevated winter baseflows starting in mid-November (0.57 cms). Interestingly, these metrics were also the ones that showed the largest discrepancies with Olema Creek metrics. For visualizations of discharge in Lagunitas Creek and Olema Creek across 2005-2022, see ***Supplementary Materials*** **(Figure S4)**.

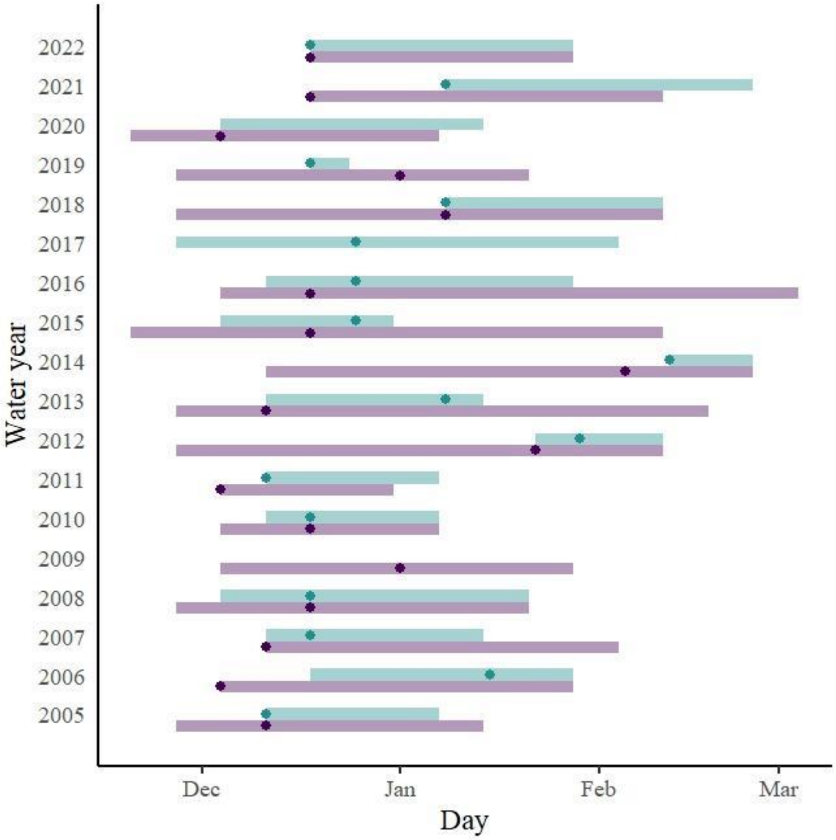


Figure 3 Spawn timing for Lagunitas Basin (purple) and Olema Basin (blue) across the study period. The x-axis is the month of year of spawning, and the y-axis is the water year of the returns (starting October 1st of the previous year). The bars start at the date at which the 5th percentile of cumulative redds is reached and continue until the date at which the 95th percentile is reached, highlighting the length of the spawning window. Dots within the bars indicate the date of peak spawning.

Table 2 Coefficient of variation (CV) and mean of discharge metrics, excluding the CV of early and full spawning season yearly CV, for Lagunitas Creek basin and Olema Creek basin across the entire study period 2005-2022. Water year day is the day from the start of the water year (October 1st) and cms is cubic metres per second. See Table S3 and Figure S4 for yearly metric values.

	Lagunitas		**Olema**	
Discharge metric	**CV**	**Mean**	**CV**	**Mean**
Day of wet season start (WY day)	0.18	43	0.40	69
First peak after wet season start (WY day)	0.30	77	0.34	85
Median discharge early season (cms)	0.36	0.77	1.29	0.30
Median discharge full season (cms)	0.68	1.03	1.21	0.39
Day of peak flow (WY day)	0.22	101	0.21	102
Total discharge Feb (cms)	0.95	290	0.69	125
CV discharge early season	-	1.08	-	1.86
CV discharge full season	-	1.52	-	2.24

The onset of spawning did not significantly differ between basins once accounting for flow variables, revealing that the later start of spawning in Olema Basin can partially be attributed to differences in discharge magnitude, variability and timing during the early spawning season (**Figure 4, Table 3A**). Early median discharge significantly affected the start of spawning in both basins, where higher flows led to earlier onset of spawning. There was no effect of discharge variability on date of the onset of spawning in Lagunitas Basin, whereas in Olema Basin there was a strong, significantly negative relationship where more variable early season flow led to an earlier onset of spawning. The onset of the wet season had a marginally positive, significant effect on spawn timing in Olema Basin where a delayed wet season resulted in a delayed onset of spawning, but in Lagunitas Basin there was no relationship. These results emphasize that the onset of spawning in Lagunitas Basin, where variability in the start of the wet season is dampened by river regulation in the mainstem, is largely driven by the amount of flow early in the season. In contrast, the onset of spawning in Olema Creek is driven by the start of the wet season, the amount of the flow, and the variability in discharge, reflecting the variation in flow conditions across years. We also modeled the onset of spawning using the first flow pulse after the start of the wet season (Model 1b), which was a relatively worse fit compared to using the start of the wet season (AIC = 256, $R^2 = 0.71$ vs AIC = 260, $R^2 = 0.68$, but see **Figure S5** & **Table S4** for results based on first pulse flow).

The model for peak spawn timing revealed marginally significant differences in the date of peak spawning once accounting for flow, with Olema Basin slightly lagging behind Lagunitas (**Table 3B**). There were significant negative effects of median flow across the spawning season, where both basins had earlier peak spawn timing when flows were higher. The day of peak flow mid-spawning season had significant positive effects, indicating that later peak flows may extend the date of peak spawning. The relationship between median flow and peak spawning date fit a logarithmic curve, with a sharper negative relationship at lower median flows (**Figure 5**). Furthermore, the relationship between median flow and peak spawning day was mediated by the day of peak flow, as the two flow variables had a significant positive interaction. This suggests that as peak flow comes later in the season, the effect of median flow becomes less negative in its influence on the date of peak spawning.

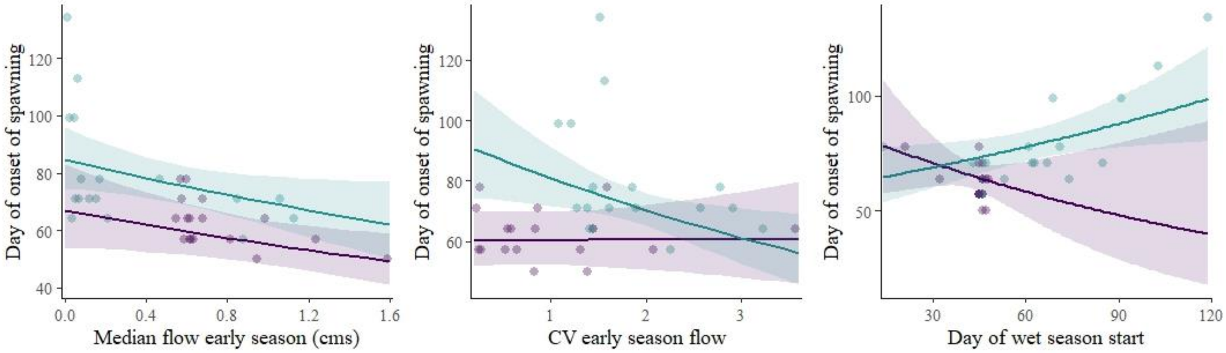


Figure 4 Observed data (points) and predicted relationships (lines with 95% confidence intervals) between the day of onset of spawning in Lagunitas Basin (purple) and Olema Basin (blue) and flow predictor variables, from left to right: median early season flow, coefficient of variation (CV) of early season flow, day of wet season start. Note that day metrics are in water year day, starting October 1st.

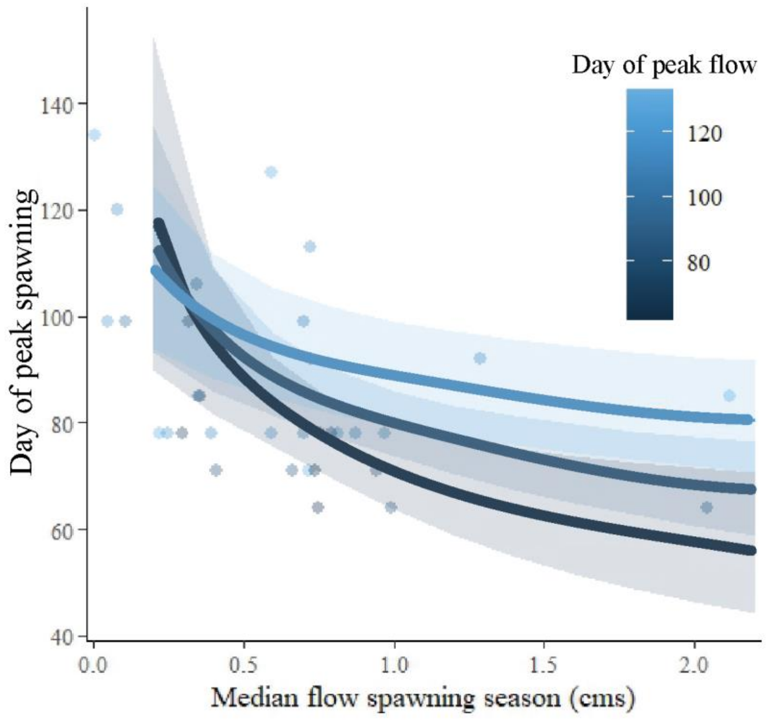


Figure 5 Observed data (points) and predicted relationships (lines with 95% confidence intervals) between the day of peak spawning (in water year day, starting October 1st) and median flow of the spawning season, mediated by the day of peak flow (water year day). Colours of the lines show how the effect of median flow varies when peak flow is early (dark blue), middle, or late (light blue) in the season.

Finally, spawning window length was not significantly different between basins once accounting for flow magnitude and variability across the spawning season (**Table 3C**). Spawning window length in both basins was negatively influenced by cumulative flow across the spawning season, showing a logarithmic relationship and no significant interaction with basin (**Figure 6**). The effect of flow variability across the spawning season on spawning window length was significantly dependent on basin; in Lagunitas, there was no significant effect, while in Olema basin the relationship was significantly negative. Thus, more variable flows across the spawning season condensed the spawning window in Olema, while lower cumulative flow lengthened of the spawning window in both basins.

Characterizing natal origin of adult returns

The number of otoliths recovered and analyzed from each basin from water years 2010-2019 represent a small subset of the total number of returning fish (1-5% of Lagunitas spawners, 3-50% of Olema spawners). Yet, ^{87}Sr/^{86}Sr profiles from otoliths revealed interesting patterns of natal contribution to spawning populations and dispersal between basins **(Figure 7)**. In Lagunitas Creek basin, most returns originated in Lagunitas (i.e., they homed to their natal basin). There was one fish reared in Olema Creek that strayed into Lagunitas in 2013, a jack from brood year 2011, while the other strays to Lagunitas Creek originated from outside of the watershed. These out-of-watershed strays were only detected in three years (2015, 2016, 2018).

Table 3 Results from generalized linear models predicting aspects of spawn timing (Model 1a = onset of spawn timing; Model 2 = peak spawn timing; Model 3 = length of window of spawning). Parameter columns contain the predictor variables used in the model, as well as the intercept. Estimate columns contain the beta estimate from the model with lower and upper 95% confidence intervals in brackets. Stars indicate significant effects, based on p-values.

