Coho Salmon Outmigration Drivers and Long-Term Trends in a Small Watershed

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ABSTRACT

Climate change presents a major threat to anadromous salmonids; increases in stream temperatures and hydrologic extremes impact all salmonid life stages by pushing the limits of tolerable stream conditions, affecting habitat availability, and altering important life history cues. Temperature and flows drive smolt outmigration; shifts to outmigration timing due to climate change can cause a mismatch with prey availability, threatening the survival and fitness of these species. I used 19 years of smolt trap data to analyze how outmigration patterns of an endangered Central California Coast coho salmon population differed in a dammed and undammed subbasin of a small watershed. I used a paired t-test to test the similarity of outmigration traits in the two creeks and a Multivariate Autoregressive State-Space model to analyze trends and the influence of abiotic drivers on timing. I found a significant difference in the median outmigration fork length ($p = 0.02599$) but no difference in the median outmigration date or length between the two subbasins. I found a negative correlation between wet season baseflow and the window length (-0.1086), but no other flow or temperature metrics significantly affected timing. Across the study period, there were only insignificant trends toward earlier and shorter migration windows. Similar outmigration timing in this watershed means this population may lack the life history diversity to buffer against mismatch or years of poor recruitment. However, stable outmigration trends indicate that if the timing of upwelling is stable, there is no immediate concern for increased mismatch events in this watershed.

KEYWORDS

MARSS model, Central California Coast coho, phenology, endangered species, ocean upwelling

INTRODUCTION

Of California's 32 native salmonid taxa, 15 are threatened or endangered, and 74 percent will likely be extirpated by the end of the century or sooner (Moyle et al. 2017). Anthropogenic activities such as dams, agriculture, and logging drastically alter salmonid habitat quality and availability as well as water quality, stream temperature, and stream flows (Moyle et al. 2017). However, climate change poses the most pressing threat to California's salmonid populations (Katz et al. 2013, Moyle et al. 2017). California's anadromous salmonids already live at or near their tolerance limit for environmental conditions, as they constitute the southernmost populations of Pacific salmonid species (Katz et al. 2013). The upper-temperature limit for salmonids is 25 ℃, but temperatures around 18 ℃ can cause higher susceptibility to disease, weight loss, or competition from species adapted to warm temperatures (Richter and Kolmes 2005). The upper range of average summer stream temperatures in Northern California is around 18 ℃ ("Western Regional Climate Center" 2018), with temperatures surging in warmer years. Salmonids living at the edge of this temperature threshold are especially vulnerable due to the experienced and projected impacts of climate change in California, including rising temperatures and more frequent and intense droughts and floods (Ehlers 2022). Anthropogenic and climate-induced hydrologic changes alter the timing and intensity of flow events. Low flows can limit access to habitat, impair stream connectivity, and cause fish stranding, while high flows can wash away redds and juveniles (Tonina et al. 2022). Such streamflow and temperature shifts may substantially impact all life stages and the phenology of anadromous salmonids.

One natural buffer against climate-related risk is the presence of different life history strategies among populations. Despite changes in climatic conditions, such 'portfolio effects' sustain salmonid metapopulations through the shifting success of different life history strategies over years (Hilborn et al. 2003, Greene et al. 2010). Portfolio effects in salmon populations stem from several factors, including habitat heterogeneity, genetic diversity, and environmental variability (Schindler et al. 2015). Portfolio effects have mostly been documented in large watersheds and spatial scales (Hilborn et al. 2003, Greene et al. 2010). However, these effects have yet to be studied in smaller watersheds, where smaller salmon populations are more vulnerable to the impacts of climate change but likely have fewer of these buffers. The timing of salmon life history events provides an important opportunity to study the synchronization or diversification of salmon populations.

One important life history event that may be particularly sensitive to changes in stream conditions is smoltification and the outmigration of smolts. Smoltification is a series of physiological changes allowing salmonids to transition from fresh to saltwater. Salmon ocean survival is largely linked to ocean conditions at the time of entry, which influence early ocean growth and consequent fitness (Holtby et al. 1990, Satterthwaite et al. 2014). In California, salmon smolts time their outmigration to arrive during ocean upwelling, a period of high marine productivity and abundant salmon prey (Spence and Hall 2010). A combination of abiotic factors, including photoperiod, stream flow, stream temperature, and moon phase, drive the timing of smolt outmigration (Holtby et al. 1989, Sykes et al. 2009, Spence and Dick 2014). Due to this relationship between environmental variables and timing, climatic conditions can change the outmigration window, increasing the possibility of a mismatch between ocean arrival and upwelling. Previous studies have shown that warmer water temperatures and drought shift outmigration timing (Munsch et al. 2019, Kastl et al. 2022). Given the projected increase in temperatures and droughts, this pattern could potentially exacerbate mismatch events and decrease the fitness and survival of California salmonids. As such, it is essential to study outmigration drivers in various systems to better understand how projected climate change might impact salmonids across their range.

Outmigration responses, drivers, and trends vary across salmonid species and geographies; studying different salmonid species across their range is important to understand the specific effects of stream conditions and climate change on different populations. One species of interest is coho salmon (*Oncorhynchus kisutch*) in the California Central Coast (CCC) region, which is a critically endangered salmonid at the southern end of their range (Moyle et al. 2017). Across three distinct regions, coho salmon smolts responded to different environmental variables and had varying responses to these drivers (Spence and Dick 2014). Additionally, coho smolts exhibit a range of outmigration strategies, with short, predictable outmigration windows at higher latitudes and wide, highly variable windows at lower latitudes (Spence and Hall 2010). With such intraspecific variability, it is important to further the understanding of outmigration drivers and traits at the southernmost end of their range. Existing research on coho outmigration is focused on northern populations (Holtby et al. 1989, Spence and Dick 2014), which are not under the same anthropogenic and climatic pressures. Additionally, CCC coho primarily occupy small coastal streams and watersheds, which creates additional concern for synchronized populations that might not have life history diversity to buffer against major change. The Lagunitas Creek watershed is a small coastal system with a dammed and an undammed subbasin with varying geologies and environments. This system provides a unique opportunity to study coho at the southern end of their range, specifically to observe the patterns of coho smolts in two environmentally distinct subbasins.

In this study, I aim to characterize coho smolt outmigration traits, drivers, and trends within the Lagunitas Creek watershed and compare these aspects of outmigration between the two subbasins. I first determined if smolts in Olema and Lagunitas Creeks exhibit differences in median outmigration date, outmigration window length, and outmigration size. Although Lagunitas is regulated, the hydrograph resembles historic conditions (Grantham 2014). Considering the relatively unchanged flow conditions and the proximity of the two creeks, I expected no difference in outmigration traits would exist. Then, I determined the extent to which stream temperature, stream flow, and moon phase influence outmigration timing and length; I expected that a combination of these three factors would best explain timing. Finally, I determined if there were any trends in outmigration timing or length from 2004 to 2023. I expected no significant trends in timing due to low life history variability in coho (Rebenack et al. 2015), but that there could be insignificant trends towards earlier outmigration and shorter windows in response to a changing climate (Kastl et al. 2022). I used smolt outmigration data in Lagunitas and Olema Creeks collected by Marin Municipal Water District (MMWD) and the National Parks Service (NPS) from 2004 to 2023, along with temperature and flow data to understand the dynamics of coho smolts across these two creeks and over time.

METHODS

Study site

The Lagunitas Creek watershed is a small coastal watershed located in Marin County, California. The watershed drains approximately 270 square kilometers (km^2), and the Lagunitas mainstem runs 40 km from Mount Tamalpais to the southern end of Tomales Bay (Figure 1).

However, four dams in the creek restrict access by anadromous fish to the lowest 19 km (Ettlinger et al. 2022b). This watershed experiences a Mediterranean climate and is a rainfall-dominated system that receives around 95% of its precipitation between the months of October and April. High intra-annual variation in rainfall causes periods of both drought and high precipitation in this system (Voeller et al. 2018).

