Received: 21 March 2025 | Accepted: 13 May 2025

DOI: 10.1002/eap.70070

ARTICLE

ECOLOGICAL APPLICATIONS
ECOLOGICAL SOCIETY OF AMERICA

Facilitated migration could bolster migrant passage through anthropogenically altered ecosystems

Benjamin P. Burford[1,2] | **Jeremy J. Notch**[1,2] | **William R. Poytress**[3] | **Cyril J. Michel**[1,2]

[1]Institute of Marine Sciences' Fisheries Collaborative Program, University of California, Santa Cruz, Santa Cruz, California, USA

[2]Fisheries Ecology Division, Southwest Fisheries Science Center, National Marine Fisheries Service, National Oceanic and Atmospheric Administration, Santa Cruz, California, USA

[3]Red Bluff Fish and Wildlife Office, U.S. Fish and Wildlife Service, Red Bluff, California, USA

Correspondence
Benjamin P. Burford
Email: bburford@ucsc.edu

Funding information
Bureau of Reclamation, Grant/Award Numbers: R18AC00039, R21AC10455, R20PG00061

Handling Editor: Angee N. Doerr

Abstract

Anthropogenic habitat change frequently outpaces the adaptive capacity of migratory taxa, placing many species and populations at risk of extirpation or extinction due to the mismatch of natural migration phenology and suitable conditions. While dynamic protection can greatly benefit migratory species, it is contingent on the flexibility of relevant management actions. For regulated ecosystems where advanced management planning is required, we present a new framework—facilitated migration—for actively matching natural migration phenology with suitable conditions for successful migrant passage. Using a case study of juvenile Chinook salmon (*Oncorhynchus tshawytscha*) oceanward migration in the Sacramento River, a major bottleneck to the recovery of imperiled populations in California, we show how the conditions associated with migration preparation, migration initiation, and successful migrant passage could be regulated to benefit migrants. Thermally shifted preparation, flow pulse-mediated initiation, and passage protection via increased flow, all accomplished by controlling the release of water from storage reservoirs, could increase the number of natural-origin Chinook salmon populations successfully migrating to the ocean by 43%–479% compared to the status quo management scenario. To further inform expected outcomes, we find that the temporal scope and diversity of juvenile salmon lifestages studied via acoustic telemetry should be expanded, and that the range of flows and flow changes that juvenile salmon experience should be increased. Facilitated migration works by synchronizing migration—thus, a prudent course of action when implementing this strategy would be to favor event quality over event quantity. In forcing scientists and managers to critically evaluate how migrations can be supported and manipulated, facilitated migration will help migratory species persist in anthropogenically altered ecosystems.

KEYWORDS
anthropogenic change, conservation science, ecosystem management, hydrology, migration ecology, salmon

---

INTRODUCTION

Many migratory taxa confronted with global environmental change and local anthropogenic habitat change face uncertain futures. Ecological networks, time-area closures, and threat mitigation can be incorporated into management plans to support natural migrations (Allen & Singh, 2016; Oestreich et al., 2020). When implemented appropriately, these dynamic management strategies can cost-effectively balance the conservation of natural migrations and human activities (Hausner et al., 2021; Reynolds et al., 2017). For example, dynamic protection of stopover foraging habitat (Hassrick et al., 2022; Phillis et al., 2018), a critical resource for long-distance migrants, is associated with greater utilization by feeding shorebirds (Golet et al., 2018) and predicted to reduce the mortality of whales due to ship strikes (Hausner et al., 2021).

Unfortunately, some migratory pathways have become anthropogenically altered to the extent that migration success is increasingly improbable. This could occur when habitat change has outpaced the adaptive capacity of migratory populations, resulting in a mismatch of migration phenology and suitable environmental conditions (McNamara et al., 2011; Stenseth & Mysterud, 2002). For example, in the highly altered Sacramento-San Joaquin River watershed of North America, as little as 0%–3% of juvenile Chinook salmon (*Oncorhynchus tshawytscha*) survive the migration from rivers to the ocean (Buchanan et al., 2018; Michel, 2019; Michel et al., 2015)—in part due to a mismatch of migration phenology with altered flow regimes (Michel et al., 2021; Sturrock et al., 2020). While rare phenotypes may allow some migratory species to persist under global environmental change (Cordoleani et al., 2021), habitat modification will likely result in the failure of even the most resilient populations if pertinent measures are not taken.

In some systems, anthropogenic changes offer an opportunity to alter ecosystems in favor of migrants (Golet et al., 2018; Reynolds et al., 2017). However, political and economic constraints on managers can stifle the implementation of dynamic management. For example, dams and associated reservoirs in the Sacramento-San Joaquin River watershed could release water to opportunistically provide more suitable conditions for Chinook salmon rearing and migration (Daniels & Danner, 2020; Michel, 2019; Michel et al., 2021, 2023; Pike et al., 2013). Yet, water demand for agricultural and municipal use largely dictates water release schedules (Gartrell et al., 2017; Reis et al., 2019), which are often set far in advance once water availability is determined (Mount et al., 2017). Such constraints make it nearly impossible to dynamically alter flows—instead, precise knowledge of wildlife requirements must be determined so they can be incorporated into watershed plans and resultant release schedules (Mount et al., 2017).

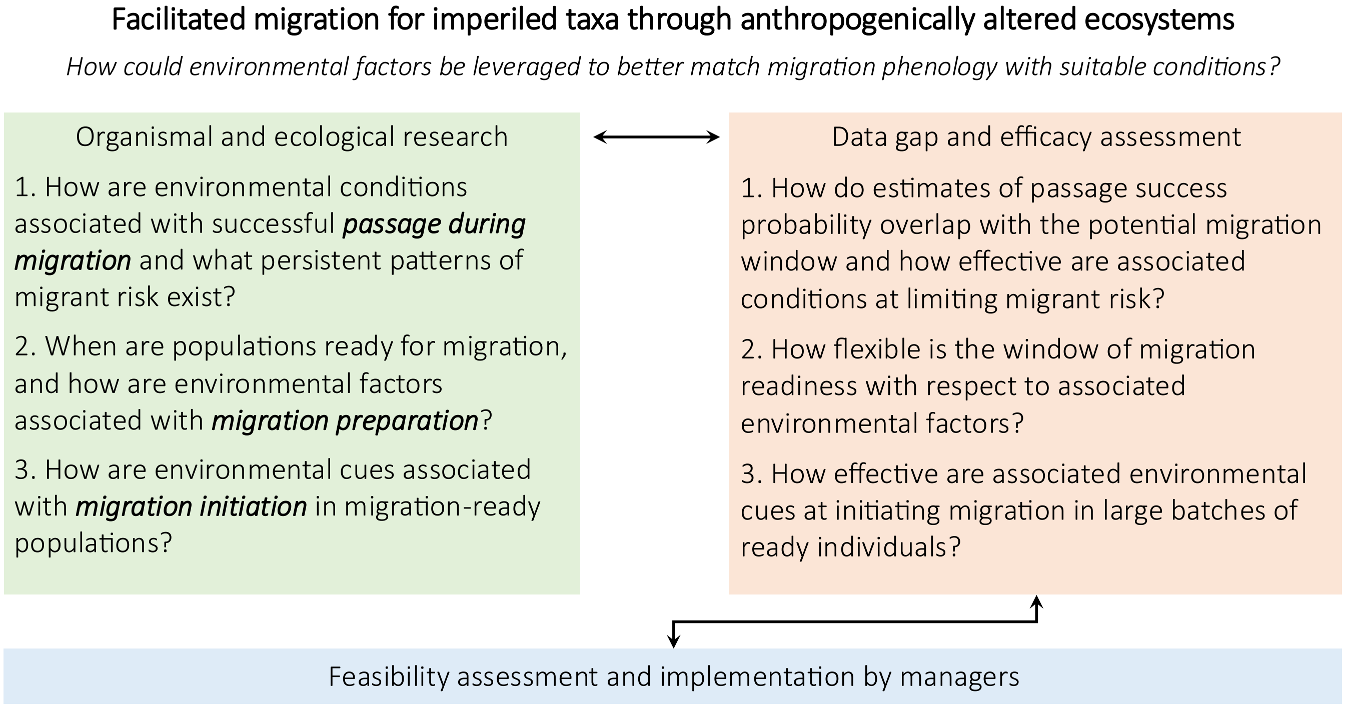
To make movement ecology more likely to be incorporated into habitat management plans (Fraser et al., 2018), we present a framework for implementing facilitated migration for migratory species conservation (Figure 1). Dynamic management strategies involve predicting when migratory species will utilize a given habitat to effectively implement conservation measures (Hausner et al., 2021; Hazen et al., 2017). In contrast, facilitated migration involves the deliberate triggering of migration to better match migration phenology with suitable conditions, and to provide more suitable conditions while migrations are underway (Figure 2). Facilitated migration will be especially relevant in degraded systems with near-irreversible land use changes and fundamentally altered environmental regimes where managers face competing demands between humans and migratory taxa for limited resources. We caution against the application of this framework to mitigate for increased exploitation of intact systems that currently support functional migrations.

