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By

Brian Kastl

A dissertation submitted in partial satisfaction of the

requirements for the degree of

Doctor of Philosophy

in

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in the

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of the

University of California, Berkeley

Committee in charge:

Professor Theodore Grantham, Chair
Professor Stephanie Carlson
Professor Mathias Kondolf

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Abstract

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Professor Theodore Grantham, Chair

Local human impacts and climate change are presenting freshwater species around the world with conditions that are more extreme than those to which they evolved. Human water use and increasing drought severity are causing unprecedented low stream flow and warm water. Consequently, cold-water, migratory fish, such as salmon and steelhead trout (*Oncorhynchus spp.*), face challenges in completing their life cycles. As Pacific salmon navigate extensive river networks during their migration, individual fish often cannot avoid heavily impaired reaches of streams and rivers, particularly in California, USA. Salmon in the southern extent of their range already experience conditions that approach or exceed their tolerance limits. Yet, we have an incomplete understanding of flow and temperature conditions required to complete their life cycles and sustain healthy populations. Are salmon approaching thresholds in low flows, minimum depths, and maximum temperatures? How do streamflow and temperature influence the critical timing of downstream migration (outmigration) of juveniles? Do minimum thresholds exist in stream water depths that salmon can navigate? How do additional environmental and ecological stressors interact with water temperature to affect physiological thermal limits of salmon?

In this dissertation, I explore how an endangered population of coho salmon (*Oncorhynchus kisutch*) near the southern extent of the species range in the agricultural Russian River watershed is affected by receding streams and warming waters. In Chapter 1 we tracked outmigration of individually marked juveniles in 7 streams over 13 years, which included an historic drought with extreme dry and warm conditions. We discovered that low-flow years during droughts contracted the outmigration window by 31% (from 11 to 7 weeks), while warm years hastened the outmigration window by approximately three weeks. In Chapter 2 we investigated minimum depth thresholds for migration by applying a novel use of water depth measurements at the riffle crest thalweg, which is the shallowest repeating geomorphic feature that salmon must navigate. We found that steep reductions and a cessation in movement occur at shallow depths, but that movement-depth thresholds varied among streams with different geomorphologies. Finally, in Chapter 3 we develop a framework to assess the degree to which

thermal tolerance may be reduced by ecological stressor interactions. Our example assessment demonstrates that temperature-stressor interactions, such as temperature interactions with predation, competition, and disease, may cause uneven distributions of impacts, such as development, growth and carrying capacity, to salmon populations.

Together, the chapters of this dissertation offer insights to better understand, manage, and mitigate the adverse impacts of low flow, shallow water, and warm water in salmon-bearing streams in coastal California. Our findings suggest that maintaining adequate streamflows from March through June is critical to preserving an outmigration window that is sufficiently long in duration to reduce risks of phenological mismatches when juvenile salmon reach the ocean to feed. Policies that set minimum water depth limits are likely needed in many of California's impaired streams to protect the salmon movement during the outmigration period. This research also underscores the importance of temperature-stressor interactions when considering the potential impacts of warming waters on salmonids. The assessment framework that we introduce can serve in any salmon-bearing system to categorize temperature-stressor interactions and the potential severity of their impacts on a salmon population. Collectively, the site-specific assessment methods and findings of this dissertation can be utilized to inform strategic instream flow policies, ecological stressor reduction, and thermal criteria development. If implemented, these solutions can reduce adverse impacts of human water use and drought on endangered migratory salmon individuals and enhance the resilience of salmon populations in a changing climate.

In dedication to my family Suzi, John, and Jessie, who inspire discovery, curiosity, and compassion for the living world.

Table of Contents

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Introduction

Growing human population pressures and climate change are increasing water scarcity globally (Vörösmarty et al., 2000). Declining access to sufficient freshwater introduces a myriad of impacts on ecosystems, which affect both people and other organisms (Crausbay et al., 2017). As a result of human water use, drought, and a changing climate, many aquatic species are pushed towards extirpation and complete species extinction (Closs et al., 2016; Katz et al., 2013; Moyle et al., 2017). Fish species around the globe are particularly threatened by changes in climate and human water consumption, including losses of up to 75% of local fish biodiversity (quartile range 4-22%) in some regions by 2070 (Xenopoulos et al., 2005). Severe droughts are also threatening freshwater fish through impacts on stream connectivity, habitat, food resources and phenology (Katz et al., 2013; Lake, 2003). Such drought impacts are exacerbated by water withdrawals because they are often greatest during periods of low precipitation and high temperatures (Kovach et al., 2019), thus compounding the impacts of natural low flow and warm water temperatures on fish.

Migratory fish species are particularly vulnerable to climate- and human-induced changes in stream condition because they must navigate extensive lengths of stream networks (Closs et al., 2016). As climate change intensifies droughts, migratory fish species on many continents will experience poleward range shifts (Lassalle & Rochard, 2009). Increasing drought frequency in California, USA as a result of climate change (Swain et al., 2018) is hastening spring flow recessions and prolonging the dry season (Grantham et al., 2018). Consequently, Pacific salmonids (*Oncorhynchus spp.*) at the southern extent of their range are threatened by worsening climate change and local anthropogenic stressors, particularly in California, where 78% of native California salmonid taxa may be extirpated by the end of the century, if current trends are not redirected (Katz et al., 2013).

Unprecedented, low streamflow and reservoir levels in the Western United States are increasing in frequency (Wahl et al., 2022) and may cause ecological thresholds of salmonids to be reached and new life stage bottlenecks to be introduced. During drought years, for example, extreme low flow reduces access to suitable habitat (Jaeger, 2012; Thorstad et al., 2003), stream connectivity (Magoulick & Kobza, 2003), and dissolved oxygen (Woelfle-Erskine et al., 2017), causing mortality of critically endangered coho salmon (*Oncorhynchus kisutch*) populations during the over-summer rearing period (Grantham et al., 2012; Obedzinski et al., 2018; Vander Vorste et al., 2020). Warming stream water, caused by climate change-induced low flow and increasing ambient air temperatures (Ficklin et al., 2013), is also contributing to more common exceedance of physiological thermal tolerance of Pacific salmonids (Hague et al., 2011). High water temperatures during extreme low flows also have indirect impacts on salmonids, including increased vulnerability to predation and disease (Nobriga et al., 2021).

A more comprehensive and refined understanding of potential streamflow and water temperature requirements for salmon could help to inform stream management and policy targets that support ecologically protective hydrology and temperature regimes. While interactions between streamflow and water temperature are common, disentangling their respective effects on salmonid life history strategies can also guide management strategies. Temperature and flow

affect salmonids at various timescales, ranging from interannual variability to seasonal to instantaneous impacts; investigations into many timescales have been previously performed (Spence & Dick, 2014; Spence & Hall, 2010; Sturrock et al., 2020). Still, unexplored flow and temperature influences on salmon phenology, behavior, and survival are vast and may vary among salmonid populations and sites (Zillig et al., 2021). Tools are urgently needed to use existing research findings and customize assessments to watersheds of interest. My dissertation addresses management and policy needs by demonstrating that juvenile salmonid outmigration in California coastal streams is influenced by drought and is a growing life cycle bottleneck of concern. I investigate how water temperature and flow independently alter outmigration timing among wet and dry years. I also explore how shallow water depths can prevent outmigration during drought years. Finally, considering the plethora of ecological/environmental stressors that interact with water temperature to impact salmonids, I introduce a new assessment technique that attempts to capture the degree to which stressors interact with temperature to influence ecological thermal tolerance, all to inform environmental policies and restoration opportunities to protect endangered salmonids in a changing climate.

In chapter 1, I investigated how intensifying severity of droughts in California (Swain et al., 2018) may affect the timing of endangered coho salmon (*Oncorhynchus kisutch)* downstream migration (outmigration). The timing and duration of outmigration is particularly important because salmon have adapted to match ocean entry timing with seasonal periods of marine conditions that promote production of prey, and consequently promote salmon growth and survival (Satterthwaite et al., 2014; Spence & Hall, 2010). Therefore, we sought to identify whether abnormally warm seasonal stream temperatures and low streamflow during drought may alter the timing and duration of outmigration or cause thresholds in the earliest and latest dates of outmigration to be reached. By tracking stream departure timing, streamflow, and water temperature in seven streams over 13 years, we captured dynamics over a wide range of interannual precipitation variability, ranging from 330 to 1570 mm (4.5 to 0.5 mm/day mean seasonal runoff), as well as 10.2 to 12.8 °C mean seasonal water temperature. We conducted linear mixed effects modeling to estimate the influences of flow and water temperature on outmigration timing. We found that drought contracts the duration of outmigration by 31%, from 11 weeks during the wettest years to 7 weeks during the driest year. During the warmest years, water temperature shifted the outmigration period earlier by approximately three weeks. Our findings suggest that droughts have the potential to cause phenological mismatches for anadromous salmonids. Contracted outmigration duration could increase the likelihood that an entire cohort of a salmon population would have low marine survival rates, given the unpredictability of productive marine conditions. Similarly, warming stream water temperatures that result in early migration may increase the frequency that out-migrating smolts encounter limited prey resources. We expect that human water use during dry years intensifies low-flow conditions during drought, underscoring the need for environmental flow protections for salmon in a warming climate.

Chapter 2 more deeply explores how a specific hydrologic parameter – stream water depth – may control outmigration of coho salmon. California streams are vulnerable to flow depletion, intermittency, and shallow water depths, as a result of drought (Grantham et al., 2018) and human water withdrawals (Deitch et al., 2009). Yet, migratory fish species such as

anadromous salmonids require connected streams to complete their migration between fresh and marine waters. We aimed to answer the questions as to what water depths juvenile salmonids successfully navigate, whether preferential movement depths exist, and whether setting minimal water depth thresholds could extend the duration of the outmigration season. We continuously measured depth and detected downstream movement of juvenile coho salmon during the spring outmigration season over ten years in 4 streams. We used an existing approach to measure depth at the shallowest repeating geomorphic feature that salmon must navigate – the riffle crest thalweg (RCT) – to convert continuous water stage data to RCT depths. We calculated population-level depth preferences by evaluating the resulting RCT depth measurements during detections, relative to RCT depths experienced throughout the outmigration season, irrespective of detections. We found that juveniles moved over a wide range of depths (interquartile range 6.1–18.0 cm), with interannual and inter-stream variance. Fish did not move at shallow depths, which varied by stream, demonstrating that movement-depth thresholds may exist. We also found that each additional day that water depths remain above an existing management threshold of 9.1 cm extended the outmigration end date by 0.25 days on average. These findings indicate that even outside of drought years, management actions to maintain minimum stream flow thresholds will enable juvenile salmon to successfully migrate downstream and contribute to coho salmon population recovery.

Chapter 3 provides a framework for assessing how maximum water temperature thresholds for salmonids may be altered by additional ecological and environmental stressors. As freshwater temperatures increase, risks grow that the temperatures will exceed thermal tolerances of salmonids (Crossin et al., 2008; Zillig et al., 2021). Interactions between ecological stressors (i.e., non-native species competition, disease, predation) and water temperature may lower the thermal tolerance of salmon, causing impacts on mortality, development/growth, carrying capacity, life history diversity, and/or community structure (Zillig et al., 2021). Considering the growing, yet incomplete, body of literature on temperature-stressor interactions (TSIs) and interspecies and inter-population variability in physiological thermal tolerance of salmonids (Zillig et al., 2023), we aim to develop a general framework to assess the potential impact of TSIs on the ecological thermal tolerance of salmonid populations, addressing both individual impacts of TSIs and their net population-level impact. We illustrate the assessment framework, using peer-reviewed literature and expert knowledge for a population of coho salmon in northern California, USA. Assessment rankings of TSI extent, strength, and expert confidence indicate the relative degree to which each TSI contributes to multiple impacts on the life stage of a salmonid population. Our example demonstrates that TSI severity (extent * strength) had a non-uniform distribution across six impacts, including mortality and phenology. The food availability TSI had the greatest severity, with the highest magnitude impacts on development/growth and carrying capacity. Based on multiple TSI assessments, restoration strategies, including stressor reduction and environmental flows to reduce water temperature, can be prioritized among salmonid populations and sites. Lastly, temperature targets can be informed by the net impact of stressors and incorporated into management and policy to reduce adverse, population-level impacts of warming water temperatures on salmonids.

Collectively, the chapters demonstrate that changing flow and temperature regimes have profound impacts on the outmigration of salmonids, particularly with respect to changing

phenology and potential population-level impacts. While drought is a natural phenomenon, the increasing severity and frequency of drought may be bringing salmonids closer to detrimental thresholds of flow, water depth, and temperature to which they have not yet adapted. Effects of intensifying drought, climate change, and human water diversions on coho salmon near the southern extent of their range may be indicators of impending threats to more northern populations. The chapters show that setting management and policy targets for these key environmental indicators can contribute to protecting endangered salmon populations. Finally, the methods and frameworks in these chapters to assess impacts of flow, water depth, temperature, and interactions with stressors can be adapted at the site-specific level to identify local ecological thresholds and set appropriate management targets that build resilience to worsening droughts among salmon populations beyond California.

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Chapter 1

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

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 7 streams over 13 years, spanning an 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.

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 along migration pathways and destinations. For example, previous studies have explored the effects of climate change and drought on the migration of terrestrial and avian species, including mismatches in the timing and duration (window) of resource availability 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 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 migratory fish species. Up to 75% of freshwater fishes risk extinction by 2070 (Xenopoulos et al., 2005), due to drought impacts on stream connectivity, habitat, and food resources (Lake, 2003). Migratory fish species are particularly at risk (Closs et al., 2016). 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 (*O. mykiss*) (Grantham et al. 2012) and coho salmon (*O. 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 has 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

an historic 2012-2016 drought 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 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 (Fig. 1). The study area has a distinct wet season (November-April), with a high degree of interannual precipitation variability. Streamflow reflects seasonal precipitation patterns, 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 liter sec^{-1} or cease to flow entirely by mid-summer (July-August), particularly in dry years (Appendix S1: Fig. 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 recovery of the population, a conservation hatchery program was established in 2001. Over the study period approximately 30,000 hatchery-raised juveniles were released into the study streams each fall. Approximately 21% 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: Fig. S2), focusing on one-year-old smolts detected between March 1 (historically when smolts begin to out-migrate) and July 3 (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.
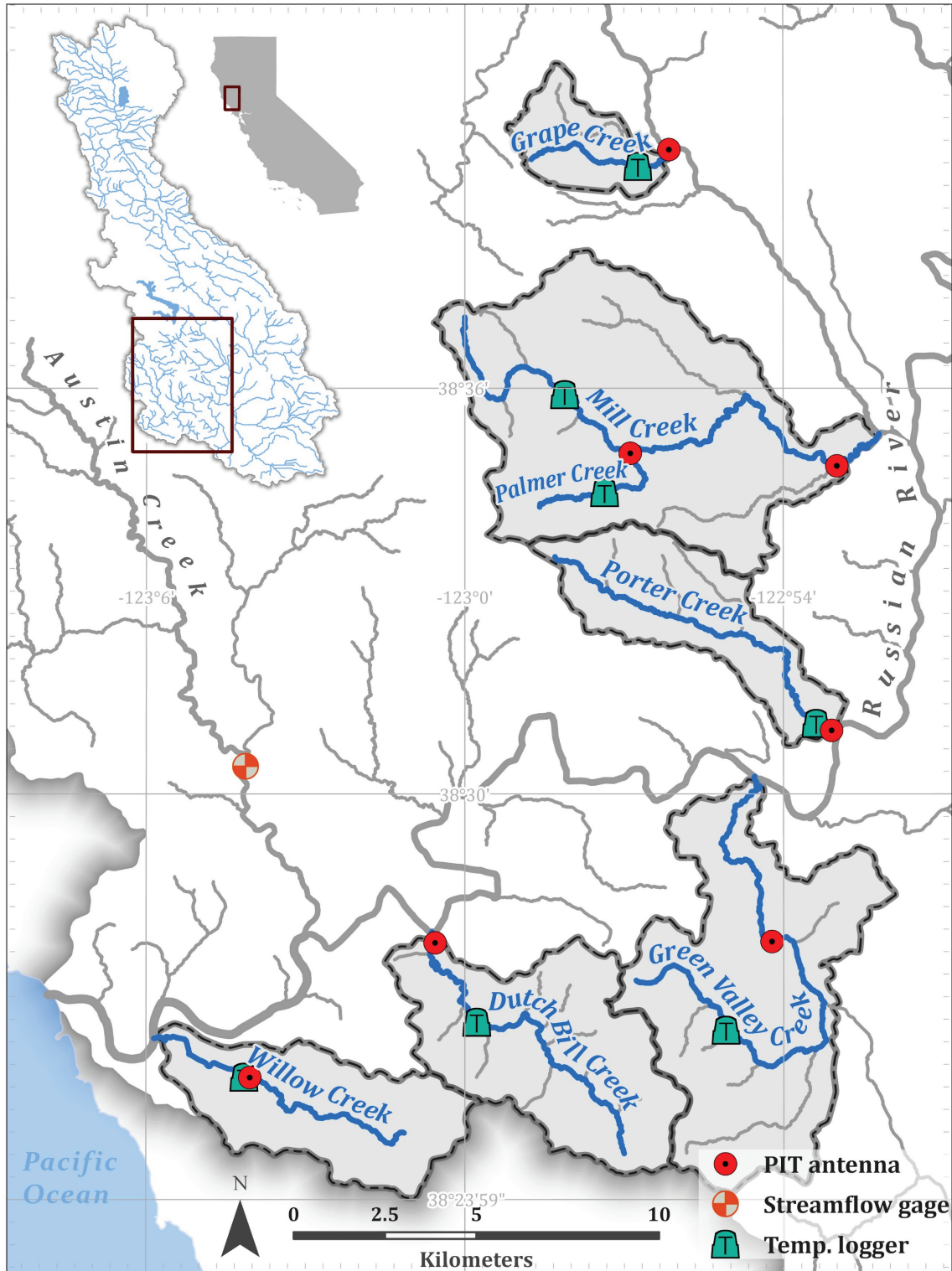
Figure 1. Map of the study streams, passive integrated transponder (PIT) antennas, Gage USGS 11467200 Austin C Nr Cazadero CA, and water temperature loggers.
Streamflow and water temperature

Seasonal streamflow of study streams was estimated using a nearby USGS flow gage (Station #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 (mm), 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 out-migrated.

