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ARTICLE

Freshwater Ecology

Migration in drought: Receding streams contract the seaward migration window of endangered salmon

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Abstract

Prolonged migration windows buffer migratory animal populations against uncertainty in resource availability. Understanding how intensifying droughts from climate change influence the migration window is critical for biodiversity conservation in a warming world. We explored how drought affects the seaward migration of endangered coho salmon (*Oncorhynchus kisutch*) near the southern extent of their range in California, USA. We tracked stream departures of juvenile coho, measuring streamflow and temperature in seven streams over 13 years, spanning a historic drought with extreme dry and warm conditions. Linear mixed effects models indicate that, over the range of observations, a decrease in seasonal streamflow (from 4.5 to 0.5 mm/day seasonal runoff) contracted the migration window by 31% (from 11 to 7 weeks). An increase from 10.2 to 12.8°C in mean seasonal water temperature hastened the migration window by three weeks. Pacific salmon have evolved to synchronize ocean arrival with productive ocean upwelling. However, earlier and shorter migration windows during drought could lead to mismatches, decreasing fitness and population stability. Our study demonstrates that drought-induced low flows and warming threaten coho salmon in California and suggests that environmental flow protections will be needed to support the seaward migration of Pacific salmon in a changing climate.

KEYWORDS
climate change, coho salmon, degree-days, environmental flow, low flow, mismatch, outmigration, phenology, smolt, streamflow, upwelling, water temperature

INTRODUCTION

Animal migration is a behavioral strategy that can increase energy intake via improved access to resources (Avgar et al., 2014). Numerous species sync migration timing with the availability and nutritional value of resources at migration destinations (Fryxell & Sinclair, 1988; Satterthwaite et al., 2014) and a prolonged window of departures among individuals can buffer populations against uncertainty in timing of resource availability (Spence & Hall, 2010). Climate change is intensifying droughts globally (Pendergrass et al., 2017) and represents a growing threat to migratory species (Visser & Both, 2005) by changing spatial and temporal patterns of resource availability. For example, previous studies have explored the effects of climate change and drought on the migration of terrestrial and avian species, including mismatches between migration and the timing/duration of resources at migration destinations and along migration routes (Both et al., 2006; Middleton et al., 2013). However, few studies have explored how worsening drought conditions at the migration origin alter the duration (window) of migration departures.

Because human water withdrawal from streams disproportionately reduces ecologically available water during periods of low precipitation and high temperatures (Kovach et al., 2019), the impacts of drought may be most pronounced for fish that migrate during the dry season (Closs et al., 2016). Up to 75% of freshwater fishes risk extinction by 2070 in some areas with reduced discharge (Xenopoulos et al., 2005), due to drought impacts on stream connectivity, habitat, and food resources (Lake, 2003). As droughts intensify in a changing climate (Swain et al., 2018), altered precipitation and flow will cause extirpations and poleward range shifts of migratory fish species on many continents (Lassalle & Rochard, 2009). Drought is already contributing to the extinction risk of Pacific salmon (*Oncorhynchus* spp.) at the southern extent of their range in California, USA (Katz et al., 2013). For example, low streamflow during the dry season has been shown to limit the over-summer survival of steelhead trout (*Oncorhynchus mykiss*) (Grantham et al., 2012) and coho salmon (*Oncorhynchus kisutch*) (Vander Vorste et al., 2020), especially during drought years when habitat becomes unsuitable or dries completely. There is also a growing risk that warming stream temperatures will exceed the physiological tolerance thresholds of Pacific salmon (Hague et al., 2011).

Seaward migration (outmigration) of juvenile salmon (i.e., smolts) from their natal streams to the ocean typically occurs in the spring (March–June), when flows recede at the transition between the wet and dry seasons. With an increasing frequency of drought in California as a result of climate change (Swain et al., 2018), rivers are expected to experience an earlier spring flow recession and prolonged dry season (Grantham et al., 2018). These projected changes in regional hydroclimatic conditions may lead to lower flows that restrict the successful downstream migration of salmon. Previous studies related to the effects of drought have found that high flow events trigger outmigration (Arevalo et al., 2021; McCormick et al., 1998; Spence & Dick, 2014), due to ease in downstream movement (Sykes et al., 2009) and increased turbidity that enables predator evasion (Aarestrup et al., 2002). Higher cumulative thermal experience has also been found to promote earlier smoltification and earlier outmigration timing (McCormick et al., 1998; Munsch et al., 2019; Sykes et al., 2009; Teichert et al., 2020). Others have documented that changes in water temperature trigger outmigration (Spence & Dick, 2014). These studies highlight that both temperature and flow are key determinants of smolt outmigration dynamics, yet their combined effects on the duration (window) of outmigration during periods of drought have not received attention. Coho salmon in California have developed a particularly prolonged outmigration window that is known to be synchronized with the long and highly variable period of ocean upwelling (Spence & Hall, 2010). These periods of productive marine conditions promote the growth of prey and have been shown to increase salmonid survival when outmigration timing coincides (Satterthwaite et al., 2014). Thus, changes in the timing of outmigration caused by drought could increase the risk of a timing mismatch between migration arrival and upwelling, adversely affecting fish fitness and survival, with potential population-level consequences.