Facilitated migration leverages associations between environmental conditions and three phases of migration: (1) preparation, or the development of relevant traits in advance of the journey ahead, (2) initiation, or the mass movement of migrants in response to environmental cues, and (3) passage, or successful transit through the migratory route (Dingle, 2014). Using a case study, we present a guide to this framework, revealing how it informs both management strategies and future research directions. This involved fitting three sets of models corresponding to the three phases of migration outlined above, and then using these models to simulate how controlled adjustments to environmental conditions may increase the number of successful migrants.

CONCEPTUAL FRAMEWORK

To increase the number of migrants that survive (Y_{ms}) out of the number of individuals that initiate migration (Y_m), facilitated migration requires an understanding of how environmental factors (E) are involved in the timing of migration preparation (T_p), Y_m, and successful migrant passage probability (ϕ_s), and a system within which such factors can be temporarily manipulated in the favor of the migratory species. While empirical research in a given study system should resolve the functional forms of the associations, four equations provide a foundation for applying facilitated migration across study systems (Equations 1–4).

First, to maximize Y_{ms}, both ϕ_s and Y_m must be simultaneously increased. While comparable changes to ϕ_s or Y_m should have similar effects on Y_{ms} (e.g., either



Facilitated migration for imperiled taxa through anthropogenically altered ecosystems

How could environmental factors be leveraged to better match migration phenology with suitable conditions?

Organismal and ecological research

1. How are environmental conditions associated with successful ***passage during migration*** and what persistent patterns of migrant risk exist?
2. When are populations ready for migration, and how are environmental factors associated with ***migration preparation***?
3. How are environmental cues associated with ***migration initiation*** in migration-ready populations?

Data gap and efficacy assessment

1. How do estimates of passage success probability overlap with the potential migration window and how effective are associated conditions at limiting migrant risk?
2. How flexible is the window of migration readiness with respect to associated environmental factors?
3. How effective are associated environmental cues at initiating migration in large batches of ready individuals?

Feasibility assessment and implementation by managers

FIGURE 1 Workflow for facilitated migration. Migrations often progress sequentially through the three phases: preparation, initiation, and passage. However, resolving patterns of passage during migration is fundamental to guiding potential management actions involved in migration preparation and initiation. We therefore present a conceptual workflow and case study example in this order.

doubling ϕ_s or Y_m results in a doubling of Y_{ms}), if one of the independent variables approaches zero, increases to the other will be of little value (Equation 1).

$$Y_{\mathrm{ms}} = \phi_s Y_m \tag{1}$$

Second, Y_{ms} depends on when and how E are altered because ϕ_s is unlikely to improve if E are already suitable, managed shifts in E are inadequate to overcome unsuitability, or Y_m is very low. Accordingly, time (T)—which, depending on the migration, could be time of day, year, etc.—could have an influence on ϕ_s that is distinct from (or interacts with) E. In addition to E and T, migrant condition (C_m) and migration distance (D_m) should also influence ϕ_s (Equation 2). For example, migrants in better condition with shorter migrations might have greater ϕ_s than those in poorer condition with longer migrations.

$$\phi_s = f(E, T, C_m, D_m) \tag{2}$$

Third, Y_{ms} might further depend on when and how E are altered because Y_m is unlikely to increase if managed shifts in E are applied outside of when populations are prepared to migrate, or if the size of the migratory population (N_m) is relatively small. Thus, E, T_p, and N_m should all directly affect Y_m, yet their relative influence might depend on the state of the study system (Equation 3). For instance, in systems where E vastly differs from historical conditions to which migrations have evolved, relevant alterations to E could have comparable effects as T_p or N_m on Y_m. Finally, if observing migration initiation causes ready individuals to initiate migration after some time lag (k), then Y_m could additionally depend on the number of time-lagged migrants (Y_{mk}).

$$Y_m = f\left(E, T_p, N_m, Y_{\mathrm{mk}}\right) \tag{3}$$

Fourth, substantially advancing or delaying Y_m to improve Y_{ms} would only be possible in populations that exhibit responsiveness of T_p to E (Equation 4) (an exception being the release of captive-raised populations into the wild). Accordingly, T_p should depend on both E and migratory population (P_m), the latter encompassing any population- or lifestage-specific timings of natural migration. Notably, for P_m that have relatively large windows over which they are naturally prepared to migrate (i.e., large range of T_p), some flexibility in temporally controlling Y_m to better align migrations with higher ϕ_s could occur without altering T_p.

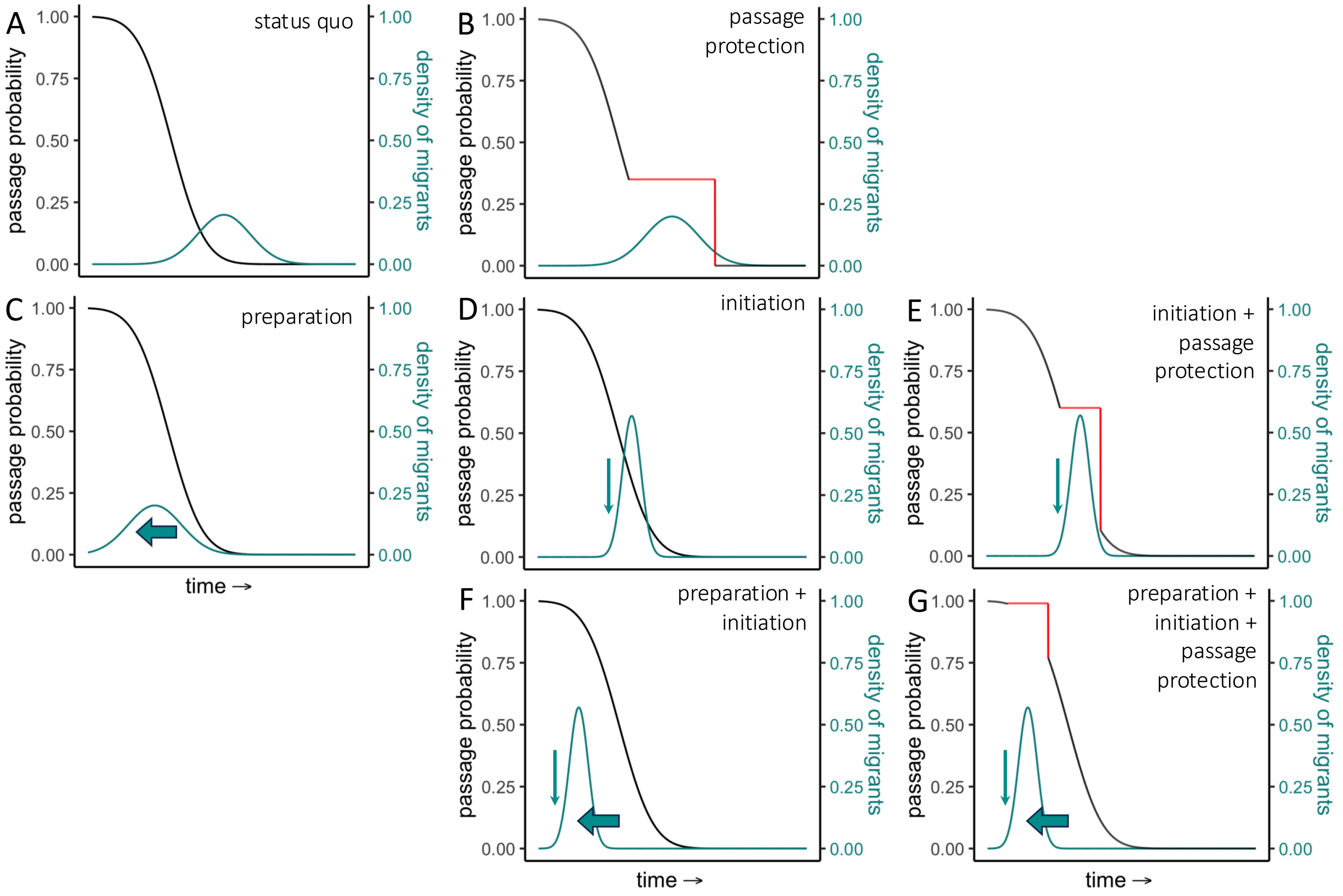


FIGURE 2 Representative scenarios of how facilitated migration could better match migration phenology with suitable conditions in an anthropogenically altered ecosystem. (A) The status quo scenario where the natural migration phenology of an imperiled population (cyan curve) is mismatched with suitable conditions (black curve), hampering population recovery. (B) One solution would be to use passage protection, or to elevate environmental suitability during natural migration phenology (red line). (C) Alternatively, by manipulating migration preparation (horizontal cyan arrow), the entire population's migration could be expedited to occur under more suitable conditions. (D) Instead, by supplying a relevant environmental cue (vertical cyan arrow), the population could be encouraged to initiate migration earlier within the natural migration phenology window, when conditions are more suitable. Finally, these three strategies are not mutually exclusive—earlier initiation could be combined with (E) passage protection, (F) expedited migration preparation, or (G) expedited preparation and passage protection.

$$T_p = f(E, P_m) \tag{4}$$

Migrations typically progress sequentially through the three phases—preparation, initiation, and passage—however, resolving temporal patterns of ϕ_s is fundamental to guiding potential management actions involved in T_p and Y_m (Figures 1 and 2). In other words, knowledge of the state of the system in terms of migrant risk is essential before managers attempt to control the timing of migrations. For example, encouraging migration to begin earlier via expedited preparation (Figure 2C), earlier initiation (Figure 2D), or both (Figure 2F) would only be appropriate if passage success was predicted to be higher earlier than (or earlier within) natural migration timing (Figure 2A). Accordingly, after describing our case study system, our approach begins by modeling patterns of ϕ_s against T and E, and then progresses to modeling T_p and Y_m using study system-specific versions of Equations (1–4).