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% CI). Variable coefficients with 95% CIs that do not overlap 0 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 2008-2020 (539 ± 376 detections per stream-year; mean ± SD). Among stream-years, mean outmigration start and end dates were March 20 ± 13.2 days and May 18 ± 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 (Fig. 2A). Outmigration during years with warmer water temperatures also generally occurred earlier than during years with cooler water temperatures (Fig. 2B).
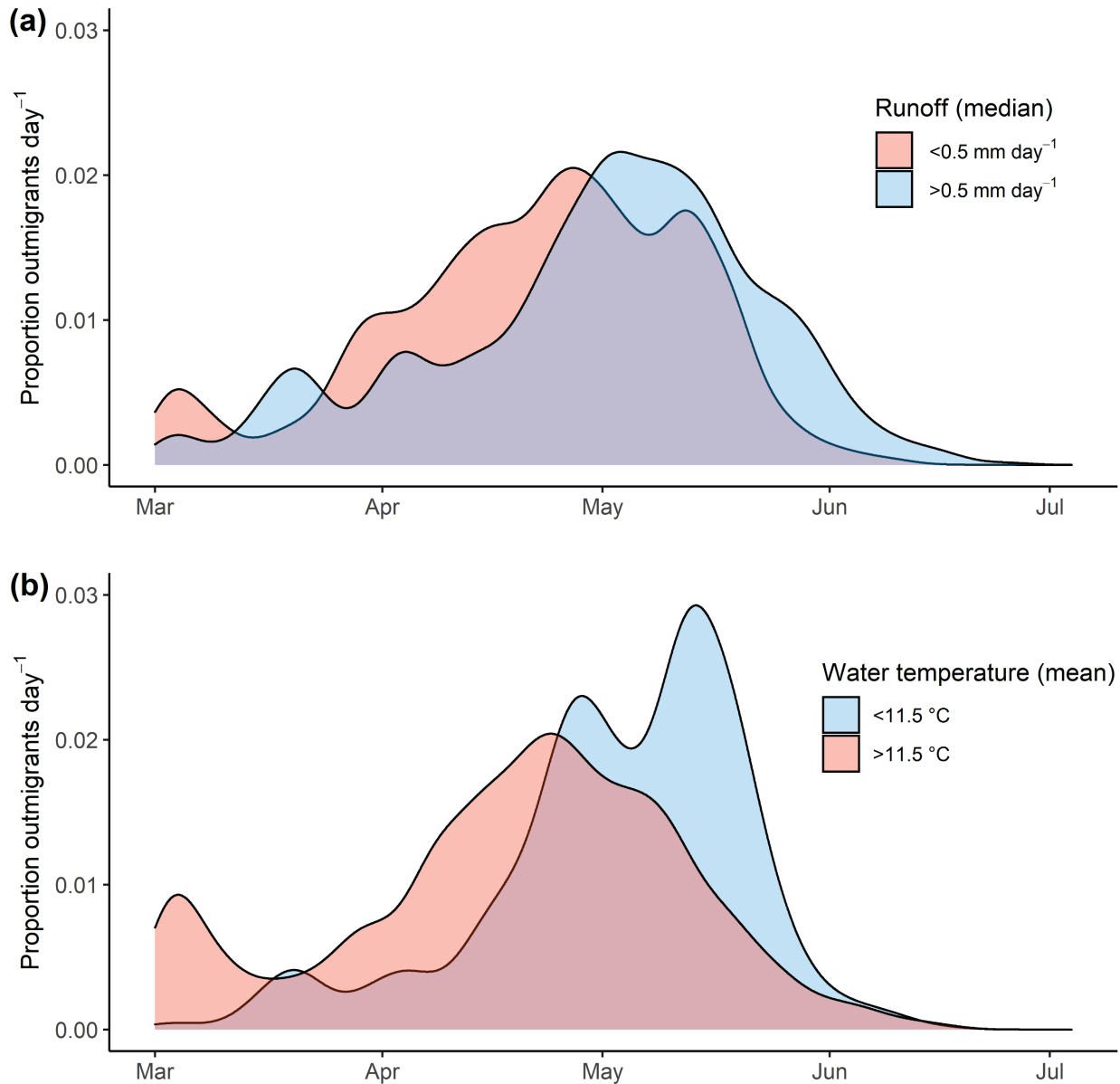
Figure 2: Outmigration timing distributions: **(a)** Low (red) vs. high (blue) streamflow years, represented by median March-June runoff (15,513 coho salmon detections), are based on an equal number of years with values above and below 0.5 mm day^{-1}. **(b)** Cool (blue) vs. warm (red) years, represented by mean March-April water temperature (7,385 detections), are based on an equal number of years with values above and below 11.5 °C.

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 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 (Fig. 3A and 3B). That is, when runoff is high, the outmigration start date is hastened and the outmigration end date is extended. In 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 (Fig. 3C). The positive effect of runoff on outmigration duration was consistent among all of our study sites (Appendix S1: Fig. S3).
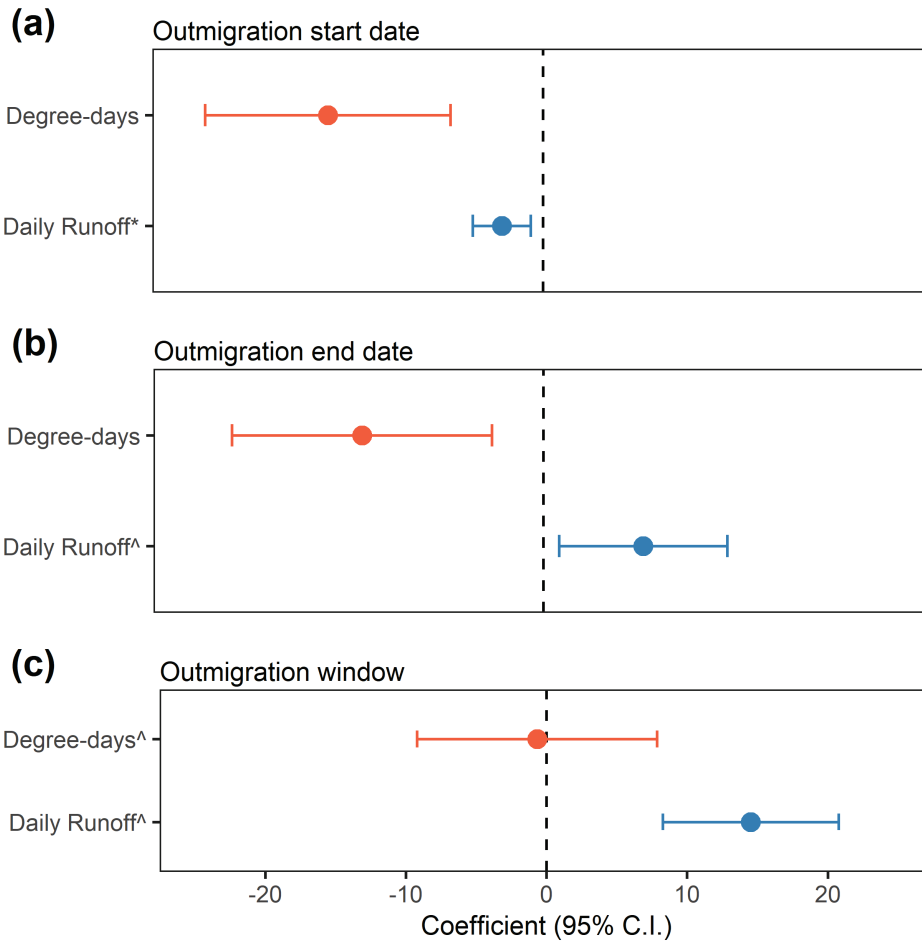
Figure 3: Coefficient effect sizes (±95% confidence interval [CI]) for explanatory variables, including degree-days (March-April; red color) and median daily runoff (*March-April, ^March-June; blue color), of the top performing model for each response variable: **(a)** outmigration start date (when 5% 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 March 12 (March 3-21 95% CI) to March 24 (March 17-31 95% CI) (Fig. 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 March 30 (March 21-April 9) to March 6 (February 24-March 16) (Fig. 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 May 25 (May 14-June 5) to May 14 (May 5-23) (Fig. 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 May 25 (May 14-June 5) to May 5 (April 23-May 16) (Fig. 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 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 (Fig. 4E). Because higher degree-days hasten both outmigration start and end dates, water temperature shifted, but did not prolong or contract, the outmigration window.
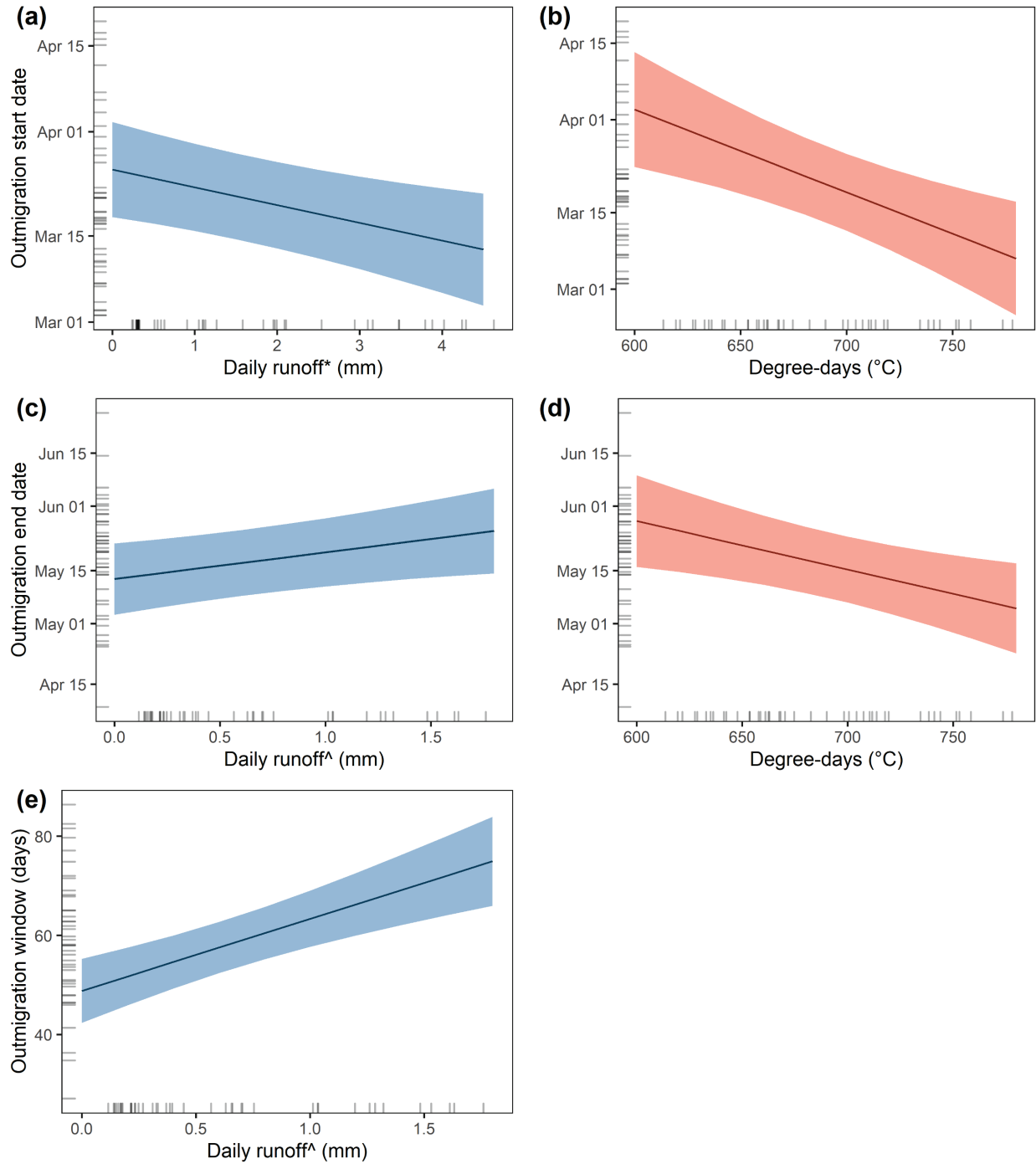
Figure 4: Partial dependence from linear mixed effects models of coho salmon smolt outmigration start date (top row), end date (middle row), and window (bottom row). Model estimates (solid lines) and 95% confidence intervals (shading) for median daily runoff (*March-April, ^March-June) and degree-days (March-April). Observations are indicated by tick marks on x- and y-axes.

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 has 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 out-migrating smolts was lower in drought versus non-drought years. Nevertheless, we can assume that smolts that do not out-migrate 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 prepares 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 impassible 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 out-migrating 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 led 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 May 27 ± 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 out-migrating 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 increases 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 out-migrating smolts during our study period was May 28, synchronized with the mean peak upwelling date (May 27) (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 ℃ 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 the year 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 to 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.

Acknowledgements

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Supplement to Chapter 1

Appendix S1 contents

- Supplemental figures (Figs. S1–S3)
- Supplemental tables (Tables S1–S2)
- Methods for upwelling timing
- Literature cited