In this study, we investigated how seasonal streamflow and water temperature affect outmigration of endangered coho salmon, during a period encompassing extreme wet years and a historic drought (2012–2016) in California (Ullrich et al., 2018). We analyzed salmon movement and environmental data between 2008 and 2020 to determine how interannual variation in stream conditions influenced the start date, end date, and window of outmigration. We predicted that low flows associated with drought years would delay the outmigration start date due to the absence of spring freshets that trigger downstream fish movement (Spence & Dick, 2014; Sturrock et al., 2020), hasten the outmigration end date due to impassable stream conditions, and, in combination, contract the outmigration window. We also expected warmer stream temperatures associated with drought to shift the migration window earlier in the year, as has been documented by others (Munsch et al., 2019; Sykes et al., 2009; Teichert et al., 2020). Our hypotheses address how the compounded impacts of water scarcity and warm temperatures during climate change-induced drought may create a novel life stage bottleneck for migrating salmon.

METHODS

Study area and coho salmon monitoring

This study focused on seven tributary streams in the lower Russian River basin, California (Figure 1). The study area has a distinct wet season (November–April), with a high degree of interannual precipitation variability. Streamflow reflects seasonal precipitation patterns,

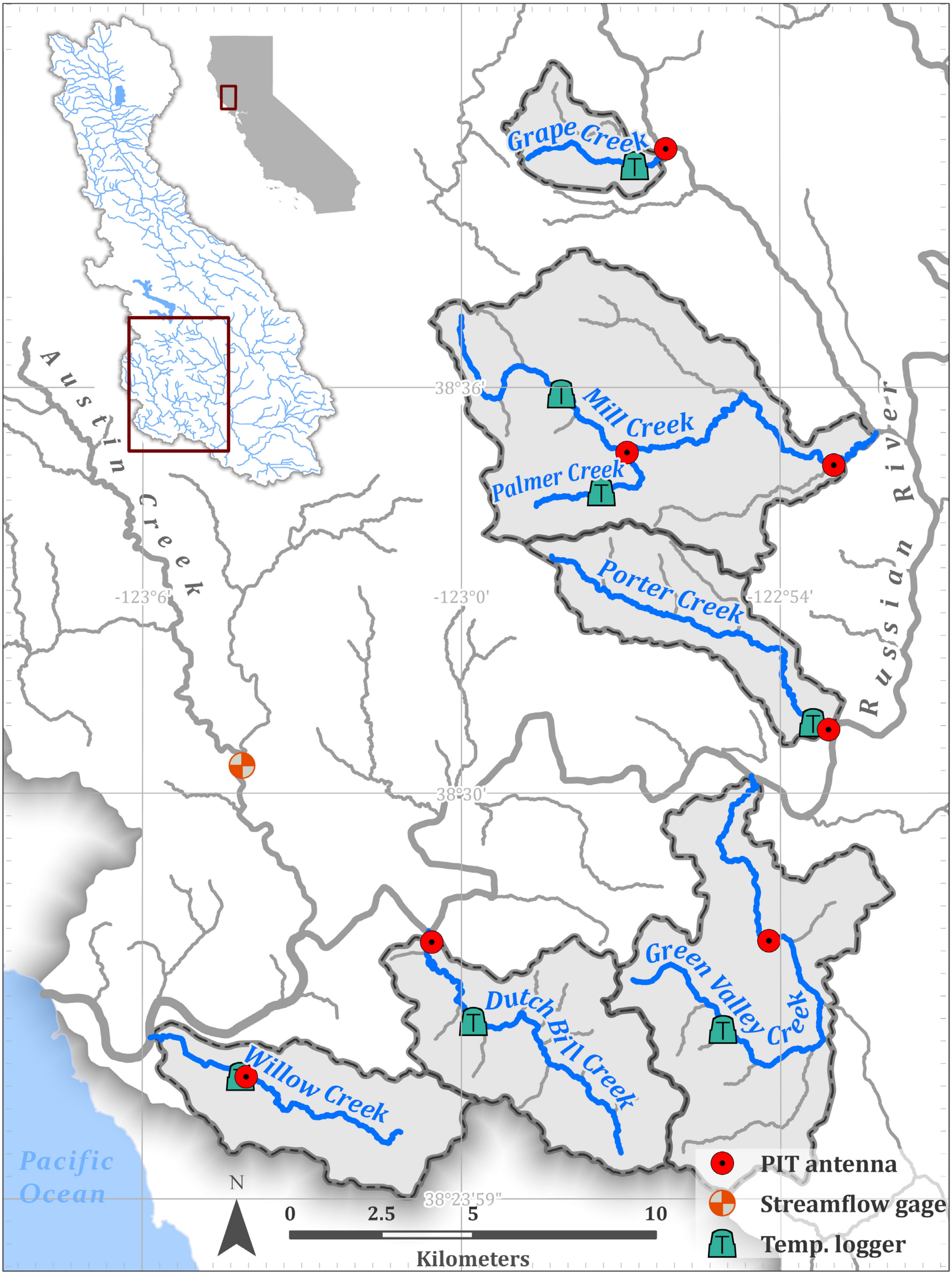

FIGURE 1 Map of the study streams, passive integrated transponder (PIT) antennas, Gage USGS 11467200 Austin C Nr Cazadero CA, and water temperature (Temp.) loggers.

with flashy, high-magnitude peaks associated with winter storms, followed by a predictable flow recession period after the last rainfall event, typically starting in April–May and continuing throughout the dry season, until late October. Flows in most of the study streams fall below 1.5 L/s or cease to flow entirely by mid-summer (July–August), particularly in dry years (Appendix S1: Figure S1).

Russian River coho salmon belong to the Central California Coast population complex, which was listed as endangered under the Federal Endangered Species Act (70 FR 37160) in 2005. To support the recovery of the population, a conservation hatchery program was established in 2001. Over the study period, approximately 54,000 hatchery-raised juveniles were released into the study streams each fall. Approximately 17% of juveniles were implanted with passive integrated transponder (PIT) tags, which were detected by PIT antennas located in the study streams near their confluence with the Russian