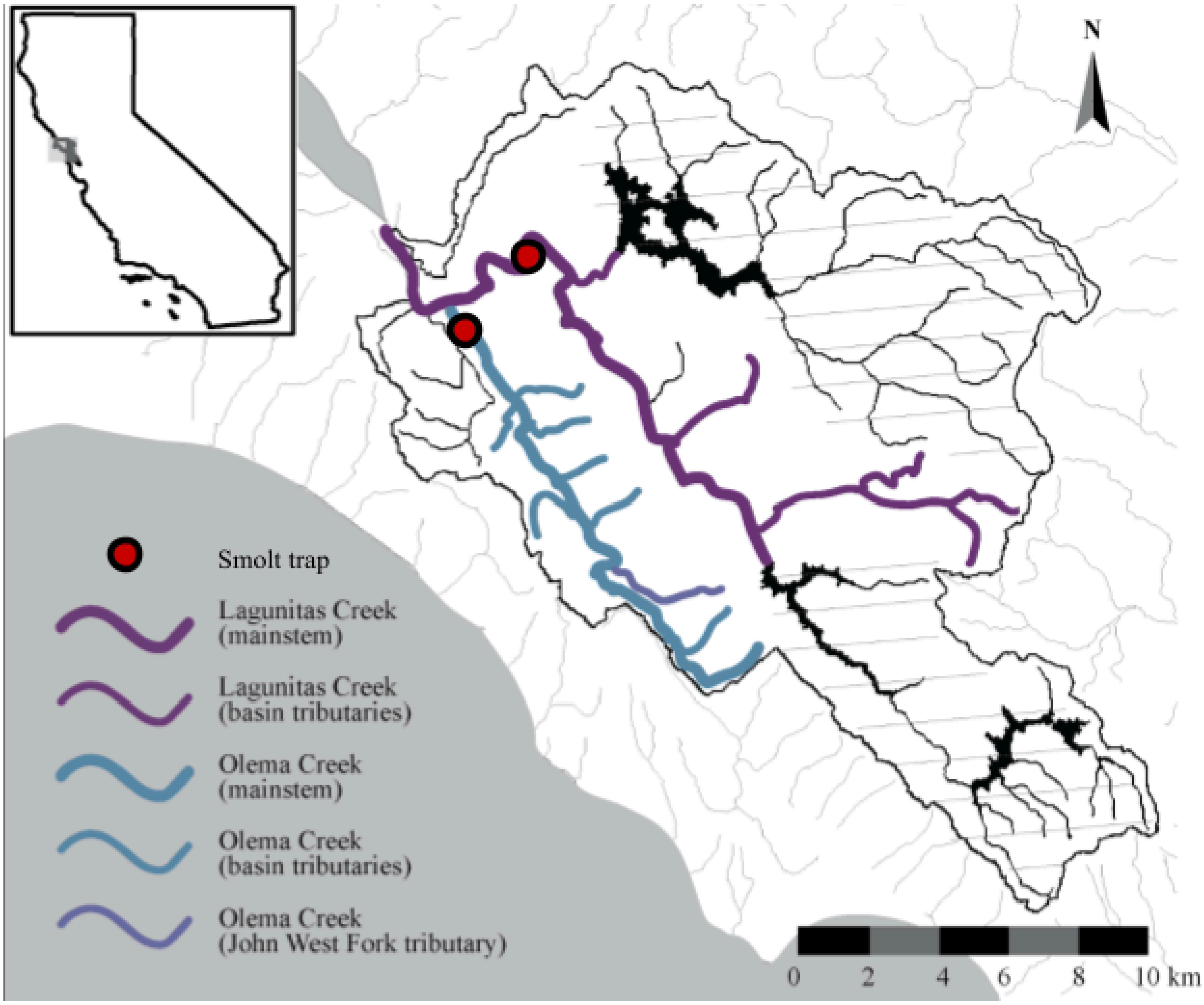


Figure 1. Map of Lagunitas Creek Watershed and sampling locations. The Lagunitas Creek mainstem and tributaries are shown in purple, along with reservoirs in this basin. Olema Creek and its tributaries are shown in blue. The two creeks converge shortly before entering Tomales Bay.

The major tributaries to Lagunitas Creek are San Geronimo Creek, Devils Gulch, Nicasio Creek, and Olema Creek. In this study, I will focus on coho salmon populations in the Lagunitas

Creek mainstem and Olema Creek, the watershed's two main subbasins. These two creeks run parallel through contrasting environments until their confluence near Tomales Bay. Additionally, the San Andreas fault line runs through the watershed, leaving the two creeks on different plates and resulting in geological differences in the subbasins. The physical separation and varying conditions in these subbasins make the Lagunitas Creek watershed a unique site to study how habitat heterogeneity in a small watershed affects smolt outmigration patterns.

Lagunitas Creek is heavily forested, running through redwood groves near Samuel P. Taylor State Park and willow and alder thickets further downstream. The shady, damp conditions along Lagunitas Creek help maintain cool water temperatures in the stream year-round ("Tomales Bay and Lagunitas land use and habitat" 2016). Additionally, managed flows release water from the hypolimnion of Kent Lake, providing cold water (< 20°C) in Lagunitas Creek (Grantham 2014). Although the management of dams on Lagunitas Creek ensures cold water and sufficient flows for salmon, these dams limit spawning habitat to nearly half of historical amounts. The Lagunitas Creek subbasin also suffers from a lack of floodplain habitat due to human-made and natural constraints, which was identified as a critical bottleneck for overwinter survival in coho salmon (Stillwater Sciences 2008). Riparian and floodplain restoration efforts to address these limitations are ongoing throughout the creek ("Lagunitas Creek Floodplain & Riparian Restoration Project" 2018).

Olema Creek is an unregulated tributary that runs primarily through NPS land, 56% of which is under grazing leases (Voeller et al. 2018). The Olema Creek subbasin is primarily characterized by annual grassland and oak woodland ecosystems (Lewis et al. 2019). While dams on Lagunitas tributaries provide water year-round, Olema tributaries are primarily intermittent, meaning they experience streamflow only during the wet season (Lewis et al. 2019). Additionally, the San Andreas Fault runs directly through Olema Valley, situating Lagunitas and Olema creeks on separate tectonic plates that have different geologies and compositions ("Faults - Point Reyes National Seashore (U.S. National Park Service)" 2021). Given these differences in land use, flow regimes, and geology, we can expect stream temperatures, flow regimes, and habitat quality to vary between Olema and Lagunitas subbasins.

Study species

Coho salmon in Lagunitas Creek

The Lagunitas Creek watershed is a stronghold for the federally endangered California Central Coast Evolutionarily Significant Unit (CCC-ESU) of coho salmon. Evolutionarily significant units delineate species' ecologically and genetically distinct populations and are important for distinguishing populations in conservation efforts (Waples 1995). This watershed has large and consistent returns of wild, naturally spawning adults and is not supplemented by hatchery production.

Coho life cycle

The coho life cycle is roughly three years long, split between freshwater and the ocean (Figure 2). Spawning in small coastal streams such as Lagunitas occurs between November and January. Eggs in the redd incubate for a few months before hatching into alevin. Once alevin absorb their egg sack, they become fry and leave the redd. Fry emergence typically occurs during late winter or spring, at which point juvenile coho spend an additional year rearing in freshwater. During the spring of their second year, salmon undergo smoltification, a process in which physiological and developmental changes prepare salmon to live in saltwater (Hoar 1988). Between March and May, smolts migrate downstream, where they may spend additional time rearing in the estuary before entering the ocean. Adults typically spend a year in the ocean before returning to their natal streams in the fall and winter, where they spawn and then die (Lestelle 2007).