A. Model 1a Results

Predictors of onset of spawning

Parameter	Estimate (95% CI)
Constant (Lagunitas Basin)	4.5*** [4.125, 5.006]
Olema Basin	-0.14 [-0.697, 0.411]
Median discharge early season (cms)	0.192* [-0.360, -0.022]
Day of wet season start (WY day)	-0.006 [-0.017, 0.003]
CV discharge early season	0.001 [-0.075, 0.081]
Olema x CV discharge early season	-0.142* [-0.278, -0.006]
Olema x Day of wet season start	0.010+ [0.000, 0.021]
Nagelkerke's R2	0.71
AIC	256.2

+ $p < 0.1$, * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$

B. Model 2 Results

Predictors of peak spawning day

Parameter	Estimate (95% CI)
Constant (Lagunitas Basin)	3.9*** [3.5, 4.2]
Olema Basin	-0.2+ [-0.3, 0.0]
Median discharge full season (cms, log-transformed)	-0.6** [-1.1, -0.2]
Day of peak flow (WY day)	0.005** [0.001, 0.009]
Median discharge x day of peak flow	0.004* [0.001, 0.008]
Nagelkerke's R2	0.5
AIC	268

+ $p < 0.1$, * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$

C. Model 3 Results

Predictors of length of spawning window

Parameter	Estimate (95% CI)
Constant (Lagunitas Basin)	141.6** [50.2, 233.0]
Olema Basin	-73.5 [-194.6, 47.7]
CV discharge full season	15.9 [-4.9, 36.6]
Total discharge Feb (cms, log-transformed)	-21.1* [-42.2, 0.0]
Olema Basin x CV discharge full season	-27.4* [-51.4, -3.4]
Olema Basin x Total discharge Feb (cms, log-transformed)	18 [-6.9, 42.9]
R2	0.51
AIC	291.4

* $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$

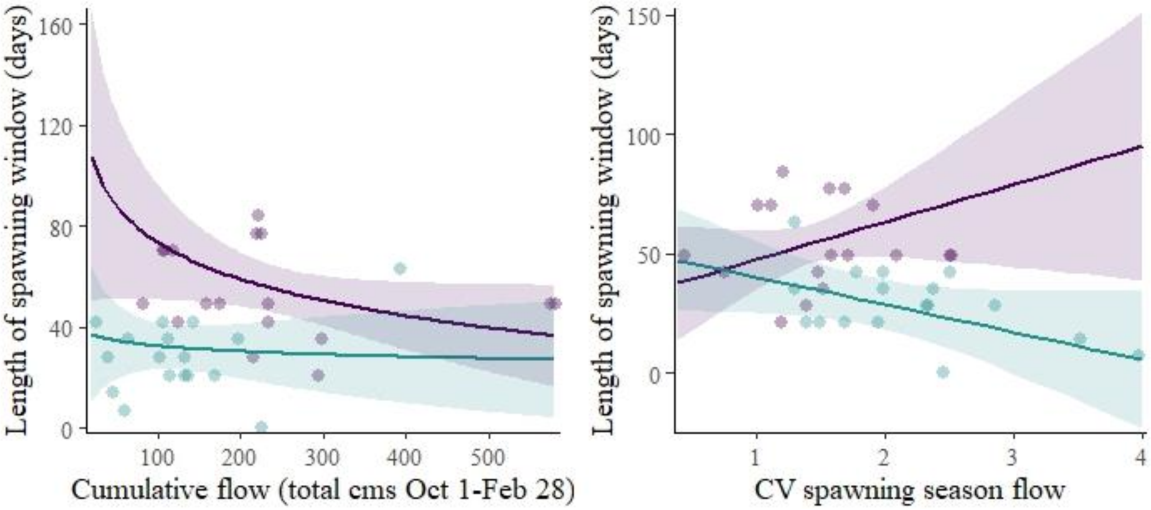


Figure 6 Observed data (points) and predicted relationships (lines) illustrating the relationship between length of the spawning window in Lagunitas (purple) and Olema (blue) Basins and the cumulative flow from October 1st to the end of February, and the coefficient of variation (CV) of the entire spawning season.

Olema Basin returning fish showed a greater diversity of natal origin contributions **(Figure 7)**. Lagunitas-origin fish strayed into Olema every year with otoliths recovered except 2019, and the contribution of fish originating in Lagunitas to the Olema Basin spawning population varied considerably across years. In 2012, for example, fish originating in the Lagunitas Basin comprised half of the spawning population in Olema Basin. In contrast, in 2019, none of the otoliths recovered from spawners in Olema Basin represented fish that originated in Lagunitas. Note that no otoliths were recovered in 2017 in Olema Basin due to challenges with surveying in this extremely wet year. Additionally, there were two years where fish from out of the watershed strayed into Olema Basin, mirroring patterns in Lagunitas. Overall, strays into Olema Basin (both from Lagunitas and outside the watershed) comprised a substantial proportion of spawners in the Olema Basin (18-67%) in all years except for 2019, and most of these originated in the Lagunitas Basin **(Table 4)**. The stray rate of Lagunitas-origin fish into Olema Basin as a function of Lagunitas-origin fish returning to the entire watershed ranged from 0 % (2019) to 11 % (2011) (avg. = 5%, SD = 4%).

Fine scale variation in ^{87}Sr/^{86}Sr signatures within the Olema Basin allowed us to further explore contributions of the intermittent John West Fork. We found that fish originating from JWF comprised a sizeable proportion of Olema Basin returns (Return WY: 2010, 2013, 2014, 2018, 2019), even during years where juveniles were impacted by drought (Brood WY: 2007, 2010, 2015, 2016), highlighting the importance of this tributary for sustaining the Olema Basin sub-population. While our sample size was small (n=6), we note that none of the adult spawners collected in Olema in 2015 showed evidence of having been born in either Olema Creek or the John West Fork in 2012. Instead, the 2015 spawning population was made up of entirely of strays and jacks from the 2013 Olema Creek cohort. Of note, returns to Olema Basin in 2012 suggested one fish originated in Olema Creek in 2009, a year when no redds were recorded. This may be attributed to a consequence of simply not detecting the redds in the field, but Sr isotopic data from the nearby Warm Springs Hatchery in the Russian River watershed overlapped with the Olema Creek Sr isotopic signature suggesting hatchery strays into Olema Basin are also plausible. More work needs to be done to investigate the possibility of hatchery-origin strays from the Russian River into the Lagunitas Basin.

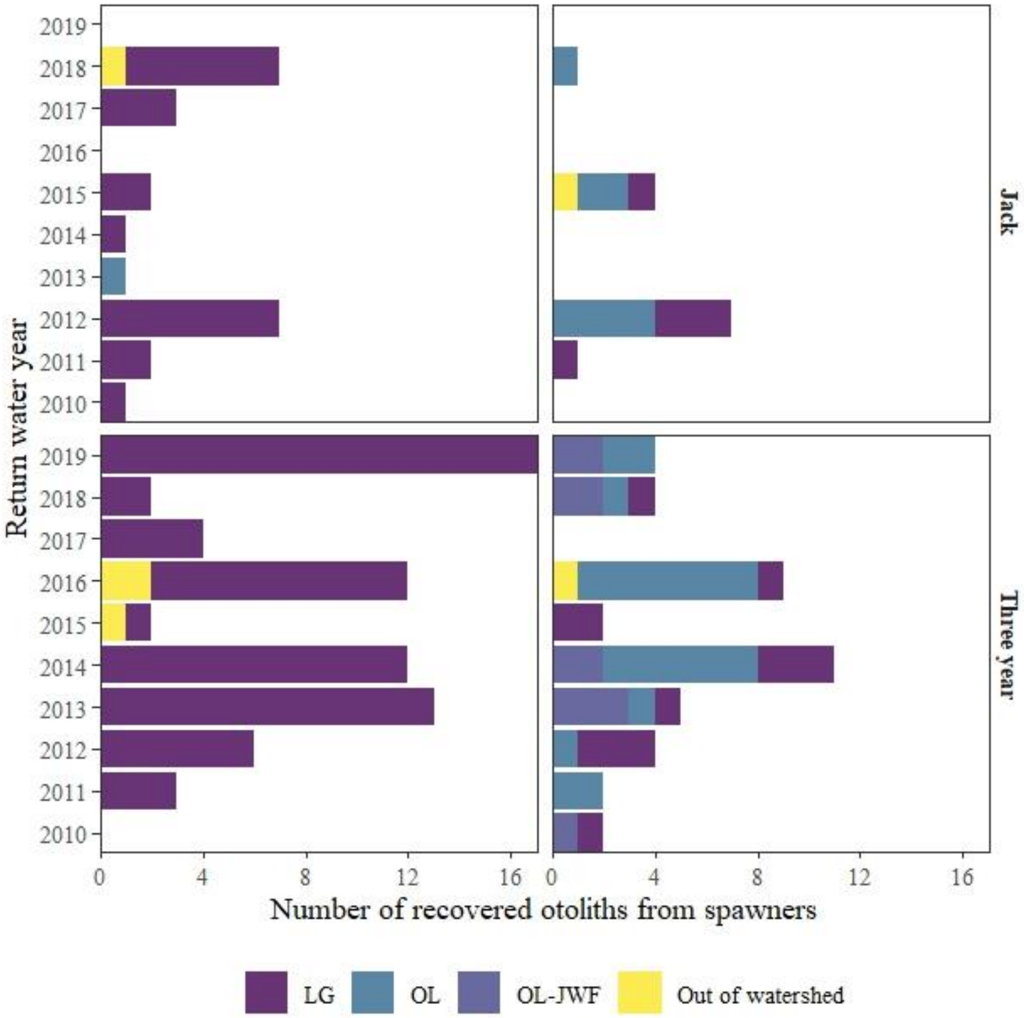


Figure 7 Natal origins and maturity of spawners as determined by recovered otoliths in Lagunitas Basin (left panel) and Olema Basin (right panel). The colour of the bar indicates the natal origin of the fish (LG = Lagunitas Creek basin, OL = Olema Creek basin, OL-JWF = John West Fork in Olema basin, Out of watershed = not traced within to an origin within the watershed). The top row show fish that returned as immature jacks (males of <1 year ocean residency) and the bottom row are fish that returned as three year old mature adults (~18 months ocean residency, either sex).

We tested for correlations between demographic variables and the proportion of the spawning population in Olema Basin of Lagunitas-origin (**Table 5A**). The proportion of Lagunitas-origin redds comprising the total Olema Basin redd count was significantly negatively correlated with the Olema Basin-origin returns that year (r = -0.88). We also tested for correlations between Olema Creek flow variables and Lagunitas Basin fish propensity to stray and only found significant correlation with Olema Creek October cumulative discharge (r = 0.84) (**Table 5B**). This suggests that wetter Octobers may facilitate dispersal of Lagunitas-origin fish into Olema Basin, but this possibility deserves further study. The number of years with strays originating from outside the watershed was too small for analysis but we note that the origin of these strays had $^{87}Sr/^{86}Sr$ signatures either from multiple possible origins, or outside of our known water sample values, suggesting that more work is needed to understand the source of the out-of-watershed strays (see ***Supplementary Materials*** for details) but these do not appear to be fish from the Warm Springs Hatchery.

Table 4 Productivity of adult spawner population in Olema Basin only across the otolith sampling period, return water years 2010-2019. Numbers of redds of natal origin has taken otolith numbers and adjusted to the number of recorded redds. Note that 2017 is omitted as no otoliths were recovered.

Water Year	Total otoliths	Total redds	*Number of redds of natal origin*				Proportion redds Lagunitas-origin	Proportion redds strays
			Olema Creek	John West Fork	Lagunitas Basin	Outside watershed		
2010	2	13	0	6	6	0	0.50	0.50
2011	3	25	17	0	8	0	0.32	0.32
2012	11	14	6	0	8	0	0.57	0.57
2013	5	44	9	26	9	0	0.20	0.20
2014	11	38	21	7	10	0	0.26	0.26
2015	6	6	2	0	3	1	0.50	0.67
2016	9	79	61	0	9	9	0.11	0.23
2018	5	17	7	7	3	0	0.18	0.18
2019	4	58	29	29	0	0	0.00	0.00

Table 5A. Pearson correlation between total redds and the proportion of Lagunitas origin redds in Olema Basin.

Demographic variable	Pearson correlation	95% confidence intervals	P value
total Lagunitas-origin redds in watershed	-0.62	-0.91, 0.08	0.08
total Olema-origin redds in watershed	**-0.88**	**-0.97, -0.52**	**0.002**

Table 5B. Pearson correlation between flow metrics and Lagunitas-origin stray rates into Olema Basin.

Flow variable	Pearson correlation	95% confidence intervals	P value
wet season start	0	-0.67, 0.66	1
CV (early)	-0.05	-0.69, 0.64	0.9
CV (full)	-0.38	-0.83, 0.38	0.3
median flow (early)	0.10	-0.60, 0.72	0.8
median flow (full)	0.07	-0.62, 0.70	0.9
cumulative discharge (Oct)	**0.84**	**0.40, 0.97**	**0.004**
cumulative discharge (Nov)	0.23	-0.51, 0.78	0.5
cumulative discharge (Dec)	0.11	-0.60, 0.72	0.7

Discussion

Prior research has emphasized that different portions of a watershed are important for producing adults in different return years (Brennan et al. 2019), which emphasizes the importance of distributing adults and juveniles across the landscape. Our work explored how aspects of hydrology influence the distribution of spawners through space and time and further explored the natal origins of the spawners in the context of endangered coho salmon in small coastal watershed. When comparing spawn timing in the regulated Lagunitas Basin versus an unregulated tributary subbasin (Olema), we found that the onset of spawning and duration of spawning in mainstem Lagunitas Basin were stable across years, reflecting the regulated flow regime, whereas the onset and duration of spawning in Olema Basin varied, reflecting natural variation in flow conditions. These differences in spawn timing are partially explained by the relationships with early season hydrological conditions between the two basins; while the initiation of spawning in Olema Basin is dependent on the onset of sustained, elevated flows caused by consistent rainfall, the larger Lagunitas Basin and its regulated flow regime potentially buffers the spawning adults against precipitation variability, especially in years of extreme drought. Information gained from analysis of otolith microchemistry of returning spawners also shed light on the importance of adult dispersal in this meta-population. The Lagunitas Basin is considerably larger and supports a consistently larger population of adult salmon, suggesting that it could be an important source population in the meta-population, and our results support this expectation. Adults in Olema Basin often originated from several natal sources and brood years, highlighting the importance of dispersal in space (between basins, from outside the watershed) and time (multiple brood years) for colonizing/recolonizing stream habitats. Dispersal by adults into diverse stream habitats across the watershed broadens the habitat mosaic for juveniles, promoting trait variation and hedging against poor conditions in the early life stages, contributing to population resilience. Importantly, one intermittent stream in Olema Creek, John West Fork, appeared to be a consistent contributor of adults to that system, emphasizing the importance of seasonally available habitats for supporting salmon populations. Overall, our study shows that habitat diversity enhances metapopulation stability even in small watersheds and endangered populations by offering varied environments that can drive variation in traits and survival to adulthood across a range of climate contexts.