River. We compiled detection data from 2008 to 2020 (Appendix S1: Figure S2), focusing on 1-year-old smolts detected between 1 March (historically when smolts begin to outmigrate) and 3 July (latest detection date during the study). We defined outmigration start and end as the dates when 5% and 95% of cumulative seasonal detections occurred, respectively. We defined outmigration window as the duration (days) between 5% and 95% of cumulative detection dates.

Streamflow and water temperature

Seasonal streamflow of study streams was estimated using a nearby US Geological Survey flow gage (station number 11467200), due to inconsistencies in gage coverage among streams and over time. We scaled the observed median March–June streamflow at the gage by the drainage area of each stream (contributing area above each PIT antenna) and by mean annual precipitation (averaged across each drainage area), following regional methods for estimating streamflow at ungaged basins (Mann, 2004), which is effective for estimating flows at streams located in close geographic proximity and for the seasonal scale of the flow variable modeled. To account for size differences in streams, we converted the estimated flow values to median daily runoff (in millimeters), by dividing mean seasonal discharge by drainage area of each site (Appendix S1: Table S1). We collected water temperature data, using Onset HOBO U22 loggers, placed in a pool of each stream during the outmigration season. To estimate cumulative thermal experience, we calculated the degree-days as the sum of daily mean water temperature (°C) (Spence & Dick, 2014) for March–April to cover the period before most smolts outmigrated.

Modeling the effects of drought on outmigration timing

We used linear mixed effects models (Zuur et al., 2009) to explore the independent effects of runoff and degree-days on outmigration timing and duration. We confirmed that the two variables were weakly correlated (Pearson correlation coefficients <0.21) and could be evaluated in the same model (Dormann et al., 2013). For each response variable (outmigration start date, end date, and window), we included runoff and degree-days as fixed effects and stream as a random effect, using the *lmer* function of the *lme4* package in R (version 4.0.4; R Core Team, 2018). We calculated the marginal R^2 (proportion of variance explained by the fixed effects) and the conditional R^2 (proportion of variance explained by both the fixed and random effects). We also extracted estimated coefficients for the explanatory variable(s) in the models and calculated their 95% confidence intervals (95% CIs). Variable coefficients with 95% CIs that did not overlap zero were considered significant.