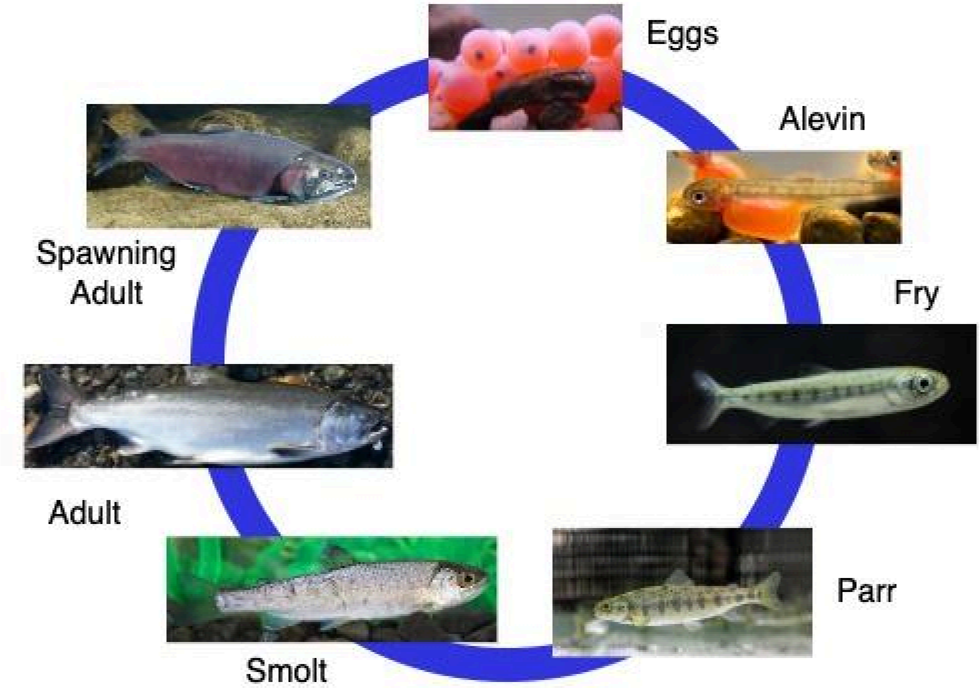


Figure 2. Salmon life cycle. Coho salmon spend about half their life in freshwater, growing from eggs to smolts. They then migrate to the ocean, where they spend a year before returning to spawn in their natal streams.

Data collection

Smolt sampling

To study outmigration patterns in this watershed, I analyzed coho smolt outmigration counts, water temperature, and streamflow time series collected by several agencies working throughout the watershed. In Lagunitas Creek, Marin Water has collected smolt outmigration data in cooperation with NPS since 2006. To collect this data, crews deployed rotary screw traps in the stream from late March to early June to capture fish migrating downstream. A rotary screw trap involves a large cone that is rotated by stream flow and funnels migrating fish into a trap. Each day during the study period, crews checked the trap, identified organisms to species level, checked salmonids for signs of smoltification, measured, weighed, and then released fish downstream of the trap. To determine trap efficiency, crews gave up to 20 smolts a day a unique fin clip depending on the week, then released them 300 meters (m) upstream. Recaptured fish were used to calculate trap efficiency using Darroch Analysis with Rank Reduction (DARR) 2.0.2 software (Bjorkstedt 2005).

On Olema Creek, the NPS ran a similar operation starting in 2004. Here, NPS used fyke/pipe traps, which consist of large cylinders of steel pipe and fencing with funnel-shaped openings inside. Fish enter the trap, follow the funnels, and once they reach the back of the trap, they have difficulty finding the entrance. Crews checked the traps daily but only measured and weighed a random subset of around ten smolts daily. As in Lagunitas, NPS deployed smolts traps from roughly late March to early June, depending on conditions. NPS used the same DARR analysis of mark-recapture data to estimate trap efficiency.

Streamflow and temperature

I used streamflow and water temperature data from the two creeks to understand the covariate effects of these factors on outmigration timing. I accessed daily water temperature records for Lagunitas that Marin Water has collected since the early 1990s. At Olema, NPS crews deployed Onset temperature loggers in the smolt trap and reported daily average temperatures during the duration of trap operation. I downloaded average daily discharge (cubic feet/second [cfs]) data from the United States Geological Survey (USGS) database. The USGS operates a flow gage in Lagunitas Creek at Samuel P. Taylor State Park (“Lagunitas C a Samuel P Taylor State Park CA” 2024). In Olema Creek, the San Francisco Bay Area Network Inventory and Monitoring Program (SFAN I&M) maintained a stream gage measuring average daily discharge until 2017, when USGS took over the site. I accessed stream flow data for Olema from these two agencies.

Data processing

Before running statistical analyses, I processed smolt trap, water temperature, and stream flow data to ensure conformity across these datasets. I cleaned and transformed the data in R (R Core Team 2024). I combined smolt trap datasets from each year and stream and converted dates to ordinal dates. From this synthesized data, I created two data frames that I used throughout my analysis - one with the median outmigration date and the other with the length of the middle 80 percent of the outmigration data, i.e. the outmigration window length. I then converted the daily flow and temperature measurements into annual metrics to be used as covariates in the models. I used the UC Davis eFlows Functional Flow Calculator (Lane et al. 2023) to extract the following flow metrics from average daily discharge: 10th percentile of wet season baseflow magnitude, peak flow magnitude, timing of the spring recession flow, and rate of change of the spring recession flow. Due to only having Olema temperature data during trap operation, there were limited options for an annual temperature metric. I used the "changepoint" package in R (Killick et al. 2022), which detects changes in the mean of a time series. I found the ordinal date of the temperature changepoint within the smolt trap dates for each year. I then downloaded a moon phase dataset and filtered for occurrences of the new moon ("1900 - 2022 Lunar Cycle" 2022).

Data analysis

Outmigration characteristics

To analyze the outmigration characteristics of smolts in Olema and Lagunitas Creeks, I used paired t-tests. I ran three paired t-tests, one each for the median outmigration date, the outmigration window length, and the median fork length (size) of smolts at outmigration. For each of these tests, I paired data in the two streams by year to account for interannual variation. I used a significance level of 0.05 to determine if there was a significant difference in outmigration traits between the two creeks.

Outmigration drivers

I used a Multivariate Auto-Regressive State-Space (MARSS) model to estimate covariate effects on timing and to determine whether the effects differ by subbasin. The MARSS framework (Holmes et al. 2021) is ideal for analyzing multiple time series of various spatial structures and how covariates drive fluctuations in the time series. In addition, MARSS models are useful in analyzing ecological data due to their ability to filter out observation error from process error. Process error refers to the actual fluctuations in population characteristics in response to environmental stochasticity. Observation error refers to the discrepancies between actual and observed values. By distinguishing observation error from process error, the MARSS model can estimate true population sizes and population changes across time. The MARSS framework consists of a process model (1) and an observation model (2), as shown in the following equations.

$$\mathbf{X_t} = \mathbf{B}\mathbf{x}_{t-1} + \mathbf{U} + \mathbf{C}\mathbf{c}_{t-1} + \mathbf{w_t}\text{, where } \mathbf{w_t} \sim \text{MVN}(0, \mathbf{Q}) \tag{1}$$

$$\mathbf{y}_t = \mathbf{Z}x_t + \mathbf{v}_t\text{, where } \mathbf{v_t} \sim \text{MVN}(0,\mathbf{R}) \tag{2}$$

Observations enter the model as **y** - for my first model, observations were the median outmigration date each year. In the second model, the observations were the length of the outmigration window. In both these models, I log-transformed the observations in order to ensure model convergence. The **Z** matrix links observations to the true states (**X**). In my model, I used an identity matrix to indicate that observations from the two sites, Olema and Lagunitas, should correspond to two separate states. $\mathbf{V_t}$ is a vector of observation errors assumed to be drawn from a multivariate normal distribution with mean zero and covariance matrix **R**. I set the **R** matrix to 'diagonal and unequal' to account for differing trapping methods in the two creeks. A 'diagonal and unequal' **R** matrix means that the observation error variance at the two sites should be estimated as different and that there is no observation error covariance between sites. The **B** matrix of the process model allows for estimates of density dependence and species interactions. For this model, I set the **B** matrix equal to 'zero' as I was not looking to estimate biotic interactions.