CASE STUDY AND APPROACH

Juvenile Chinook salmon oceanward migration through California's Sacramento River

In western North America, year-to-year variability in precipitation has made it extremely challenging for managers to balance water allocation from storage reservoirs for humans and wildlife (DWR, 2022; Swain et al., 2018). Recent and ongoing droughts have exacerbated this challenge, resulting in record low water reserves (Diffenbaugh et al., 2015; Lund et al., 2018). This is particularly evident in the Sacramento-San Joaquin River watershed, where new management approaches are currently being considered for more effective water allocation. Precise wildlife water requirements will be crucial for the success of this plan. Given climate change projections (Diffenbaugh et al., 2015; Swain et al., 2018), understanding how to successfully balance water demand for humans and wildlife will also be relevant for higher-latitude watersheds. Indeed, mitigation of hydroelectric development on the Columbia and Snake Rivers involves water allocation for migratory species, and aspects of facilitated migration for anadromous salmonids are supported by many stakeholders (NPCC, 2014).

Anadromous salmonids, such as Chinook salmon, are exceptionally important constituents of watersheds in western North America where they spawn and rear (Quinn, 2018). The vast majority of historical freshwater spawning habitat is blocked by dams (Yoshiyama et al., 2001), but natural-origin populations still exist downstream of these barriers (Munsch et al., 2022). There are two critical migrations where facilitation could be impactful: the juvenile migration from freshwater-rearing habitats to the ocean, and the adult return migration from the ocean to freshwater spawning habitats (Quinn, 2018). Examining Chinook salmon in the Sacramento River, we focus on juveniles as an example of the facilitated migration framework, as they inhabit the southernmost freshwater range populated by this species (Quinn, 2018) and experience dramatic fluctuations in environmental conditions that influence abundance (Michel, 2019) and survival (Cordoleani et al., 2018; Notch et al., 2020). Furthermore, it is difficult to overstate how modified the Sacramento River and its flow regimes are—most habitat outside of the river channels has been destroyed or blocked (Whipple et al., 2012), and flows within the channels are currently reduced and homogenized compared to historical conditions (Buer et al., 1990). The silver lining of the extensive anthropogenic modification is that relevant environmental conditions in the Sacramento River are controllable (Daniels & Danner, 2020; Michel et al., 2023; Pike et al., 2013), potentially offering the opportunity to facilitate the migrations of Chinook salmon.

A potential pitfall of management actions that target single species or populations is that it could be to the detriment of others (e.g., Zarri et al., 2019). Thus, it is important that facilitated migration strategies account for the full portfolio of relevant phenotypes. Four populations of Chinook salmon with distinct migratory strategies currently exist in the Sacramento-San Joaquin River watershed (winter-, spring-, fall-, and late-fall-run). Each is named for the season that adults enter freshwater on their spawning migration, but the timing of juvenile migration to the ocean also differs among populations (Fisher, 1994). In addition, the timing of juvenile downstream migration can depend on lifestage. While the smolt lifestage is that which migrates to the ocean, earlier ontogenetic stages can also move downstream from natal reaches in the upper river to feed and grow in the warmer, more productive downstream reaches (Gaines & Martin, 2002; Quinn, 2018). The full portfolio of populations and lifestages within the study system, although a small fraction of its historical diversity (Munsch et al., 2022), deserves special attention within the facilitated migration framework.

Passage during migration (ϕ_s)

To guide potential actions involved in preparation, initiation, and passage protection (Figure 2), we began our case study by modeling successful passage probability (ϕ_s) using telemetry studies of smolts. As described in detail below, this was accomplished by fitting a version of Equation (2) with non-parametric associations between ϕ_s and environmental factors (E), time (T), migrant condition (C_m), and migration distance (D_m). We then contextualized the temporal pattern of ϕ_s, as revealed by this model, by comparing it to the full scope of natural migration in the study system, as revealed by daily numbers of individuals initiating migration enumerated by long-term monitoring.

While an exception is the use of stopover foraging habitat to rebuild energy reserves or continue growth (e.g., Golet et al., 2018; Hassrick et al., 2022; Phillis et al., 2018), once underway, migrations typically continue until the destination is reached (Dingle, 2014). Migratory delays outside of stopover behavior are often associated with increased migrant mortality or cessation of migration due to the depletion of energy reserves or increased exposure to threats (e.g., Marschall et al., 2011; McCormick et al., 1999; Zydlewski et al., 2005). When synchronized with environmental data, telemetry enables a spatiotemporal understanding of movement dynamics in an environmental context and can also elucidate patterns of migrant risk (Hausner et al., 2021; Hazen et al., 2017). Due to technological limitations impacting acoustic tag size, however, measurements of successful passage at the level of the individual are only elucidated in the larger smolt lifestage in juvenile Chinook salmon (Cooke et al., 2011; Smircich & Kelly, 2014). We therefore estimated ϕ_s using acoustic telemetry studies of smolts.

Thousands of acoustically tagged hatchery- and natural-origin smolts of all populations were released in groups across 24 locations in the Sacramento River watershed from 2007 to 2023 (ITAG, 2024) (Figure 3). Our goal was to broadly understand temporal variation in ϕ_s from release to estuary exit. Although dozens of strategically positioned acoustic receivers recorded fish movements

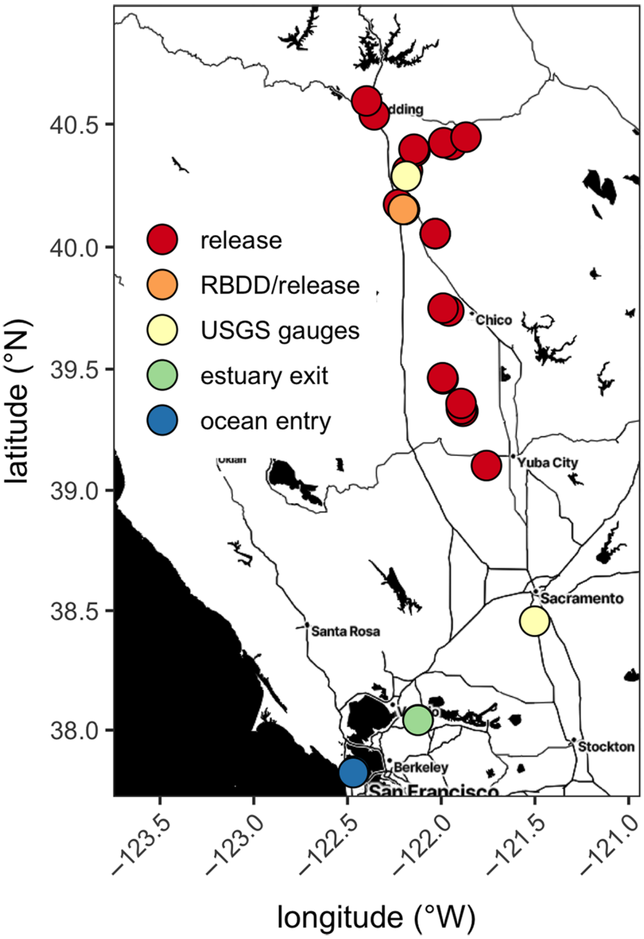


FIGURE 3 Map of the case study area with relevant locations color-coded. Note that some release locations are closer together than is distinguishable at the map's resolution, so are encompassed by a single dot. As indicated in the legend, the decommissioned Red Bluff Diversion Dam (RBDD) is also a release location.

throughout the system, we were mainly interested in detections recorded at the estuary exit (Benicia Bridge) and ocean entry (Golden Gate Bridge), the latter being used to determine the detection efficiency of the former (Figure 3). We performed this analysis outside of the traditional mark-recapture framework, and therefore only examined smolts ($n = 25{,}581$) from release groups exhibiting ≥0.8 detection efficiency at the estuary exit (mean detection efficiency = 1.0). Passage success was represented by the detection of a tagged fish at acoustic receivers located near Benicia Bridge or downstream (Figure 3).