Hydrological variability influences spawn timing

To initiate spawning at the southern edge of their range, coho salmon typically require an increase in discharge that elevates and sustains baseflow as well as a drop in temperature (Tillotson et al. 2019; LovellFord et al. 2020). Subsequent increases in flow enhance the amount of spawning habitat and attract spawners throughout the season on the ascending and descending limbs of flow pulses (Shapovalov & Taft 1954; Alabaster 1970; van den Berghe & Gross 1989; Beechie et al. 2008). Here, we found that higher variability in discharge and the timing of winter baseflow led to more variable spawn timing in the unregulated Olema Basin, while flow regulation in Lagunitas Creek - that decoupled baseflow elevation from precipitation and lowered flow variability - had a stabilizing effect on spawn timing. Returning adults to the Olema Basin were likely restricted from migrating upstream or accessing adequate spawning habitat until there significant precipitation to increase the discharge sufficiently so that it would not quickly recede to summer baseflow levels. This led to extremely delayed spawning or condensed windows of spawning in years of later precipitation, smaller amounts of precipitation, and/or low discharge variability resulting from few precipitation events. The most striking instances of delayed access due to precipitation limitation were observed in drought years such as 2012 and 2014, where the onset of spawning in Olema closely tracked the start of the wet season at the end of January and mid-February, respectively, and the spawning window was delayed and shortened as a consequence. Antecedent conditions likely compounded these effects, as it takes more precipitation to elevate baseflow after more intensively dry summers where discharge can be as low as <0.01 cms (Van Loon 2015). In contrast, regardless of rainfall patterns, reservoir releases started on November 15th in Lagunitas Creek, in effect marking the start of the wet season in Lagunitas Creek and dampening flow variability. Returning adults thus had access to upriver spawning reaches earlier in the season in Lagunitas irrespective of rainfall patterns and, in drought conditions, river regulation extended the length of the spawning window. Removing barriers to the onset of spawn timing through flow regulation leads to remarkable consistency in spawn timing start dates, likely explained by a combination of the stable flows (Davidson et al. 1943) and the underlying genetic component of spawning (Stewart et al. 2003; Cauwelier et al. 2018). It is also possible that flow regulation is inducing an evolutionary response in narrowing the variation of spawn timing, as the phenology of breeding is a highly heritable trait (Carlson & Seamons 2008) and can shift in response to selection over a relatively short period (Quinn et al. 2002; Tillotson et al. 2019). In the Lagunitas watershed, the last dam was constructed in 1960 and mandated minimum flow requirements were implemented in 1995, leading to 23 generations of coho salmon adapting to a reduced watershed and 10 generations experiencing a consistent wet season start which could be exerting some selective pressure (Marin Municipal Water District 2011).

Yet, Lagunitas Creek spawn timing was not entirely independent of precipitation. A higher median discharge in the early spawning season explained earlier spawn timing in both basins, and a higher median discharge across the entire season contributed to earlier peak spawning across both basins too. One possible explanation is that while artificial baseflow elevation ensures access, greater magnitude and frequency of precipitation can further increase discharge and therefore spawning habitat, including access to upriver tributary spawning sites, and provide a flow pulse (high rate of change in discharge) that is a cue for adults to migrate upstream (Alabaster 1970; Moir et al. 2004). Peak flows, caused by precipitation events, were more strongly associated with peak spawning dates when precipitation was lower overall, a result that was consistent in both the regulated and unregulated basin. Even when fish had ample access to the spawning grounds from elevated baseflow in Lagunitas, most fish still waited for precipitation events to spawn in dry years. In fact, in years with extremely reduced precipitation (e.g., 2014) spawning windows were longer in Lagunitas, as spawning started in December and steadily continued throughout the season, but the first precipitation events in February also motivated spawning activity, greatly extending the spawning window. In addition, we found the date of the first flow pulse caused by precipitation or dam operations (in lieu of precipitation) did not explain the onset of spawning, suggesting that this alone is not a sufficient cue to initiate spawning. This suggests that flow regulation does not modify the peak flow timing and pulse flows caused by precipitation, and that fish are dependent on precipitation cues and other associated atmospheric changes (e.g., changes in pressure) for initiating spawning events rather than dam-released flow pulses meant to imitate these events, similar to what has been observed in other flow regulated systems (Hasler et al. 2014; Peterson et al. 2017; Tillotson et al. 2021). Thus, while we can extend the start and duration of spawning with flow modifications, the central tendency is conserved and still dependent on rainfall itself. Precipitation may play a more complex role in Lagunitas Creek that our metrics do not capture, or temperature may be interacting with flow, with fish avoiding streams or delaying spawning until temperatures are more suitable (Beechie et al. 2008; LovellFord et al. 2020; Austin et al. 2023). While flow releases from reservoirs are typically from the hypolimnion (the bottom, cold layer in the reservoir), this assumption may be violated when multi-year droughts stress water systems and temperatures of flow releases may play a larger role in determining spawn timing.

Overall, the differences in hydrological variability observed in the Lagunitas Creek watershed appear to influence the onset, peak, and window of spawning in this rain-fed system, with more predictable winter flows stabilizing the spawn timing in Lagunitas Basin relative to the unregulated Olema Basin. As the mainstem river of the watershed, Lagunitas Creek is much larger in catchment area and therefore discharge than Olema Creek, thus we would expect discharge to be of higher magnitude and less variable in Lagunitas versus Olema and, hence, spawn timing to be less variable with a wider distribution. Estimates of unimpaired flows for Lagunitas Creek also indicate inflated monthly flow magnitudes in November (average 57% inflation) and December (28% inflation), with less flow modification in January and February (<12% inflation or deflation) (California Environmental Flows Working Group 2021; Grantham et al. 2022). This suggests that flow regulation is increasing discharge higher than would be expected in most years, hinting at some positive influences of flow regulation in the early part of the spawning season. However, it is also important to keep in mind that Lagunitas is simply a much larger system, with less discharge variability to begin with, and a much larger spawner populations, so some of the reduced variation observed in the spawning traits of fish in Lagunitas are very likely a consequence of the differences in size. However, our results suggest that beyond number of returns and basin size, hydrological variables that captured the variability, timing, rate of change, and magnitude of discharge explained differences in spawn timing between the two basins suggesting an important role of hydrology and flow alteration in influencing the location and timing of spawning.

Spawner dispersal through space and time contributes to small populations

Otoliths from adult coho salmon carcasses that returned to the watershed as adults revealed that fish of various natal origins contributed to the adult spawning population within the Lagunitas Creek watershed coho salmon complex. Due to the much larger size of the Lagunitas system, including a consistently larger adult population, we expected to find evidence that the Lagunitas subpopulation is a “source” population that subsidizes other subpopulations within the complex through dispersal (e.g., Lin et al. 2011) – and we did. In brief, our analyses of otolith microchemistry revealed that adults breeding in Olema Basin regularly originated elsewhere, while most spawners in Lagunitas Basin originated from within the Lagunitas Basin. Basin subpopulations are separated by unsuitable spawning habitat at the lower reaches of the stream, leaving discrete breeding patches that lend themselves to some degree of homing; however, these basins remain connected by flow during most of the year, facilitating dispersal between basins for colonizing/recolonizing of spawning habitat when conditions are suitable (Schtickzelle & Quinn 2007). This concept can be extended to the entire region, with fish from unknown natal origins dispersing into the Lagunitas Watershed and contributing to the adult spawners, particularly in the Olema subpopulation but also, to a lesser degree, the Lagunitas subpopulations. Dispersal from outside the Olema Basin contributed the most to productivity in years of lowest returns overall, when the Olema-origin fish survival to adulthood was presumably lower, highlighting the role of the dispersal and metapopulation functioning in supporting persistence of this subpopulation and expanding habitat use across the watershed. The expansion of the usable watershed habitat is especially notable considering the contributions of the intermittent tributary, John West Fork, a tributary of Olema Creek. Our results show that this small seasonal tributary regularly contributed adults to the Olema subpopulation – suggesting that this habitat is a crucial natal rearing habitat contributing to the breeding population. This finding also supports earlier work that highlights the value of this tributary as juvenile rearing habitat (Hwan et al. 2018). Interestingly, the John West Fork shows evidence of contributing adults even during extreme dry years. For example, we see evidence that fish originating in the John West Fork in 2015 and 2016, during a multi-year drought in California, survived to adulthood. Given that the wetted habitat available in the John West Fork contracts considerably during drought years (Hwan & Carlson 2016), this hints that the successful adults originating from the John West Fork may have emigrated early and reared elsewhere (e.g., Olema Creek, lower Lagunitas mainstem, Tomales Bay) during the extreme drought conditions. Overall, this work adds to the growing body of literature on the value of intermittent streams as highly productive habitat for juvenile salmonids (Wigington et al. 2006; Hwan et al. 2018; Rossi et al. 2022) and emphasizes the importance of maintaining sub-populations distributed across the full habitat mosaic for adult returns and resilience (Cordoleani et al. 2021, 2024).

Dispersal through time also contributed to subpopulation persistence and habitat use, underscoring the importance of life history diversity (e.g., age complexity, iteroparity) in dispersing risk (Buoro & Carlson 2014). Here, we found that early returning jacks made up a considerable proportion of the spawning population in years where the cohort survival to adulthood was low. For example, in 2015 no Olema-origin otoliths were recovered from fish born three years prior in 2012, yet two Olema-origin fish from the 2013 cohort were recovered. Ultimately, dispersal via space and/or time are both important sources of adults into small populations that can have positive effects on recipient population growth, fitness, and viability (Keefer & Caudill 2014; Bett et al. 2017).

Interbasin straying on such a small scale has not been previously explored in California, and we acknowledge that the classification of a “stray” is dependent on the scale of homing and an ongoing discussion in the literature (Quinn et al. 1999; Neville et al. 2006; Quinn 2018). There is some evidence of fine-scale homing in Pacific salmon at the river reach-scale (Bentzen et al. 2001) and even to precise natal sites (Stewart et al. 2003; Quinn et al. 2006; May et al. 2023), but in systems with weak subpopulation structure, it may be more appropriate to consider homing at the sub-watershed scale (Neville et al. 2006). Analysis of otoliths in our watershed detected Olema-origin fish returning to Olema in all but one instance, providing evidence for homing at the basin scale. However, homing in the watershed may be operating more on a gradient, with fish more likely to stray to nearby sites where conditions may be better than natal sites for spawning (Labelle 1992; Hamann & Kennedy 2012; Cram et al. 2013; Keefer & Caudill 2014). Notably, we also observed straying into the Lagunitas Creek watershed from out of the basin, including during very dry years. This is especially interesting when considering that the Lagunitas complex is part of a larger metapopulation within the CCC ESU and that the Lagunitas watershed is unique in the region as the system drains into an estuary that is perennially open, potentially attracting more strays from outside the watershed under drought conditions. Unfortunately, we were unable to determine the source of out of basin strays, though they do not appear to be from the nearest conservation hatchery (Warm Springs Fish Hatchery on the Russian River). As the otolith time series builds in the system and with additional water sampling outside the system, future studies will be able to explore the provenance of these out-of-basin strays and environmental drivers of straying within and outside of the watershed.