Before adding covariates, I tested different **Q** and **U** matrix specifications to determine which best fit the data. $\mathbf{W_t}$ is a vector of process errors drawn from a multivariate normal distribution with mean zero and variance-covariance matrix **Q**. I ran the model with **Q** as 'diagonal and unequal,' 'diagonal and equal,' 'equalvarcovar,' and 'unconstrained.' The **U** matrix is used to specify trends seen in the data over time. I tested an 'equal,' 'unequal,' and 'zero' **U** to determine if the two creeks were experiencing the same, different, or no trends over the study period. I compared the Akaike information criterion corrected for small sample sizes (AICc) of these models to determine which **Q** and **U** matrices best fit the data.

I then added covariates to the best-fit models to determine what factors smolts respond to and how these responses vary between streams. I used four annual flow metrics - 10th percentile of wet season baseflow magnitude, peak flow magnitude, timing of the spring recession flow, and rate of change of the spring recession flow - along with the ordinal date of the temperature changepoint and the ordinal date of the March new moon. I tested two **C** matrices to model different responses to covariates. One **C** matrix tested a 'watershed' hypothesis, in which smolts in the two streams respond similarly to the covariates. The other **C** matrix tested a 'stream specific' hypothesis, where smolts in each stream have separate responses to covariates.

I first ran each of the six covariates individually, once with the 'watershed' and once with the 'stream specific' **C** matrix, for a total of 12 models. I then tested a combination of the best covariates, again testing both **C** matrices. I compared the AICc scores of all the models to determine which combination of flow, temperature, and moon phase metrics best explained variation in the outmigration timing. The model estimates maximum-likelihood (ML) parameters via an Expectation-Maximization algorithm, and I bootstrapped the best-fit model to obtain 95% confidence intervals for the model parameters. I looked at whether or not the confidence intervals overlapped with zero to determine whether any of the covariate effects were significant, i.e. did not overlap with zero. I repeated all of the above steps for the second model, in which the length of the outmigration window was the response variable. I did not include the moon phase in the outmigration window models as I did not expect there to be a relationship between these variables.

Long-term trends

To determine long-term trends in outmigration timing and length, I analyzed the estimations of the **U** matrix. I used the best-fit model from above and ran models with the **U** matrix as 'equal,' 'unequal,' and 'zero' to determine if the trend was the same, different, or insignificant at the two sites. I bootstrapped the models with the 'equal' and 'unequal' **U** matrix and obtained the 95% confidence interval to see if there was a significant trend and if there were different trends in the two creeks.

RESULTS

Outmigration traits

I found that smolts in Lagunitas and Olema creeks exhibit similar outmigration timing but different outmigration fork lengths. In the first paired t-test, I found that the median outmigration date did not significantly differ between the two creeks when paired by year ($t_{(15)}$ = -0.69499, p = 0.4977) (Figure 3a). Similarly, I found no difference in the outmigration window length between Lagunitas and Olema creeks ($t_{(15)}$ = 1.2846, p = 0.2184) (Figure 3b). However, I found a significant difference in the median fork length at outmigration in the two creeks ($t_{(15)}$ = -2.4701, p = 0.02599), with generally larger smolts in Olema Creek across years (Figure 3c).

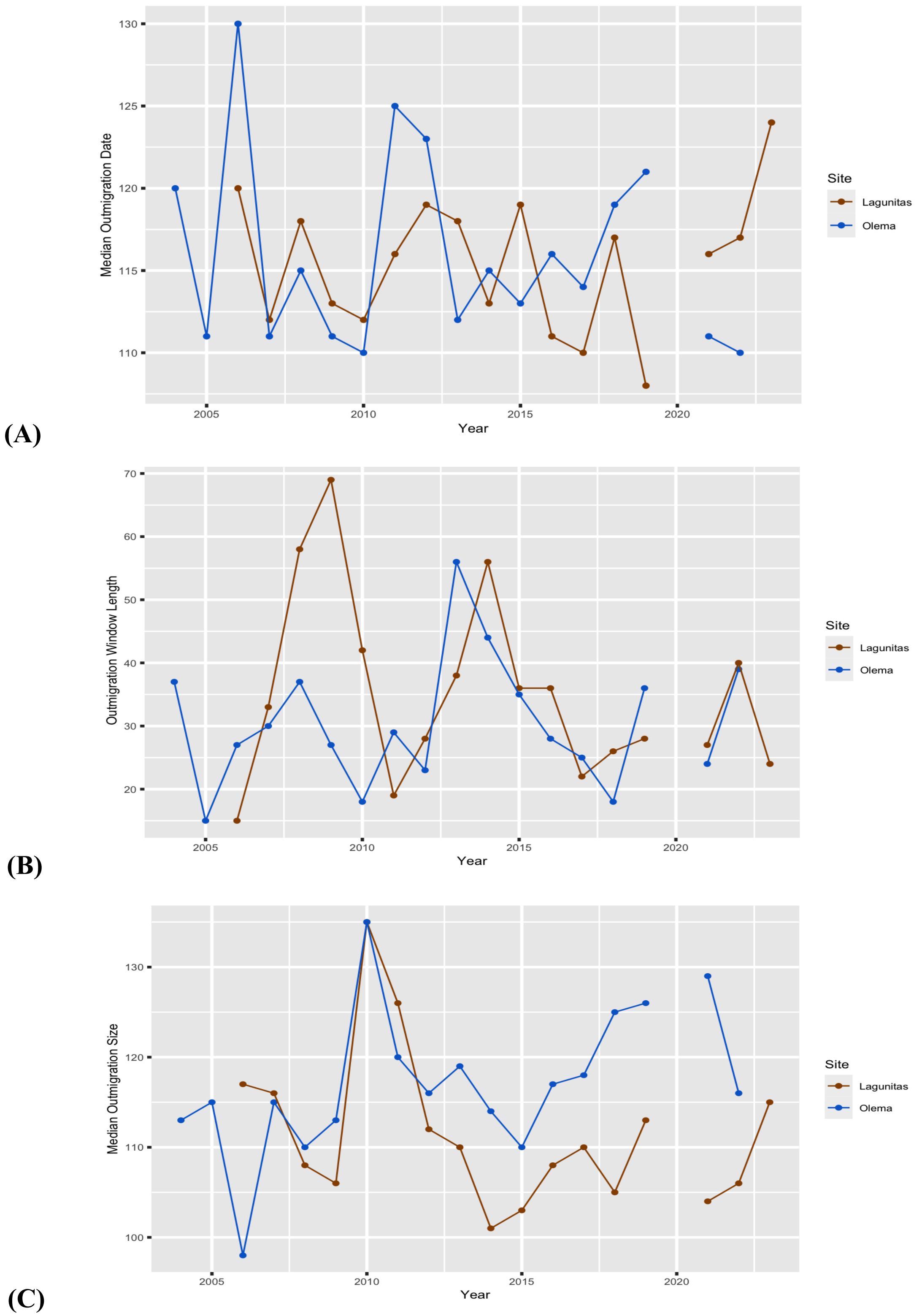


Figure 3. Outmigration traits in Lagunitas and Olema Creeks. Line graphs show outmigration traits in the two creeks over the study period, with Lagunitas shown in brown and Olema shown in blue: (a) median outmigration date, (b) length of the outmigration window, and (c) median fork length at outmigration (outmigration size).

Outmigration drivers

Median outmigration date

Across models, I found that the timing of smolts in the two creeks varied similarly across time and that there were no strong drivers of outmigration timing. Among the four **Q** matrices I tested, the model with **Q** as ‘diagonal and equal’ had the highest support (AICc = -111.929). I followed the standard assumption that models within two AICc have similar support (Burnham and Anderson 2004). Following this assumption, the ‘diagonal and equal’ model fit the data significantly better than the next best model (AICc = -109.0826, ΔAICc = 2.8464).