RESULTS

Juvenile coho salmon outmigration timing

We detected 25,047 one-year-old coho salmon migrating out of our study streams between 2008 and 2020 (539 ± 376 detections per stream-year; mean ± SD). Among stream-years, mean outmigration start and end dates were 20 March ± 13.2 days and 18 May ± 14.3 days (Appendix S1: Table S2). Mean outmigration window was 59.3 ± 13.3 days. Outmigration during dry years generally occurred earlier and for a shorter window than during wet years (Figure 2a). Outmigration during years with warmer water temperatures also generally occurred earlier than during years with cooler water temperatures (Figure 2b).

Effects of streamflow and water temperature on outmigration timing

Streamflow and water temperature explained a higher degree of variation in outmigration start date (marginal $R^2 = 0.34$) than outmigration end date (marginal $R^2 = 0.17$), but when accounting for the random effect of

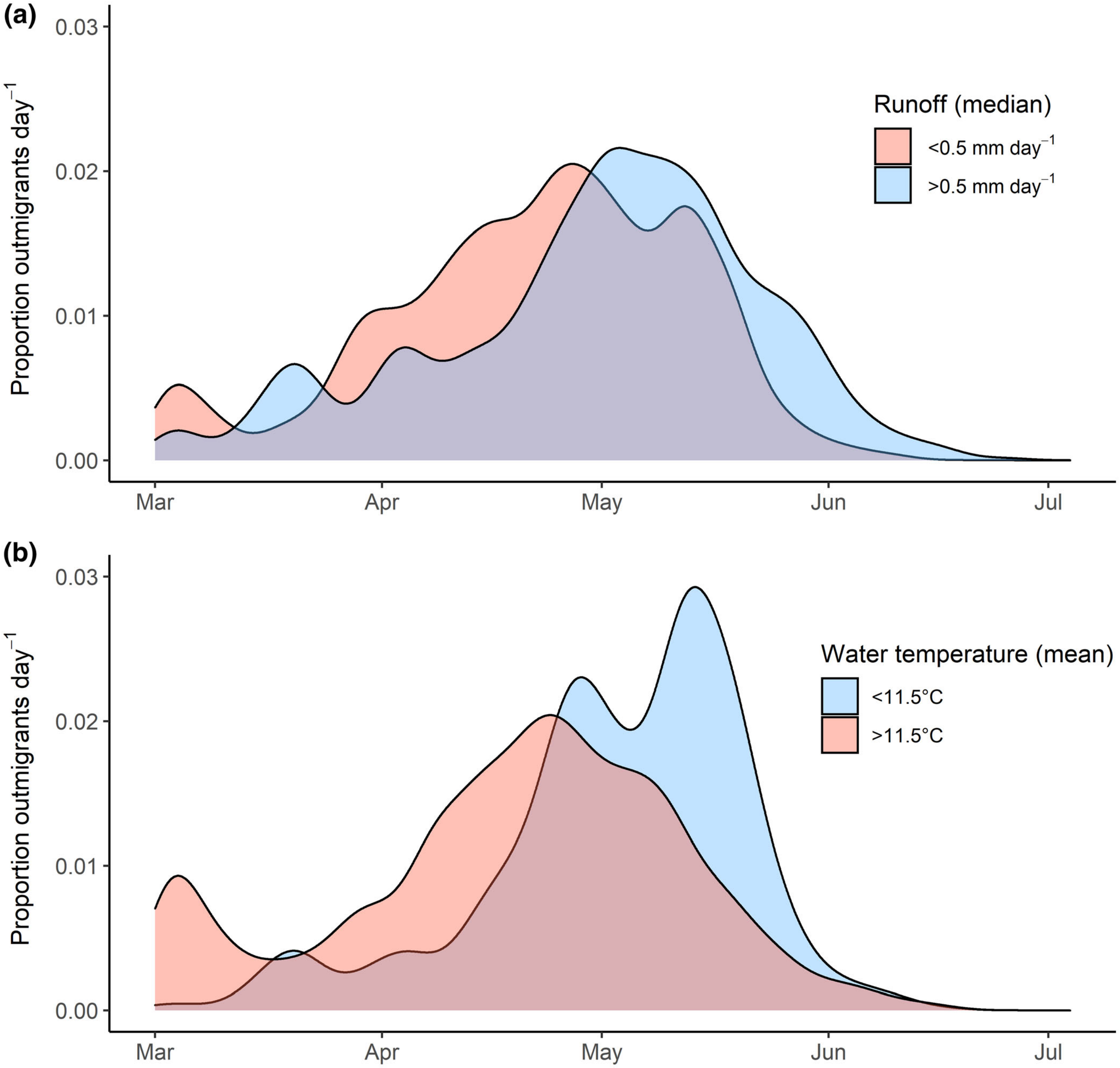

FIGURE 2 Outmigration timing distributions: (a) low (orange) versus high (blue) streamflow years, represented by median March–June runoff (15,513 coho salmon detections), are based on an equal number of years with values above and below 0.5 mm/day. (b) Cool (blue) versus warm (orange) years, represented by mean March–April water temperature (7385 detections), are based on an equal number of years with values above and below 11.5°C.