Implications for population resilience

Coho salmon at the southern end of their range in California are highly restricted in spawn timing by the onset of winter rains, which are highly variable in the region (Weitkamp et al. 1995). California is already experiencing more volatility in wet season rainfall patterns, and this is only projected to intensify in the coming decades (Swain et al. 2018). Predicted larger winter floods can threaten survival during the early stages of coho salmon development by scouring eggs or displacing juveniles (Beechie et al. 2013), and drier conditions can lead to earlier disconnection of streams, inhibiting juvenile dispersal to better habitats (Vander Vorste et al. 2020). When these populations are distributed across the landscape and spawning across a protracted period, this contributes to diversity of rearing and emergence conditions. However, the ability of the population to spread risk through space and time may be constrained by rainfall and runoff conditions (Kastl et al. 2022). For example, during the extreme drought of 2013-14 reduced and delayed rainfall restricted spawning access to coho salmon in the nearby Russian River system, resulting in a major range contraction and a subsequent cohort collapse (Carlson et al. *in prep*). In our system, the delayed spawning access and more concentrated spawn timing due to late winter rains could lead to higher competition on the spawning grounds and subsequently in offspring, later emergence timing, and less variation in emergence timing. There could also be a mismatch in mating opportunities, as there can be sex differences in the timing of arrival on the spawning grounds (Dahl et al. 2004). These factors likely all contributed to some degree to a large decrease in juvenile production in the summer of 2014 in Olema Creek basin, despite an average number of adult spawners (Carlisle et al. 2016), and potentially impacted the survival of an entire cohort in 2012. The downstream consequences of concentrated rainfall and concentrated adult breeding on juvenile emergence and early life performance is an underexplored consequence of shifting rainfall patterns that deserves more attention. While our results highlight the potential impacts of a much later, more condensed spawning period on offspring life stages and survival, we also found that flow regulation may play a role in mitigating these effects to some degree.

The multi-year, historical drought of 2012-2016 captured within our study period best illustrated effects of precipitation variability on spawning in an unregulated system and the mitigating effects of flow regulation and provides multiple insights into adult coho salmon response to drought in the region. In particular, we found that not all drought years are equivalent, and that drought years that had multiple rainfall events early in the spawning season, regardless of amount, did not considerably impact spawn timing. Second, we also found that flow regulation can buffer against some of the effects of delayed precipitation in a drought year by ensuring fish can access spawning grounds in the absence of significant precipitation events. Third, despite this buffering effect, most fish still relied on precipitation for cues to begin spawning, with artificial pulse flows attracting some, but not all, spawners. Finally, the watershed (and potentially regional) metapopulation and variation in age-structure of adults serve to enable recolonization of stream habitat following cohort failure, maintaining the utilization of a wide range of habitats by the next generation of coho salmon.

Overall, we find that adult dispersal through space and time play important roles in metapopulation persistence, spreading risk within a season, as well as contributing demographic subsidies to weak sub-population and allowing recolonization of stream habitat when conditions are suitable. Furthermore, our work highlights the importance of better understanding of metapopulation structure, including sources and sinks, and using a suite of approaches - from restoring habitat heterogeneity to environmental flows that increase connectivity - as strategies for supporting salmon complexes in the face of increasing variability and change.

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Supplementary Materials

Baseline ^{87}Sr/^{86}Sr stream values

Methods: Creating the isoscape

The first step to uncovering the natal origin of returning coho salmon is to characterize the variation in stream water chemistry in the watershed and develop an "isoscape" of ^{87}Sr/^{86}Sr signatures for major rearing areas (Barnett-Johnson et al. 2008; Sturrock et al. 2015; Willmes et al. 2018). The ^{87}Sr/^{86}Sr signature of a stream is a product of weathering of the underlying geology of the entire upstream watershed; thus, in a geologically diverse watershed such as Lagunitas, we expected distinct ^{87}Sr/^{86}Sr signatures for Olema Creek and Lagunitas Creek basins. Furthermore, because Olema Creek basin spans two different plates, tributaries on the east and west side of the basin may also have different ^{87}Sr/^{86}Sr signatures, giving us even finer-scale natal origin information in that basin.

We did three rounds of water sampling from 2020-2024, first to establish differences between basins within the Lagunitas Creek watershed, then expanding our sampling to smaller tributaries within the watershed, as well as other coho-rearing watersheds in the region, encompassing the southern range of Central California Coast coho salmon **(Table S1, Figure S1a-c)**.The ^{87}Sr/^{86}Sr signature of a stream section was obtained by collecting water with a sterile 60mL syringe and a 0.45µm syringe filter, filtering ~120mL of stream water into a sterile plastic bottle. This sample was then processed on a Nu Plasma HR (Nu Instruments, Inc.) which is a multiple-collection, double-focusing, plasma-source mass spectrometer (MC-ICP-MS), providing us with an ^{87}Sr/^{86}Sr estimate and standard error (see Willmes et al. 2018 for detailed methods).

Beyond the Lagunitas Creek watershed, the other major CCC coho salmon populations in the southern region of the ESU are in the Russian River, Sonoma County and Scott Creek, Santa Cruz County. These populations are severely depleted and supplemented by conservation hatcheries, Warm Springs hatchery run by the US Army Corps of Engineers on Dry Creek in the Russian River, and Kingfisher Flat Fish Hatchery run by the Monterey Bay Salmon and Trout Project on a tributary of Scott Creek in the Scott Creek watershed. As the hatcheries produce the largest numbers of juveniles in these watersheds, we aimed to account for these sources by obtaining ^{87}Sr/^{86}Sr values from otoliths of fish in these systems. We were given 10 frozen, spawned-out adult coho salmon carcasses from the Warm Springs hatchery from fish that spent their entire lives in the hatchery to obtain the hatchery fish ^{87}Sr/^{86}Sr signature. There were no hatchery mortalities from Scott Creek available and instead we obtained 10 frozen natural-origin juvenile coho salmon from Scott Creek that were incidental mortalities to get the Scott Creek ^{87}Sr/^{86}Sr signature. We dissected fish for their otoliths and polished and analyzed otoliths according to the same protocol as Lagunitas Creek spawner otoliths, then calculated the average ^{87}Sr/^{86}Sr and 95% CI for the entire profile post-exogenous feeding check, as these fish remained in the same stream or hatchery system for the whole juvenile period. We then averaged the signature across all fish for each system and included those values in our regional isoscape.

To determine if ^{87}Sr/^{86}Sr water signatures were different between basins within Lagunitas

Creek and surrounding streams in the county, we ran a one-factor ANOVA. For the ANOVA, we grouped samples into subbasins or similar regions: Lagunitas Creek (mainstem Lagunitas Creek and tributaries Nicasio Creek, Cheda Creek, Devil's Gulch), San Geronimo Creek (major tributary of Lagunitas Creek but within the basin), Olema Creek (mainstem), Western Olema tributaries, Eastern Olema tributaries (John West Fork, Five Brooks Gulch), lower Lagunitas (including tributary Bear Valley Creek), and Western Marin (Redwood Creek, Pine Gulch) and Walker Creek (nearest major stream). We performed a post-hoc Tukey test to assess which subbasins significantly differed. We did not include hatchery samples because Warm Springs hatchery had a wide range and overlapped with other signatures.

Results: Strontium isoscape for the southern range of CCC coho salmon

Our results showed large variability in $^{87}Sr/^{86}Sr$ values across the region, providing a potential blueprint for tracing natal origins of CCC coho salmon returns across their southern range to assess region-wide dispersal **(Table S1, Figure S1)**. Despite this diversity of Sr isotopic signatures, there were some overlapping values (e.g., JWF and Lagunitas, Dry Creek and Olema Creek). We addressed the overlap between JWF and Lagunitas basin, but considering Dry Creek fish are better represented by hatchery fish otolith signatures that incorporate hatchery feed, we deferred to the hatchery Sr isotopic signature. The ANOVA and post-hoc Tukey test revealed significant differences between water samples ($F(7,16) = 150.42$, $p < .001$). Olema Creek significantly differed from all subbasins ($p < 0.05$), and Lagunitas Creek differed from all subbasins except JWF ($p = 0.13$). San Geronimo Creek also did not differ from JWF ($p = 0.35$). While Lagunitas Creek and San Geronimo Creek differed at the subbasin level ($p < 0.001$), we kept these together in the Lagunitas Basin category as there was already uncertainty in overlap with JWF, and because we did not sample the entirety of the Lagunitas Creek mainstem it is likely there is more of a gradient than we have in our samples. There was some additional overlap in water signatures between Western Marin and Walker Creek ($p = 0.33$) and Western Olema tributaries and Lower Lagunitas ($p = 0.16$). Overall, the results enabled us to assign natal origin of fish based on $^{87}Sr/^{86}Sr$ otolith profiles to the discrete basins and we leaned on other evidence for determining natal origin between overlapping signatures.

There are opportunities to expand upon the foundational strontium isoscape in the coastal region that we have built. The diverse geological composition of the Lagunitas Creek watershed results in fine-scale diversity in stream microchemistry, which we were able to leverage to assign natal origins of returning spawners at the sub-watershed scale based on their otolith microchemistry. This method has been widely used in larger river systems, most notably in the Central Valley (Barnett-Johnson et al. 2008; Sturrock et al. 2015; Willmes et al. 2018; Cordoleani et al. 2021) and the Klamath River systems (Hodge et al. 2016) in California, and the Bristol Bay system in Alaska (Brennan & Schindler 2017; Brennan et al. 2019). However, this is the first study to our knowledge to map part of the isoscape for CCC ESU coho salmon and to elucidate natal origin at such a fine scale. The ability to track local movement within a watershed gives us valuable information on habitat use as juveniles, and what habitats contribute disproportionately to adult returns in years of different conditions. In modified systems with reduced populations, understanding what habitats support survival under different environmental conditions can help guide restoration efforts of diverse habitats and enhance watershed connectivity (Beechie et al. 2013; Flitcroft et al. 2016; Cordoleani et al. 2024). Furthermore, using otoliths across the wider CCC ESU coho salmon complex and expanding the isoscape could also lead to a better understanding of the regional metapopulation and contributions of different populations in years of different conditions, linking dispersal of adults to their donor and recipient populations and allowing assessment of source-sink dynamics across the range of this endangered coho ESU.

Otolith preparation & analysis

Methods: Polishing otoliths & analyzing $^{87}Sr/^{86}Sr$ signatures

There were 322 otoliths collected from coho salmon carcasses within the Lagunitas Creek watershed from water years 2010-2019, 10 otoliths from Warm Springs hatchery fish, and 10 otoliths from Scott Creek juvenile fish. We polished 167 of the otoliths, using established methods (Barnett-Johnson et al. 2007, 2008). Briefly, we mounted otoliths on slides using Crystalbond resin and polished with 1500 grit paper and 3µm lapping film until the primorida were exposed and daily increment rings were visible. We then flipped otoliths and repeated the process on the other side, until daily increments were clearly defined under the microscope. At this point, otoliths were a flat, thin layer. We transferred polished otoliths to petrographic slides, fitting 12 otoliths on a slide.

We measured otolith ^{87}Sr/^{86}Sr from the furthest dorsal primordia along a 90° transect on the dorsal side until ~1000µm, capturing ocean entry, using laser ablation inductively coupled plasma mass spectrometry (LA-ICPMS; Nu plasma HR interfaced with a New Wave Research Nd:YAG 213 nm laser). Laser diameter was 40µm with a run speed of 5µm/s, pulse rate of 10Hz and fluence of 4.2-5.5 J/cm^2**.** The marine portion of the coho adult otoliths for Lagunitas samples and marine rockfish (Sebastes *sp*) for hatchery and Scott Creek juvenile samples were used as a marine standard for each slide to control for instrument bias and drift and used to correct ^{87}Sr/^{86}Sr values from otolith transects. We created ^{87}Sr/^{86}Sr profiles from the transects by discarding outliers (>2 SD) and applying a loess smooth (span = 0.1) with 95% confidence intervals.

Results: Otolith $^{87}Sr/^{86}Sr$ profiles

We obtained ^{87}Sr/^{86}Sr otolith profiles for 151 returning fish in the Lagunitas Creek watershed. In addition, we generated profiles for 10 Warm Springs hatchery fish and 6 Scott Creek fish.