All covariates aside from wet season baseflow and peak flow had higher support for the ‘watershed’ **C** matrix than the ‘stream-specific’ matrix, but none of the models had significant covariate effects (Table 1). The peak flow model had similar support across the ‘watershed’ and ‘stream-specific’ models (ΔAICc = 0.2865). The influence of wet season baseflow on outmigration timing varied in the two creeks, creating higher support for the ‘stream-specific’ **C** matrix. When testing individual covariates, I found that the model with the wet season baseflow covariate and the ‘stream-specific’ **C** matrix had the highest support (AICc = -112.1378). The wet season baseflow model explained significantly more than the other covariate models. However, wet season baseflow did not explain more than the base model, which had an AICc within two points of this model (ΔAICc = 0.2088).

Table 1. Median outmigration date covariate model scores. AICc scores for the six covariates under both the ‘stream-specific’ and ‘watershed’ hypotheses. The final model tested both wet season baseflow and temperature as covariates. ΔAICc indicates the deviance from the lowest AICc score.

C matrix - hypothesis tested	Covariates	AICc	ΔAICc
Stream-specific	Wet season baseflow	-112.1378	0.000
Watershed	Wet season baseflow	-109.3986	2.739
Stream-specific	Timing of spring recession	-109.3136	2.824
Watershed	Timing of spring recession	-109.0271	3.111
Stream-specific	Spring recession rate of change	-106.8596	5.278
Watershed	Spring recession rate of change	-109.0792	3.059
Stream-specific	Peak flow	-106.7796	5.358
Watershed	Peak flow	-108.9997	3.138
Stream-specific	Date of March new moon	-106.6415	5.496
Watershed	Date of March new moon	-109.0824	3.055
Stream-specific	Temperature changepoint	-106.6274	5.510
Watershed	Temperature changepoint	-109.0747	3.063
Watershed	Wet season baseflow, temperature	-106.3983	5.739

None of the covariates had significant estimates, as they all had confidence intervals that overlapped with zero. The estimates for the spring recession rate of change, peak flow, temperature changepoint, and moon phase centered around zero, while estimates for wet season baseflow and timing of the spring recession only overlapped slightly with zero (Figure 4).

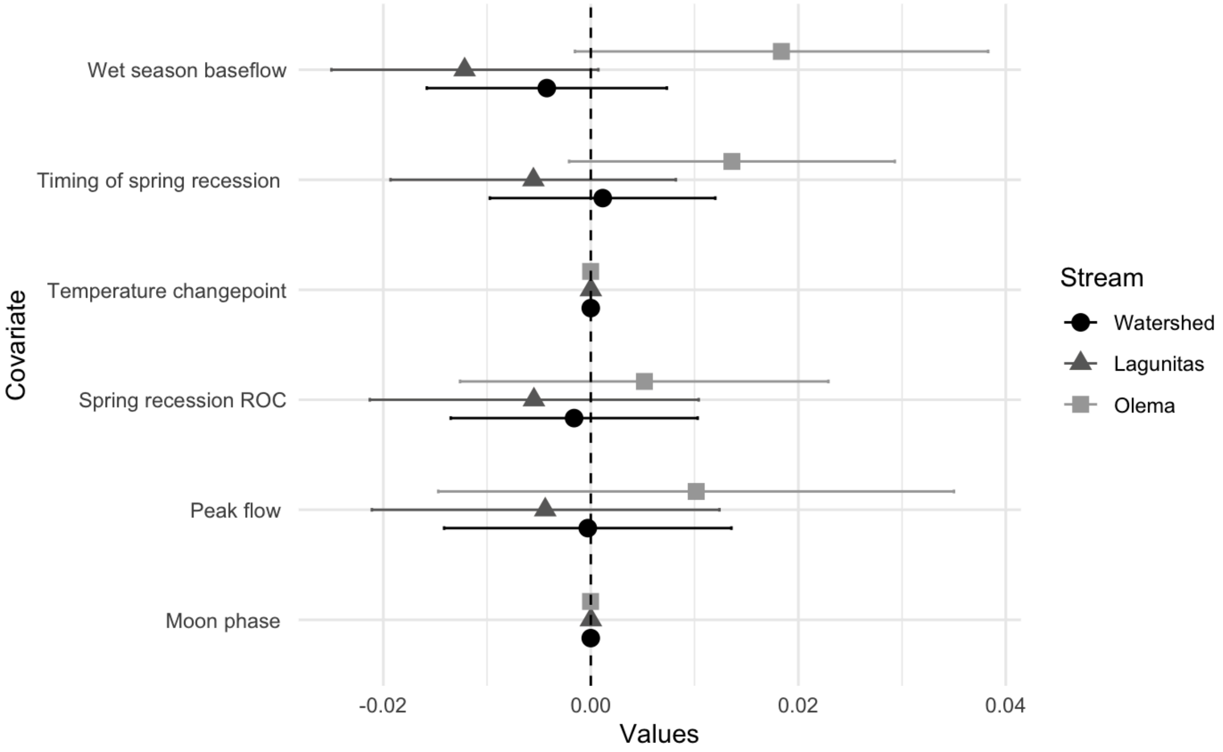
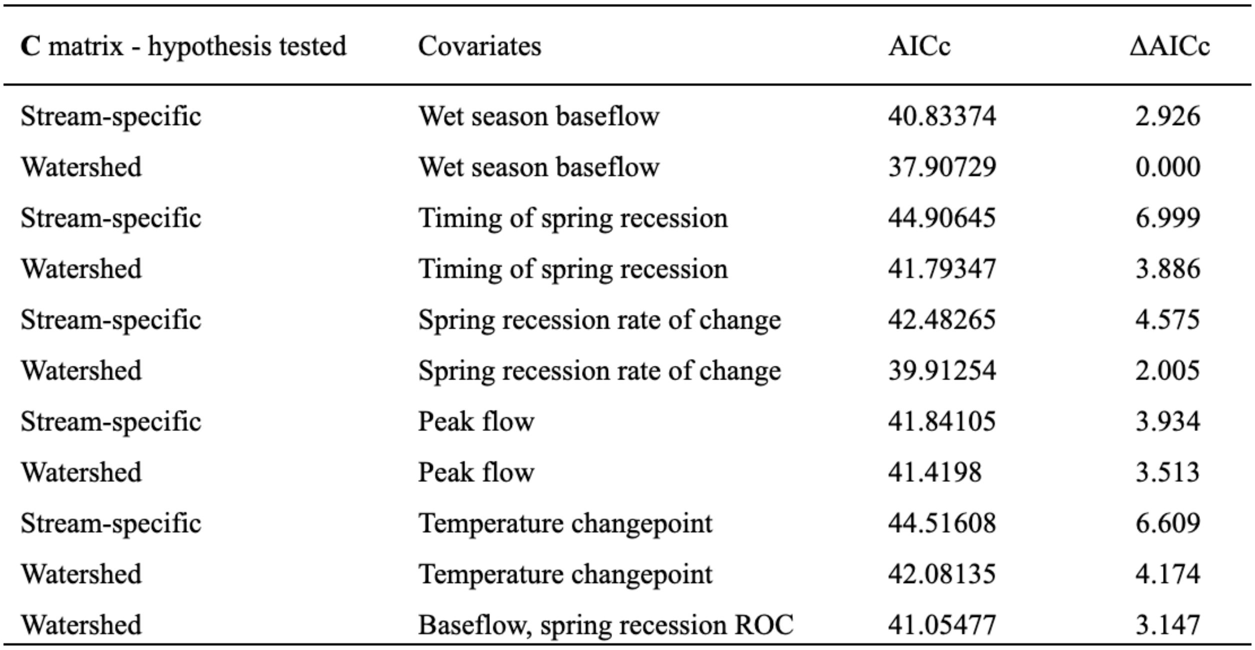


Figure 4. Estimates and confidence intervals for covariate effects on median outmigration date. The graph shows estimates of covariate effects for the six covariates under the 'watershed' hypothesis and 'stream-specific' hypothesis, with separate effects on Lagunitas and Olema creeks. Bars indicate the width of the confidence intervals, where insignificant effects overlap with the dotted line (zero).