Supplemental figures
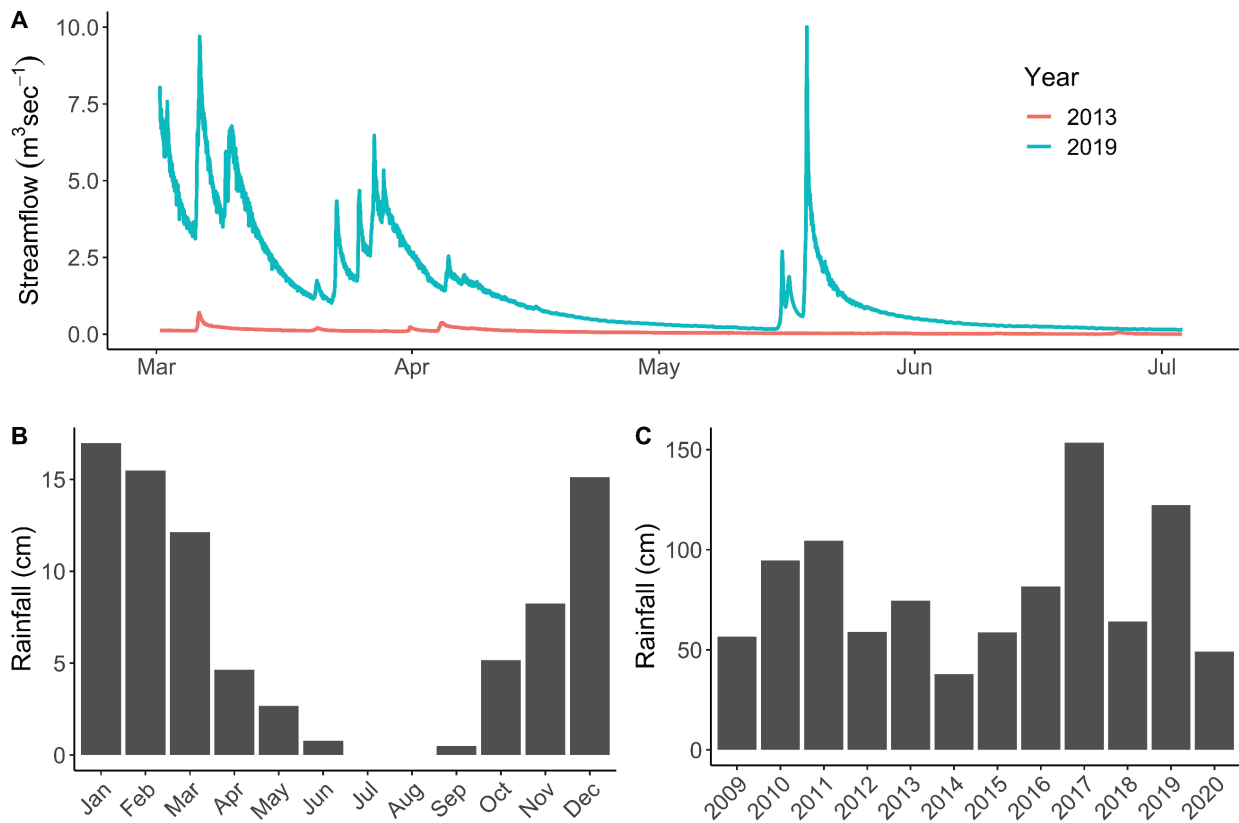
Fig. S1. (A) Streamflow at Mill Creek (2.2 km upstream of confluence with Russian River) for a wet year (blue) vs. dry year (red), during the outmigration season. (B) Mean monthly precipitation (2008-2019). (C) Annual precipitation (October-September). Precipitation measured at Santa Rosa County Airport, within 80 km of all study streams.
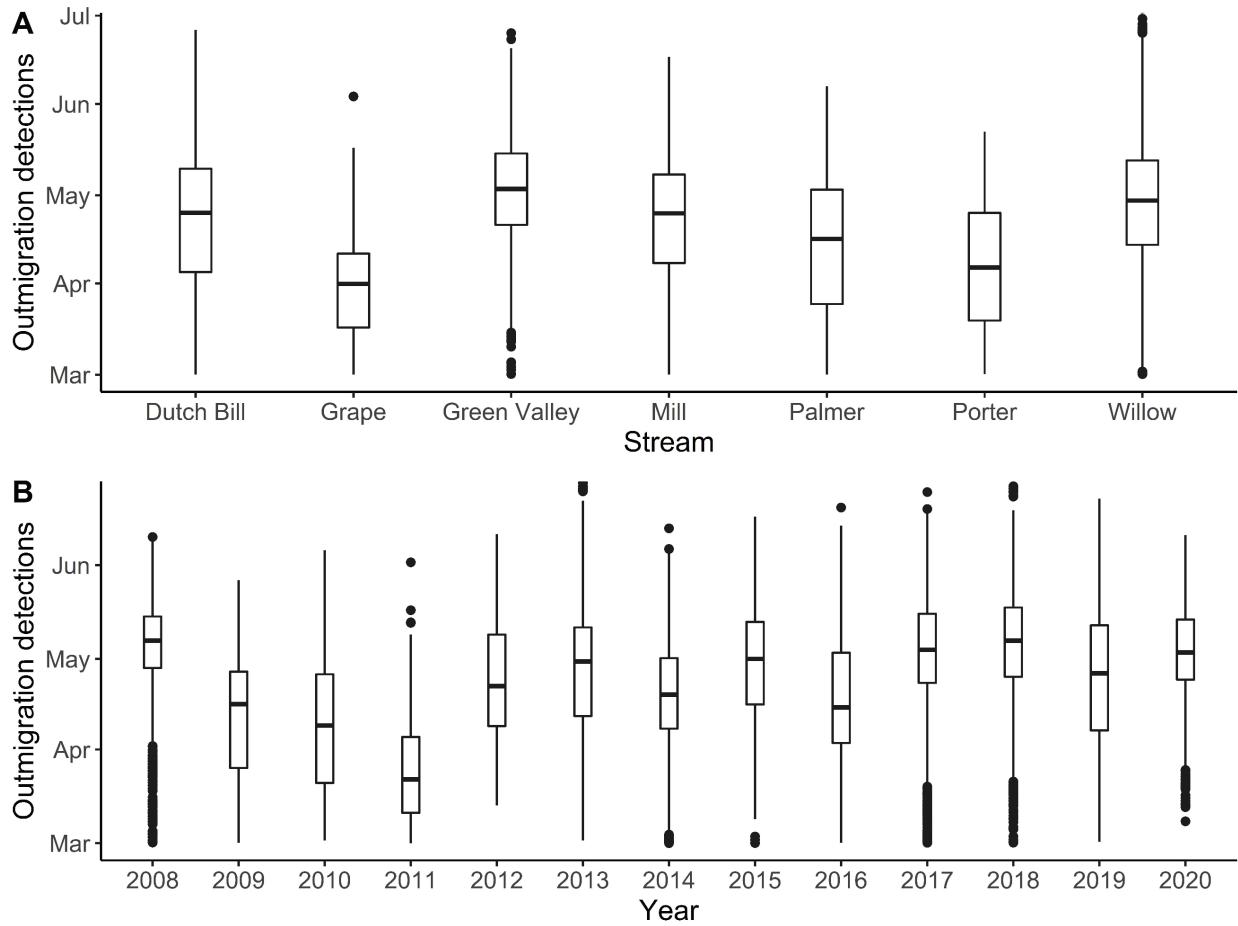
Fig. S2: Outmigration timing of age-1 coho salmon from seven study streams within the Russian River watershed. Box plots (A) among streams, and (B) among years, represent 47 stream-years (25,047 detections). Thick lines show median, box ends show upper and lower quartile, ends of whiskers show 1.5 times the IQR, and dots show outliers. Due to variable periods among streams of no data collection, years include variable numbers of streams, and streams include variable numbers of years.
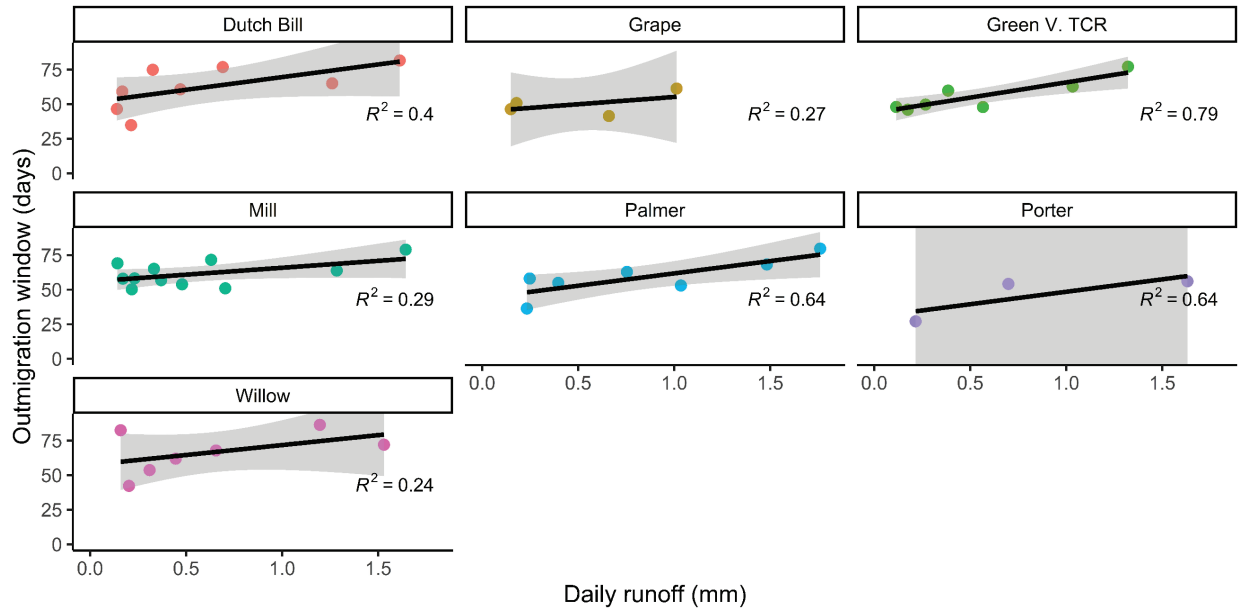
Fig. S3: Plots of estimated March-June daily runoff (mm) vs. outmigration window (duration 5th – 95th cumulative outmigration). All study streams demonstrate a positive relationship between the two variables.

Supplemental tables

Table S1. Study stream attributes and value ranges for each explanatory variable that is used in the linear mixed effects models. Degree-days are the sum of the daily mean water temperature (°C) March-April. Median daily runoff estimates (mm day^{-1}) are available for all years of outmigration and degree-day.

Stream	Drainage area (km^2)	Years of outmigration data	Years of degree-days data	Degree-days March-April	Runoff March-April (mm day^{-1})	Runoff March-June (mm day^{-1})
Dutch Bill	30.2	8	6	627 - 718	0.29 - 4.24	0.14 - 1.61
Grape	8.4	4	4	708 - 758	0.33 - 3.80	0.15 - 1.01
Green Valley	89.3	7	7	670 - 778	0.24 - 3.48	0.11 - 1.32
Mill	48.8	11	9	629 - 704	0.30 - 4.32	0.14 - 1.64
Palmer	9.8	7	7	614 - 714	0.32 - 4.63	0.23 - 1.76
Porter	19.2	3	3	710 - 774	0.29 - 4.29	0.22 - 1.63
Willow	18.5	7	6	619 - 712	0.27 - 4.02	0.16 - 1.53

Table S2. Statistics of outmigration window/timing, degree-days, and runoff for 42 stream-years that were used in the linear mixed effects models. *March-April, ^March-June.

Stream	Year	Window (days)	Start (5th %tile)	End (95th %tile)	Degree -days*	Scaled degree-days*	Runoff* (mm day^{-1})	Runoff^ (mm day^{-1})
Dutch Bill	2013	59.1	22-Mar	20-May	636	6.36	0.31	0.17
Dutch Bill	2014	74.9	2-Mar	15-May	701	7.01	1.11	0.33
Dutch Bill	2015	46.5	10-Mar	26-Apr	683	6.83	0.31	0.14
Dutch Bill	2017	65.0	17-Mar	21-May	662	6.62	3.10	1.26
Dutch Bill	2019	81.6	7-Mar	27-May	718	7.18	4.24	1.61
Dutch Bill	2020	34.8	15-Apr	19-May	627	6.27	0.29	0.21
Grape	2011	61.3	2-Mar	3-May	719	7.19	3.80	1.01
Grape	2012	41.4	17-Mar	28-Apr	708	7.08	2.09	0.66
Grape	2013	50.8	10-Mar	30-Apr	758	7.58	0.33	0.18
Grape	2015	46.4	10-Mar	25-Apr	753	7.53	0.33	0.15
Green V.	2014	49.7	28-Mar	16-May	741	7.41	0.91	0.27
Green V.	2015	47.9	19-Apr	5-Jun	735	7.35	0.25	0.11
Green V.	2016	59.8	31-Mar	29-May	778	7.78	1.09	0.39
Green V.	2017	62.8	29-Mar	31-May	744	7.44	2.54	1.03
Green V.	2018	47.9	17-Apr	4-Jun	698	6.98	1.58	0.57
Green V.	2019	77.1	17-Mar	3-Jun	752	7.52	3.48	1.32
Green V.	2020	46.0	16-Apr	1-Jun	670	6.70	0.24	0.17
Mill	2008	58.2	26-Mar	24-May	629	6.29	0.51	0.23
Mill	2009	56.9	18-Mar	13-May	653	6.53	0.59	0.37
Mill	2012	71.5	17-Mar	27-May	635	6.35	1.99	0.63
Mill	2013	57.9	18-Mar	15-May	659	6.59	0.31	0.17
Mill	2014	65.1	2-Mar	6-May	690	6.90	1.13	0.33
Mill	2015	69.1	16-Mar	25-May	704	7.04	0.31	0.14
Mill	2017	63.8	21-Mar	24-May	648	6.48	3.16	1.28
Mill	2018	51.0	6-Apr	27-May	658	6.58	1.97	0.70
Mill	2020	50.3	1-Apr	22-May	633	6.33	0.30	0.22
Palmer	2008	58.0	22-Mar	19-May	614	6.14	0.55	0.25
Palmer	2009	54.9	16-Mar	10-May	643	6.43	0.63	0.40
Palmer	2010	68.2	6-Mar	13-May	654	6.54	3.48	1.48
Palmer	2011	53.0	2-Mar	24-Apr	668	6.68	3.88	1.04
Palmer	2018	62.8	21-Mar	23-May	663	6.63	2.11	0.75
Palmer	2019	79.7	4-Mar	22-May	714	7.14	4.63	1.76
Palmer	2020	36.3	11-Apr	18-May	641	6.41	0.32	0.23
Porter	2018	54.1	9-Mar	2-May	710	7.10	1.95	0.70
Porter	2019	56.1	11-Mar	7-May	774	7.74	4.29	1.63
Porter	2020	27.1	12-Mar	9-Apr	739	7.39	0.29	0.22
Willow	2013	82.5	4-Apr	25-Jun	619	6.19	0.29	0.16

Willow	2014	53.6	22-Mar	14-May	668	6.68	1.05	0.31
Willow	2016	61.9	21-Mar	22-May	712	7.12	1.27	0.45
Willow	2017	86.4	7-Mar	1-Jun	661	6.61	2.94	1.20
Willow	2018	67.9	7-Apr	14-Jun	622	6.22	1.83	0.66
Willow	2019	72.0	18-Mar	29-May	675	6.75	4.02	1.53

Methods for upwelling timing

Upwelling data are based on the mean of estimates at 38° and 39° N latitude for the years used in the mixed effects modeling (2008-2020) from the Biologically Effective Upwelling Transport Index (BEUTI), developed by the National Oceanic and Atmospheric Administration, which can be found here:
https://oceanview.pfeg.noaa.gov/products/upwelling/cutibeuti
https://mjacox.com/upwelling-indices/

Dates of peak upwelling are based on the greatest rate of change in cumulative upwelling (Bograd et al., 2009; Jacox et al., 2018; Oestreich et al., 2022) and were calculated, using an R script that was adapted from https://github.com/woestreich/blue-whale-phenology/blob/main/scripts/cumulative_beuti.R.

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Chapter 2

Deep enough to swim? Stream water depths that support endangered coho salmon outmigration

Abstract

Streamflow depletion is occurring globally, due to land use change, climate change, and increasing human water demand. Ecological effects of low flows are particularly significant for diadromous fish, which require connected stream networks to migrate between fresh and marine waters. In coastal California, USA, drying streams are known to limit rearing habitat for juvenile salmon, but effects on their seaward migration remain poorly understood. In this study, we evaluated the outmigration of endangered, juvenile coho salmon (*Oncorhynchus kisutch*) during the late spring flow recession in four streams over 10 years. We monitored the outmigration of fish tagged with passive integrated transponders via detections at stationary antennas, and we measured stream water depths when movement was detected. We assessed depths at multiple riffle crest thalwegs (RCTs), the shallowest geomorphic feature that fish must navigate. Finally, we calculated population-level outmigration depth preferences by evaluating depths during fish movement, relative to depths available during the potential outmigration window. Juvenile fish moved over a wide range of depths (interquartile range 6.1–18.0 cm), which varied by year and stream. Fish ceased to move at shallow water depths, which limited late-season outmigration as stream drying occurred. Our findings suggest that management actions to increase streamflow during the spring would benefit salmon outmigration and could contribute to population recovery. Streamflow-RCT depth relationships, used to assess coho depth preferences during movement, is a relatively simple and effective method for assessing environmental flow needs, a priority for aquatic conservation in California and globally.

Introduction

Water scarcity is increasing in many regions of the world, due to growing human population pressures and climate change (Vörösmarty et al., 2000). Consequently, declining freshwater availability is placing both people and ecosystems at risk (Crausbay et al., 2017). In the Western United States, for example, record-low streamflow and reservoir levels in recent decades have had major impacts on water supplies for agriculture, industry, and municipalities (Wahl et al., 2022). Streamflow depletion has also had significant ecological effects, pushing many aquatic species to the brink of extinction (Closs et al., 2016). For example, periods of extreme low flow have been shown to cause water temperatures to increase the susceptibility of organisms to predation and disease (Nobriga et al., 2021), limit hydrologic connectivity (Magoulick & Kobza, 2003) and reduce access to suitable habitats (Jaeger, 2012; Thorstad et al., 2003).

California's Pacific salmon are particularly vulnerable to declining streamflow. In fact, it is estimated that 78% of native California salmonid taxa face extirpation or extinction within the century, if current trends in water use and climate change continue (Katz et al., 2013). Occurring

at the southern end of their range, California's Pacific salmon utilize habitats that experience a more intense dry season than populations further north. Naturally limited water supplies, coupled with high human demands, increase the risk of flow depletion in salmon-bearing streams (Deitch & Dolman, 2017). As a result, low flow is recognized as an important limiting factor to juvenile salmon rearing in coastal California streams (Grantham et al., 2012; Obedzinski et al., 2018), including critically endangered coho salmon (*Oncorhynchus kisutch*) populations (Vander Vorste et al., 2020). For example, previous studies have shown that over-summer survival of juvenile coho salmon is lowest in drought years, when extreme low flows limit habitat availability, disconnect streams, and cause dissolved oxygen levels to fall below tolerance limits (Obedzinski et al., 2018; Vander Vorste et al., 2020).

Low streamflow can also influence the spring seaward migration (outmigration) of juvenile salmon (smolts) in California (Sturrock et al., 2020; Sykes et al., 2009). Unlike in the northern, temperate-climate region of their range, coastal streams in the Mediterranean climate of California experience a predictable flow recession throughout the spring that reaches zero or near-zero values by summer (Deitch & Dolman, 2017). This transition between wet and dry seasons is accelerated in drought years and, in coastal streams, an earlier flow recession is associated with both an earlier end, and a contraction, of the migration window for coho salmon smolts (Kastl et al., 2022). This suggests that low streamflow may be an important limiting factor to smolt migration, although it has received less attention than flow impacts on other life stages. Although previous research has shown that juvenile passage through fishways can be limited by insufficient water depths (Ohms et al., 2022), the effects of low flows on fish outmigration through natural stream channels is not well understood. There is a particular need to understand smolt outmigration passage requirements and the relationship between streamflow, water depths, and movement patterns in coastal California streams, which are vulnerable to flow depletion from both drought (Grantham et al., 2018) and human water withdrawals (Deitch et al., 2009).

In this study, we characterized coho salmon smolt movement patterns in relation to flow and water depths encountered throughout the spring outmigration season. Specifically, we asked: 1) What are the depths that smolts navigate during their outmigration? 2) Is there evidence of preferential movement depths (at a population level), and how do migration depth preferences vary among streams and among years? 3) Is the outmigration season prolonged when water depths remain above a minimum passage depth requirement? To address these questions, we tracked the movement of individually marked fish and monitored flow and water depths at riffle crests—the shallowest section of repeating pool-riffle habitat units—at four study streams over 10 years. We calculated depth preferences as the frequency of outmigration detections at specific depths, relative to the frequency of depth occurrence over the outmigration season (Kong et al., 2018; Mäki-Petäys et al., 1997; Van Liefferinge et al., 2005). We hypothesized that smolts prefer deeper water, due to more frequent outmigration associated with high-flow events (Spence & Dick, 2014; Sturrock et al., 2020). We also hypothesized that smolts would avoid water depths below previously reported passage depth requirements. Finally, we predicted that movement would cease entirely when a shallow water depth threshold was exceeded in our study streams, each with a unique depth-to-flow relationship. Overall, this work advances the understanding of outmigration depth preferences, informs management strategies that reduce the impacts of low

streamflow during migration, and highlights the need to protect environmental flows for migratory fishes.