Natal origin of spawners from recovered otoliths

Methods: Assigning natal origin

To assign natal origin, we first had to visually identify the exogenous feeding check. On the otolith, the exogenous feeding check is exemplified by a strong, thick depositional band ~ 200-250 µm from the furthest dorsal primordia. The point of exogenous feeding in otolith profiles is where fish cease to feed upon the maternal yolk sac and start incorporating only material from their environment in their otoliths. We also did visual inspections of the otolith microstructure to mark secondary points of thicker depositional bands, usually associated with some major habitat change or point of stress in the fish, and marked the otolith radius of these on the $^{87}Sr/^{86}Sr$ profiles, giving us multiple “tags”. We took the length along the transect from the exogenous feeding check, added 25 μm to adjust for some profiles showing a small lag, then averaged the $^{87}Sr/^{86}Sr$ value across the next 25 μm, designating this as the natal rearing segment. We established methods from the Central Valley (e.g., Barnett-Johnson et al. 2008), taking the natal origin signature and classifying it to a natal origin using linear discriminant function analysis (LDFA). We grouped water samples into subbasins (as in the ANOVA) as the training data, then assigned natal origin for each fish, taking a 60% threshold for assigning natal origin because of the large swaths of our isoscape that remain unknown and manually assigning the “NA” samples. We visually inspected each otolith profile and the exogenous feeding check to verify the LDFA results, and manually changed some assignments based on whether the 95% confidence intervals of the known water signatures overlapped with the 95% confidence intervals of the otolith profile (e.g., signatures that had lower $^{87}Sr/^{86}Sr$ values than the known water signatures). These were assigned to “Out of watershed”. In addition, any fish assigned to Western Marin were also assigned as “Out of watershed”; these are possibly from the Western Marin watersheds, or Warm Springs hatchery given the overlap and need to be further inspected to determine origin.

We assumed homing to the watershed as the baseline, and thus we only pursued potential stray locations if the Sr isotopic signatures were not overlapping with either known location. This meant that fish classified by the LDFA as likely of JWF-origin but that returned to Lagunitas Basin were assigned as Lagunitas Basin, as it is a much larger system with a larger returning adult population and homing is more common in fish. Given the wider range of Warm Springs hatchery fish signatures (**Figure S1c**), there is some overlap with Olema Creek mainstem Sr isotopic values. This meant that some hatchery fish may have been overlooked if they strayed into Olema. However, as we only detected one Olema-origin (or potentially hatchery-origin) fish in Lagunitas, it suggests that hatchery strays are very few if we assume the probability of straying into Olema Creek is the same (or less) than the probability of straying into Lagunitas.

For fish that were returned to Olema Creek basin but had an $^{87}Sr/^{86}Sr$ signature matching that of Lagunitas Creek basin, we needed to determine whether these fish were in fact from Lagunitas basin, or from John West Fork (JWF), an intermittent tributary of Olema Creek that has an $^{87}Sr/^{86}Sr$ signature within the range of Lagunitas basin. For the majority of fish returning to Olema with this signature, their $^{87}Sr/^{86}Sr$ profiles showed the JWF/Lagunitas $^{87}Sr/^{86}Sr$ value just after natal rearing before they jumped to the Olema Creek mainstem $^{87}Sr/^{86}Sr$ value. This indicated that the fish were born in JWF but quickly migrated out into the mainstem, a common strategy of fish in intermittent streams that start to contract in the summer. For these fish, we manually assigned them to JWF as the most likely natal origin. However, there were 17 other fish that showed the JWF/Lagunitas $^{87}Sr/^{86}Sr$ signature for the entirety of their rearing period before going out to the ocean.

For these Lagunitas natal signature but Olema-returning fish, we initially compiled three lines of evidence to assess the likelihood of them rearing in JWF versus Lagunitas basin, designating fish natal origin in JWF as “unlikely” or “possible” (**Table S2**). First, we looked at the number of redds in JWF and Olema Creek basin as a whole in the cohort's brood year (3 years earlier for three year olds, 2 years earlier for jacks) as well as the estimated number of juveniles from the brood year from end-of-summer juvenile monitoring surveys. Second, we assigned juvenile rearing conditions based on the California Department of Water Resource's Sacramento River water year index for the brood water year (https://cdec.water.ca.gov/). Third, we took the probability of the natal origin being classified as JWF (or Eastern Olema Tributary) based on the LDFA. The $^{87}Sr/^{86}Sr$ value in a small, intermittent stream can change based on groundwater input during the summer, but as water collection from JWF was taken in the summer when groundwater influence should be strongest and it matched $^{87}Sr/^{86}Sr$ values from fish that only reared in the tributary for a short period before migrating to the Olema Creek mainstem, we felt confident in capturing the JWF signature. Given these three lines of evidence, we assessed the 17 possible JWF-origin fish and deemed them "unlikely" if they met two of the three following criteria: no redds in the basin in brood year and no juveniles, reared in a dry or critically dry year, <60% probability of being assigned to JWF natal origin from the LDFA.

After this initial pass, 11 fish were labelled as "possible" for JWF origin. We then performed additional analyses using LA-ICPMS, this time doing spot analyses with the laser in the habitat transition area where fish exited freshwater and moved into the ocean (Sturrock et al. 2015). We ran 5-8 spots, covering ~40µm each with some semi-overlapping spots for even higher resolution (run speed 5µm/s, pulse rate 10 Hz, fluence 5 J/cm^2). For each spot, we calculated the average $^{87}Sr/^{86}Sr$ value, adjusted for drift using a marine standard (Sebastes *sp*) at the beginning, midpoint, and end point of the session. The high resolution enabled us to capture small changes in $^{87}Sr/^{86}Sr$ values as fish moved through different habitats during the phase of outmigration, and if any of these spots matched $^{87}Sr/^{86}Sr$ values for Olema Creek, we took this as evidence of fish moving through Olema Creek. Considering fish rearing in JWF need to move through Olema Creek on their way to the estuary, we designated fish with an Olema Creek Sr isotopic value as "confirmed" JWF-origin. Any "possible" fish without evidence of movement through Olema Creek were treated as Lagunitas-origin fish.

Results: Natal origin assignments

Overall, of the 151 otoliths from the Lagunitas Creek watershed, we matched 145 to a natal origin within the watershed (107 Lagunitas Creek basin, 28 Olema Creek, 10 JWF). Three JWF-origin fish were designated as a result of the spot analysis. **Figure S2** shows a typical otolith profile for a fish of each natal origin. We were unable to identify the origin of 6 fish, as the $^{87}Sr/^{86}Sr$ signatures during the freshwater phase did not match up with any of the stream signatures identified in our isoscape (or were not able to be distinguished, e.g., Warm Springs and Western Marin) and varied in their Sr isotopic signatures. Only one fish is of possible hatchery origin based on $^{87}Sr/^{86}Sr$ signature, but the otolith microstructure will need to be assessed to confirm (Barnett-Johnson et al. 2007). We ruled out that the remaining unknown fish were of hatchery origin from the Russian River or Scott Creek systems, or from nearby streams with smaller coho salmon populations. It is probable that some of these fish came from other regions of the Russian River that are not hatchery supplemented, as the headwaters of the region had a similar strontium isotopic signature (~0.706, J. Christensen, personal communication) and it is the next largest coastal system with CCC coho salmon. Interestingly, the Russian River has also experienced an increase in returns starting in 2014 (Pregler et al. 2023), around the same time we see out of basin strays appear in our otolith time series. Another possibility is the

Klamath River, where some sections of the Klamath system have a similar signature (0.705-0.706; Hodge et al. 2016), with coho salmon populations outside of the CCC coho salmon ESU. The origin of these fish warrants further investigation.

Tables

Table S1 Location of water samples (A) and fish (B) collected within the southern range of CCC coho salmon, with a focus on the Lagunitas Creek watershed, and their associated ^{87}Sr/^{86}Sr, including the standard error multiplied by two. Fish ^{87}Sr/^{86}Sr values were averaged across 5-10 otoliths.

A

Watershed	Stream	Sample ID	Collection Date	Latitude	Longitude	Sr87/86	2SE
Lagunitas Creek	Bear Valley Creek	Bear Valley Creek @ NPS Offices	8/02/23	38.0435671	-122.7986637	0.709134	1.12E-05
Lagunitas Creek	John West Fork	John West Fork - Eastern Olema Tributary	8/02/23	37.9951978	-122.7543972	0.706690	1.18E-05
Lagunitas Creek	Five Brooks Gulch	Five Brooks Gulch - Eastern Olema Tributary	1/09/24	38.0023044	-122.7588963	0.706481	0.0000116
Lagunitas Creek	Western Olema Tributary	Vedanta crossing - Western Olema Tributary	1/09/24	38.0386842	-122.7860614	0.709520	1.42E-05
Lagunitas Creek	Western Olema Tributary	Upstream tributary - Western Olema Tributary	1/09/24	38.008971	-122.7674881	0.709487	1.35E-05
Lagunitas Creek	Lagunitas Creek	Lagunitas Creek @ Shafter Bridge	6/02/20	38.004460	-122.708732	0.706416	1.11E-05
Lagunitas Creek	Lagunitas Creek	Lagunitas Creek @ Cheda Creek	6/02/20	38.037855	-122.746331	0.706308	1.23E-05
Lagunitas Creek	Lagunitas Creek	Lagunitas Creek @ Cheda Creek	6/02/20	38.037855	-122.746331	0.706293	1.19E-05
Lagunitas Creek	Lagunitas Creek	Lower Lagunitas Creek Near Mouth	8/02/23	38.0628466	-122.8195159	0.708936	1.53E-05
Lagunitas Creek	Olema Creek	Olema Creek @ Five Brooks Bridge	7/01/20	37.999449	-122.756059	0.707392	8.68E-06
Lagunitas Creek	Olema Creek	Olema Creek @ Bear Velly Road Bridge	7/02/20	38.041933	-122.789775	0.707565	1.08E-05
Lagunitas Creek	Olema Creek	Olema Creek @ Randall	7/26/23	37.974088	-122.734187	0.707628	1.07E-05
Lagunitas Creek	Nicasio Creek	Nicasio Creek downstream of reservoir	1/07/24	38.0698456	-122.7632099	0.705994	1.49E-05
Lagunitas Creek	Cheda Creek	Cheda Creek	1/07/24	38.042113	-122.7393192	0.706348	1.22E-05
Lagunitas Creek	Devil's Gulch	Lower Devil's Gulch	1/07/24	38.0312589	-122.7324926	0.705808	1.03E-05
Lagunitas Creek	Devil's Gulch	Upper Devil's Gulch	1/07/24	38.0388646	-122.7167219	0.706177	1.30E-05
Lagunitas Creek	San Geronimo Creek	San Geronimo Creek @ Roy's Pools	6/02/20	38.012688	-122.662622	0.706728	1.31E-05
Lagunitas Creek	San Geronimo Creek	San Geronimo Creek @ Woodacre confluence	1/07/24	38.0131722	-122.6476889	0.706983	1.39E-05
Lagunitas Creek	Woodacre Creek	Upper Woodacre Creek	1/07/24	38.0074821	-122.6385593	0.707096	1.41E-05
Pine Gulch	Pine Gulch	Pine Gulch @ Olema Bolinas Rd	7/26/23	37.9187396	-122.6927983	0.708057	1.16E-05
Redwood Creek	Redwood Creek	Redwood Creek @ Muir Beach	7/26/23	37.8635845	-122.5753738	0.707975	1.19E-05
Redwood Creek	Redwood Creek	Redwood Creek @ Santos Meadow	7/26/23	37.8756065	-122.581978	0.707919	1.43E-05
Russian River	Dry Creek	Dry Creek @ Hatchery	7/26/23	38.7192965	-122.9951517	0.707555	1.10E-05
Salmon Creek	Salmon Creek	Salmon Creek @ Watson School	8/28/23	38.3552413	-122.9386851	0.706809	1.20E-05
Walker Creek	Walker Creek	Walker Creek @ Jackrabbit Flat	8/02/23	38.174734	-122.824328	0.708284	2.66E-05
Walker Creek	Walker Creek	Walker Creek @ Suspension Bridge	8/02/23	38.170913	-122.815215	0.708398	1.12E-05

B

Watershed	Stream	Fish Origin	Collection Date	Latitude	Longitude	Mean Sr87/86	2SE
Scott Creek	Scott Creek	Natural-origin juveniles from 2021 (brought to Monterey Bay Salmon & Trout Project hatchery)	7/26/23	37.074625	-122.221558	0.708740	7.31E-06
Russian River	Dry Creek	Warm Springs hatchery, adult broodstock	12/11/23	38.717754	-122.999761	0.707730	9.83E-06

Table S2 Compiled evidence for the assignment of fish to Lagunitas Basin natal origin versus John West Fork (see *Methods*). Otolith ID refers to the ID of the polished and analyzed otolith. Return Basin where the fish carcass was found. Maturity is whether the fish carcass was determined to be a three-year-old, a jack, or unknown. Return Water Year is the water year in which the fish spawned, and Brood Water Year is the water year in which the fish was born, based on their maturity status. Redds in JWF and Olema Creek Basin are the number of redds in the brood year, indicating whether fish were born in that creek. Olema Basin Juvenile Estimate is the basinwide estimate of juveniles, with 95% confidence intervals, as calculated from summer surveys done by National Park Service. In 2009, zero coho salmon were detected during surveys. Brood WY Condition is a designation of water conditions during the juvenile rearing phase. Probability of JWF Natal Origin Classification is the probability of the fish natal signature being from JWF based on a linear discriminant factor analysis. Outmigration Movement is whether there is microchemical evidence that the fish moved through Olema Creek upon outmigration. The final column is a determination of likelihood that the fish originated from JWF instead of Lagunitas Creek basin, where only “confirmed” fish were designated as JWF-origin.