Outmigration window length

I found that the outmigration window length varied similarly in the two creeks and that wet season baseflow significantly influenced the length of the window. The model with **Q** as 'diagonal and equal' had the highest support (AICc = 39.15979). The next best model had an AICc score more than two points away, making this the best model (ΔAICc = 2.92702). As in the median outmigration date models, the 'watershed' **C** matrix had the highest support for covariates except peak flow (Table 2). The model with the peak flow covariate had equal support for the two **C** matrices (ΔAICc = 0.42125). The strongest covariate model had wet season baseflow with the 'watershed' matrix (AICc = 37.90729) but did not explain more than the base model (ΔAICc = 1.2525).

Table 2. Outmigration window length covariate model scores. AICc scores for the six covariates under both the ‘stream-specific’ and ‘watershed’ hypotheses. The final model tested both wet season baseflow and the spring recession rate of change as covariates. ΔAICc indicates the deviance from the lowest AICc score.



C matrix - hypothesis tested	Covariates	AICc	ΔAICc
Stream-specific	Wet season baseflow	40.83374	2.926
Watershed	Wet season baseflow	37.90729	0.000
Stream-specific	Timing of spring recession	44.90645	6.999
Watershed	Timing of spring recession	41.79347	3.886
Stream-specific	Spring recession rate of change	42.48265	4.575
Watershed	Spring recession rate of change	39.91254	2.005
Stream-specific	Peak flow	41.84105	3.934
Watershed	Peak flow	41.4198	3.513
Stream-specific	Temperature changepoint	44.51608	6.609
Watershed	Temperature changepoint	42.08135	4.174
Watershed	Baseflow, spring recession ROC	41.05477	3.147

The wet season baseflow model had a significant negative maximum-likelihood (ML) estimate (-0.1086), with a confidence interval that did not overlap with zero. The confidence intervals for all other covariates overlapped with zero, although the spring recession rate of change and peak flow did not center around zero (Figure 5).

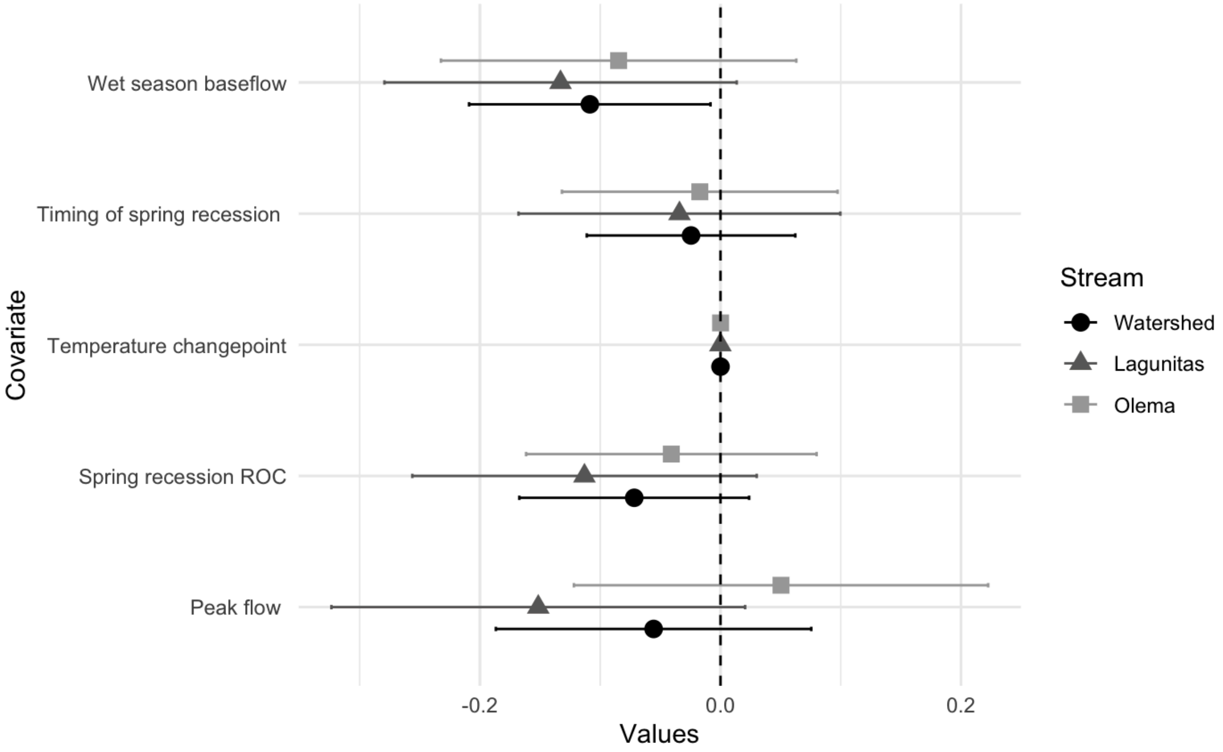


Figure 5. Estimates and confidence intervals for covariate effects on outmigration window length. The graph shows estimates of covariate effects for the six covariates under the 'watershed' hypothesis and 'stream-specific' hypothesis, with separate effects on Lagunitas and Olema creeks. Bars indicate the width of the confidence intervals, where insignificant effects overlap with the dotted line (zero).

Long-term trends

I found no significant trend in smolt outmigration timing throughout the study period. Among the three models with **U** set to 'equal,' 'unequal,' and 'zero,' the model with no trend, i.e., 'zero,' had the highest support. Although I set **U** to 'zero' in the covariate models, I ran models with **U** as 'unequal' to obtain estimates for trends in the two creeks. In the median outmigration date model, MARSS estimated trend coefficients of 0.0606 and -0.212 in Lagunitas and Olema, respectively (Figure 6a). The confidence intervals for both values overlapped with zero, although the CI for Olema did not strongly center around zero (-0.696 to 0.270). In the outmigration window model, MARSS estimated trend coefficients of -0.01169 and 0.00819 in Lagunitas and Olema, respectively (Figure 6b). Again, confidence intervals for these estimates overlapped with zero, with both relatively centered around zero.