stream, both models explained a similar degree of variation in the data (conditional $R^2 = 0.67$). A similar degree of variation was explained by the two explanatory variables in the outmigration window model (marginal $R^2 = 0.30$; conditional $R^2 = 0.47$). The models indicate that runoff has a significant negative effect on outmigration start date and a significant positive effect on outmigration end date (Figure 3a,b). That is, when runoff is high, the outmigration start date is hastened and the outmigration end date is extended. By contrast, degree-days had a significant negative effect on both outmigration start date and end date. Thus, warmer temperatures (higher degree-days) both hasten the start date and end date of outmigration. These effects are consistent with the outmigration window model, which indicates that runoff significantly expands the duration of outmigration but that temperature has no effect (Figure 3c). The positive effect of runoff on outmigration duration was consistent among all of our study sites (Appendix S1: Figure S3).

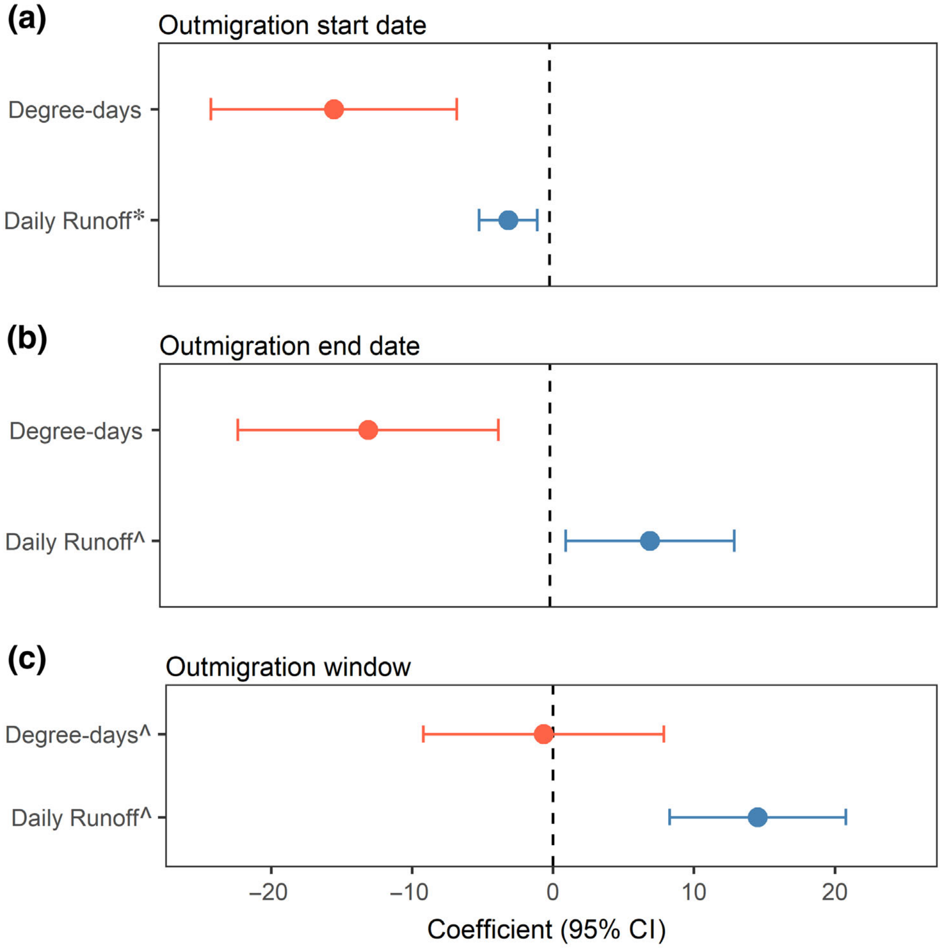

FIGURE 3 Coefficient effect sizes (±95% confidence interval [CI]) for explanatory variables, including degree-days (March–April; red color) and median daily runoff (*March–April, ^March–June; blue color), of the top performing model for each response variable: (a) outmigration start date (when 5% of cumulative seasonal detections was reached), (b) outmigration end dates (when 95% of cumulative seasonal detections was reached), and (c) outmigration window (number of days between start and end dates).