A large body of work has shown that river flow, or volumetric discharge, is the primary variable governing ϕ_s across Chinook salmon populations in the Sacramento-San Joaquin River watershed (Buchanan et al., 2018; Michel, 2019; Michel et al., 2015, 2021). Flow is associated with the efficacy of salmon movements (Olivetti et al., 2021) and navigation (Perry et al., 2018), and threat exposure (Henderson et al., 2019). Although its effects can be difficult to decouple from those of flow, temperature is also important for ϕ_s: it is associated with the metabolic performance of juvenile Chinook salmon and predators (McInturf et al., 2022; Zillig et al., 2023), as well as the activity of predators (Michel et al., 2020; Ward & Morton-Starner, 2015), pathogens (Fryer & Pilcher, 1974), and humans (Reis et al., 2019). We therefore hypothesized that flow control could be a valuable tool to facilitate the successful passage of juvenile Chinook salmon during oceanward migration. However, the impact of flow on ϕ_s was likely dependent on timing, magnitude, and temperature, reflecting the myriad of periodic threats facing juvenile salmon in this system.

Each smolt was associated with mean temperature (in degrees Celsius) and tidally filtered flow (in cubic meters per second) (United States Geological Survey [USGS] gauge 11447650; USGS, 2024; Figure 3) for the period of time it was present, assumed to be present, or would have been present (in the case of mortality) in the Sacramento River. Missing detections at the estuary exit were interpolated using the shortest river distance between the temporally closest detection and the missing location, and the most precise average travel rate available.

All analyses were conducted using R version 4.1.0 (R Core Team, 2021). We used generalized additive models (GAMs) implemented with the "mgcv" R package (Wood, 2017) to incorporate non-parametric associations between ϕ_s and E, T, C_m, and D_m as smoothed terms (s []) (Equation (5)). Please note that intercepts and error terms, unless a key component of the conceptual framework, are not explicitly written in the following equations for simplicity.

$$\phi_s = s[E] + s[T] + s[C_m] + s[D_m] \tag{5}$$

In this version of Equation (2), E was represented by flow, D_m by distance from release to estuary exit (in kilometers), and C_m by fish condition factor, or the quotient of fish weight in hectograms (100× g) and cubed fish length (in cubic centimeters). Our intent was to include both flow and temperature as E terms in the same model. However, T (which in our case was represented by the day of water year—October 1 to September 30) and temperature were highly correlated leading to excessive concurvity (≥0.7) when included in the same GAM. We, therefore, assessed their effect using two separate GAMs of the same form: one where T was represented by the day of water year (Equation 6) and another where T was represented by temperature (Equation 7).

$$\phi_s = s[\text{Flow}] + s[\text{Day of water year}] + s[\text{Condition factor}] + s[\text{Migration distance}] \tag{6}$$

$$\phi_s = s[\text{Flow}] + s[\text{Temperature}] + s[\text{Condition factor}] + s[\text{Migration distance}] \tag{7}$$

We did not distinguish between natural- versus hatchery-origin salmon given that T and origin covaried (i.e., telemetry studies of natural-origin fish always occurred later in the water year than those of hatchery-origin fish). For both GAMs, a binomial error distribution was used (the response variable was binary: $1 =$ successful passage, $0 =$ unsuccessful passage); 5 knots ($k = 5$) were sufficient to represent non-parametric associations, concurvity was minimal, and diagnostics were found to be satisfactory (Appendix S1: Figures S1 and S2) using the "DHARMa" R package (Hartig, 2022).

The full temporal scope of natural migration initiation (Y_m) was compared to ϕ_s using an array of rotary screw traps (RSTs) attached directly to the decommissioned Red Bluff Diversion Dam (RBDD; Figure 3) (Voss, 2024). RSTs estimated the daily number of unmarked juvenile Chinook salmon passing RBDD from 2006 to 2019. The traps sampled juveniles produced by natural spawning in the upstream tributaries and a 95-km reach of the main stem Sacramento River downstream of Keswick Dam, the flow-regulating afterbay of Shasta Dam. The traps are therefore spatially situated just downstream of the major spawning grounds of the upper Sacramento River watershed and just upstream of habitat that is only seasonally thermally suitable for salmon, and therefore represents the beginning of the migratory corridor.

Daily Y_m totals were estimated based on the quotient of the daily combined catch of active RSTs and flow-based modeled trap efficiency (Martin et al., 2001; Voss & Poytress, 2022). All juvenile Chinook salmon caught were field identified to lifestage using an established size threshold (fry <46 mm fork length, pre-smolts/smolts ≥46 mm fork length) (Voss & Poytress, 2022), and to run using established length-at-date criteria (see Harvey et al., 2014). While length-at-date population assignments are directly applicable for managers, there is substantial uncertainty associated with population assignments based on length-at-date alone (Harvey et al., 2014). Accordingly, for some Endangered and Threatened winter and spring-run Chinook salmon (NMFS, 1994, 1999), genetic analyses have also been used since 2017 to validate population assignments and to increase the precision of run-based passage estimates at RBDD (Voss & Poytress, 2022). Hatchery-origin juvenile salmon were excluded from daily estimates by removing all adipose fin clipped individuals. When appropriate, a proportion of non-adipose fin clipped fish was also removed from estimates (based on 25% fractional marking rates of hatchery fall-run Chinook salmon).

To represent the natural phenology of Y_m, we determined the 10% passage threshold, or the day of the water year when a cumulative 10% of each population and lifestage was estimated to have passed RBDD ($n = 107$ thresholds, 1 datum per year per population per lifestage when available). The 10% threshold was low enough to represent when the majority of each population was prepared to migrate, and thus receptive to migration-triggering stimuli, yet high enough to be relatively consistent from year to year. In addition, we determined the 50% and 90% thresholds for subsequent relation to the 10% thresholds ($n = 107$ each).

Migration preparation (T_p)

To facilitate migration, it is necessary to understand the timeframe over which potential migrants would be prepared to migrate (T_p), and therefore be receptive to environmental cues that would initiate migration. We quantified T_p using annual 10% passage thresholds obtained from daily numbers of individuals initiating migration. As described in detail below, our version of Equation (4) used parametric associations between T_p and both E, migratory population (P_m), and their interaction. We then related 10% thresholds to 50% and 90% thresholds to understand how a change in T_p was reflected in the phenology of the entire migration.

Migration preparation can involve the buildup of energy reserves and physiological, behavioral, and biochemical changes (Dingle, 2014; Ramenofsky & Wingfield, 2007). Juvenile salmon have a distinct preparatory phase that occurs in advance of oceanward migration called smoltification. Their bodies become slender, more streamlined, and silvered; they become more pelagic and social; and numerous biochemical changes involved in osmoregulation and metabolism occur (Folmar & Dickhoff, 1980; Quinn, 2018). Photoperiod and temperature have been associated with smoltification across anadromous salmonids (Hoar, 1976); smoltification typically occurs within a specific photoperiod timeframe within which it can be advanced or delayed by temperature (Bourret et al., 2016; Muir et al., 1994). In fact, earlier migration of juvenile salmonids over multidecadal timeseries has been linked to increased air, water, and ocean temperature associated with global climate change

(Kovach et al., 2013; Otero et al., 2014). Upstream storage reservoirs could be used to regulate downstream temperature (Daniels & Danner, 2020; Macdonald et al., 2012; Michel et al., 2023) in watersheds where many natural-spawning populations of salmon still exist (Munsch et al., 2022). Indeed, some studies have examined how temperature could be used to expedite or delay migration preparation in juvenile Chinook salmon (Muir et al., 1994), although application has not occurred (NPCC, 2014).

Through temperature's impact on development, we hypothesized that temperature control could be a valuable tool to facilitate the timely preparation of juvenile Chinook salmon for migration readiness in the study system. However, we expected that different populations and lifestages could have unique responses to temperature given that salmonid thermal physiology can reflect unique migratory phenology (Eliason et al., 2011; Zillig et al., 2023).

To assess how T_p was associated with thermal history for natural-origin juvenile Chinook salmon, we related 10% passage thresholds from daily passage estimates at RBDD to accumulated thermal units (ATU; the sum of average daily temperatures) for fry and smolt lifestages of all populations. Daily temperature (in degrees Celsius) and flow (in cubic meters per second) of the Sacramento River over the study period were gathered from USGS gauge 11377100 near Red Bluff, CA, 23 km upstream of RBDD (USGS, 2024). Two passage thresholds were omitted from this analysis owing to missing temperature data (thus, $n = 105$).