Methods

Study area and reach characterization

The study area includes four tributaries to the Russian River, in Sonoma County, California (Fig. 1). The region has a distinct winter rainfall regime (November–April) with streams experiencing flashy, high flows during winter storms, followed by a flow recession in spring and through the summer dry season. During most years, streamflow in the study streams fell to less than 0.1 cubic feet per second (cfs) (0.003 m^3sec^{-1}) by 1 August, or as early as 1 May in dry years. Mean annual precipitation over the study period (2010–2020) at the Sonoma County Airport in Santa Rosa, California was 80.3 cm (CV = 0.42). The study watersheds include Willow, Dutch Bill, Porter, and Mill creeks (Figure 1), which have drainage areas between 9.8 and 20.2 km^2 (Table 1), and support oak woodlands, grassland, mixed coniferous forest, and redwood forest. The watersheds also support vineyard agriculture and rural residential development that rely on stream diversions and/or shallow wells to satisfy water demands (Deitch et al., 2009).
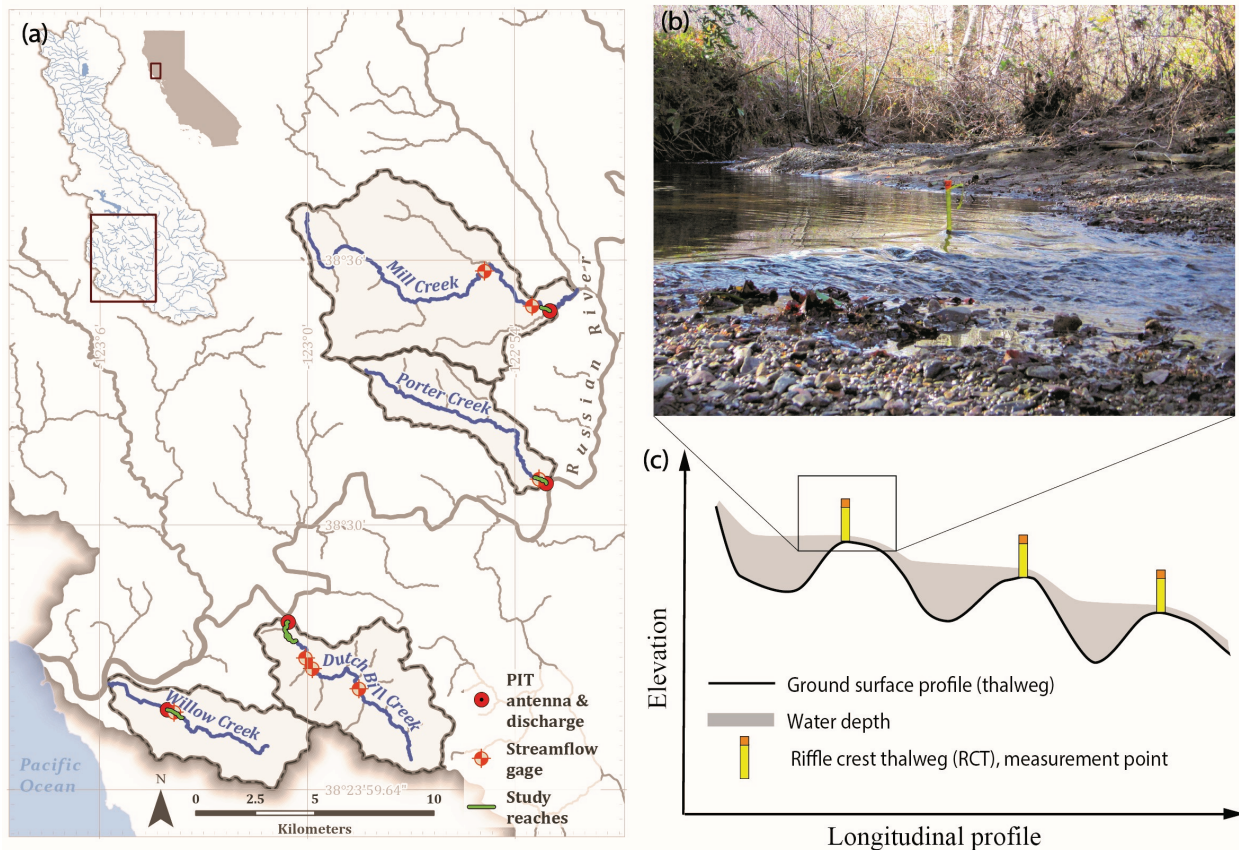

Figure 1: **(a)** Study streams, passive integrated transponder (PIT) antenna arrays and discharge measurement locations, and the study reaches. **(b)** Example of riffle crest thalweg (RCT) field

measurement location, marked by rebar. **(c)** Pool-riffle sequence (vertical exaggeration) and RCTs (adapted from Rossi et al., 2021).

Table 1: Study stream characteristics and geomorphic attributes.

Stream	Study reach length (km)	Catchment Area (km^2)	Geomorphic classification	Slope (%)	Substrate size (mm)	Channel width depth ratio
Dutch Bill	2.0	30.2	Pool-riffle	0.4	54.0	18.5
Mill	0.5	9.8	Step-pool	0.6	61.5	12.5
Porter	0.8	19.2	Pool-riffle	0.5	40.8	21.0
Willow	0.9	18.5	Pool-riffle	0.6	18.7	18.5

Notes: Slope, substrate, and width-depth ratio values are based on the means of field measurements made within each study reach, at five locations before and five locations after the >50-year flood in 2019 (geomorphic data collection methods described in Appendix S1).

Study population

The Russian River historically supported large runs of coho salmon that were fished for subsistence by local tribes for thousands of years and, after European settlement, supported a commercial fishery through the 1950s (Steiner, 1996). However, dam construction, flow and temperature changes, invasive species, habitat modification and loss, and hatchery impacts drove the population to near extinction by the late 1990s (Steiner, 1996). The Central California Coast coho salmon population complex was listed as threatened under the Federal Endangered Species Act (70 FR 37160) in 1996 and endangered in 2005. The streams in this study have all been identified as priorities for coho salmon recovery (National Marine Fisheries Service, 2012).

Efforts to restore coho in the Russian River have included physical habitat restoration and instream flow enhancement projects. In 2001, a conservation hatchery was established to accelerate population recovery (Pregler et al., in press). During the study period, approximately 43,000 hatchery, age-0 juvenile coho salmon were released in the study tributary streams each fall to allow for acclimatization to the local stream environment prior to outmigration as smolts the following spring (March–June). Passive integrated transponder (PIT) tags with unique identifiers were implanted into approximately 15% of the hatchery releases each year. PIT antennas were deployed into tributary streams to track the movement of fish and to determine the timing of outmigration to the Russian River.

Assessing movement depths during smolt outmigration

We analyzed PIT antenna detections during the smolt outmigration season from 2010 to 2020. Among Russian River tributaries, the historical outmigration start date is 1 March and the latest detection date during the study period is 3 July. However, we limited our analysis to 1 May – 3 July, when we hypothesized migration-limiting depths could occur. This time window also

made it possible to increase our number of observations from 18 stream-years without data gaps (for 1 March – 3 July) to 26 stream-years without data gaps. To account for multiple detections of some individuals, we included only the earliest detection date of each individual in our analysis.

To estimate the water depths that fish were navigating at the time of detection, we used a combination of real-time measurements, long-term discharge datasets, and values estimated from depth-discharge relationships. In each stream, we established a 0.5–2 km study reach in proximity to the PIT antenna nearest the confluence with the Russian River (Fig. 1). During the outmigration season in 2018 and 2019, we measured the depth of water within the channel across a range of flow conditions using a stadia rod. Specifically, we measured water depths at the riffle crest thalweg (RCT), which is the deepest point of the channel (thalweg) at the riffle crest (Rossi et al., 2021). The riffle crest occurs immediately downstream of the pool tail and is the shallowest depth in the longitudinal profile of riffle-pool sequences. The RCT therefore represents the deepest path in the shallowest section of the stream that out-migrating juvenile salmon must pass as water levels recede. We measured 9–15 RCT depths per stream during each site visit and each site was visited 15–18 times over the 2-year study period, resulting in over 1300 RCT depth measurements. During each site visit, discharge was also measured with a FlowTracker handheld acoustic doppler velocimeter within 100 m of antenna arrays, following standard flow measurement protocols (Rantz, 1982). In-situ pressure transducer gauges in pools of each study stream near antenna arrays continuously measured water depth (stage) in 15-minute intervals (stage measurement details in Appendix S1). Depths were then transformed to discharge, using stage-discharge rating curve power-law relations, from discharge measurements collected at each site across a range of flows (Harrelson et al., 1994).

We next converted our continuous discharge data to continuous RCT depth using rating curves developed at each site. Specifically, we used power law regression analysis to develop mathematical relationships between median RCT depth and discharge (i.e., the RCT rating curve). Relationships between discharge at a given channel cross-section and the associated average water depth generally have been shown to follow power-law relationships (Leopold & Maddock, 1953) and have been specifically used for describing the relationship between discharge and RCT depth (Mierau et al., 2017; Rossi et al., 2021):

$$Q = a(RCTd)^b,$$

where Q is the volumetric flow rate, RCTd is the riffle crest thalweg depth, and a and b are empirically-determined values. We fit nonlinear (weighted) least-squares models to each stream, using 12–15 points that represent the median RCT depth and a discharge measurement per stream, producing a unique power-law equation for each stream. Then the power law equations were used to convert past years of continuous streamflow data into continuous RCT depth data. Since we were interested in applying rating curve equations to 10 years of stream data, we checked whether rating curves were stable among years, using the discharge and RCT depth measurements collected in 2018 and 2019. All 2019 discharge and RCT depth measurements were made after a >50-year flood event in late February 2019, which induced greater channel geomorphic change than any other period of the study. Rating curve points from 2018 and 2019

plot similarly along rating curves (Figure 3), indicating that the median RCT-Q relationships are stable over time.

Finally, we estimated the depth at which each fish out-migrated by matching the timing of the first detection with the closest 15-minute time interval at which median RCT depth in the study reach was estimated. We also calculated the depths above which outmigration occurred for cumulative percentiles of seasonal detections, and we summarized all RCT depth quantiles across streams, years, and stream-years.

Evaluating coho depth preferences
To determine if there is evidence of preferential movement of out-migrating juveniles at particular depths, we compared the distribution of depths encountered *during outmigration detections* with the distribution of depths occurring *throughout the outmigration period*. To test if there was a statistically significant difference between the two distributions, we applied the non-parametric Kruskal-Wallis test, using the package *rstatix* and the functions *kruskal_test* and *kruskal_effsize*. The eta^2, based on the H-statistic, was used as the measure of the Kruskal-Wallis test effect size:

$$Eta^2[H] = (H - k + 1)/(n - k),$$

where *H* is the value obtained in the Kruskal-Wallis test, *k* is the number of groups, and *n* is the total number of observations (Tomczak & Tomczak, 2014). The eta^2 estimate assumes values from 0 to 1 and when multiplied by 100 indicates the percentage of variance in the dependent variable explained by the independent variable.

We next calculated depth preferences by comparing the RCT depths of the stream channel *during outmigration detections*, relative to the depths occurring *throughout the outmigration period*. All depths were assigned to 1-cm depth intervals and depth preference, defined as the relationship between habitat use and habitat availability (Mäki-Petäys et al., 1997), was estimated for each interval by dividing the proportion of RCT depths encountered *during outmigration detections* (proportion use) by the proportion of RCT depths occurring *throughout the outmigration period* (proportional habitat availability), following methods by (Bozek & Rahel, 1992; Mäki-Petäys et al., 1997). We limited depth preference analysis to non-zero RCT values to include only potentially navigable depths and to intervals that constituted a minimum of 3% of RCT depths occurring *throughout the outmigration period*. We divided depth preferences by the maximum preference to standardize values from low suitability (0.0) to high suitability (1.0) per stream (Mäki-Petäys et al., 1997).

Assessing effects of passage depths on end date of outmigration
To determine if the seasonal end of outmigration coincided with declining water depths, we further evaluated outmigration in relation to timing at which water depths fall below previously reported minimum passage depth requirements. We used linear mixed effects models to explore how *outmigration end date* was influenced by the maximum date that depths were above 9.1 cm, a passage depth threshold for juvenile salmonids at riffles used by the California Department of Fish & Wildlife (CDFW, 2017). *Outmigration end date* was calculated for each stream-year as the date at which 95% of the seasonal migration detections occurred, to limit the

influence of outliers (e.g., detections of individual fish moving outside of the typical migration period; e.g., (Kastl et al., 2022). It was used as the response variable in a linear mixed-effects model with *maximum date >9.1 cm depth* as an explanatory variable 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 conditional coefficients (including stream as a random effect) and marginal coefficients (excluding stream as a random effect) of determination (R^2) (Nakagawa & Schielzeth, 2013), using the *r.squaredGLMM* function of the *MuMIn* package. We also reported the model coefficient and 95% confidence intervals, as measures of effect size, and generated partial dependence plots using the *plot_model* function of the *sjPlot* package. To further investigate the influence of shallow water depths on outmigration duration, we developed a separate linear mixed model to evaluate the effects of the *number of days RCT depth < 9.1 cm* on the *number of days with no outmigration*.

Results

Outmigration depths

Each study stream had a unique RCT depth-to-flow relationship, represented by a power law relationship (Fig. 2). As a result, the streamflow required to reach a particular RCT depth varied significantly among streams. For example, the streamflow required to reach a depth of 9.1 cm ranged from 0.71 to 3.89 cfs (0.02 to 0.11 m³sec⁻¹) among streams. Based on the RCT depth-to-flow relationships, Mill Creek required the lowest magnitude streamflow to reach this depth threshold, while Dutch Bill Creek required the highest flows. The differences in their RCT depth-to-flow relations are explained by differences in channel morphology: the study reach of Mill Creek is characterized by a narrow, confined channel, large-grained substrate, and a step-pool geomorphic channel type, whereas Dutch Bill Creek has a wide channel, moderate size substrate, and a pool-riffle geomorphic channel type (Montgomery & Buffington, 1997) (Table 1).
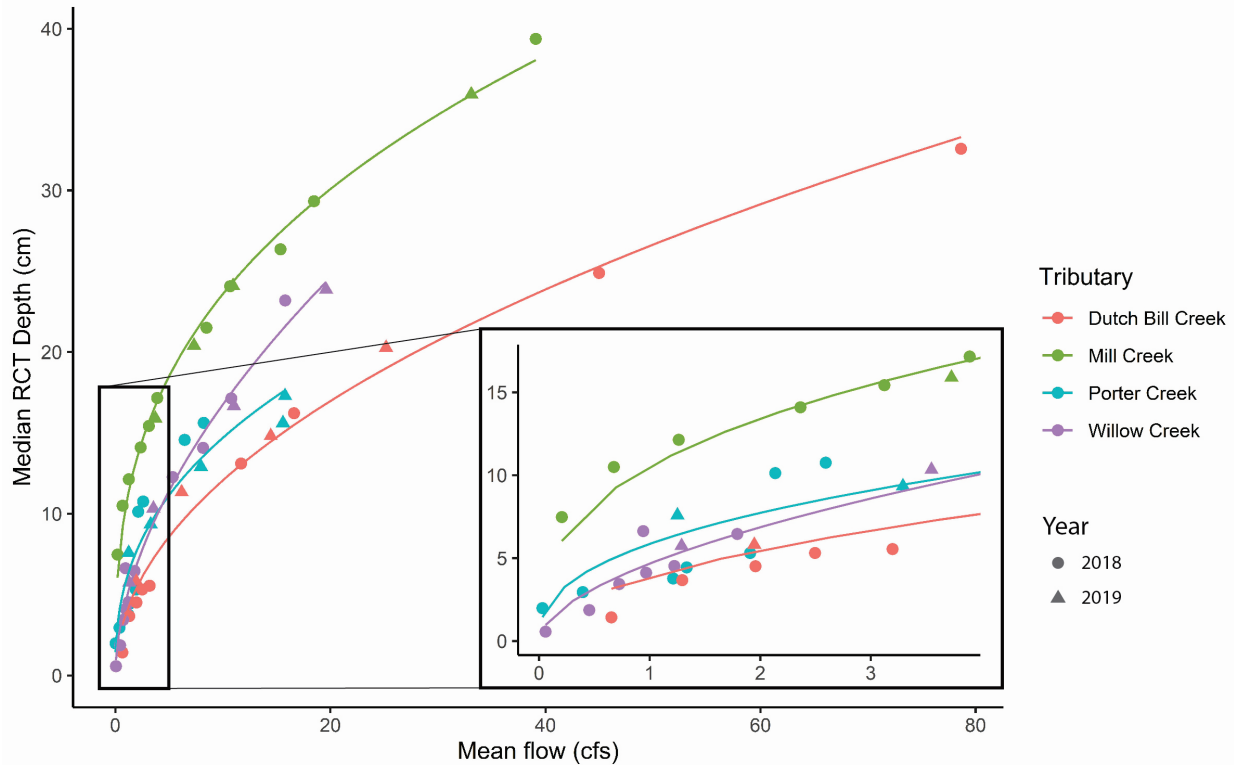
Figure 2: Riffle crest thalweg (RCT) depth-discharge rating curves for the study streams over the full range of data collected and for shallow depths (inset figure). cfs = cubic feet per second.