Otolith ID	Return Basin	Maturity	Return Water Year	Brood Water Year	Redds in JWF (Brood WY)	Redds in Olema Basin (Brood WY)	Olema Basin Juvenile Estimate (Brood WY)	Brood WY Condition	Probability of JWF Natal Origin Classification from LDFA	Outmigration Movement Through Olema Creek	Likelihood of JWF Natal Origin
1011_OL_2	OL	Jack	2011	2009	0	0	0	Dry	0.29		unlikely
1112_OL_2	OL	Three	2012	2009	0	0	0	Dry	0.04		unlikely
1112_OL_1	OL	Three	2012	2009	0	0	0	Dry	0.37		unlikely
1112_OL_3	OL	Three	2012	2009	0	0	0	Dry	0.27		unlikely
1112_OL_8	OL	Jack	2012	2010	3	13	1755, 95% CI [1062, 2448]	Below Normal	0.13	N	possible
1112_OL_6	OL	Three	2012	2009	0	0	0	Dry	0.55		unlikely
1112_OL_5	OL	Three	2012	2009	0	0	0	Dry	0.64		unlikely
1213_OL_2	OL	Three	2013	2010	3	13	1755, 95% CI [1062, 2448]	Below Normal	0.01	N	possible
1213_OL_3	OL	Three	2013	2010	3	13	1755, 95% CI [1062, 2448]	Below Normal		Y	confirmed
1314_OL_15	OL	Three	2014	2011	11	25	4690, 95% CI [1761, 7619]	Wet	0.21	Y	confirmed
1314_OL_6	OL	Three	2014	2011	11	25	4690, 95% CI [1761, 7619]	Wet	0.72	N	possible
1314_OL_12	OL	Three	2014	2011	11	25	4690, 95% CI [1761, 7619]	Wet	0.66	N	possible
1314_OL_17	OL	Three	2014	2011	11	25	4690, 95% CI [1761, 7619]	Wet	0.63	N	possible
1415_OL_6	OL	Three	2015	2012	2	14	4690, 95% CI [1761, 7619]	Below Normal	0.04	N	possible
1415_OL_5	OL	Jack	2015	2013	5	44	16599, 95% CI [13075, 20123]	Dry	0.02	N	possible
1516_OL_10	OL	Three*	2016	2013	5	44	16599, 95% CI [13075, 20123]	Dry	0.61	N	possible
1718_OL_5	OL	Three*	2018	2015	3	6	1006, 95% CI [229, 2069]	Critical	0.68	Y	confirmed

*length, age or sex not recorded - assumed to be three year old unless otherwise stated

Table S3 Spawning, straying, and discharge metrics for the entire study period, 2005-2022, for both Lagunitas Creek and Olema Creek basins. Strays into the basin and the proportion of returns as strays are based on the number of recovered otoliths and their natal origins. Note that we only had otolith data for spawning seasons 2010-2019.

Water Year	Basin	Total redds	Recovered otoliths	Strays into basin	Proportion of returns as strays	Day of wet season start (water year days)	First rain pulse after wet season start (water year days)	CV discharge early season	CV discharge full spawning season	Median discharge early season (cms)	Median discharge full spawning season (cms)	Day of peak flow (water year day)	Total discharge Oct (cms)	Total discharge Nov (cms)	Total discharge Dec (cms)	Total discharge Feb (cms)
2005	LG	370				45	68	2.07	1.49	0.63	0.94	89	9.0	23.4	107	233
2005	OL	138				63	69	2.57	1.50	0.12	0.41	89	1.0	1.7	38	115
2006	LG	134				46	79	3.56	2.53	0.68	2.04	93	7.0	21.5	263	574
2006	OL	9				61	68	2.78	1.99	0.08	0.35	89	1.2	2.9	42	113
2007	LG	301				45	73	0.87	1.59	0.68	0.72	133	7.2	23.0	53	159
2007	OL	95				62	73	1.89	2.34	0.15	0.22	133	0.7	2.7	31	102
2008	LG	133				46	79	0.64	1.72	0.62	0.81	118	7.9	22.5	50	233
2008	OL	33				74	81	3.23	2.00	0.03	0.25	118	0.8	1.7	12	144
2009	LG	26				32	86	0.55	2.10	0.55	0.72	87	7.8	25.6	49	176
2009	OL	0				124	136	2.04	3.11	0.02	0.05	87	0.4	1.5	4	48
2010	LG	50	1	0	0.00	48	74	0.58	1.39	0.61	0.97	112	11.9	23.8	49	216
2010	OL	13	2	1	0.50	85	110	1.38	1.69	0.05	0.40	111	3.9	5.6	14	132
2011	LG	65	5	0	0.00	47	79	1.44	1.20	0.99	0.99	91	9.5	26.6	136	295
2011	OL	25	3	1	0.33	47	67	1.27	1.40	1.06	0.66	90	5.3	17.7	112	169
2012	LG	123	13	0	0.00	46	112	0.24	1.12	0.59	0.72	114	7.9	23.9	42	109
2012	OL	14	11	6	0.55	103	112	1.57	3.51	0.06	0.08	114	1.3	4.8	7	47
2013	LG	211	14	1	0.07	45	48	1.32	1.58	1.23	0.74	62	7.8	41.2	165	220
2013	OL	44	5	1	0.20	43	52	1.62	2.33	0.85	0.32	62	1.0	25.8	119	134
2014	LG	191	13	0	0.00	46	131	0.23	1.91	0.57	0.59	132	7.6	21.3	40	119
2014	OL	38	11	3	0.27	119	131	1.52	3.97	0.01	0.01	132	0.2	0.6	1	61
2015	LG	128	4	1	0.25	47	64	1.39	1.69	1.59	0.79	73	5.9	20.9	171	226
2015	OL	6	6	4	0.67	46	63	1.44	1.95	1.13	0.36	73	0.7	2.7	113	137
2016	LG	185	12	2	0.17	46	82	0.84	1.22	0.60	0.87	111	7.2	21.0	51	223
2016	OL	79	9	2	0.22	67	81	2.91	1.78	0.07	0.35	110	0.0	0.5	24	108
2017	LG	125	7	0	0.00	27	76	2.21	1.52	0.99	3.47	131	11.1	39.1	120	1237
2017	OL	14	0	0	0.00	46	71	2.26	1.30	0.88	2.12	131	2.8	11.8	78	393
2018	LG	85	9	1	0.11	45	93	0.27	1.02	0.61	0.70	101	7.5	24.3	43	107
2018	OL	17	5	1	0.20	91	100	1.08	2.86	0.04	0.11	101	0.6	6.2	8	40
2019	LG	212	17	0	0.00	45	98	0.52	2.51	0.81	1.29	109	7.6	27.2	58	581
2019	OL	58	4	0	0.00	71	98	1.44	2.46	0.17	0.70	109	0.6	4.9	18	226
2020	LG	56				46	62	0.83	0.75	0.95	0.75	68	7.1	21.2	74	124
2020	OL	3				53	68	1.41	1.30	0.21	0.28	91	0.6	1.3	35	65
2021	LG	155				45	62	0.25	0.45	0.60	0.59	120	5.5	19.8	41	83
2021	OL	16				69	119	1.21	2.50	0.02	0.05	120	0.1	0.7	2	25
2022	LG	223				21	24	1.59	1.52	0.57	0.75	75	66.3	93.6	200	298
2022	OL	90				14	24	1.85	2.38	0.47	0.30	75	69.3	100.9	178	197

Table S4 Results from generalized linear model of onset of spawning using the first peak post-wet season start instead of wet season start time. The parameters are the intercept and predictors and the estimate is the beta estimate with 95% confidence intervals in brackets. Stars represent significant results.

Model 1b Results

Predictors of onset of spawning

Parameters	Estimate (95% CI)
Constant (Lagunitas Basin)	4.453*** [4.125, 4.786]
Olema Basin	0.033 [-0.425, 0.494]
Median discharge early season (cms)	-0.259** [-0.433, -0.081]
First peak post-wet season start (WY day)	-0.002 [-0.005, 0.001]
CV discharge early season	-0.007 [-0.093, 0.084]
Olema x CV discharge early season	-0.132+ [-0.284, 0.019]
Olema x First peak post-wet season start	0.004+ [0.000, 0.008]
Nagelkerke's R2	0.68
AIC	260.1

+ p < 0.1, * p < 0.05, ** p < 0.01, *** p < 0.001

Figures

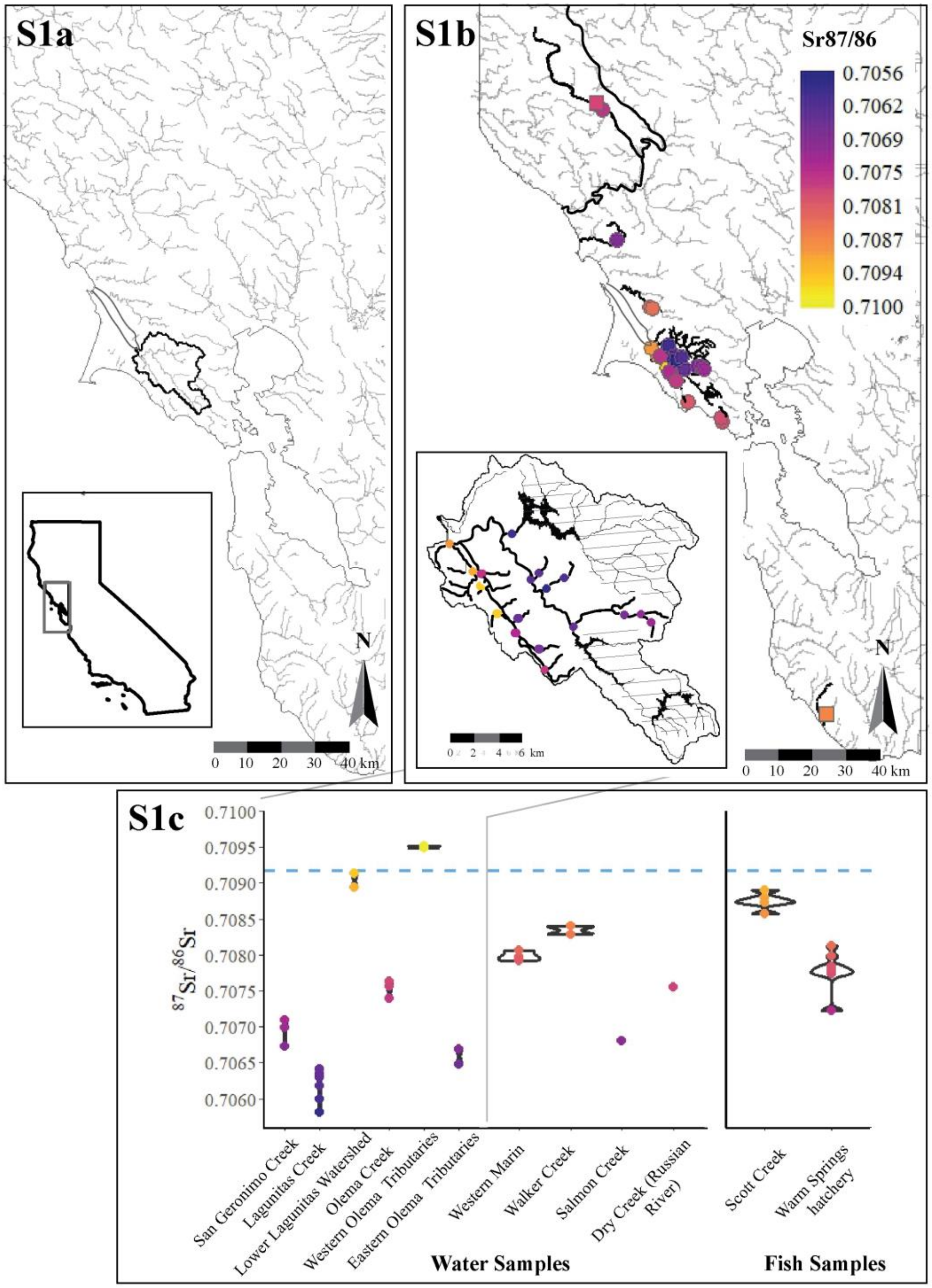

Figure S1 Regional "isoscape" map of Central California Coast coho salmon streams with ^{87}Sr/^{86}Sr values. (S1a) Map of California (inset) with the region of focus in grey rectangle, and close up of the region and its watersheds. The Lagunitas Creek watershed is outlined in black. (S1b) The same southern CCC coho salmon region, with streams that were sampled to create the isoscape in black. Sampling locations for water samples (circles) and fish otoliths (rectangles) and their associated ^{87}Sr/^{86}Sr values are shown. Inset map is a more detailed sampling map of the Lagunitas Creek watershed. (S1c) The resulting ^{87}Sr/^{86}Sr values from water and fish samples across the region, grouped by subbasin or area, plotted in ^{87}Sr/^{86}Sr space to visualize differences.