We used multiple regression to parametrically relate T_p to E, P_m, and their interaction (Equation 8).

$$T_p = E \times P_m \tag{8}$$

In this version of Equation (4), E was represented by ATU, average flow for the ATU period, and the interaction between flow and ATU. This accounted for any effect of flow on thermal history associations. P_m was represented by both lifestage and population because T_p differs between fry and smolts of the same population. Our hypothesized association between T_p and E depended on P_m, which we represented using a three-way interaction between ATU, population, and lifestage (Equation 9).

$$T_p = \text{Flow} + \text{ATU} : \text{Flow} + \text{ATU} \times \text{Population} \times \text{Lifestage} \tag{9}$$

We tested the goodness of fit between models that included 15-, 30-, 45-, or 60-day ATU and flow using Bayesian information criterion (BIC). BIC favored 15- or 30-day periods, but the difference between these two was trivial (<2 BIC points, Appendix S1: Table S1). Thus, we selected the 15-day model. Diagnostics were examined using standard plotting functions in base R (Appendix S1: Figure S3). One observation (point 36 in Appendix S1: Figure S3, spring-run smolts in 2015) was particularly influential, likely due to the low flows and high temperatures observed during that water year (Cordoleani et al., 2018; Notch et al., 2020).

To determine how a change in T_p corresponded to a change in the rest of the migration's phenology, we compared 10% thresholds to 50% and 90% thresholds using a linear regression ($n = 107$).

Migration initiation (Y_m)

To understand how environmental cues could be used to control Y_m, we modeled daily numbers of individuals initiating migration recorded at the beginning of the migratory corridor. As described in detail below, we fit a version of Equation (3) with non-parametric associations between Y_m and E and T_p, a random effect for the size of the migratory population (N_m), and an autoregressive term for the number of time-lagged migrants (Y_{mk}).

The timing of migrations evolves to optimize the suitability of conditions along the migratory path and in the destination ecosystem, and migration initiation is a critical step in this process (Dingle, 2014). For example, some taxa use celestial cues, like moon phase, to synchronize the arrival of migrants at reproductive areas (Adamczewska & Morris, 2001; Grant et al., 2009; Tsukamoto et al., 2003), while foraging migrations in others can be cued by environmental conditions that directly give rise to food sources (Dingle, 2014; Pedgley et al., 1995). Given that social information influences decision-making in migratory taxa (Gil et al., 2018), the density-dependence of migration initiation itself could also be a major factor influencing the timing of migration.

In juvenile salmonids, flow is a commonly identified environmental cue that initiates migration in large batches of ready individuals (Antonsson & Gudjonsson, 2002; Raymond, 1979; Whalen et al., 1999). However, some studies find that temperature is the better predictor of migration initiation (e.g., Frechette et al., 2023; Jonsson & Ruud-Hansen, 1985) and there could be methodological reasons for this. First, it can be difficult to decouple how environmental conditions impact preparation and initiation, respectively. Timing, for example, the date at which different proportions of the population have migrated, is often the response variable in both analyses. This can be useful for assessing readiness but misses higher-frequency variability attributable to pulses in migration initiation. Second, flow metrics vary from study to study. Most use averaged flow (Aldvén et al., 2015; Stich et al., 2015; Sykes et al., 2009) or flow timing (Frechette et al., 2023; Kovach et al., 2013; Teichert et al., 2020), while fewer incorporate metrics of flow change (Otero et al., 2014; Sturrock et al., 2020; Zeug et al., 2014). Finally, the importance of flow likely varies from population to population and watershed to watershed within a species. For example, juvenile Chinook salmon in the Columbia River tend to migrate with or before peak flows (Quinn, 2018; Raymond, 1979), while those in the Nechako River in central British Columbia tend to migrate at non-peak flows (Sykes et al., 2009).

We hypothesized that flow change control could be a valuable tool to facilitate juvenile Chinook salmon Y_m in the study system. We additionally expected that migratory responses to flow change could depend on lifestage and population, given that differences in natural migration phenology (Fisher, 1994) imply adaptation to distinct portions of the historical hydrograph (Kiernan et al., 2012). The efficacy of flow changes for moving fry downstream or initiating migration in smolts could therefore depend on magnitude, timing, and background flow, as well as Y_{mk}.

We used daily passage estimates obtained at RBDD to examine how flow change was related to Y_m for natural-origin juvenile Chinook salmon. While we were interested in the response of different populations, we modeled daily counts of all populations combined. Population-specific effects were approximated by examining time-specific effects, as this framework is more easily utilized by managers and has broader relevance to other watersheds. Only 3 days out of the entire 13-year timeseries reported zero natural-origin juvenile Chinook salmon catch; however, sampling efficiency was exceptionally low on these days due to low trapping effort in response to high flows and large numbers of migrating hatchery-origin fish. Because the low sampling efficiency could not be incorporated into these observations (i.e., 0 catch/flow-based sampling efficiency $= 0$), we, therefore, excluded these three observations, bringing the total number to 3916. Two separate analyses were conducted for passage estimates of each lifestage, given that fry and smolts had distinct timing of downstream movements, and that fry vastly outnumbered smolts. Only days when a given lifestage was observed were included in the respective analysis ($n = 3374$ and 3798 for fry and smolts, respectively).

Based on migration rates revealed by acoustic tagging experiments of smolts (ITAG, 2024), we made the reasonable assumption that sampled fish began moving oceanward within the 24 h preceding their capture. Daily flow of the Sacramento River over the study period was gathered from USGS gauge 11377100 (USGS, 2024), the same monitoring station used for temperature in the preparation analysis. Each sampling date at RBDD was associated with baseline flow, that is, flow averaged over the 7 days leading up to (and including) the day before a given sampling date, and daily flow change, or the difference between baseline flow and flow on the day before a given sampling date.

We used generalized additive mixed-effects models (GAMMs) implemented with the “mgcv” R package (Wood, 2011) to incorporate non-parametric associations between Y_m and E and T_p as smoothed terms, and to include N_m as a random effect (re[]); Y_{mk} was included parametrically. Both response variables (Y_m of fry and smolts, respectively) were modeled using GAMMs of the same form (Equation 10).

$$Y_m = s[E] + s\left[T_p\right] + \text{re}[N_m] + Y_{\text{mk}} \tag{10}$$

In this version of Equation (3), E was represented by flow change and baseline flow, T_p by day of water year, and N_m by a random intercept of water year. The latter two terms respectively captured seasonal and year-to-year variability in Y_m, allowing us to resolve the specific influence of E on Y_m. Reflecting the anticipated effects of density-dependence, the modeled timeseries contained short-term autocorrelation. Specifically, the number of fish initiating migration on a given day depended on the number initiating migration the day before. We therefore specified a first-order autoregressive autocorrelation structure error term, AR(1), to represent Y_{mk}. Since both responses were non-zero, over-dispersed discrete counts, and a negative binomial family with a log link function was not available in the model fitting framework, we log-transformed the response variable before fitting models. We also tested the parsimony benefit of including interactions between smoothed terms using tensor products (i.e., smoothed interactions) and parametric interactions. We found that parametric interactions between flow change and baseline flow smoothed terms were the best-supported additions for models of both lifestages given the lack of concurvity and modest decrease in BIC over the next best model (Appendix S1: Table S2). A parametric interaction between time and flow change smoothed terms was marginally more parsimonious for smolts (<5 BIC points), but we selected the model with the parametric interactions between flow change and baseline flow for consistency with the fry GAMM (Equation 11).

$$\log\left(Y_m\right) = s[\text{Baseline flow}] \times s[\text{Flow change}] + s[\text{Day of water year}] + \text{re}[\text{Water year}] + \text{AR}(1) \quad (11)$$

For day of water year, we used a cyclic cubic regression spline, as the seasonal pattern of migration repeated from year to year; all other smoothed terms used a cubic regression spline. For both GAMMs, 10 knots ($k = 10$) were sufficient to represent non-parametric associations and diagnostics were satisfactory (Appendix S1: Figures S4 and S5) (Wood, 2011). We additionally confirmed the absence of standardized residual autocorrelation.

Facilitated migration efficacy

To assess the potential efficacy of facilitated migration in our study system, we simulated how relatively simple temperature and flow manipulations could change the number of natural-origin Chinook salmon smolts that successfully completed oceanward migration (Y_{ms}) via alterations to natural migration phenology. Specifically, we assessed how Y_{ms} under a "status quo" scenario (i.e., the normal migration timeframe with mean flows) (Figure 2A) compared to Y_{ms} under (1) a safer migration timeframe with mean flows (Figure 2F), (2) the normal migration timeframe and passage protection (i.e., increased flow) (Figure 2E), and (3) a safer migration timeframe with passage protection (Figure 2G). We focused on fall- and spring-run smolts for this exercise given that the preparation model temperature coefficients for late-fall and winter-run smolts, like fry of all populations, were not statistically distinguishable from 0. Furthermore, passage success was quantified using smolts, not fry.