All streams exhibited similar seasonal streamflow patterns, due to their proximity and shared watershed characteristics. Over the study period and across all four streams, we detected 5,022 juvenile coho moving downstream. Downstream movement of smolts generally occurred during storms in early spring, as water depths rapidly increased and then receded over several days, and throughout the late spring, as water depths gradually receded over several weeks. However, streams with shallower water depths during the spring flow recession experienced an earlier cessation in outmigration detections, as water depths approached zero (Fig. 3).
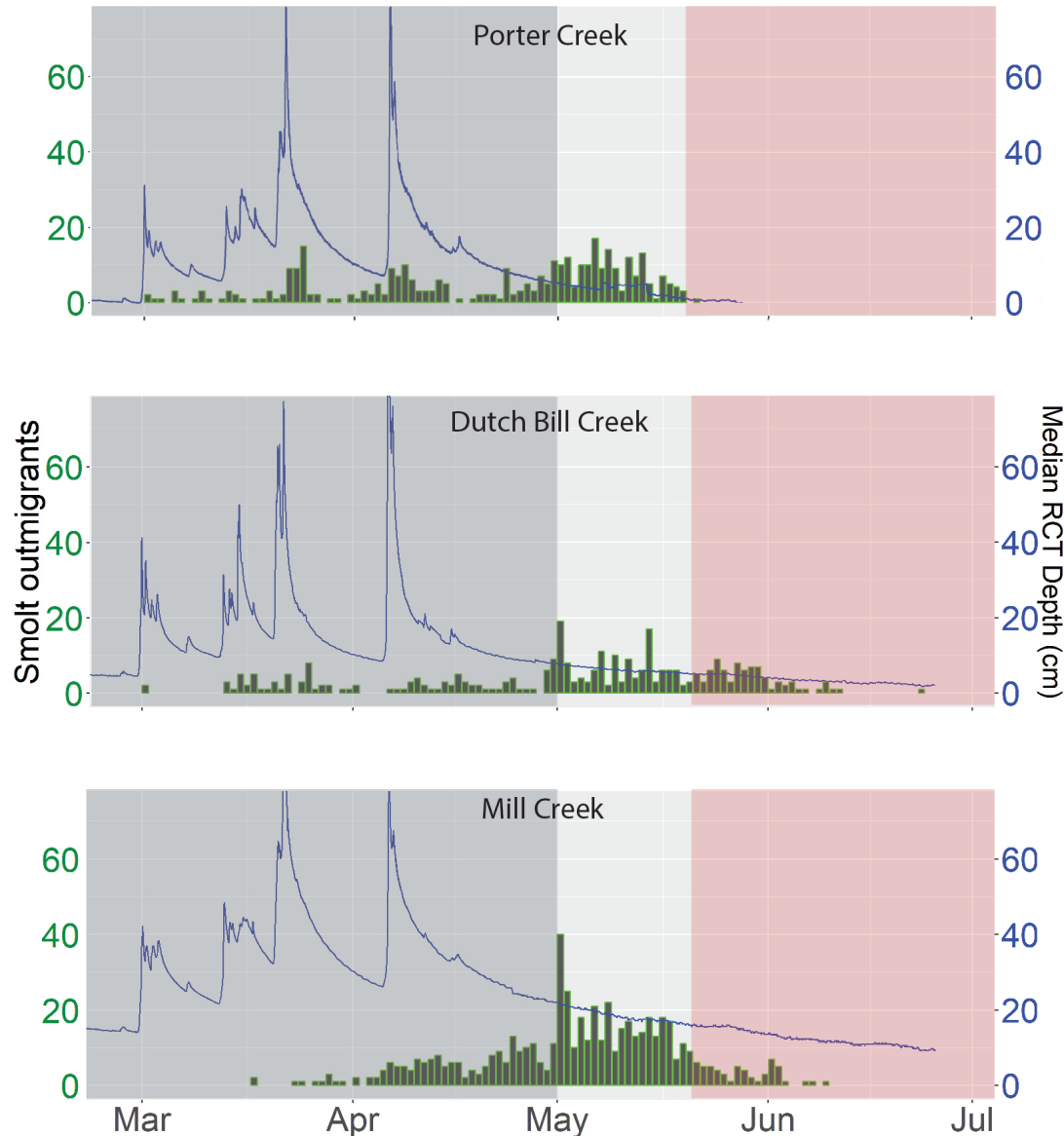
Figure 3: Daily smolt detections (green bars) and median RCT (riffle crest thalweg) depths (blue lines) available for three of four study streams, during the 2018 outmigration season (a dry year). Dark gray shading indicates the early-season outmigration not considered in this analysis. Red shading indicates the period when shallow water depths impacted Porter Creek outmigration.

RCT depths varied *throughout the outmigration period* and *during outmigration detections*. The range of median RCT depths *throughout the outmigration period* was 1.2–14.3 cm (mean 5.9 cm, CV 1.0 cm) among streams and 2.3–18.4 cm (mean 8.8, CV 0.7 cm) among years. The range of median RCT depths *during outmigration detections* was 3.8–18.0 cm (mean 9.3 cm, CV 0.7 cm) among streams and 3.8–23.6 cm (mean 12.7, CV 0.5 cm) among years (Appendix S1: Table S1). Percentiles of outmigration indicate the depths above which the 25th, 50th (median), and 75th percentiles of seasonal outmigration detections occurred. In 24 of 26 stream-years, median depths *during outmigration detections* were deeper and interquartile ranges were narrower than depths occurring *throughout the outmigration period* (Fig. 4).
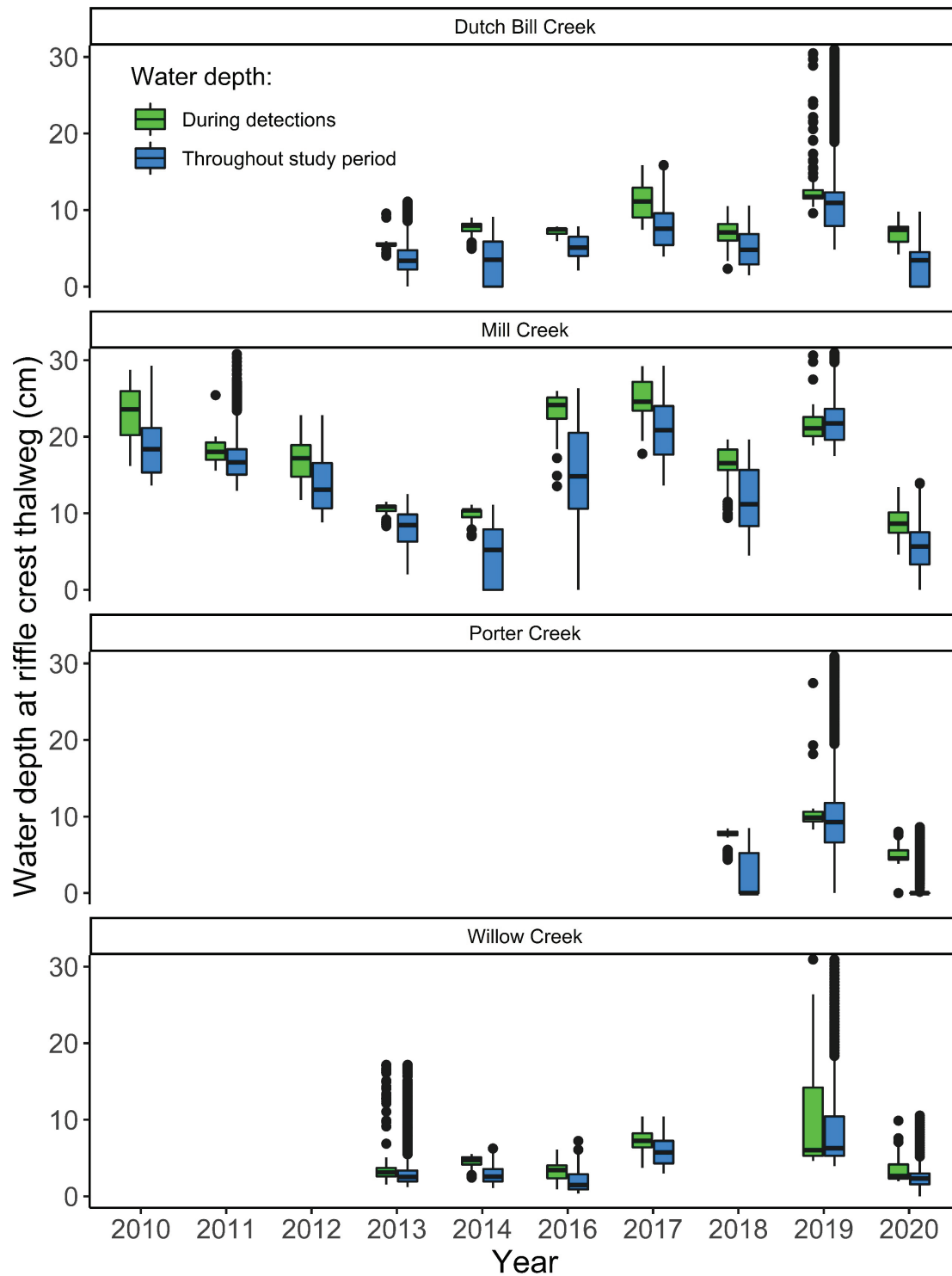
35

Figure 4: Box plots of riffle crest thalweg (RCT) water depths during outmigration detections (green) and throughout the 1 May – 3 July study period (blue). Thick horizontal lines represent the median, box top and bottom show upper and lower quartiles, ends of whiskers show 1.5 times the interquartile range, and dots are outliers.

Depth preferences

We found a significant difference between depths encountered *during outmigration detections* (habitat use) and depths occurring *throughout the outmigration period* (habitat availability), with $p < 0.001$ and an effect size of $eta^2 = 0.006$. When analyzed separately, we found that each stream also had a significant variance: Willow Creek $p < 0.001$, $eta^2 = 0.005$; Mill Creek $p < 0.001$, $eta^2 = 0.007$; Dutch Bill Creek $p < 0.001$, $eta^2 = 0.017$; Porter Creek $p < 0.001$, $eta^2 = 0.002$.

During the late outmigration period (1 May – 3 July), smolts were not detected at the shallowest RCT depths that occurred in each stream (Fig. 5). Preference curves, calculated as habitat use divided by availability, indicated that smolts rarely moved at depths below 8 cm in Mill Creek, 5 cm in Dutch Bill Creek, 4 cm in Porter Creek, and 2 cm in Willow Creek. Movement increased above these depths and peaked at different levels among streams. In Dutch Bill Creek and Willow Creek, the smolts showed the greatest preference for movement at depths above 7 cm. In Porter Creek, smolt depth preference was greatest at 4–9 cm. Peak depth preference was highest for Mill Creek, estimated above 23 cm.

Effects of shallow depths on outmigration timing

The maximum date that RCT depths reached 9.1 cm explained a high degree of variation in outmigration end date (95% cumulative seasonal outmigration date; $p < 0.01$; marginal $R^2 = 0.32$; conditional $R^2 = 0.52$) and with stronger support than the null model, based on AIC values (delta 5.68). The significant positive relationship indicated that later dates of flows falling below 9.1 cm RCT depths are associated with longer periods in which smolts are capable of out-migrating. On average, a one day increase in the *maximum date >9.1 cm depth* extends the *outmigration end date* by 0.25 days (0.11–0.40 days 95% CI) (Fig. 6). Over the range of conditions observed, an extension from 1 May to 3 July in *maximum date >9.1 cm depth* is expected to extend the *outmigration end date* 16 days: from 20 May (13–27 May 95% CI) to 5 June (28 May – 13 June 95% CI). The model with a response variable *number of days with no outmigration* has a positive but insignificant (-0.037–0.250 95% CI) relationship with *number of days below 9.1 cm* (marginal $R^2 = 0.09$; conditional $R^2 = 0.36$).
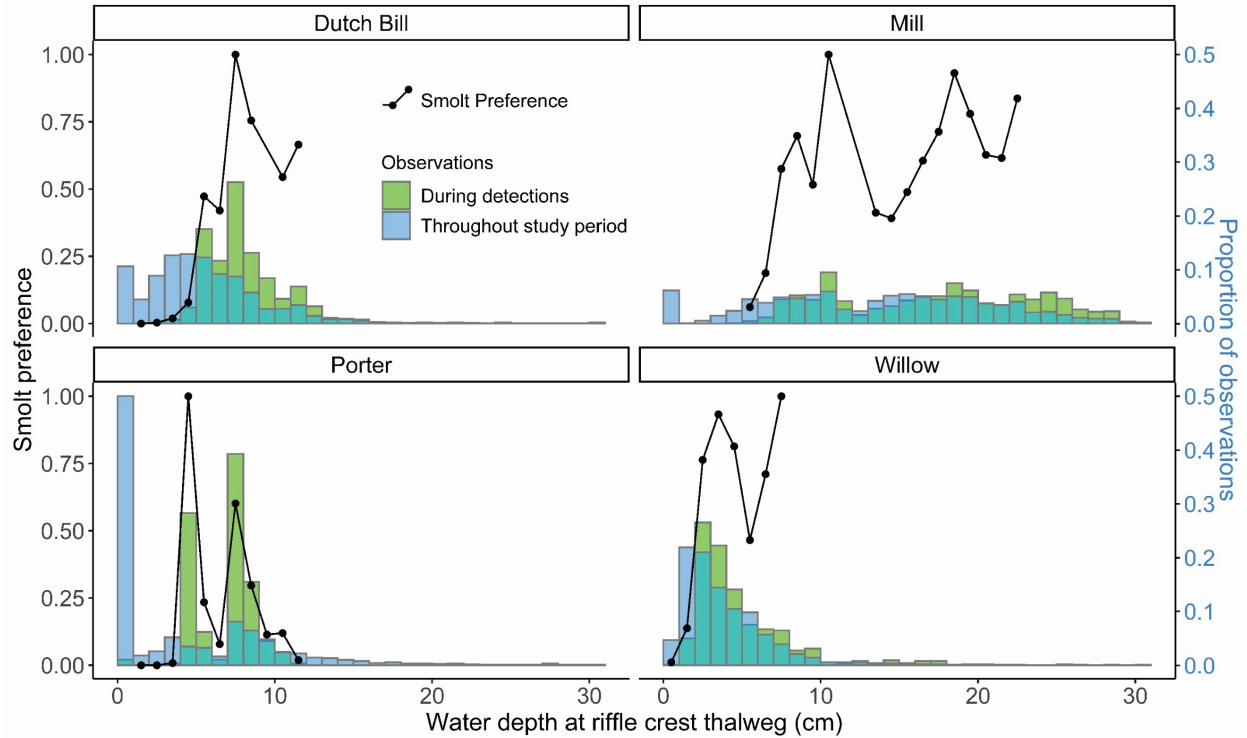
Figure 6: Partial dependence plot including model estimate (solid line) and 95% confidence interval (shading) for maximum date that RCT depth was greater than 9.1 cm vs. outmigration end date (95% cumulative seasonal outmigration) from linear-mixed effect model. Tick marks on x- and y-axes indicate observations. Conditional R^2 values include the study stream as a random effect.

Discussion

During the late outmigration period (1 May – 3 July) in California's Russian River watershed, coho salmon smolts were detected migrating over a wide range of depths in all streams and years, but consistently ceased to migrate when depths were shallowest. In most streams, little movement was observed at estimated depths below 4 cm. The exception was Willow Creek, in which movement was reduced below 2 cm. Overall, detection depths recorded in our study were shallower than expected. Avoidance of shallow depths might have occurred due to low-flow channel obstructions or adaptations related to heightened predation risk (Power, 1984) that deter smolt movement during outmigration.

Observations of smolt movement over shallow depths suggests that flow conditions only partially explain outmigration patterns and that other environmental and endogenous controls may be influencing smolt movement. For example, previous work has shown that temperature affects outmigration timing, with higher cumulative thermal experience associated with earlier outmigration of coho salmon along the North American west coast (Spence and Hall 2010), including the Russian River (Kastl et al., 2022). Thus, years with cooler winters and springs could lead to later outmigration and increase the likelihood of fish encountering shallow, low-flow conditions. There is also evidence that the outmigration of coho salmon is naturally

prolonged and in synchrony with the long and highly variable ocean upwelling period in California (Spence & Hall, 2010), which increases the chance that smolts will arrive to the ocean when food resources are plentiful. Such factors may explain outmigration during periods of low streamflow, despite the risks of stranding and predation.

Each of our study streams had unique outmigration depth preferences and a distinct range of shallow depths that smolts avoided. Our depth preference calculations (depth *use* divided by depth *availability*) minimize a potential bias toward depths that are available for longer periods. Still, we assume that seasonal phenology of outmigration (time of year when endogenous and environmental controls favor outmigration) is constant, although late-June outmigration may be less common, irrespective of water depths. Because the juvenile coho we monitored originated from the same local genetic stock, we conclude that variation in depth preferences is related to environmental factors and not local adaptation. Smolts in some streams have consistently greater depth preferences than in other streams. We suggest that channel characteristics likely explain the differences in outmigration depths among streams. For example, we found that stream reaches with narrower channels and coarser substrates, such as at our Mill Creek site (Table 1), were associated with higher depth preferences. This could be because these channel types are more difficult to navigate under shallow depths than wider, more uniform channels with smaller grain sizes.