Variable effect size on outmigration start date, end date, and window

Controlling for the effects of other explanatory variables, a 1 mm/day decrease in median March–April runoff delays the outmigration start by 2.9 days (0.8–4.9 days 95% CI). Over the range of conditions observed, a decrease from 4.5 to 0.5 mm/day runoff is expected to delay the outmigration start by 12 days—from 12 March (3–21 March 95% CI) to 24 March (17–31 March 95% CI) (Figure 4a). Each 1°C increase in mean daily water temperature (61 degree-days for March–April) hastens the outmigration start by 9.2 days (4.0–14.5 days). Over the range of conditions observed, increasing mean daily water temperatures from 10.2 to 12.8°C (from 620 to 780 degree-days) hastens the outmigration start by 24 days, from 30 March (21 March–9 April) to 6 March (24 February–16 March) (Figure 4b).

Controlling for the effects of other explanatory variables, a 1 mm/day decrease in median March–June runoff hastens the outmigration end by 7.0 days (1.1–13.0 days 95% CI). Over the range of conditions observed, a decrease from 1.8 to 0.2 mm/day runoff is expected to hasten the outmigration end by 11 days—from 25 May (14 May–5 June) to 14 May (5–23 May) (Figure 4c). Each increase in 1°C mean daily water temperature (61 degree-days for March–April) hastens the outmigration end by 7.8 days (2.2–13.4 days). Over the range of conditions observed, increasing mean daily water temperature from 10.2 to 12.8°C (from 620 to 780 degree-days) hastens the outmigration end by 20 days—from 25 May (14 May–5 June) to 5 May (23 April–16 May) (Figure 4d).

Lower median runoff delays the outmigration start and hastens the outmigration end, resulting in the contraction of the outmigration window. Controlling for the effects of