To better align migrations with safer passage timeframes, model fits described in previous sections were used to test the effect of a modest feasible migration phenology advance for fall- and spring-run smolts. The difference between the median and minimum date of 10% passage was 68 and 48 days in fall- and spring-run smolts, respectively. Thus, a 25-day advance seemed both modest and feasible for both populations. We determined the 15-day ATU required for this shift in both populations under mean baseline flow (264 $\text{m}^3\ \text{s}^{-1}$ [9340 $\text{ft}^3\ \text{s}^{-1}$]), and the flow pulse required to initiate migration in the maximum number of fish possible against mean baseline flow (458 $\text{m}^3\ \text{s}^{-1}$ [16,187 $\text{ft}^3\ \text{s}^{-1}$]). The simple passage protection scenario investigated was sustaining flow pulses used for initiation for the duration of migration (i.e., flow became the sum of mean baseline flow and the flow pulse).

We investigated the efficacy of different scenarios for important migration days. Important migration days were defined as those encompassing the days when 10%–90% of the population was predicted to have initiated migration ($n = 69$ and 71 days each year for fall- and spring-run, respectively). Given the correlation of 10% thresholds with 50% and 90% thresholds, we assumed that any shift to 10% thresholds would be reflected in the entire population.

When determining Y_{ms} for each scenario, ϕ_s predictions were multiplied by Y_m predictions (Equation 1). Uncertainty (δ) around these predictions, which we quantified using 95% CIs, was therefore used to estimate uncertainty around Y_{ms} by summing fractional uncertainties and multiplying by Y_{ms} (Taylor, 1997) (Equation 12).

$$\delta Y_{\text{ms}} \approx \left|Y_{\text{ms}}\right| \left(\frac{\delta\phi_s}{\left|\phi_s\right|} + \frac{\delta Y_m}{\left|Y_m\right|} \right) \quad (12)$$

When subtracting the Y_{ms} of the "status quo" scenario from Y_{ms} of alternative scenarios, the uncertainty of the resulting change in Y_{ms} (ΔY_{ms}) was estimated by the sum of each scenario's uncertainty (Taylor, 1997) (Equation 13).

$$\delta\Delta Y_{\text{ms}} \approx \delta \text{Y}_{\text{ms}}\,\text{Status quo} + \delta Y_{\text{ms}}\,\text{Alternative} \quad (13)$$

Results should therefore encompass as close to the full range of outcomes as is quantifiable. To contextualize efficacy, we divided the predicted Y_{ms} for each scenario by the maximum predicted Y_{ms} from 2006 to 2019 under the "status quo" scenario.

RESULTS

Passage during migration (ϕ_s)

Our results show that we have a broad but incomplete understanding of successful migrant passage probability (ϕ_s) by juvenile Chinook salmon in the study system. Monitoring efforts revealed that migration initiation occurred year-round in natural-origin populations. However, available acoustic telemetry data were only based on smolts and collected within the winter and spring periods (Figure 4). The passage of most natural-origin winter-run fry and smolts, which comprise an endangered ecologically significant unit (NMFS, 1994), fell mainly outside this scope.

Within the timeframe of available data, average ϕ_s across the study period was 0.06 ± 0.004 (value ± 95% CI). In general, migrants in better condition (higher C_m) with shorter migrations (lower D_m) had greater ϕ_s than those in poorer condition with longer migrations

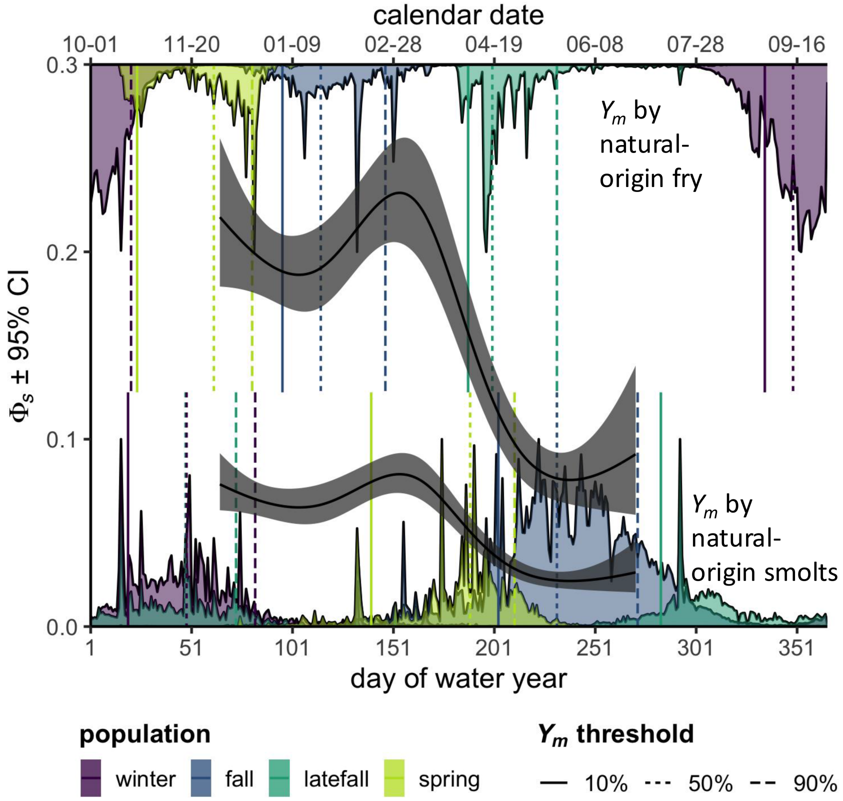


FIGURE 4 Successful passage during migration in juvenile Chinook salmon varied seasonally, but our knowledge of this pattern only partially overlapped with natural migration phenology. Lines and shaded ribbons show how the probability of smolt passage (ϕ_s) from release to estuary exit, at mean (737 $m^3 s^{-1}$ [26,027 $ft^3 s^{-1}$]) and median (423 $m^3 s^{-1}$ [14,938 $ft^3 s^{-1}$]) flow (upper and lower dark lines and ribbons, respectively), fluctuated over the course of the water year, holding all other predictors at median values. Shaded curves above and below probability predictions respectively show the phenology of natural-origin fry and smolt migration initiation (Y_m) for each population, as revealed by 13 years of rotary screw trap (RST) data collected at Red Bluff Diversion Dam (RBDD). Each curve shows the within-run cumulative initiation (0–0.1 scale) for each day of water year over the timeseries. Vertical dashed lines show the median date of 10%, 50%, and 90% initiation for both lifestages of all populations. A secondary *x*-axis (above) shows calendar dates in relation to the day of water year. Note that this figure shows the study system as is—the purpose of facilitated migration is to use this information to plan when and how resources should be devoted to increase the number of individuals that successfully complete migration by best aligning the colored curves with the gray curves while shifting the gray curve up.

(Appendix S1: Figure S6). Averaging over the effects of C_m and D_m clearly indicated that time (T) not only affected ϕ_s (Figure 4), but also the influence of environmental factors (E) on ϕ_s (Figure 4). E (i.e., flow) had 1.57 times the maximum effect size of T on ϕ_s, suggesting that passage protection (Figure 2B) may generally be more efficient than phenology shifting (Figure 2C,D) at increasing ϕ_s. However, the effect size of T increased with E such that more suitable E (i.e., higher flow) enhanced the potential ϕ_s benefit of phenology shifting (Figure 2E,G) (Appendix S1: Figure S7).

There was a distinct temporal pattern of ϕ_s showing peaks and troughs that informed how the migration phenology of different populations could be shifted to improve passage success (time GAM: $R^2 = 0.10$, $df = 13$, residual $df = 25{,}567$). While higher versus lower flows within the range of typical values shifted this pattern up or down, respectively (Figure 4), we also found an association between the temporal pattern and flow that informed how flow events could be used to effectively boost ϕ_s (Figure 5A). Later in the water year, higher flows were required to achieve the same ϕ_s that lower flows elicited earlier in the water year, perhaps owing to higher temperatures (temperature GAM: $R^2 = 0.11$, $df = 14$, residual $df = 25{,}567$) (Figure 5B). From early April through June, when spring- and fall-run smolts naturally migrated, relatively large flow additions were required to boost ϕ_s (Figure 5C,E). On the other hand, from early December through late March, when fry of the same runs (and late-fall smolts) traveled downstream, smaller flow additions resulted in the same ϕ_s. Once conditions approached 20°C, migration was unlikely to succeed regardless of flow additions (Figure 5D,F). Flow additions were of minimal or currently unpredictable benefit to ϕ_s if baseline flow already exceeded approximately 1000 $m^3 s^{-1}$ (35,315 $ft^3 s^{-1}$).