Our modeling results also demonstrate that persistent shallow water depths, associated with streamflow recession at the beginning of the dry season, can inhibit outmigration. While low flow in Russian River tributaries has been shown to hasten the coho salmon outmigration end date (Kastl et al., 2022), the findings of the present study suggest that shallow water depth is the mechanism by which smolt movement is limited during low flow. If water depths are not sufficiently deep before the full potential outmigration season concludes, smolts likely become trapped upstream, where over-summer survival of smolts is uncommon, due to expansive stream network drying (Moidu et al., 2021). In-person observations of trapped coho smolts are made regularly after stream disconnection during drought years (Sonoma Resource Conservation District 2022). Thus, our study provides empirical evidence that shallow water depths are a significant limiting factor to smolt outmigration, although our study does not directly explore flow effects on smolt survival. We also suggest that impassable shallow water depths in the late outmigration season can have non-lethal, but significant effects on salmon populations, by contracting the outmigration window and limiting the likelihood that smolts reach the ocean during favorable upwelling conditions, which could reduce growth rates, marine survival rates, and reproductive success (Satterthwaite et al., 2014).

Management implications

Our study demonstrates the application of new methods to monitor smolt movement in streams to assess stream-specific, fish passage depth requirements. By deploying stage loggers in pools with the shallowest downstream RCTs, it is possible to obtain continuous estimates of shallow-passage depths for a channel reach. Monitoring of downstream smolt movement via PIT tags/antennas can then be coupled with depth measurements to assess the depths that fish navigate or avoid. We suggest that these methods represent an important advancement over

traditional approaches that estimate passage depths based on generic body size dimensions of salmon (Thompson, 1972). We also note that while our approach to estimate movement depths at RCTs differs from the "critical riffle method" used by the California Department of Fish and Wildlife (CDFW) to estimate passage flow requirements (CDFW 2017), our analyses indicate that the 9.1 cm minimum passage requirement used by CDFW is likely protective of smolt movement in our study streams.

As the effects of climate change become more pronounced, low streamflows in the spring and summer season are expected to further decline in coastal California streams (Grantham et al. 2018). Moreover, human water use pressures are likely to grow, particularly during periods of drought, increasing the risk of streamflow depletion. Here we showed that shallow water depths associated with low streamflow may be a significant limiting factor to the outmigration of juvenile coho salmon in Russian River tributaries. This work suggests that efforts to protect and enhance streamflow in coastal streams during the spring flow recession—such as water conservation, environmental flow protection, water collection during winter for use during spring, flow augmentation from off-channel storage (Rossi et al. in prep), and watershed restoration activities that enhance dry-season baseflow—are warranted and are likely to benefit out-migrating salmon.

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Supplement to Chapter 2

Appendix S1 contents

- Geomorphic data collection methods
- Stream stage measurement methods
- Supplemental table: outmigration depths

Geomorphic data collection methods

We characterized the channel substrate and dimensions in each of our study reaches in autumn 2018 and 2019 to relate stream characteristics with RCT rating curves and smolt depth preferences. To measure channel substrate, we conducted pebble count measurements by blindly selecting 100 substrate samples within one square meter quadrats at each RCT, selecting the first piece of substrate to come in contact with the sampler's finger each time. Pebble measurements were counted into bins, and the mean 84th percentile pebble diameter (D_{84}) was used to characterize site substrate (Table 1) (Kondolf, 1997; Wolman, 1954). We calculated slope as the mean of six gradients per stream, based on elevational differences (measured with an automatic level) and distances between every other RCT marker. We also calculated the mean channel width-to-depth ratio, based on the active width and maximum depth of the channel below the height of the active width, as measured in the field at six cross-sections per stream. Active channel elevation was determined, based on the upper elevation of the scoured channel and height of unvegetated lateral bars. Geomorphologic classification was characterized based on field observations, according to (Montgomery & Buffington, 1997).

Stream stage measurement methods

Where gauges were located more than 200 m from antenna arrays in our study reach, we performed linear regressions between discharge measurements at the gauged location and discharge measurements near the antenna to estimate continuous discharge values in our study reaches. Discharge measurements and conversions from flow to RCT depth, instead of direct stage-to-RCT depth conversions, were required because long-term continuous stage data was often measured upstream, where streamflow was frequently higher or lower than downstream study areas. Outmigrant detections and RCT measurements were made near the tributary confluence with the Russian River because fish movement detections at downstream locations are most representative of outmigration and late-season depths were shallower than upstream.

Supplemental table

Table S1: Riffle crest thalweg (RCT) depths (cm) above which outmigration occurred for specified cumulative seasonal outmigration, by stream and year. The 75th percentile RCT depth is the mean depth above which 75% of cumulative seasonal outmigration occurred. Flow to reach 9.1 cm riffle crest thalweg (RCT) depth threshold for juvenile salmonid movement is based on minimum depth for juvenile salmonid movement (Woodard & Haas, 2017) and RCT rating curves of our study.

Stream	25 pctl RCTd	50 pctl RCTd	75th pctl RCTd	Flow (m^3s^{-1}) at 9.1 cm
Dutch Bill	9.3	7.6	6.2	0.11
Mill	22.6	18	11	0.02
Porter	8	7.6	4.8	0.06
Willow	5.9	3.8	2.8	0.10
mean	11.4	9.3	6.2	0.07
CV	0.7	0.7	0.6	0.6
Year				
2010	25.9	23.6	20.2	
2011	19.2	18.0	17.0	
2012	18.9	17.2	14.7	
2013	10.4	3.8	2.9	
2014	9.5	8.0	5.7	
2016	22.6	6.9	3.4	
2017	24.5	13.4	7.7	
2018	17.5	13.6	7.8	
2019	22.3	15.5	11.5	
2020	8.8	7.4	5.1	
mean	18.0	12.7	9.6	
CV	0.3	0.5	0.6	

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Chapter 3

Accounting for temperature-stressor interactions in ecological thermal tolerance assessments of Pacific salmon

Abstract

River and stream temperatures continue to rise, due to modifications to the natural flow regime and a warming climate. As a result, there is a growing risk that water temperatures will exceed the thermal physiological tolerance thresholds of aquatic organisms, especially cold-water fishes. The threat of rising temperatures can be intensified by other ecological stressors that influence their thermal tolerance. For Pacific salmon and trout (*Oncorhynchus spp.*), such "temperature stressor interactions" (TSIs) include low food availability/production, heightened competition, poor habitat quality, disease, predation, low dissolved oxygen, and toxins. Where present, TSIs can increase the adverse effects of thermal stress on mortality, development/growth, carrying capacity, life history diversity, community structure, and reproduction, contributing to extinction risks for threatened populations. We propose a framework to assess the potential impact of TSIs on the ecological thermal tolerance of salmonid populations, including the individual impacts of each TSI and their net population-level impact. We demonstrate how information on local TSIs can be synthesized from peer-reviewed literature and expert knowledge through an assessment of a coho salmon (*O. kisutch*) population in northern California, USA. Assessment rankings of TSI extent, strength, and expert confidence can be used to estimate the relative degree to which each TSI contributes to multiple impacts on the life stage of a salmonid population. From our example assessment, TSI severity (extent * strength) was non-uniformly distributed across six impacts. The food availability TSI had the greatest severity, most severely impacting development/growth and carrying capacity. However, the impact of the habitat quality TSI on life history diversity was three times greater than that of the food availability TSI. Results from the TSI assessment can guide restoration strategies designed to reduce the influence of stressors on thermal tolerance. For example, if managers aim to prioritize mortality rate reduction, our example assessment indicates that the dissolved oxygen TSI has the most severe impacts on mortality. In addition to stressor reduction, restoration may be achieved via water temperature reduction and biophysical resilience enhancement. Lastly, the net population-level impact from our TSI framework represents the reduction from physiological to ecological thermal tolerance. Therefore, our TSI framework may help to inform the development of temperature targets to protect salmonid populations that are increasingly at risk from warming waters.

Introduction

Pacific salmonids (*Oncorhynchus* spp.) in their native ranges face a plethora of stressors that threaten several populations with extinction (Katz et al., 2013; Lichatowich, 1999). These include competition with and predation by non-native species (Nobriga et al., 2021; Reeves et al., 1987), alteration of flow regimes by dams and diversions (Crozier et al., 2020), impacts from hatcheries (Lichatowich, 1999), and disease (Richter & Kolmes, 2005). Present-day climate

change is increasing stream and river water temperatures (Ficklin et al., 2013), which may exceed the rate at which salmonids can adapt and evolve to warming water (e.g., Crozier et al. 2021), especially at the southern extent of their range in California, where temperatures already approach or exceed physiological tolerance thresholds (Michel et al., 2021). It is estimated that California may lose most runs of Pacific salmon and steelhead trout by the end of the century, if changes in management are not made (Katz et al., 2013; Moyle et al., 2017). Strategies for maintaining suitable water temperatures for salmon in a warming climate will be particularly important.

West coast Pacific salmonids, including all species and runs, evolved over time (i.e., during glacial maxima and warm periods) to colonize cold-water environments (Bernatchez & Wilson, 1998). Variations in thermal tolerance occur among species, runs, populations, sites, and life stages, due to spatial variability in habitat-forming processes, such as climate, elevation, and hydrologic regime (Fangue et al., 2006; Zillig et al., 2021). As ectotherms, water temperature is critical to salmon and steelhead physiology and ecology during all life stages. Excessive water temperature can have adverse impacts on mortality rates, metabolism, growth and feeding rates, reproductive success, development of embryos and alevins, phenology (migration, spawning, rearing, smoltification), competition (e.g. invasives and predators), disease risk, sublethal/chronic effects, and community structure (Crossin et al., 2008; Zillig et al., 2021). The thermal capacity of salmonids is governed by numerous intrinsic physiological traits and is known as the fundamental thermal physiology (Zillig et al., 2021). In laboratory experiments, fundamental thermal physiology is measured by growth rates (Marine & Cech, 2004), aerobic scope, and other indices in the absence of other stressors (Eliason et al., 2011).

Ecological thermal physiology, on the other hand, is defined as the circumscription of the fundamental thermal physiology by environmental and ecological stressors that interact with water temperature to modify a population's thermal performance (Brett, 1971; Zillig et al., 2021). The resulting ecological thermal physiology window of suitable temperatures may have steep reductions (or thresholds) in ecological fitness at the upper temperature range (Zillig et al., 2021). These interactions (hereafter, *temperature-stressor interactions* or TSIs) exist in most salmonid environments, vary by site. Each TSI can reduce the upper limit of suitable temperatures, or the ecological thermal tolerance (hereafter, *thermal tolerance*), often to a degree greater than the influence of the stressor acting independently. Existing TSIs can reduce the ability of an individual salmonid to withstand high water temperatures (EPA 2003). For example, impacts of thermal exposure may more adversely impact salmonids when they are additionally exposed to adverse biotic interactions (predation), malnutrition (low food availability), or compromised habitat structure (Adams et al., 2022; Michel et al., 2021; Webb & Erskine, 2005). The ecological thermal physiology of salmonids represents an increasingly influential component of the thermal vulnerability of salmonids (Zillig et al., 2021).

While information on TSIs may exist in the form of peer-reviewed literature, researcher/manager knowledge, and indigenous ecological knowledge, an operational framework is still needed to assess the influence of TSIs in lowering ecological thermal physiology thresholds and to consider their effects in management decisions. An assessment of TSIs can inform site-specific management by determining the *relative* degrees of TSI impacts within and

among life stages and populations. With limited resources for restoration, a TSI assessment may aid in the prioritization of TSIs to reduce via restoration, which may include targeting the ecological stressors of each TSI. For example, an assessment that demonstrates a high degree of impacts from the temperature-predator interaction TSI, relative to other TSIs, may suggest that non-native predator population management could be prioritized. Furthermore, a comparison of TSI impacts among populations may reveal, for example, the watershed in which water temperature reduction via environmental flows may dampen TSI impacts most significantly, allowing evaluation of costs and benefits to inform prioritization. Finally, the degree of deviation in ecological thermal physiology from fundamental thermal physiology may inform salmonid temperature targets – recommendations or regulations that set maximum temperatures to reduce adverse thermal impacts during specific life stages – to increase ecological thermal tolerance, and consequently strengthen salmonid population resilience in a warming world.

Here, we introduce a framework for assessing the potential impacts of temperature stressor interactions on the ecological thermal performance of individual salmonid population life stages. We attempt to answer the following questions: i) How can TSI impacts on salmonid population life stages be assessed, based on expert knowledge of TSI spatial extent, strength, and expert confidence, when quantitative data are limited? ii) How can this information be used to prioritize restoration and inform site-specific thermal targets that reduce adverse impacts of TSIs and increase the ecological thermal tolerance of salmonids? We illustrate the framework with an example of a juvenile coho salmon (*O. kisutch*) population in northern California. Using an expert elicitation process, we evaluated the spatial extent, strength, uncertainty, and impact of distinct TSIs on different life stages. We also explore how the evaluation of TSIs can be used to inform restoration strategies that limit thermal stress on salmon populations. Finally, we identify key data gaps and research needs to improve our understanding of TSIs and to guide development of management actions and regulatory standards that are protective of salmon and cold-water fishes in a warming world.

Methods

Collecting information on TSIs

Here we propose a method to assess the degree to which TSIs may alter ecological thermal tolerance for a life stage of a salmonid population. First, identify all known TSIs and list the associated impacts (i.e., mortality, carrying capacity, etc) of each TSI in their system for the salmonid life stage of interest. We provide a template of common TSIs and associated impacts (Figure 1, blue and orange ellipses, respectively) as a starting point, recognizing that not all populations will exhibit all of these TSIs and impacts, and that other populations may be subject to other TSIs and impacts not identified here. Multiple impacts often exist for each TSI (Table 1). We define TSI impacts as adverse individual or population-level effects on mortality, physiology, life histories, or community structure. Second, conduct a literature search of peer-reviewed studies, as well as reports written by agencies, non-profits, and consulting firms. Many TSI studies may have been conducted on specific salmonid species, but not conducted on other species. In some cases, TSIs may be specific to a particular species or salmonid run. Yet, in other cases, the interactions may be similar across salmonids. Therefore, it is best to start a literature search for each TSI, focused on the most specific salmonid unit (i.e. Sacramento River spring-

run Chinook). For some populations, viability assessment or life cycle modeling efforts may provide important context for understanding the relative contributions of various stressors and limiting factors. When insufficient studies exist to identify impacts, expand the literature search from population to run, then to species in the Evolutionary Significant Unit (ESU), then to the species as a whole.
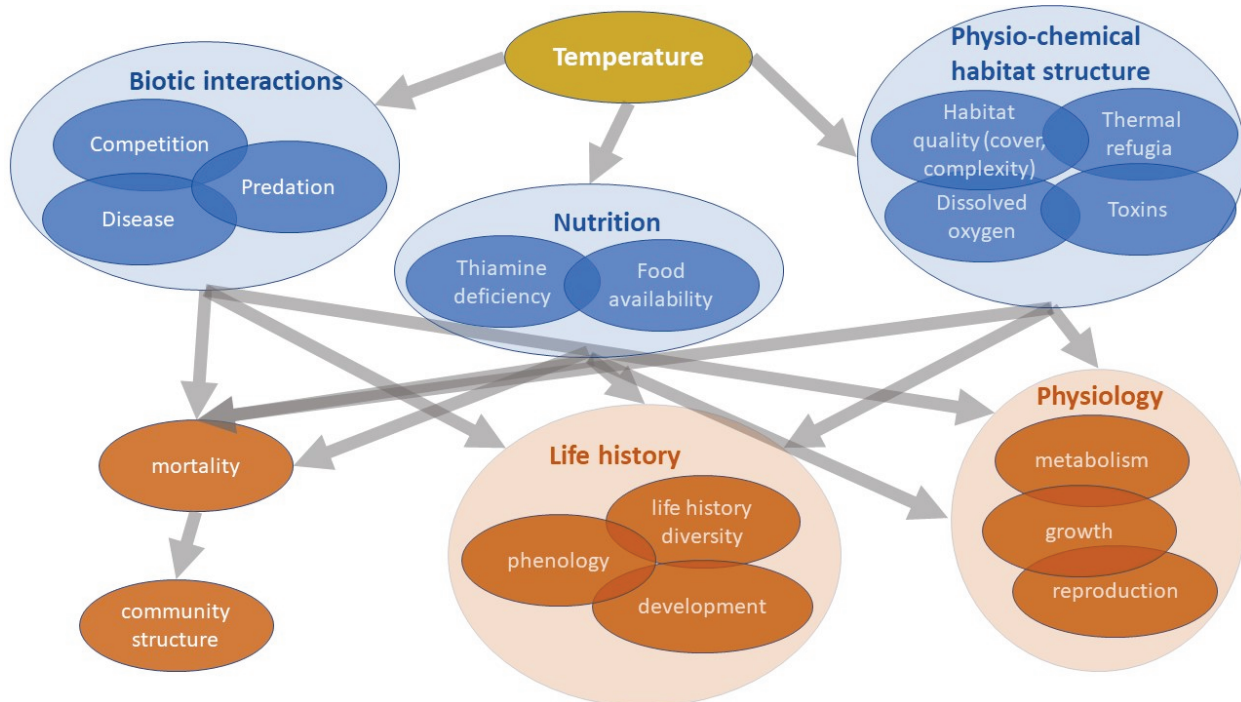

Figure 1: Possible temperature interactions with ecological stressors (blue), resulting in impacts (orange) on salmonids. Temperature can also have direct impacts on salmonids, irrespective of stressors; however, this diagram focuses only on interactions. The diagram is not exhaustive of all temperature-stressor-interactions (TSIs) and depends on the specific system of interest.

A wealth of previous studies that have found significant compounded impacts of several TSIs on ecological thermal tolerance (Fig. 1), including Zillig et al. (2021), which summarizes key mechanisms by which biotic interactions, nutrition, and physio-chemical habitat structure can each interact synergistically with temperature to alter ecological thermal physiology. More specifically, food availability is well-recognized in bioenergetics models as interacting with temperature to impact growth, including greater production of macroinvertebrate food subsidies with increasing temperature (Moyle and Cech 2004), although metabolic rates, consumption, and growth decrease as temperatures approach upper ecological thermal tolerance limits (Adams et al., 2022). Competition of juvenile steelhead with redside shiner, which affects food availability, has been shown to decrease growth rates of juvenile steelhead by 54% when reared at temperatures above 19 °C, in comparison to growth rates in the absence of redside shiner, while growth rates were independent of temperatures under the same competition levels at temperatures below 15 °C (Reeves et al., 1987).