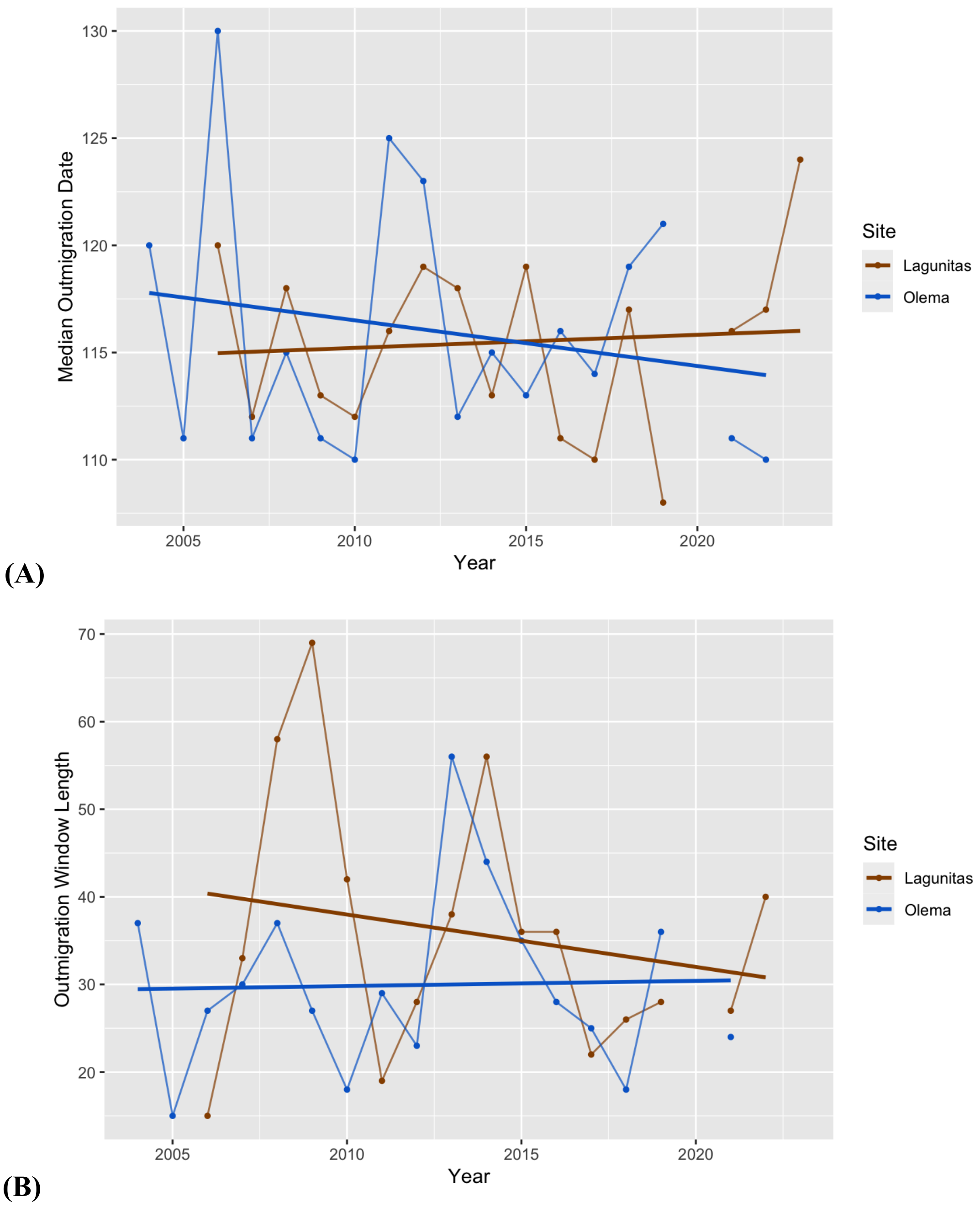


Figure 6. Trends in outmigration timing. Line graph with trend lines for both (a) median outmigration date and (b) outmigration window length. Trend lines reflect estimates from the 'unequal' **U** matrix models, with a negative estimate for median date in Olema and a negative trend in Lagunitas window length.

DISCUSSION

Coho salmon smolts in the two main tributaries of the Lagunitas Creek watershed generally exhibited similar outmigration traits and patterns across this study. Smolts in Lagunitas and Olema Creeks had median outmigration dates and windows that did not significantly differ. Evidence of similar life history patterns across the watershed supports the idea that smolts in the two creeks behave as a single population. This lack of a portfolio effect raised concern about the stability of the population in the face of a changing climate; without life history diversity, this population lacks a natural butter against the potential negative effects of extreme climate events. However, smolts in both creeks showed no significant trend in median outmigration date or window length throughout the study period. A primary motivation for this study was to understand trends in migration timing, as changes in timing seen in other populations have raised concern about increased mismatch events between ocean arrival and ocean upwelling. I also wanted to determine how environmental factors influence outmigration timing to better understand the possible drivers of dynamics and trends in timing. Overall, the 'watershed' covariate matrices had the highest support, implying that smolts across the watershed respond similarly to environmental drivers. Although only wet season baseflow had a significant estimate, similar support among covariate models suggests that multiple factors may influence outmigration timing, effects are inconsistent across years, or these covariates do not capture the primary driver.

Outmigration traits

Outmigration timing

Similarities in outmigration timing in the two creeks support the idea that smolts in the watershed act as a single population. I found no significant difference in the median outmigration date or length of the outmigration window between Lagunitas and Olema Creeks. While smolt outmigration represents just a single facet of the definition of a population, it provides a starting point for understanding population dynamics across the watershed. The observed similarities in smolt timing most likely stem from conserved genetics between smolts in the two creeks and parallel responses to the regional climate. A small genomic region controls and cues migration in salmon (Thompson et al. 2020, Harringmeyer et al. 2021); although I did not study genetics in this watershed, salmon in the two creeks likely have a high degree of shared genetics due to their proximity. It is probable that smolts have similar interactions between genetics and broader regional climate effects in this watershed. Regional climate or synchrony of environmental factors strongly influences outmigration timing and can drive the synchronization of multiple populations (Liebhold et al. 2004). In one study, a summer low flow synchronized juvenile salmonids across 18 Atlantic salmon populations (Bouchard et al. 2022). Likewise, analogous hydrology synchronized smolt migrations in populations across four rivers (Bjerck et al. 2021). Although my analysis does not test for the synchrony of smolts in the two creeks, it is important to consider what factors may drive the observed similarities in outmigration timing. Although dams generally dampen flow regimes and base flows (Poff et al. 2007) and affect stream temperatures (Zaidel et al. 2021), Lagunitas Creek does not experience such extreme alterations. Through natural flows from San Geronimo Creek, as well as spillover and managed releases from Kent Dam, Lagunitas Creek's hydrology remains similar to historical conditions, with only slightly lower monthly flows (Grantham 2014). Outmigration timing in the two creeks may have differed more had dam regulation been significantly affected by the Lagunitas Creek flow and temperature regimes.

Outmigration size

Differences in median outmigration size point to differences in habitat quality and availability, as well as stream conditions between the two creeks. I found a significant difference in outmigration size in the creeks, with larger Olema smolts in most years. While similarities in timing may point to watershed-wide responses of smolt to regional climatic conditions, differences in size suggest varying qualities of habitat in the creeks (Cordoleani et al. 2022). Food availability, temperature, fish density, and availability of high-quality habitat are several factors affecting juvenile salmonids' growth rates (Gibson 2002, Iino et al. 2022). A number of these factors could account for this difference, and further analysis of the relationships between size, temperature, fish density, and habitat quality in these two creeks would help to elucidate the drivers behind observed differences in smolt size.

MARSS model variance and covariance

Support for ‘diagonal and equal’ **Q** matrices supports the idea that coho salmon in this watershed act as a single population. The ‘diagonal and equal’ matrix indicates that both median outmigration date and outmigration window in Lagunitas and Olema Creeks vary by the same amount but vary independently in time. The paired t-test examined the distribution of means over time, finding overall similar timing in the two streams. The MARSS model **Q** matrix examined fluctuations in the data, so while the data do not differ much overall, the direction in which they fluctuate year to year may differ. This pattern of similar means but different dynamics is especially apparent in drought years. For example, the median outmigration date appears to match closely between the creeks from 2006-2011, then becomes more asynchronous around 2012 (Figure 3a), a year which marked the start of an extreme four-year drought period (“California | Drought.gov” 2024). The lack of significant covariate effects fails to offer a robust explanation for how drought causes asynchronous timing in this watershed. This observation contradicts other findings that drought conditions synchronize salmon populations (Bouchard et al. 2022). Smolts in these two creeks may respond to different environmental or demographic factors that differ between the subbasins during drought conditions.

Covariate effects on median outmigration date

A lack of support for any specific outmigration driver suggests that several factors may influence timing, drivers may fluctuate between years, or the drivers may not be captured in this study. Wet season baseflow had equal support as the base model, while the remaining covariates had AICc scores more than two points above the base model but had equal support among each other. None of the covariates had a significant effect on the median outmigration date. Equal support across covariates may point to alignment with other studies, which have found that a combination of temperature and flow best explain outmigration timing and that the specific factors may vary among populations or time scales (Holtby et al. 1989, Hvidsten et al. 1995, Sykes et al. 2009, Spence and Dick 2014). Models with multiple covariates did not have high support, but this likely reflects the nature of the data and model setup, not evidence against there being multiple controlling factors. The aforementioned studies used cumulative, absolute, or rate-of-change temperature variables in models. While the temperature changepoint metric captures a large shift in temperature, I was unable to capture finer-scale temperature patterns that smolts appear to respond to. Similarly, the functional flow metrics sufficiently describe key aspects of the hydrograph but may miss the scale of change to which smolts appear to respond. A visual assessment of Figure 4 reveals that larger and longer flows, i.e. higher baseflow and later spring recession, correspond to later outmigration dates in Olema Creek and earlier outmigration in Lagunitas. None of these covariates had any significance, but this observation provides a point of interest for future studies that delve deeper into the role of flow in outmigration timing in this watershed. Despite preliminary findings that smolt migration peaked in Lagunitas Creek during the new moon (Ettlinger et al. 2022a) and previous work showing a relationship between the two (Spence and Dick 2014), the moon phase did not significantly impact migration timing. Overall, these findings suggest that multiple factors influence timing, that the driving factor varies across years, or that annual metrics can not sufficiently capture the variation in outmigration timing.