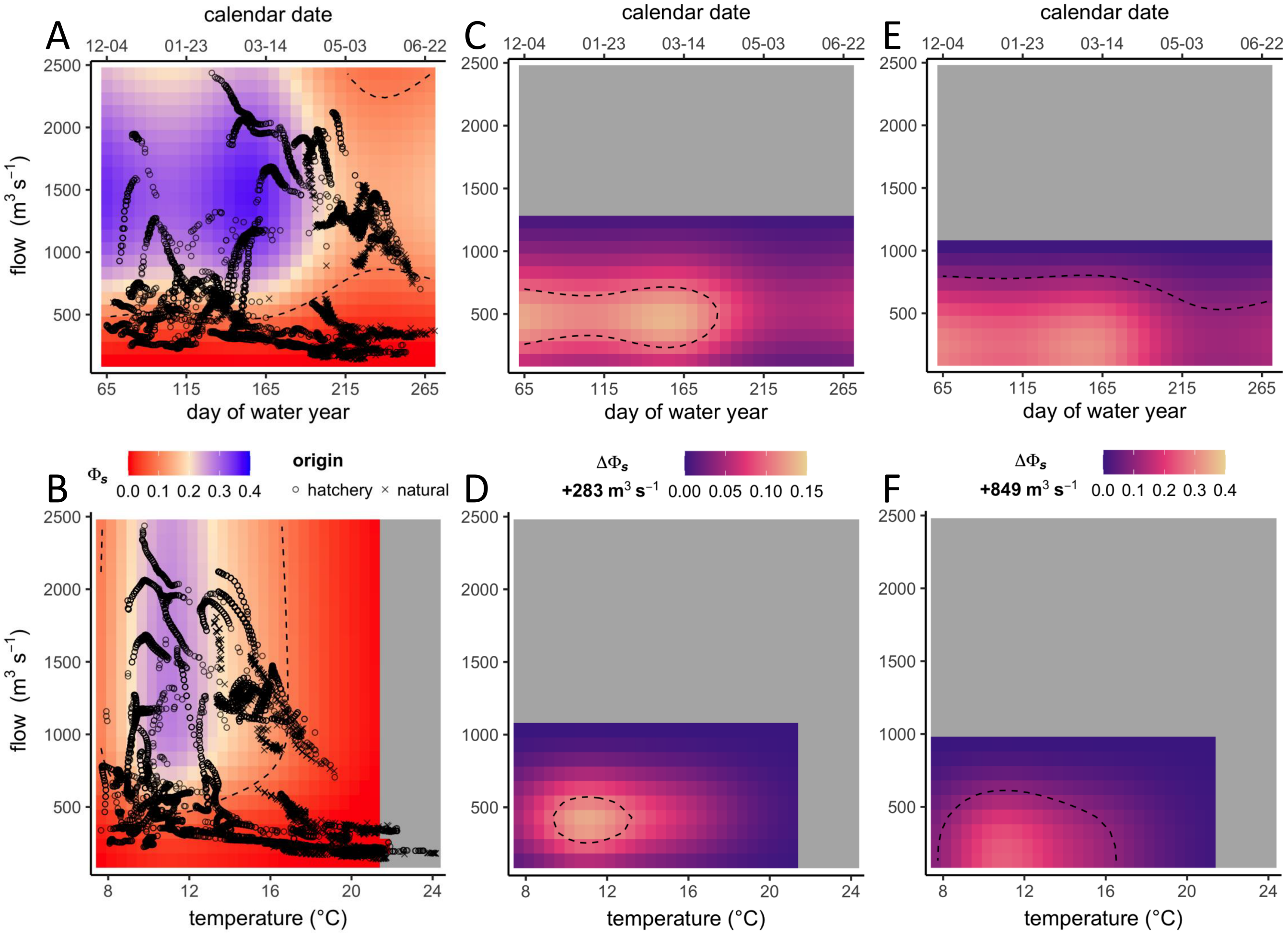


FIGURE 5 The association between the probability of successful migration and the time of year or temperature depended on flow in juvenile Chinook salmon. The interaction between baseline flow and (A) time or (B) temperature. Points show the parameters at the predicted midpoint of the migration of each individual and are shaped by origin; dashed lines show the 0.1 probability (ϕ_s) contour, or the conditions associated with a 10% chance of successful passage from release to estuary exit; and a secondary *x*-axis (above) shows calendar dates in relation to the day of water year in (A, C, and E). Predicted 283 $m^3 s^{-1}$ (10,000 $ft^3 s^{-1}$) flow addition impact on passage success with respect to (C) time or (D) temperature. Predicted 849 $m^3 s^{-1}$ (30,000 $ft^3 s^{-1}$) flow addition impact on passage success with respect to (E) time or (F) temperature. In panels (C–F), dashed lines show the 0.1 probability change ($\Delta\phi_s$) contour, or the regions where the given flow increase was associated with a successful passage probability increase of 10%. In all panels, gray shading indicates where predictions were less than half the 95% CI, indicating low confidence in the result. Note that the shading scales correspond to vertical pairs of panels; the scale is different for (C and D) compared to (A and B, E and F) in order to make patterns of successful passage probability more apparent.

Conversely, if baseline flow was below approximately 1000 $m^3 s^{-1}$, almost any flow addition was predicted to improve ϕ_s, the caveat being that larger flow additions were necessary to improve ϕ_s if baseline flow was exceedingly low (i.e., <250 $m^3 s^{-1}$ [8829 $ft^3 s^{-1}$]).

Migration preparation (T_p)

We found that lifestages of different migratory populations (P_m) tended to migrate at specific times of year (Figure 4), and only some P_m showed variation in the timing of migration preparation (T_p) that was potentially controllable using E (Figure 6A,B). Thermal history (i.e., ATU) was associated with T_p, but the association varied by lifestage, population, and flow (multiple regression: $R^2 = 0.90$, $F_{17,87} = 57$, $p < 0.001$) (Figure 6A), suggesting some thermally induced flexibility in migration phenology. As we hypothesized, variation in 10% passage thresholds for fry showed little association with 15-day ATU across all populations, whereas smolts had population-specific associations. However, all associations were dependent on 15-day average flow: for every increase in 1 $m^3 s^{-1}$, the 10% threshold change granted by a 1°C temperature increase sustained for 15 days declined by -0.02 ± 0.01 days ($p = 0.01$). Thus, the higher the flow, the more T_p shifts trended toward advances under increased temperature.

For example, under mean 15-day average flow in this dataset (307 $m^3 s^{-1}$ [10,844 $ft^3 s^{-1}$]), fall- and spring-run smolts delayed T_p with increasing temperature. A 1°C temperature increase sustained for 15 days delayed spring-run by (coefficient ± 95% CI) 17.8 ± 7.98 days but fall-run only by 11.8 ± 7.39 days (Figure 6B). Under 15-day maximum flow in this dataset (1620 $m^3 s^{-1}$ [57,210 $ft^3 s^{-1}$]), a 1°C temperature increase sustained for 15 days would advance spring-run smolt T_p by 8.45 ± 8.05 days and fall-run smolt T_p by 14.5 ± 7.46 days. While late-fall- and winter-run smolts trended toward expedited T_p with increasing 15-day ATU, their coefficients overlapped with 0 (i.e., no predictable change with 15-day ATU), similar to coefficients of all fry populations.

We also found that migration phenology shifted with advances or delays in T_p, suggesting that thermally induced shifts in 10% thresholds could result in shifts of the available population (50% threshold linear regression: $R^2 = 0.89$, $F_{1,105} = 863$, $p < 0.001$; 90% threshold linear regression: $R^2 = 0.81$, $F_{1,105} = 466$, $p < 0.001$) (Figure 6C). For example, if a 10% threshold was advanced by 1 day, the 50% and 90% thresholds would be advanced by 1.14 (±0.08) and 1.13 (±0.10) days, respectively.

Given that some P_m have relatively large windows over which they are naturally prepared to migrate (e.g., a median of 43–96 days in our study), some flexibility in temporally controlling the number of individuals that initiate migration (Y_m) to better align migrations with higher ϕ_s could occur without altering T_p. Furthermore, potentially through flexibility in release timing, a higher degree of T_p manipulation might be possible for hatchery-origin fish.

Migration initiation (Y_m)

Consistent with raw initiation data (Figure 4), our models (fry GAMM: $R^2 = 0.71$, df = 20, residual df = 3354; smolt GAMM: $R^2 = 0.57$, df = 21, residual df = 3777) captured a cyclic pattern of Y_m characterized by four peaks every water year (Figure 7A). This consisted of two peaks of fry downstream movement, one comprising spring- and fall-run (fry peak 1) and the other winter-run