Table 1: Key metrics evaluated via expert elicitation for a life stage of a salmonid run of concern, based on TSIs identified in the system of interest and impacts identified in existing literature. The example represents the mean values from four interview-based expert surveys.

Temperature-stressor interaction (TSI)	TSI extent	Impact	Impact strength	Confidence in impact strength	Severity
(i.e., competition, disease/parasites, predation, nutrition [thiamine deficiency], food availability, dissolved oxygen, toxins, habitat, etc)	A) Proportion of salmonid population's freshwater range affected by TSI, or B) proportion of salmonid population affected by TSI. *Scale 0-1*	(i.e., mortality, community structure, phenology, development/metabolism/growth, carrying capacity, reproduction, life history diversity {migration})	Degree of impact on salmonid individuals from the temperature-stressor interaction, irrespective of stressor impacts without temperature influence. *Scale 0-3 (0 = no recognition, 1 = low, 2 = moderate, 3 = strong impacts).*	Confidence in TSI strength. *Scale 0-3 (0 = complete suspicion with no evidence, 1 = little evidence, 2 = moderate evidence, 3 = evidence for most impacts) .*	TSI extent impact strength
Disease/parasites	0.23	mortality	1.00	1.25	0.23
		development/metabolism	1.50	1.25	0.34
		carrying capacity	0.75	0.50	0.17
					0.73
Dissolved oxygen	0.77	mortality	2.00	1.75	1.53
		development/metabolism	2.00	1.75	1.53
		carrying capacity	1.50	1.00	1.15
					4.22
Habitat quality	0.58	mortality	0.50	0.50	0.29
		development/metabolism	1.50	0.75	0.86
		carrying capacity	2.25	2.00	1.29
		life history diversity	1.75	1.25	1.01
					3.45
Food availability/production	0.86	mortality	0.75	0.75	0.65
		development/metabolism	2.00	1.50	1.73
		carrying capacity	2.00	1.75	1.73
		life history diversity	0.50	0.50	0.43
					4.53
Toxins	0.35	mortality	1.00	0.75	0.35
		development/metabolism	1.00	0.75	0.35
		life history diversity	0.50	0.50	0.18
		reproduction	0.50	0.50	0.18
					1.05
Competition	0.30	development/metabolism	1.00	1.25	0.30
		carrying capacity	1.00	0.50	0.30
		community structure	0.50	0.50	0.15
					0.75
Predation	0.60	mortality	1.50	1.00	0.90
		development/metabolism	1.50	1.00	0.90
		life history diversity	0.50	0.50	0.30
		community structure	0.75	0.25	0.45
					2.55
				Net impact	**17.28**

Impacts of several other TSIs increase in severity as a function of temperature. Parasite-based diseases can have adverse interactions with temperature, due to faster growth rates at high temperatures for some harmful fungi, such as *Saprolegnia parasitica*, and by increasing mortality rates as temperatures approach salmonid growth limits (Richter & Kolmes, 2005). Dissolved oxygen, which is critical for metabolism, decreases as a function of temperature, and low dissolved oxygen levels hinder development, decrease performance, and increase mortality (Carter 2005). Low dissolved oxygen levels also increase the toxicity of heavy metal contaminants when present (Colt et al. 1979). Predation rates of non-native fishes on cold water-adapted native salmonids often increase at temperatures above 20 °C, as activity of predators increases, due to higher physiological thermal tolerances and activity of native salmonids slows, according to bioenergetic modeling (Marine & Cech, 2004; Nobriga et al., 2021; Petersen & Kitchell, 2001; Vigg & Burley, 1991; Zillig et al., 2021). Lastly, habitat complexity, including riparian shading and large wood can cool and deepen pools, providing access to thermal refuges and protection from predators (Ebersole et al., 2003; Webb & Erskine, 2005), which can decrease other TSI impacts.

Estimating TSI strength, extent, severity & confidence

Once TSIs have been identified for each life stage of interest, assessors can evaluate the magnitude of the TSI net impact on a population. This is accomplished by assessing the *strength* and the *extent* of each TSI component. We define impact *strength* for each TSI as the degree of impacts that occur on a salmonid life history stage, as a result of interactions between stressors and temperature, excluding stressor impacts that would occur without adverse thermal temperature influences. based only on impacts that occur as a, excluding impacts of stressors that would still exist, even at low temperatures. Assign *strength* values for each impact on a scale of 0–3 (0 = no recognition, 1 = low, 2 = moderate, 3 = strong impacts). Then estimate TSI *extent*, which we define as the proportion of the freshwater range that is affected by each TSI, on a scale of 0–1. *Extent* of each TSI can be calculated by first estimating the spatial extent to which the temperature targets will be applied, based on the maximum river network area, where the salmon population life stage is present. In some states, spatial areas of salmon life stage presence have already been identified in state water quality standards, including data from the National Marine Fisheries Service for ESA-listed species in California via the Regional Waterboards, and in Oregon via Clean Water Act beneficial use designation processes. Typically, the spatial extent will cover a portion of a watershed. Next, estimate the stream network length impacted by the TSI, and divide it by the spatial extent of each salmon life stage, which yields the TSI *extent*. For spatially dynamic TSIs, such as parasites, viruses, and bacteria affecting salmonids (Lehman et al., 2020), *extent* may be more appropriately calculated, based on the proportion of the salmonid study population affected by the TSI.

The product of impact *strength* and *extent* for each impact represents the *severity*. The sum of multiple *severity* values from all TSIs represents the *net impact*, or the degree to which TSIs decrease ecological thermal tolerance. It may provide insights into developing new ecologically based thermal targets for a salmonid population. Finally, the *confidence* level of the expert assessor is useful in ranking uncertainty in impact strength (Krueger et al., 2012). For example, the assessor may assign a high level of *confidence* to a TSI impact that recent studies have repeatedly identified for the life stage and population of interest. A lower level of

confidence may be assigned to impacts that are based on studies conducted on different populations in similar environments. We assessed confidence on a scale of 0–3; 0 = complete suspicion, no evidence, 1 = little evidence, 2 = moderate evidence, 3 = evidence for most impacts. Consistency in data collection and ranking on TSI metrics among repeat studies for a given salmonid population will allow for the comparison of results over time to monitor changes in TSIs over time.

Assessing TSIs via expert elicitation

Expert elicitation can be used to complement or substitute peer-reviewed literature for populations for which data on TSI impacts are limited or gaps exist in data on TSI *strength* or *extent*. The process of incorporating expert knowledge into research studies is known as expert elicitation and can include the opinion of experts in the form of words, numbers or figures (Ayyub, 2001). When quantitative data are insufficient or unavailable, expert elicitation is often used and study-specific survey methods are developed to acquire data for the assessment of freshwater fish (Moyle et al., 2013). For our purposes, experts may include scientists, researchers, managers, monitoring teams, and indigenous and local communities to capture the range of valid scientific information. To demonstrate the aforementioned TSI assessment process using expert elicitation, we conducted structured interviews with four experts, including researchers and managers, to assess TSIs impacting the juvenile life stage of coho salmon in a Northern California watershed. Respondents preferred to stay anonymous and to have the watershed remain anonymous.

Results

Expert elicitation results from the example TSI assessment show the presence of seven distinct TSIs in the example system, including disease/parasites, dissolved oxygen, habitat quality, food availability/production, toxins, competition, and predation (Table 1). Among TSIs, mean values from expert respondents of e*xtent* ranged from 0.23 (disease/parasites) to 0.86 (food availability/production). Values reflected the proportion of the salmonid population's range affected by each TSI, except for the disease/parasites TSI *extent*, which interviewed experts determined to represent the proportion of the salmonid population affected. Each TSI had three to five impacts. Collectively, six impacts were recorded, including mortality, development/growth, carrying capacity, life history, community structure, and reproduction. Toxins was the only TSI to have five impacts. Development/growth was the only impact that had contributions from all TSIs.

Among TSIs, mean expert respondent *strength* values, represented by the sum of individual impacts, ranged from 2.5 (competition) to 6.0 (habitat quality). Among individual TSI impacts, the range of mean *strength* values for each TSI was 0 – 2.0 (maximum possible value 3.0). Among TSIs, mean expert respondent *confidence* values, represented by the sum of individual impacts, ranged from 2.25 (competition) to 4.5 (habitat quality; dissolved oxygen, food availability/production). Among individual TSI impacts, the range of mean *confidence* values for each TSI was 0 – 2.0 (maximum possible value 3.0).

The *severity* (*extent * strength*) of impacts among TSIs ranged from 0.73 to 4.53. The disease/parasites TSI had the lowest mean *severity*, impacting mortality, development/growth, and carrying capacity. The food availability/production TSI had the greatest *severity*, impacting mortality, development/growth, carrying capacity, and life history diversity over a large proportion (0.86) of coho salmon distributional extent in the watershed. The proportion of impact *severity* contributions from TSIs varied among TSIs (Fig. 2). For example, although the food availability/production TSI had the greatest *severity*, the habitat quality TSI had approximately three times greater impacts on life history diversity. Among individual TSI impacts, the minimum *severity* value of 0.17 was attributed to the impact of the disease/parasites TSI on carrying capacity, and two maximum *severity* values of 1.73 were attributed to the impacts of the food availability/production TSI on both development/growth and carrying capacity. Among impacts, development/growth had the greatest severity, and it is the only impact category with contributions from all TSIs, while reproduction had the lowest severity with contributions from only toxins.
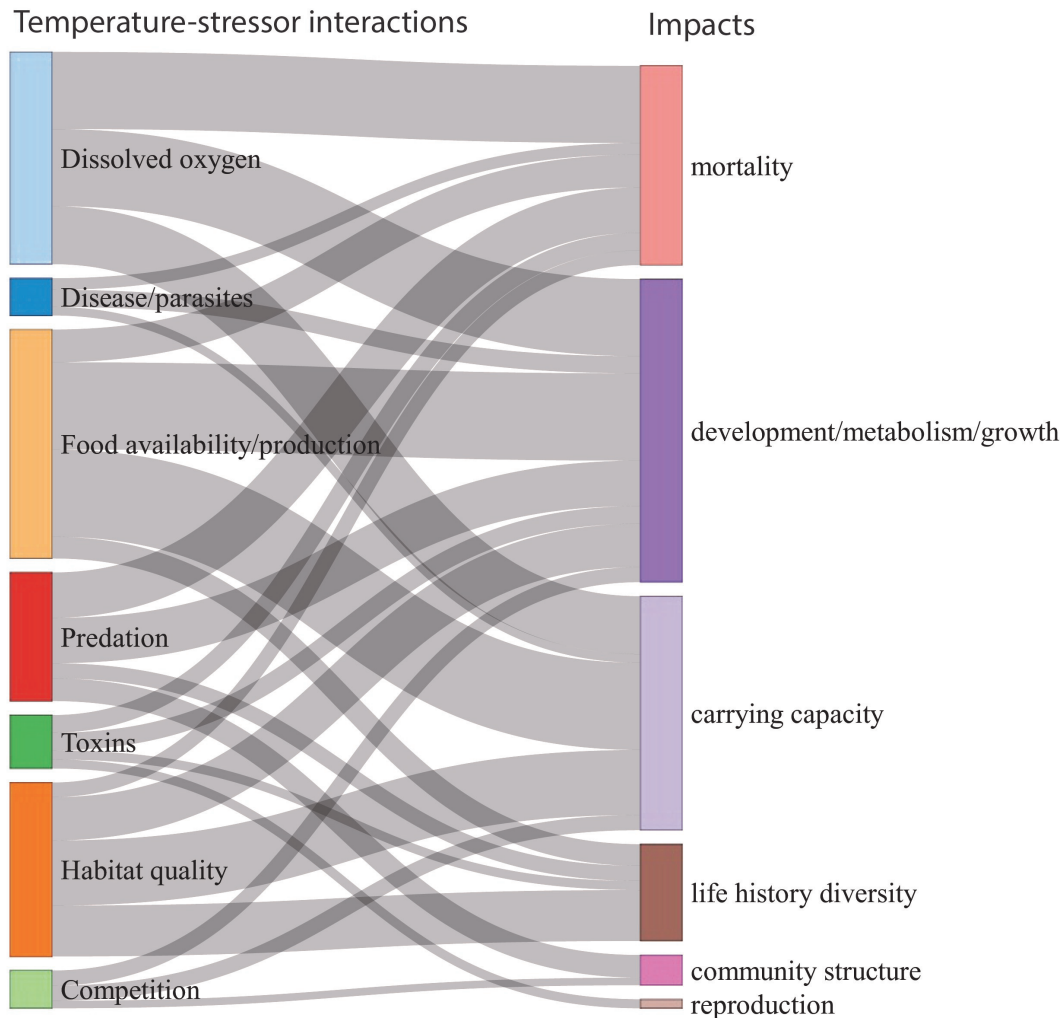

Figure 2: Sankey diagram from example expert elicitation for a coho salmon population, demonstrating the relative impacts of TSIs for a salmonid life stage. Height represents relative *severity* (*strength * extent*).

Discussion

Informing restoration

This is a first framework to use expert elicitation to consider interactions between physiological thermal tolerance and TSIs to prioritize restoration and refine the ecological thermal tolerance for life stages of salmonid populations. The universe of stressors that we provide in our approach is not meant to be exhaustive, and we acknowledge that additional TSIs in scholarly articles, gray literature, and traditional ecological knowledge may be utilized. This approach, when applied to a specific region and species, will require regionally- and species-appropriate data, drawing on existing data where available and may require professional judgment. We applied our knowledge and elicited additional information from salmon biologists in northern California to provide a hypothetical example of how temperature-stressor interactions for a salmon population could be evaluated.

Results demonstrate that when field-based data limitations exist, expert elicitation can provide a summary of current understanding on temperature-stressor interactions and their impacts for a life stage of a salmonid population. The values of TSI *extent*, *strength*, *severity*, and expert *confidence* can be used to estimate the relative (not absolute) contributions of TSIs and TSI impacts. This knowledge can be used in management practices to increase ecological thermal tolerance. Increasing ecological thermal tolerance can occur via: i) stressor reduction (i.e., non-native predator control), ii) water temperatures reduction (i.e., stream diversion reduction), and iii) protection and enhancement of biophysical resilience (i.e., phenological diversity).

Stressor reduction

Stressor reduction can target specific stressors to reduce the strength of TSIs and be achieved in several ways via existing or new restoration strategies and policies. For example, dissolved oxygen levels can be increased with environmental flows or protection of groundwater levels (Larsen & Woelfle-Erskine, 2018). Impacts of 6PPD-quinone, which is a toxic stressor that causes salmonid mortality (Brinkmann et al., 2022) and may interact with temperature, can be reduced via new state or federal policy limitations on the use of toxic chemicals in automobile tire production.
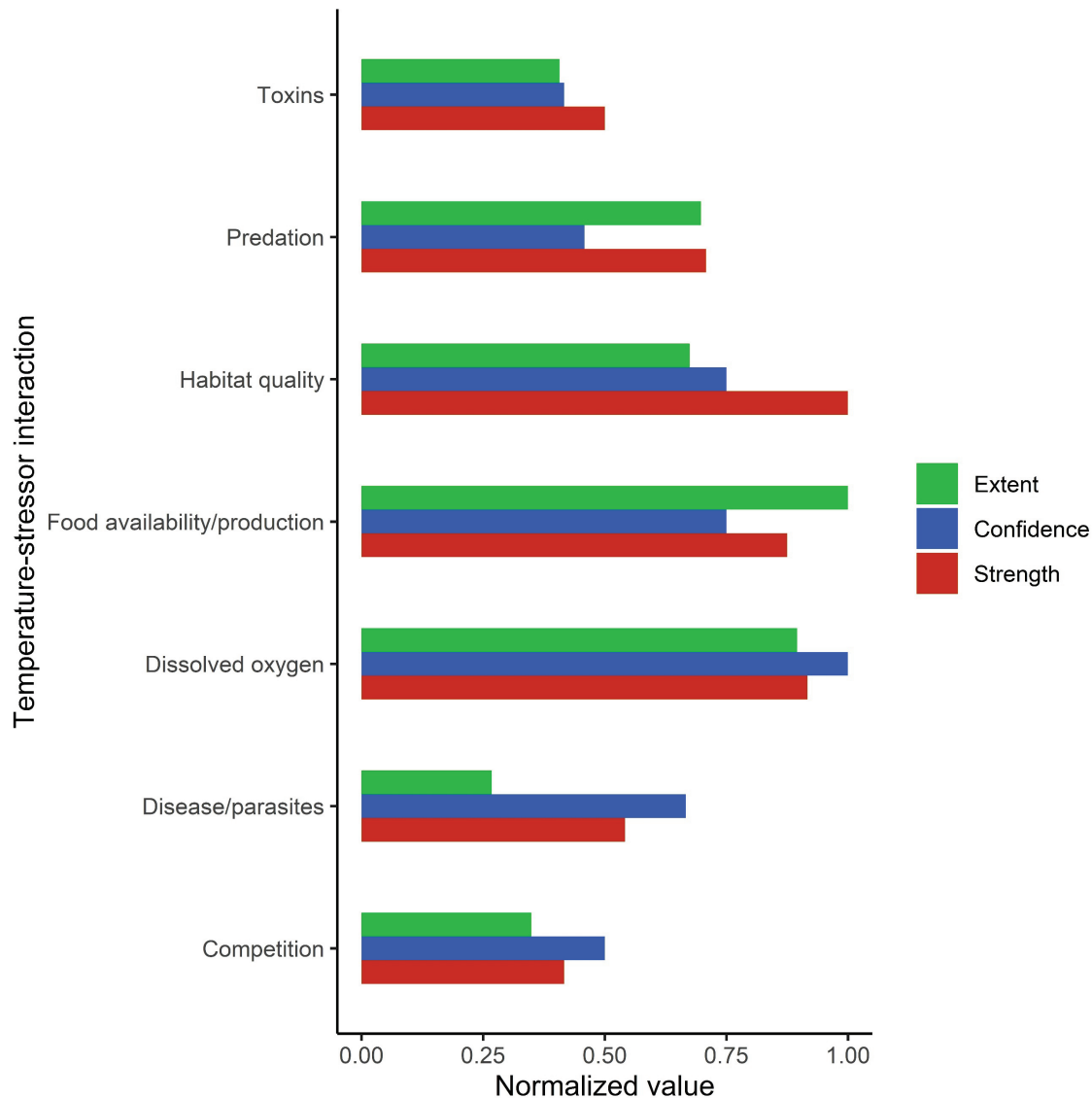
Figure 3: Temperature-stressor interactions (TSI) characteristics from an example expert elicitation, including spatial/population extent, expert confidence, and strength, for a coho salmon population. Normalized values were calculated by dividing values by the maximum category value among TSIs.