For all covariates aside from wet season baseflow and timing of the spring recession, models with a 'watershed' **C** matrix had better support than the 'stream-specific' matrices. Support for a watershed response suggests that the timing of smolts in the two creeks had similar responses to most covariates. Smolts in the two creeks responding the same to environmental drivers support the idea that smolts in the watershed act as a single population. Conserved genetics across the watershed could explain why smolts respond similarly to environmental cues (Harringmeyer et al. 2021). Differing responses to the wet season baseflow could point to differences in connectivity or habitat availability in the two creeks (Grantham 2013) or indicate that baseflows determine the strength of other hydrologic signals (Yarnell et al. 2020).

Covariate effects on outmigration window length

Support for wet season baseflow in the outmigration window model suggests that stream flow is an important factor in the length of outmigration. The model with wet season baseflow and a 'watershed' **C** matrix had the highest support and a significant covariate effect. There was equal support among the other covariates, but all had less support than wet season baseflow. A negative maximum-likelihood estimate of the wet season baseflow coefficient means that the outmigration window contracted as baseflow increased. I hypothesized that a lower baseflow would restrict connectivity and access to habitats, causing fish to be pushed out earlier

(Grantham 2013). Additional findings that drought-induced low flows caused a contracted outmigration window for coho supported this hypothesis (Kastl et al. 2022). However, both these studies were conducted in the Russian River watershed, a system characterized by intermittent tributaries. Lagunitas and Olema are perennial streams and do not face the same pressures as smolts in the Russian River. A longer window in response to lower baseflows might indicate a lack of strong hydrologic cues in years with high baseflows. Salmon respond to relative changes in flow, and in years with high baseflows, a larger flow event is needed to create a significant relative change. As such, there may be fewer hydrologic cues in years with high baseflows, causing a smaller outmigration window. A similar result was found in a study of Chinook outmigration, where high flows and high accumulated temperature caused a shorter migration period (Sykes et al. 2009).

Other studies have found temperature to be the primary determinant of the window length, with cooler or slow increases in temperature causing a longer migration window and warmer or rapid increases in temperature leading to shorter migration windows (Zydlewski et al. 2005, Sykes et al. 2009, Munsch et al. 2019). While temperature was not well supported in my models, the temperature metric I used did not capture absolute temperature, cumulative temperature, or rate of change of temperature, all of which were important in other studies. All models - aside from peak flow, which had equal support - had significantly higher support for the 'watershed' covariate matrix over the 'stream specific' model, suggesting that the outmigration window of smolts in the two creeks responded similarly to flow and temperature changes. A watershed response to environmental drivers supports the idea that regional climate conditions may drive similar timing in the two creeks.

Long-term trends

The lack of a significant trend in median outmigration date or window length suggests that the Lagunitas Creek watershed population of coho is relatively stable over time and is not noticeably responding to widescale climate changes. No change in migration timing is consistent with other studies and the general understanding of coho salmon phenology. Coho have relatively little life history variability compared to other salmonids (Rebenack et al. 2015). A study of changes in peak migration timing of Pacific salmonids found that coho had low rates of change compared to other salmonids, with an average change of 0.1 days per decade (Wilson et al. 2023). The aforementioned study consisted of salmonids in the Oregon to Alaska range and can only provide insight into trends of coho in their northern range but not the southern end. In the nearby Russian River, findings that drought contracted the migration window and increased temperatures hastened the migration window have generated concern for this population in the face of projected increases in stream temperature and decreases in spring flows (Kastl et al. 2022). In the 20th Century, hydroclimate trends in California show an increase in extremes rather than movement in a specific direction (Zamora-Reyes et al. 2022). This lack of strong trends in environmental conditions could also explain the absence of timing trends in my study.

Limitations and future directions

The data and analyses employed in this paper possess certain limitations, which constrain the extent of inference that can be drawn from my findings. The smolt traps only operated from March to May, meaning there is no information on smolts that may have migrated outside this window. There is evidence of an early emigration life history for coho in some watersheds (Nordholm 2014, Rebenack et al. 2015), meaning this data does not capture the full range of life history variation. Temperature data in Olema Creek only exists within the window of smolt sampling, which restricted the possibility of using cumulative temperature metrics or rate of change data, two important metrics in past studies (Zydlewski et al. 2005, Sykes et al. 2009, Spence and Dick 2014). The MARSS models and their interpretation were limited in several ways: the time series contained only 19 time steps, which is relatively short for a MARSS model. As a result, I had to log transform the response variables to ensure model convergence, which may have altered covariate relationships. Furthermore, the use of a single metric of outmigration, and especially a single temperature metric, limited the ability to understand what factors are truly driving outmigration. Due to these limitations and the unique characteristics of the Lagunitas Creek watershed, my results should be considered in tandem with other research and site-specific knowledge when assessing outmigration in other Central California Coast coho salmon populations.

My findings that the median outmigration date and outmigration window do not significantly differ in the two creeks warrant a more in-depth analysis of synchrony in the watershed. Analysis methods such as wavelets or dynamic factor analysis (DFA) could be used to understand the extent and patterns of synchrony between smolts in these two creeks. Tests of synchrony between flow and temperature could further this understanding of the drivers or causes of apparent synchronization of smolt timing. Running yearly MARSS models with the daily counts of outmigrating fish and flow and temperature covariates would allow for a better understanding of smolt outmigration fluctuations and drivers than is possible with a yearly metric. Yearly MARSS models or DFA could also provide insight into how drivers change across years, allowing for a deeper analysis of how climate change impacts stream conditions and outmigration. Furthering the use of the complete Lagunitas temperature data and finding a way to interpolate Olema temperature data starting in January would be extremely useful and allow for the calculation of alternative temperature metrics.

Broader implications

In this study, I investigated the population dynamics of coho salmon in a small watershed, looking at how outmigration varies across the watershed, what factors drive outmigration, and how outmigration has fluctuated over the past 19 years. Ultimately, I studied the dynamics and responses of this population in order to understand the implications of projected climate change. The literature shows that salmonid smolts respond to stream temperature and hydrology - two environmental factors that climate change impacts (Wilson et al. 2023). Although I didn’t find strong evidence that temperature or streamflow drives outmigration, I did find that variation in median date and window length in the two creeks respond similarly to covariates. Similar responses to covariates, along with similar outmigration characteristics, provide evidence that smolts in the watershed act as a single population. A lack of significant portfolio effects in the watershed raises possible concerns for the system’s ability to buffer against environmental extremes. Despite this concern, coho in the watershed have remained relatively stable over the past 19 years, with smolt estimates in Lagunitas Creek increasing over the last 10 years (Ettlinger et al. 2022b) and smolt estimates in Olema Creek exhibiting more variability (McNeill et al. 2020). In addition to consistent numbers, there is no evidence of earlier outmigration dates or shrinking outmigration windows, two concerning impacts of a changing climate. The implications of an unchanged migration pattern depend primarily on whether or not the timing of ocean upwelling shifts, i.e. if there will be an increase in mismatch events. For now, the stability of the Lagunitas Creek watershed coho salmon and its resilience against climatic extremes provide both hope for the revitalization of Central California Coast coho and an essential opportunity to study population dynamics in a small watershed with a natural population.

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