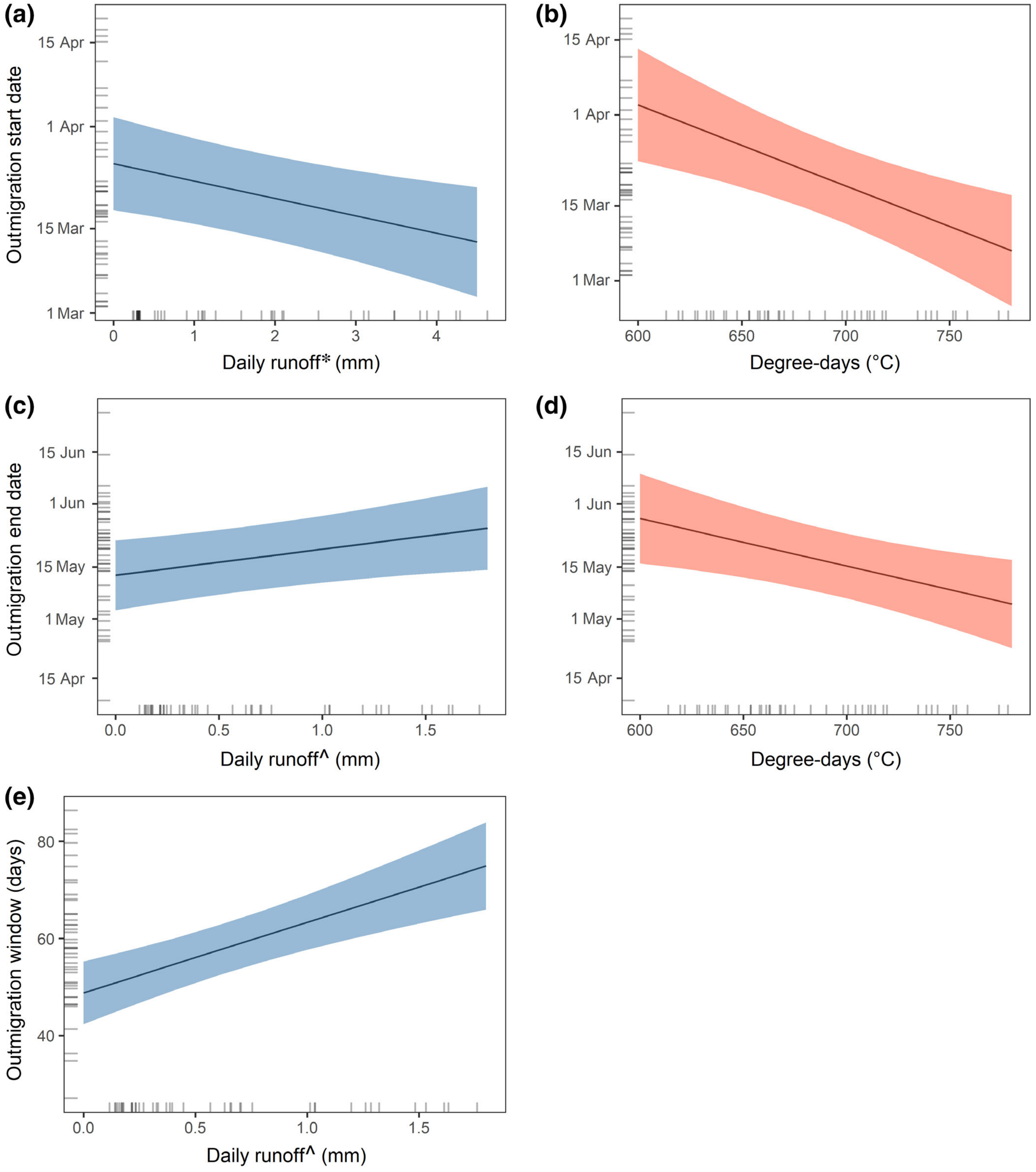

FIGURE 4 Partial dependence from linear mixed effects models of coho salmon smolt outmigration start date (a, b), end date (c, d), and window (e). Model estimates (solid lines) and 95% confidence intervals (shading) for median daily runoff (*March–April, ^March–June) and degree-days (March–April). Observations are indicated by tick marks on *x*- and *y*-axes.

other explanatory variables, a 1-mm/day decrease in median March–June runoff is expected to contract the outmigration window by 14.5 days (8.3–20.8 days 95% CI). Over the range of conditions observed, a decrease from 1.8 to 0.2 mm/day runoff contracts the outmigration window from 74.9 (66.0–83.9) days to 51.7 (45.9–57.5) days, or a 31.0% decline in the total window (Figure 4e). Because higher degree-days hasten both outmigration start and end dates, water temperature shifted, but did not prolong or contract, the outmigration window.

DISCUSSION

Our results indicate that drought-induced low streamflow contracted the outmigration window of coho salmon smolts from streams by delaying the start date and hastening the end date of outmigration. The juveniles in this study are all hatchery raised and therefore relatively genetically homogenous among streams and years, which suggests that interannual and interstream variability in outmigration timing represents responses to environmental conditions and does not reflect local adaptation. While the effects of high flows in initiating outmigration have been reported by others (Spence & Dick, 2014), the effects of low flows in contracting the outmigration window during the onset of the dry season have not been previously documented. Low flows may restrict fish migration due to shallow water depths that deter movement via physical barriers or increased risk of mortality from avian and mammalian predators. Because fish are planted in the previous fall and most often experience >50% overwinter mortality (California Sea Grant, 2021b), we could not test whether the total number of outmigrating smolts was lower in drought versus non-drought years. Nevertheless, we can assume that smolts that do not outmigrate in the spring are unlikely to survive until the rainy season, owing to the extensive stream drying that occurs in tributaries of the Russian River watershed (Moidu et al., 2021).

Our results also suggest that water temperature has a significant influence on outmigration timing that appears to act independently from the effects of flow. At our study sites, streamflow and water temperature were not correlated, likely due to the mediating effects of groundwater inputs on stream temperature that become more pronounced as surface flows decline. Our results indicate that warming water temperatures do not contract the migration window, but rather cause a shift in outmigration start and end timing to earlier in the season. This is consistent with previous studies, which demonstrate that cumulative thermal experience hastens the physiological development of juveniles that prepare them for their transition to the marine environment (Sykes et al., 2009).