Considering the high quantity and severity of TSIs from the example TSI assessment, prioritizing stressors for reduction can increase ecological thermal tolerance, when restoration resources are limited. The metrics that we developed offer multiple methods by which to prioritize stressors. First, TSIs with the greatest *severity* (*extent * strength* in Fig. 3), which the example assessment results indicate is the food availability/production TSI, may be prioritized for stressor reduction to maximize the geographic/population proportion and impact. Restoration may include enhancing trophic pathways to increase macroinvertebrate food subsidies. Second, TSIs with the greatest *strength* may be prioritized for stressor reduction to maximize impact depth, irrespective of space/population affected. The example assessment demonstrates that the

habitat quality TSI had the greatest *strength* (Fig. 3). Therefore, microhabitat buffering may increase thermal adaptive capacity for many species (Williams et al., 2008). Restoration of habitat heterogeneity can create thermal refuges that salmonids are known to preferentially utilize, particularly during periods of daily maximum temperatures (Ebersole et al., 2001, 2003). Third, TSIs with the greatest *confidence* may be prioritized for stressor reduction to maximize certainty in ecological thermal tolerance benefits. Dissolved oxygen had the greatest level of expert *confidence* and the greatest contribution to mortality from the example assessment. Therefore, increasing dissolved oxygen levels may be a restoration priority. Salmon fry are known to preferentially select stream reaches in Mediterranean climates with relatively high dissolved oxygen levels, associated with significant groundwater inflow (Larsen & Woelfle-Erskine, 2018), which can be maintained via groundwater pumping reductions. Fourth, TSIs with either the greatest or lowest *extent* may be prioritized for stressor reduction. For example, disease/parasites may be most manageably targeted while their *extent* is low before the disease/parasites spread. Lastly, prioritizing TSIs with a high combination of *severity* and *confidence* values can be used to select restoration actions that increase ecological thermal tolerance. In this case, the example expert elicitation shows that dissolved oxygen, food availability/production, and habitat quality have the greatest impacts (Fig. 4A).
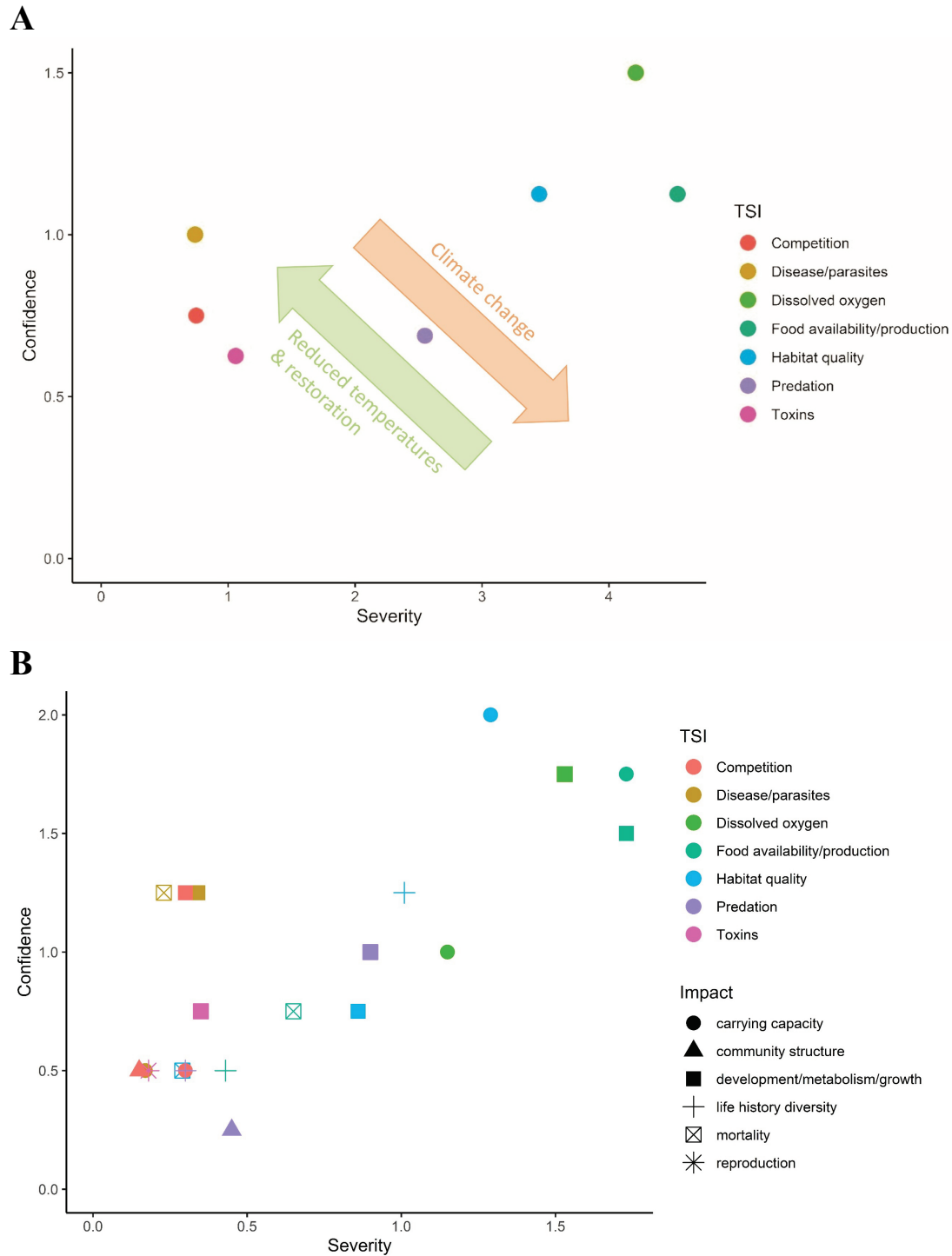
Figure 4: Plots show TSI impact severity (strength * extent) vs. assessor confidence results from the example TSI assessment process per: **A)** TSI, based on the sum of impact severity values for each TSI, and **B)** individual impacts of each TSI. Arrows represent the anticipated direction that points of future TSI assessments are expected to migrate, as TSI impact severity and assessor confidence are expected to respond to climate change and restoration.

The proposed expert elicitation process also provides an opportunity to use preexisting impact reduction goals such as those derived from population viability assessments or life cycle modeling (Jorgensen et al., 2021). These can then be used to inform the prioritization of TSI stressors for reduction. For example, mortality impacts may be of greater concern for an endangered population than a healthy population, in order to prevent extirpation. Assessment results reveal that mortality has the greatest contributions from the dissolved oxygen TSI, which may be prioritized for stressor reduction. On the other hand, life history diversity impacts may be of greater concern for a healthy population, which results reveal has the greatest contributions from the habitat quality TSI. Parsing out TSI severity and confidence by individual impacts yields insights into more specific restoration prioritization options, particularly for systems in which life stage bottlenecks are pronounced (Fig. 4B). For example, development/growth may be a priority to increase survival rates of smolt outmigrants upon ocean entry, in which case dissolved oxygen and food availability appear to have the highest combined confidence and severity values.

All assessment results can similarly be compared among multiple assessments, if the same data collection methods and the same expert judgments are used. Moreover, the *net impact* of TSIs can be compared among populations and life stages to prioritize investment in resources for restoration. Assessment of TSIs and restoration can be an iterative process. Stressor reduction restoration may decrease TSI *severity* and increase expert *confidence* (Fig. 4A), as experts learn more about TSI responses to restoration. Climate change may be having the reverse effects, increasing TSI severity, as global temperatures rise. Meanwhile, expert *confidence* may decrease, as climate change causes the probability of co-occurring warm-dry conditions to rise (Diffenbaugh et al., 2015), increasing interannual variability in temperature, and increasing expert uncertainty in TSI impacts during a given year. Still, the positive correlation between confidence & severity from example expert elicitation data suggests that the severity of TSIs that are less apparent to experts, represented by low confidence (Fig. 4), may be underestimated.

Water temperature reduction
Reduction of water temperatures will presumably lower the *strength* of TSIs by reducing the strength of temperature in interacting with stressors, thereby increasing ecological thermal tolerance. More natural flow regimes, functional flows, and natural thermal regimes support water temperatures of the hydroclimatic region to which native salmonids have adapted (Olden & Naiman, 2010; Poff et al., 1997; Yarnell et al., 2015). Several restoration strategies can be used to decrease temperatures, which may be stream or river-dependent. Environmental flows via diversion reductions and more strategic dam releases can increase flow magnitude, thereby reducing water temperatures, particularly during the summer months when solar radiation levels are high and impactful in shallow rivers. Increasing riparian vegetation and canopy cover of streams can also reduce water temperature (Justice et al., 2017), thereby having the potential to restore salmonid populations via TSI severity reductions. Groundwater recharge can also help in reducing instream temperatures.

Moreover, reducing water temperatures can also directly reduce the strength of *stressors* in interacting with temperature. For example, competition by non-native species that are not adapted to the local, natural thermal regime can be reduced under natural flow regime (Lytle & Poff, 2004), thereby reducing the severity of the competition TSI. Similarly, naturally high flows during the onset of the spring flow recession in California increase dissolved oxygen levels (Patil et al., 2022), reducing the dissolved oxygen TSI severity relative to impaired streams. Naturally high flows also submerge a diversity of habitat types in stream channels (Poff et al., 1997), reducing severity of the poor habitat quality TSI.

Biophysical resilience

Strength of TSIs can additionally be lowered when the salmonid population resilience and the capacity of the biophysical system (the watershed) to respond to restoration efforts are high. A gaining stream that is connected to the groundwater table may retain environmental flow augmentations and maintain lower temperatures than a losing stream that is disconnected from groundwater contributions. Species and population-level resilience factors can also increase restoration responses in raising ecological thermal tolerance. Populations with life history diversity, plasticity, high capacity for adaptive response may be most resilient. While thermal physiological stress impacts are realized at the individual level (albeit often multiplied across individuals in a population), genetic and phenotypic diversity can build resilience at the population level. Resilience factors may include life history diversity, inbreeding susceptibility, dispersal/colonization (straying) potential, population dynamics, a strong portfolio effect, and phenological diversity (Schindler et al., 2015; Williams et al., 2008).

Potential Additional Use of TSIs

The use of TSIs is applied in this paper primarily to ecological restoration. TSIs, and the broader concept of temperature ecological interactions, potentially could also be applied to other aspects of aquatic systems management, such as the development of temperature targets, including water quality criteria. The accuracy of temperature targets can be improved by including field-based information, including temperature ecological interactions, in their derivation.   For instance, if a TSI adverse impact score has a high magnitude, indicative of reduced ecological thermal tolerance, then a lower temperature criterion for that location may be needed to offset the stress of those high TSI adverse impacts. Hence, investigating the use of TSIs in determining water quality targets may be a relevant follow-up application to this study.

Conclusion

We find that our framework is a useful tool to prioritize restoration that reduces TSI impacts, and it is a necessary step towards the development of site-specific temperature targets. Based on the current state of existing studies, it is challenging, yet critical, to isolate TSI impacts from stressor impacts. Expert elicitation can fill this research gap to facilitate restoration and to avoid setting water temperature targets that exceed ecological thermal tolerance. The simple, proposed expert elicitation process is recommended when data on TSI impacts are commonly unavailable, since expert opinion introduces the opportunity for the introduction of biases and varying perceptions of TSI metric ranking values. Furthermore, the proposed framework assumes that TSI impacts are additive, although further interactions among TSIs may have non-

linear cumulative impacts. Future research is needed to investigate how multiple TSIs may collectively interact to alter ecological thermal tolerances of salmonids. Testing the assessment approach for multiple population life stages, utilizing a higher number of experts, may refine the accuracy of the TSI assessment approach in identifying the degree to which TSIs reduce ecological thermal tolerance of Pacific salmonids.

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Conclusion

In this dissertation, I explored the impacts of low flows and rising water temperatures on salmonids at the frontlines of a warming climate and human water use pressures. I demonstrated that springtime streamflow and water temperature are key drivers of outmigration timing, with potential for drought to cause phenological mismatches, for an endangered coho salmon population at the southern extent of the species range. I evaluated whether water depth thresholds exist and could prevent downstream movement of juvenile salmon, showing that outmigration indeed ceases when shallow water depths are reached. Considering the nascent field of research on temperature-stressor interactions, I developed a framework to help practitioners assess temperature-stressor interactions and use their assessment results to inform management and policy that can prevent adverse population-level effects on salmonids.

As I described in Chapter 1, hydrologic conditions at the origin of a migration path for a migratory fish species have profound impacts on key migration attributes. Drought and human water use shortened the outmigration season and hastened the outmigration end date, which could lead to low cohort survival rates and further threaten an already endangered population. The controls of streamflow and water temperature on this newly discovered life cycle bottleneck provide insights to managers and policymakers about opportunities to potentially increase marine survival rates by setting minimum mean flow standards and cooling water temperatures via groundwater protection and riparian vegetation. Still, future research is needed to investigate whether earlier and contracted outmigration windows affect marine survival rates, by tracking interannual adult return rates. While it is expected that both drought and human water use (i.e., stream diversions and groundwater extraction) affect outmigration, data on human water use are often not readily available. Thus, improved access to water use data would aid researchers in developing a more precise understanding of how the timing and amount of human water withdrawals affects streamflow, potentially informing solutions to water management that better balance human and ecosystem needs.

Chapter 2 demonstrates that hydrologic thresholds, namely specific shallow water depths, exist in controlling the outmigration of juvenile salmon. While such a threshold is a key determinant of outmigration during drought conditions, the exact water depths at which salmon prefer to migrate vary by stream. Geomorphology and other environmental factors are likely to influence water depth preferences. The method we explain of measuring water depths at riffle crest thalweg locations allows local managers to determine site-specific water depth thresholds, which can be used as criteria to optimize human and environmental water use in ways that reduce adverse impacts on native salmonids. However, in the absence of resources to conduct site-specific studies using our method, our findings show that existing, broadly applicable water minimum depth recommendations are still helpful in significantly extending the end date of outmigration, a potentially important factor in controlling marine survival rates. Future research is needed to explore the extent to which cessations in outmigration below specific depth thresholds are associated with upstream entrapment of juveniles and shifts in outmigration timing.

In Chapter 3 I develop an assessment framework to guide practitioners in assessing how water temperature interactions with ecological stressors may reduce the thermal tolerance of salmonids. Having recognized the variability in hydrologic thresholds from the previous chapters, the tool offers an opportunity to use local knowledge and information to develop a site-specific understanding of temperature thresholds. Furthermore, the framework helps to prioritize restoration actions, such as non-native predator removal and instream flow protections. The framework also represents an important step towards developing site- and population-specific temperature criteria. While studies on specific temperature-stressor interactions that were conducted other salmonid populations should be considered, the tool may also be used to fill data gaps in local studies by using expert elicitation. In fact, the simple expert elicitation process may illuminate priorities for peer-reviewed studies on specific temperature-stressor interactions. Experts indicated low confidence in disease, competition, and predation TSIs, suggesting that further field-based research in these TSIs may improve the accuracy of future expert elicitation. Moreover, future research to investigate how multiple TSIs may interact in combination to modify ecological thermal tolerances of salmonids is needed to accurately develop site-specific thermal criteria.

Together these chapters reveal specific impacts that receding streams and rising water temperatures have on an endangered migratory salmonid species near the southern-most extent of its range. Heightened drought impacts that California coho salmon are currently experiencing may be a precursor to similar impacts that populations to the north may experience, as climate change continues. Exacerbated by local human water use, unprecedented hydrologic conditions push migratory aquatic species towards thresholds in conditions to which they have not evolved. Our findings shed light on the hydrologic mechanisms, such as shallow water depths, that adversely impact salmonid juveniles and populations. With a new understanding of how streamflow, water depth, and water temperature affect outmigration, our research shows that minimum depth requirements support migration and can prevent the life cycle bottleneck from threatening salmonid populations. Furthermore, our research shows that hydrologic and temperature thresholds vary among populations and sites. Therefore, the approaches and assessment framework that we introduce can be used to efficiently gather data and expert knowledge to implement instream flow standards, restoration, and thermal criteria that will build resilience of salmonid populations. As climate change continues, our techniques can contribute to optimizing environmental and human water uses, providing co-benefits, and preventing ecological thresholds of migratory aquatic species from being reached.