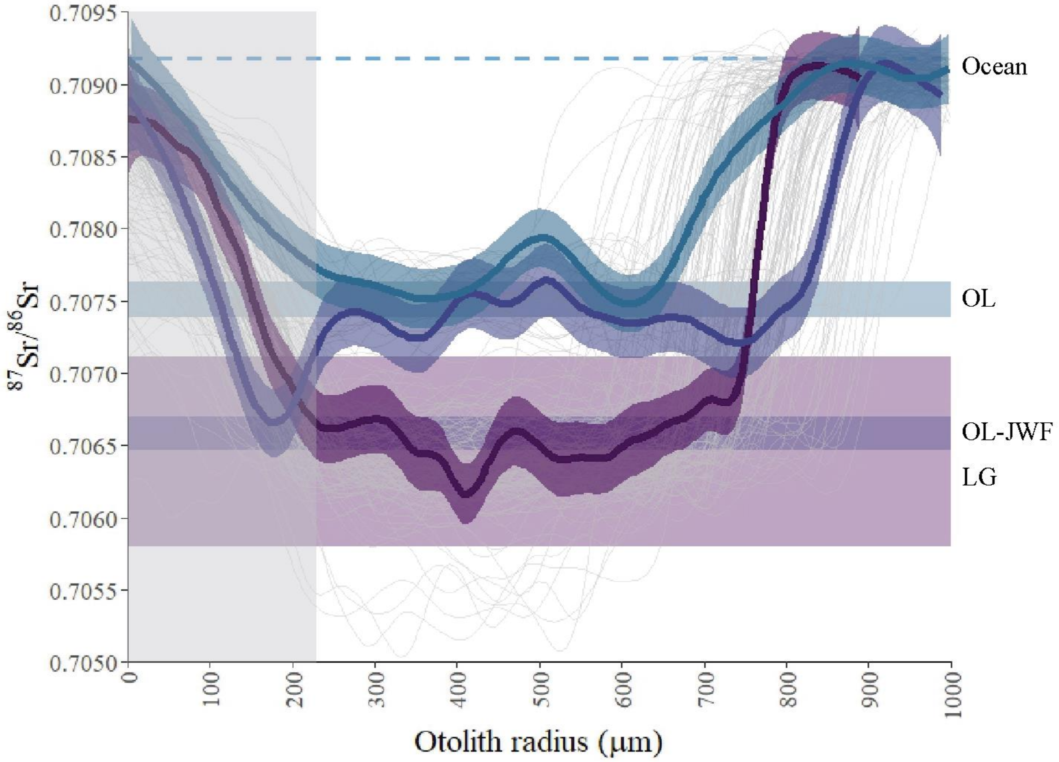

Figure S2 Example of otolith profiles for fish of each known natal origin. The distance from the otolith core along the laser transect is along the x-axis, and the resulting $^{87}Sr/^{86}Sr$ value from point of the otolith is along the y-axis. Stream $^{87}Sr/^{86}Sr$ values are colour-coded in blocks, and associated example profiles (smoothed $^{87}Sr/^{86}Sr$ values with 95% confidence intervals) of each stream natal origin are similarly colour-coded. The grey shading indicates the region of the otolith before exogenous feeding begins.

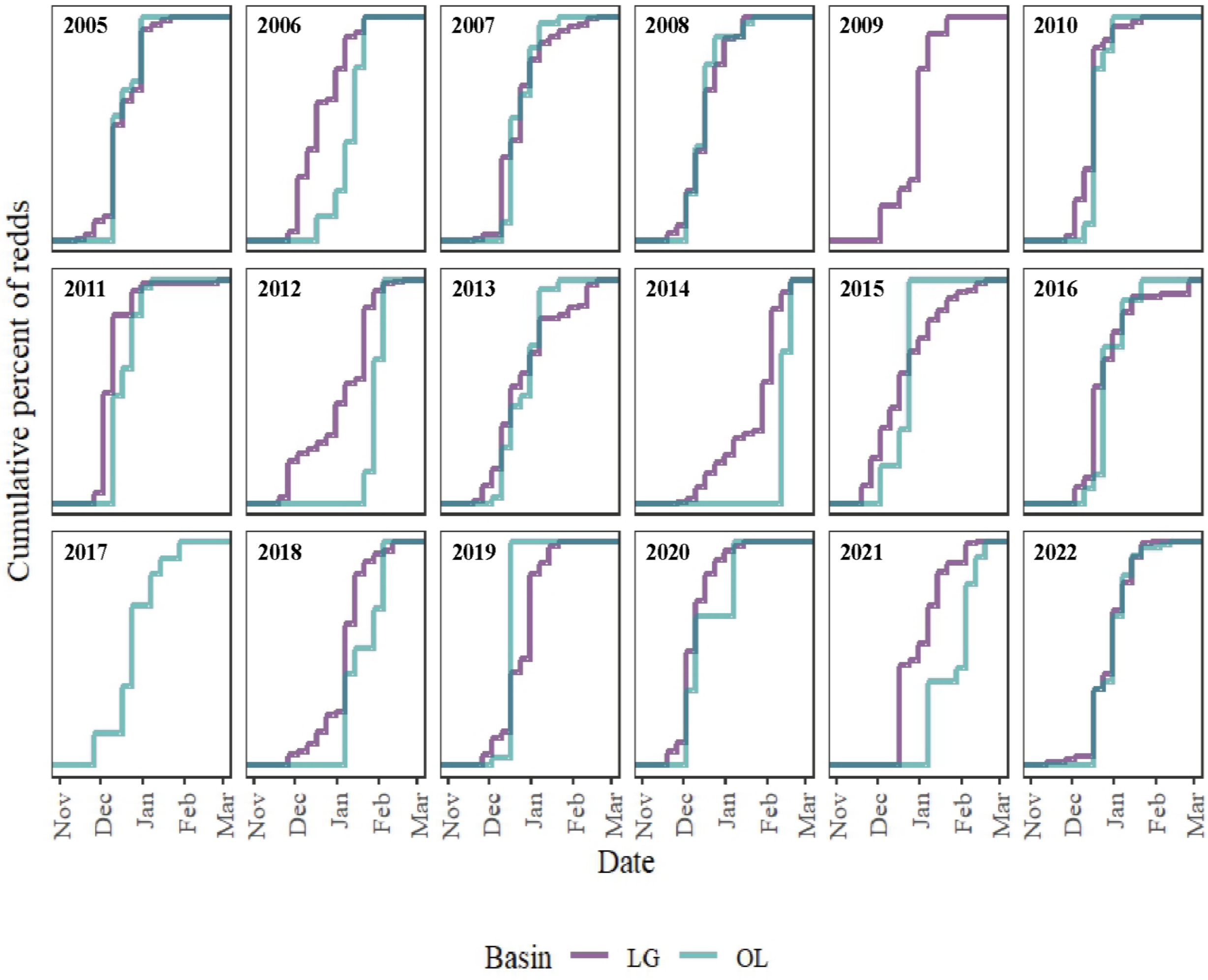

Figure S3 Curves for the accumulation of redds across the spawning season, from 0-100%, for Lagunitas Basin and Olema Basin.

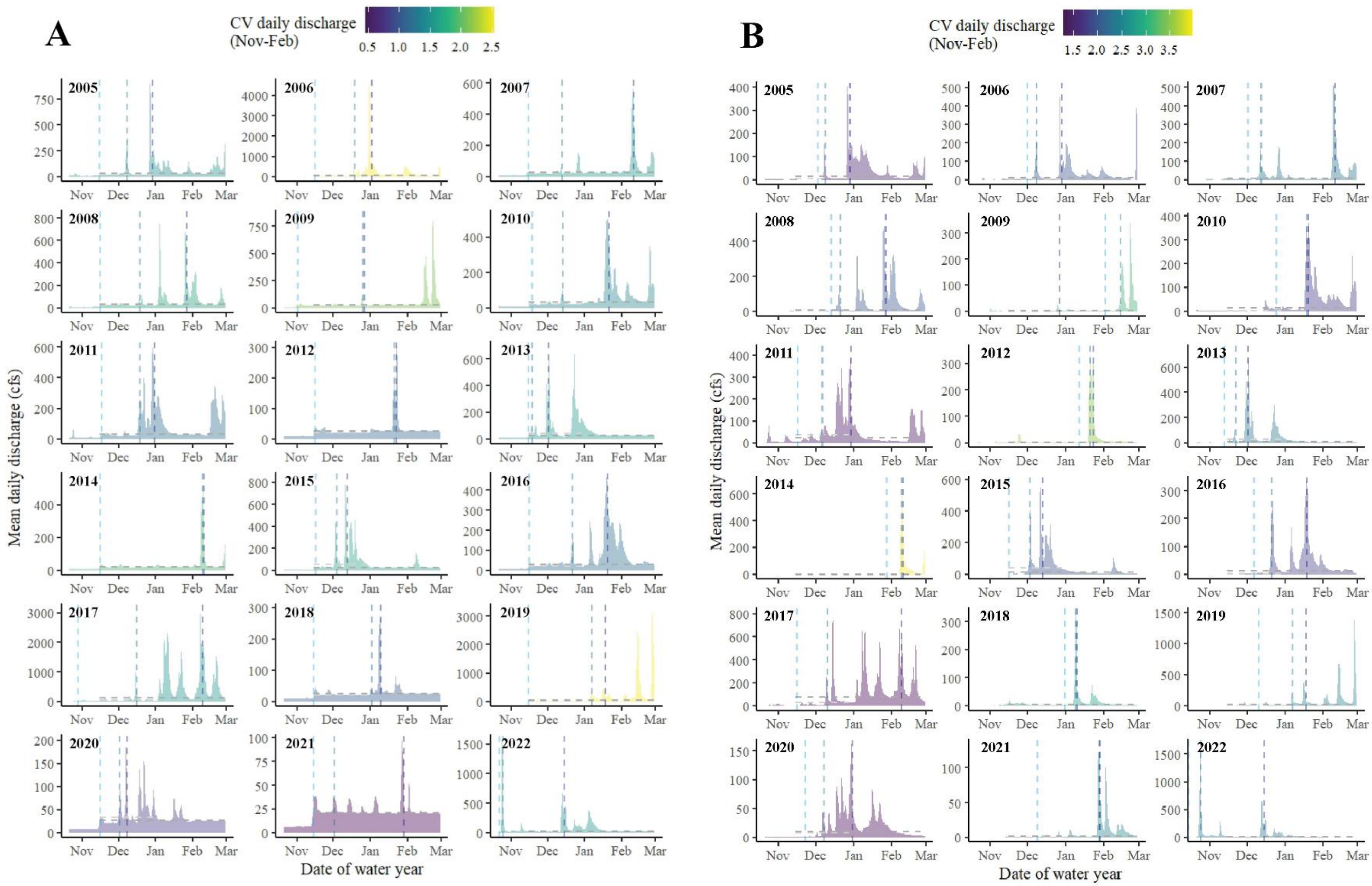

Figure S4 Mean daily discharge and discharge metrics for Lagunitas Creek (A) and Olema Creek (B) for each water year of the study period from the start of the water year to the end of the spawning period. The area under the discharge curves are coloured based on the coefficient of variation of discharge across the full spawning season. Vertical lines indicate timing of wet season metrics: onset of the wet season (light blue), first pulse flow after the wet season (medium blue), peak flow (dark blue). Horizontal gray lines indicate the early season median flow (light gray) and full spawning season median flow (dark gray).