An earlier end to the outmigration window observed in dry, low-flow years could be the result of shallow depths and impassable stream conditions. Earlier outmigration during drought could also represent a behavioral adaptation by juvenile salmon to leave the system when conditions are suitable, thereby avoiding stressful habitat conditions later in the season, including closure of estuary mouths, including the mouth of the Russian River, which occurs earlier in drought years (Behrens et al., 2013). However, earlier outmigration also has potential costs. For example, earlier outmigrating fish may be smaller, which has been associated with lower survival in the marine environment, particularly during periods with unproductive ocean conditions (Holtby et al., 1990).

Overall, we report that drought conditions lead to a contracted outmigration season, which may increase the risk of a hydro-phenological mismatch with productive marine conditions delivered by seasonal upwelling (Satterthwaite et al., 2014). The timing of upwelling along the California coast is highly variable among years (Macias et al., 2012), and near the mouth of the Russian River (38.45° N) peak upwelling occurred on 27 May ± 30 days (mean ± SD) during the study period (Appendix S1). A prolonged outmigration window for coho salmon in California likely reflects an adaptive response to this natural variability in upwelling timing (Spence & Hall, 2010), increasing the likelihood that at least a subset of the population of outmigrating smolts will encounter favorable marine conditions (Satterthwaite et al., 2014). Thus, the effect of drought in contracting the outmigration window increases the risk that a larger proportion of individuals will enter the ocean outside of the optimal period, potentially reducing their fitness and survival and further suppressing populations already on the brink of extinction. As the frequency and severity of droughts increase in California (Swain et al., 2018), such risks are likely to grow. Still, we acknowledge that since adult returns are extremely low in this system, typically <30 tagged fish per stream-year (California Sea Grant, 2021a), it is currently not possible to test whether observed outmigration shifts have population-level consequences for coho salmon.

Stream warming associated with climate change could also contribute to a phenological mismatch. Based on an average swim speed of approximately 7 km per day (Furey et al., 2016), we estimate that the mean ocean entry end date of outmigrating smolts during our study period was 28 May, synchronized with the mean peak upwelling date (27 May) (Appendix S1). However, climate change projections indicate that stream temperatures will warm substantially in the coming decades. For example, spring temperatures in streams of California's Sierra Nevada (200 km eastward) are expected to rise by 1.9°C by the 2050s (Ficklin et al., 2013). If similar temperature increases occur in the study streams, our models predict that mean ocean entry end date would occur 2 weeks earlier. Projected declines in spring stream flows (Grantham et al., 2018) suggest that migration end dates may shift even earlier. Meanwhile, predictions of annual upwelling onset date, termination date, and duration are not expected to change significantly at the latitude of the Russian River mouth by 2100 (Wang et al., 2015), exacerbating the potential phenological mismatch. Conservation in a warming climate may benefit from further identification of phenotypic traits, such as sensitivity to starvation during phenological mismatches (Wilson et al., 2022), that may influence population resilience.

Here, we demonstrate that drought both contracts and shifts the window of migration for salmon and may contribute to population-level phenological mismatches with food resource availability in the marine environment. Whereas previous studies on the impacts of drought on migratory species have largely focused on resource dynamics along migration routes (Both et al., 2006; Middleton et al., 2013), our study demonstrates how drought conditions at the origin of migration can affect the timing of departures. Our finding that drought narrows the migration window for fishes may be true for additional migratory taxa. For example, while warming has been shown to accelerate bird migration rates (Marra et al., 2005), drought-induced water scarcity could also be expected to contract the migration window for birds and other species that rely on the production of aquatic plants and insects in the spring season. As climate change increases drought severity and frequency, the influence of water scarcity and warming on temporal migration patterns of other species warrants greater attention. For salmon in California, our findings indicate that climate-induced drought may be creating new life history bottlenecks. Protecting environmental flows by limiting surface water diversions and reducing groundwater withdrawals could help expand the outmigration window for coho salmon smolts and mitigate the effects of drought in this system and in other salmon-bearing streams projected to experience more severe droughts.

AUTHOR CONTRIBUTIONS

Brian Kastl, Theodore E. Grantham, and Mariska Obedzinski conceived this study. All authors designed the study. Mariska Obedzinski directed data collection. Mariska Obedzinski and William T. Boucher collected field data. Brian Kastl analyzed data and developed models. Brian Kastl and Theodore E. Grantham wrote the initial manuscript draft with critical revisions by Mariska Obedzinski, Stephanie M. Carlson, and William T. Boucher.

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CONFLICT OF INTEREST

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

Data and code (Kastl et al., 2022) are available from Dryad: https://doi.org/10.6078/D1FD73.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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