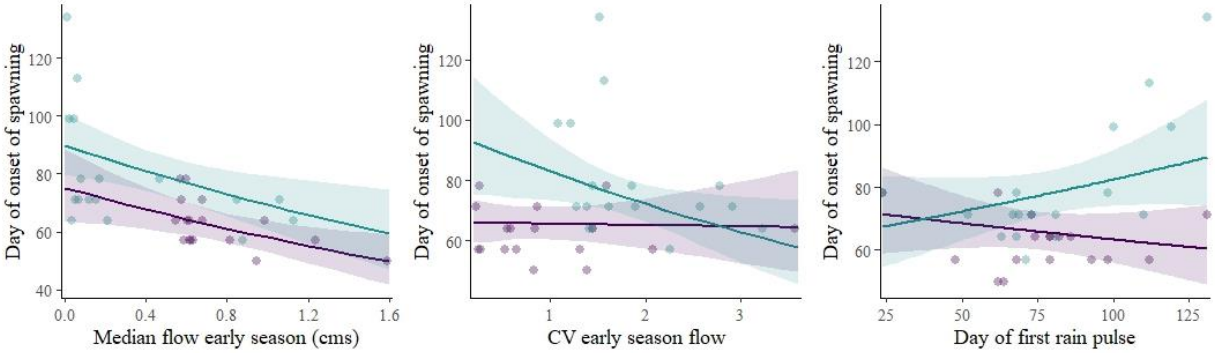

Figure S5 Observed data and predicted effects on day of onset of spawning from model 1b (see main text) using a generalized linear model with a gamma distribution and log-link. Predicted relationships (solid lines) and raw data (points) are for Lagunitas (purple) and Olema (blue) Basins. Days are in water year day (starting October 1st). CV is the coefficient of variation.

Conclusion

In this dissertation, I explored the interactions between habitat, climate, and population diversity within an endangered salmon complex to improve our understanding of factors influencing the stability and resilience of vulnerable populations. I found that all habitats within a small, modified watershed can play a role in generating trait diversity and contributing to successful adult returns in different climate contexts. However, habitat heterogeneity and trait diversity did not generate asynchrony in juvenile dynamics, with fish facing similar conditions in most years, suggesting that there is a risk of synchronized population collapse. Yet, the ability of some parts of the watershed to consistently provide refuge during drought, and the capacity of salmon to recolonize habitats following disturbance events highlights the resilience of the population.

Overall, my dissertation research offers three key insights into management and conservation of salmon populations near their southern edge in California. First, drought is a unique threat to salmon in the way it collapses the habitat mosaic for salmon at multiple life stages, but flow management is a tool for mitigating drought effects. Second, viewing the watershed as a metapopulation enables a more comprehensive understanding of risks to salmon and resilience of the population, and can inform novel restoration strategies. Third, coho salmon in California have the capacity to express a diversity of life histories, a hopeful sign that fish can exploit a range of strategies to cope with climate stress.

Drought as a unique threat

Working during the summer of 2021 amidst a historic drought had its unique challenges, one of them being the weight of seeing juvenile coho salmon struggle to survive in extremely poor habitats. Even in freshwater systems subject to strong seasonal and interannual variation where species have adaptations to such disturbances, the abiotic and biotic effects of drought are significant and culminate in the disruption of ecosystem processes (Lake 2003). Drought has been an increasingly frequent occurrence in California, and the unusual drying of perennial streams I witnessed will become more commonplace (Ayers et al. 2024; Carlson et al. 2024). My dissertation attempted to assess effects of drought at the watershed level to understand to what extent habitat heterogeneity and population diversity support persistence during drought. By examining relationships between regional climatic conditions and local-scale environmental conditions during a summer of extreme drought in Chapter 1, I found that parts of the watershed can act as refuge during drought, while others may become mortality traps (Vander Vorste et al. 2020). Though the collapse of part of the habitat mosaic due to extreme drought reduced the capacity of the watershed to support coho salmon, fish in refuge habitats displayed diverse foraging behaviours, suggesting potential for variation in growth trajectories and diverse life history strategies.

My analysis of adult spawning distributions in Chapter 3 revealed that the timing of spawning can also be heavily impacted by drought. For example, we found that delayed and reduced winter rains can push back spawning time, such as in 2021, when many fish were unable to access the system to spawn until late spring. This has important consequences for the progeny. First, late spawning can cause late emergence, potentially resulting in smaller juveniles because of reduced growth opportunities and more competition (Einum & Fleming 2000; Armstrong et al. 2010; Skoglund et al. 2012). Second, a more restricted window of spawning during drought also limits the window of emergence, increasing the risk of mass mortality from disturbance events during incubation and upon emergence. Third, delayed spawners may be building nests in marginal habitats that are less suitable for rearing resulting in a mismatch between adult spawning location and juvenile habitat (Jeffres & Moyle 2012). Under extreme drought conditions where dispersal downstream was constrained, this mismatch led to mortality in natal sites. Considering the cascading effects of delayed spawn timing in drought years, this could also have contributed to unexplained fluctuations in density when examining juvenile dynamics in Chapter 2.

My dissertation adds to a growing body of work highlighting the dangers of drought in causing mortality to juvenile coho salmon (Woelfle-Erskine et al. 2017; Obedzinski et al. 2018; Vander Vorste et al. 2020) and provides new evidence for drought reducing life history diversity in coho salmon (Kastl et al. 2022). While I mainly focused on consequences of drought within a single year, multiyear droughts can intensify ecological impacts and are a cause for concern as they become more common (Bêche et al. 2009; Wang et al. 2018). Yet my findings also offer insight into tools for mitigating drought effects. Ecological flow management helped buffer adults and juveniles against drought and contributed to diversifying the life history trajectories available for salmon, and the importance of a mosaic of habitats and connectivity to exploit it also has clear implications for stream restoration efforts designed to recover salmon.

Metapopulation dynamics offer resilience

Despite the threat of drought, a hopeful lesson from this work is that the regional metapopulation - i.e., a complex of populations connected by dispersal - provides some degree of stability to my study population. I observed how larger source populations can be critical for re-establishing subpopulations and expanding the distribution of fish when conditions allowed (Lin et al. 2011). Results in Chapter 2 and my analysis of spawning distributions in Chapter 3 highlight how streams (and watersheds) utilized by coho salmon are connected by dispersal. I found that mainstem Lagunitas Creek subpopulation was the most stable and least impacted by drought during the juvenile and adult stages, partly due to its size and regulated minimum flows. The consistent spawning and rearing in Lagunitas Creek provided a source population from which fish could disperse to other streams and watersheds, colonizing and recolonizing stream subpopulations that collapsed during drought years, as revealed by analyses of otolith microchemistry.

Lagunitas Creek may be the main source subpopulation of the watershed (and region), yet this work shows that all pieces of the metapopulation are important in different contexts. In extreme drought years, intermittent streams can be poor rearing habitats, yet under different conditions they may disproportionately contribute to adult returns as I found in Chapter 3. Tributaries may experience synchronized declines in juveniles as modelled in Chapter 2, but in years where fish have adequate access to habitat in these streams this expanded mosaic can produce variation in traits as seen in my first chapter, which can lead to adult returns. Thus, viewing the system as a diverse mosaic of habitats that support a metapopulation of endangered coho salmon, the mosaic shifts, expands, and contracts with hydrological conditions but is constantly repopulated, offering resilience to the overall population.

A caveat to these findings is that metapopulation dynamics provide resilience if environmental synchronizing agents are minimized. While Lagunitas Creek buffered the metapopulation against drought impacts, I found less evidence of buffering effects in wet years when streams across the region experienced similar winter-spring conditions. Chapter 2 results indicated that early-life high flow events can reduce salmon metapopulation stability and resilience through the Moran effect, whereby correlated local environmental conditions synchronize population dynamics (Moran 1953; Cattanéo et al. 2003; Bouchard et al. 2022; Castorani et al. 2022). Climate change is projected to exacerbate extreme flow events (Kim 2005) and increase spatial synchrony in flow conditions, further synchronizing subpopulations and eroding resilience from metapopulation dynamics (Hansen et al. 2020). However, synchronizing effects of high flows may be counteracted by trait variation that staggers the timing of vulnerable life stages like emergence, spreading risk through time.

An emerging picture of coho salmon diversity

Among Pacific salmon species, coho salmon have some of the lowest levels of life history diversity (Waples et al. 2001). Yet, past studies (Shapovalov & Taft 1954; Nielsen 1992a, 1992b, 1994) combined with recent research (Bennett et al. 2011, 2015; Roni et al. 2012; Nordholm 2014; Ghrist 2019; Halloran 2020) paint a picture that includes a variety of "hidden" life history strategies that are less common, but play important roles in population persistence. My dissertation illuminates a variety of known and potential life history pathways, with some proven to contribute to successful adult returns. For example, otolith profiles confirmed the prevalence of successful rearing in intermittent streams, including in drier years, adding to the growing appreciation of the role of intermittent streams for supporting salmon populations in arid regions (Wigington et al. 2006; Hwan et al. 2018). Some successful intermittent stream rearing involved non-natal dispersal to other streams, reinforcing that juvenile coho may be highly mobile and seek non-natal habitats to rear (Nielsen 1994; Halloran 2020). In addition, fish are utilizing habitats and resources in dynamic ways, such as using different foraging behaviours, unlocking a variety of growth pathways (Nielsen 1992a, 1992b, 1994). Growth rate can drive life history variation as it is linked to timing of outmigration to the ocean (Thorpe 1977; Metcalfe et al. 1988; Beckman et al. 1998). Growth rate variation can also contribute to age complexity of populations which is important to buffer against risk of cohort collapse. Faster growing male fish are more likely to return early from the ocean as 2-year-olds, called "jacks" (Watters et al. 2003) and slower growing fish are hypothesized to stay in freshwater longer and leave as 2-year-old smolts, though this strategy is rare (Nielsen 1992b, 1994). My observations of 1-year-old coho salmon in stream pools over the summer suggests that drought may contribute to age complexity as well by inhibiting outmigration, potentially leading to 4-year old adults.

Finally, some of the most interesting insights into coho salmon life history are not the results from my dissertation chapters, but the new questions generated. My findings point toward potentially a wide range of growth trajectories and dispersal opportunities for juvenile salmon across the watershed, yet further work needs to be done to investigate which of these growth trajectories are realized and if they indeed lead to variation in other life history traits such as outmigration timing. With growth opportunities spread across the watershed, it is hypothesized that fish track resource pulses across the watershed (e.g., Bellmore et al. 2022), including in productive habitats such as downstream wetlands and the estuary (Rossi et al. 2024), which remains to be tested. Wetland and estuary use in this system is especially understudied, despite the potential for the perennially open estuary to provide high quality rearing habitat. Further investigation of the otolith profiles I produced for this dissertation, which hinted at some unusual rearing habitats, and additional sulphur isotopic analyses may be able to advance our understanding of the contributions of wetland and estuary rearing to the returning adult population (Bell-Tilcock et al. 2021). The large variation in the timing and magnitude of growth opportunities also raises the question of whether this drives a broader distribution of outmigration timing. Though outmigration is typically in the late winter-spring, studies of coho salmon in California, Oregon and Washington are increasingly finding support for a wider range of outmigration timing starting as early as the fall (Roni et al. 2012; Nordholm 2014; Bennett et al. 2015), and that these strategies can be successful in producing adult returns. Building on work in this dissertation, further research needs to be done to expand our understanding of coho salmon life history strategies near their southern edge.

The literature on the benefits of life history diversity and its contribution to population persistence is vast, but rarely focuses on the role of small-scale habitat heterogeneity as part of the building blocks for population stability (see also Lusardi et al. 2023; Cordoleani et al. 2024). I found that the mosaic of habitats within the watershed generated meaningful population diversity, with differences between unregulated tributaries and the flow-regulated mainstem Lagunitas Creek particularly important for ensuring a wider range traits and outcomes for coho salmon. These insights highlight the importance of lesser-known life histories, habitats supporting these strategies, and their potential to contribute to species resilience to climate variability.

Importance & implications

Challenges to the conservation and recovery of endangered species are plentiful, but my work shows that salmon can generate a diversity of life history strategies to cope with, and exploit, variable environments. However, this is predicated on the availability of cold, clean, connected and complex habitat – considered the four C's of salmon restoration (Quinn 2018). We can provide salmon the blueprint to succeed by taking a holistic watershed approach, using a variety of tools at our disposal. For example, ecological flow releases from reservoirs and small holding pools can enhance stream connectivity and water quality (Yarnell et al. 2015, 2020; Poff 2018; Rossi et al. 2023). A better understanding of subsurface flows that sustain unregulated streams in the dry season and the impacts of human activities can help with planning for sustainable groundwater use and maintenance of streamflow. The removal of barriers, creation of side channels and deep pools, reintroduction of beavers, reconnection of floodplains, and other watershed restoration actions that expand the usable habitat can increase habitat heterogeneity and enhance flow connectivity to exploit it. Restoration planning and management at the watershed scale is critical to achieving high quality connected habitat that buffers against environmental variability and creates a "foodscape" - a rich mosaic of resources and growth opportunities for salmon that supports a multitude of life history trajectories (Rossi et al. 2024). In wake of climate change and challenges, supporting population diversity is a key part of species persistence. I've learned that these vulnerable populations are far more resilient and adaptable than I imagined, and it is my hope that we find ways to support these beautiful species in their recovery.

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