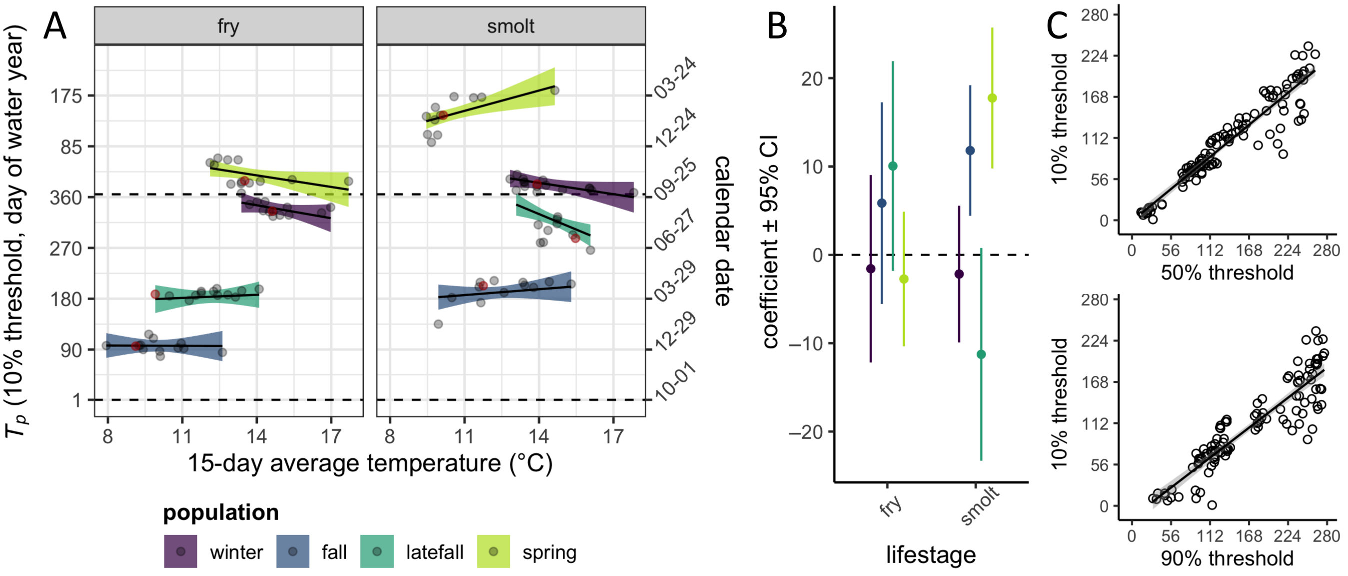


FIGURE 6 The association between migration preparation and thermal history depended on lifestage and population in juvenile Chinook salmon. (A) The association between 15-day average temperature (in degrees Celsius) and the day of the water year when 10% of each natural-origin population and lifestage had left natal grounds (10% threshold), which signifies the timing of migration preparation (T_p). Points are data, lines represent the fit of a multiple regression, and shaded ribbons represent the 95% CIs. Predictions were made at the average 15-day mean flow experienced for both lifestages of all populations (307 $m^3 s^{-1}$ [10,844 $ft^3 s^{-1}$]). Red points show the median 10% threshold from the data, and the beginning and end of the water year are shown with dashed horizontal lines. Calendar dates (right) are included for reference. (B) Coefficients from the fit shown in (A), or changes (days) in the 10% threshold with every 1°C increase over 15 days. Only fall- and spring-run smolt populations had coefficients significantly different from 0. (C) Upper and lower panels respectively show the association between 10% thresholds and 50% or 90% thresholds. The day of the water year is on a common scale to runs—that is, 0 would be the earliest recorded threshold for a given run, while the largest number would be the latest.

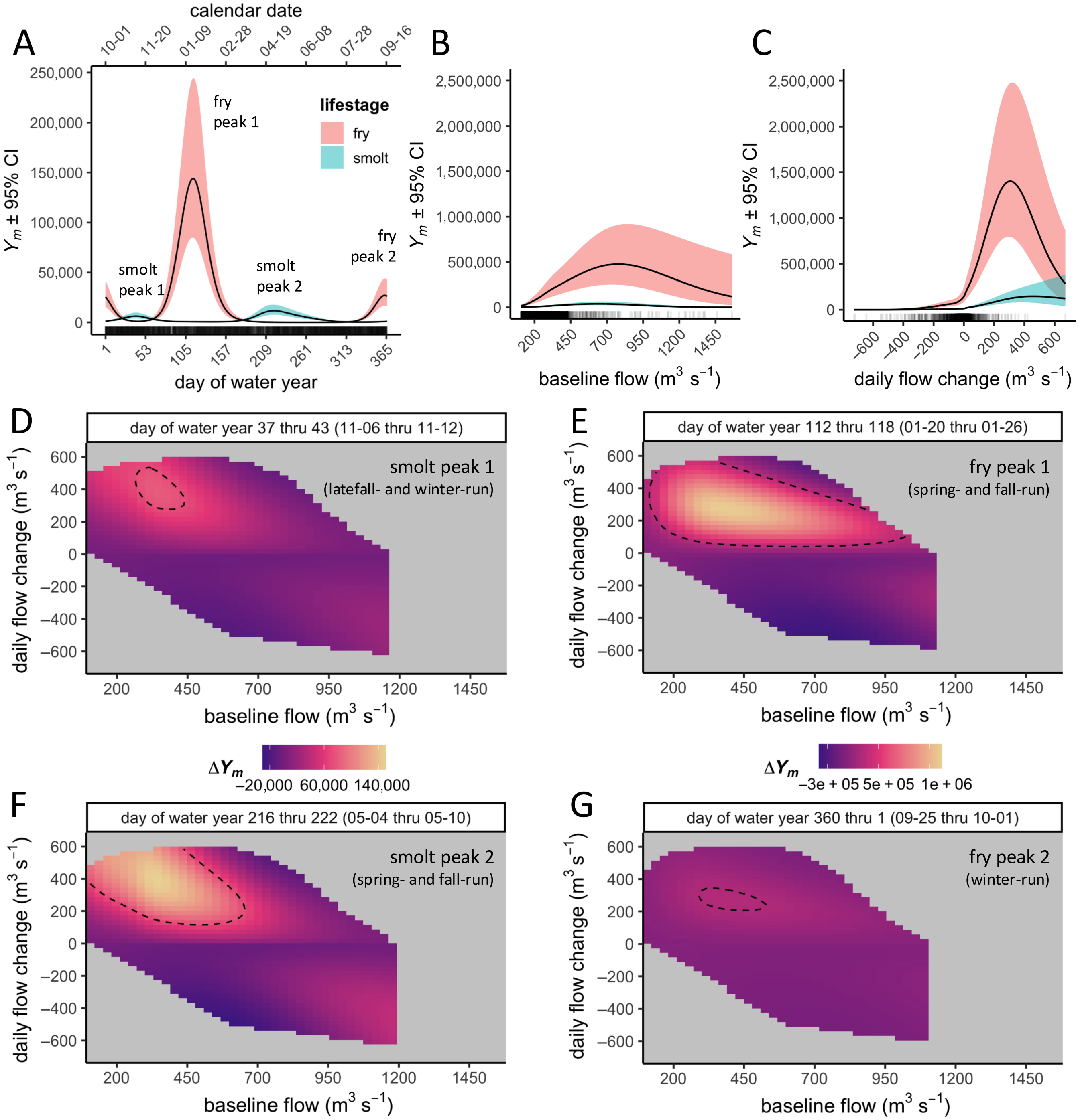


FIGURE 7 The association between migration initiation and flow change depended on baseline flow in juvenile Chinook salmon. (A) The cyclic annual pattern of migration initiation (Y_m) for each lifestage, with baseline flow set to the average value and flow change set to 0. The secondary *x*-axis (above) shows calendar dates in relation to day of water year. (B) Association between baseline flow and initiation, with time set to the day of water year of maximum initiation for each lifestage (fry = 115 [01/23] and smolt = 219 [05/07]), and flow change set to 0. (C) Association between flow change and initiation, with baseline flow set to the average value (264 $m^3\ s^{-1}$ [9340 $ft^3\ s^{-1}$]) and time set to day of water year of maximum initiation. (D–G) Predictions of initiation at different baseline flow by flow change combinations at different periods of the water year corresponding to peak migration initiation of different lifestages and runs (shown in panel [A]). Initiation change (ΔY_m) refers to the difference in initiation between a given baseline flow by flow change combination, and the corresponding baseline flow with no flow change. Note that the shading scales corresponds to vertical pairs of panels (D and F, E and G). Dashed contours show the number of fish corresponding with the 5% median total annual initiation (4% in panel [G]). In all panels, gray shading indicates where predictions were less than half the 95% CI, indicating low confidence in the result. Note the appearance of sharp transitions around $y = 0$ in panels (D)–(G), which reflect the association between initiation and flow change in panel (C)—even relatively small flow increases resulted in initiation increases, whereas flow reductions typically resulted in initiation reductions unless they occurred under large baseline flows.

(fry peak 2), and two peaks of smolt migration, one comprising late-fall- and winter-run (smolt peak 1) and the other spring- and fall-run (smolt peak 2).

We found that Y_m was related to daily flow change, and that this association depended on baseline flow. With no flow change, baseline flows had limited efficacy in initiating downstream movement (Figure 7B); however, once flow changes were incorporated, efficacy drastically changed (Figure 7C). For example, at average baseline flow (264 $m^3 s^{-1}$ [9340 $ft^3 s^{-1}$]), a daily flow increase of about 300 $m^3 s^{-1}$ (10,595 $ft^3 s^{-1}$) was predicted to result in a 1.90- and 2.70-fold initiation increase in fry and smolts, respectively, than was achievable at a baseline flow of the sum of these flows (i.e., 564 $m^3 s^{-1}$ [19,935 $ft^3 s^{-1}$]) (Figure 7B,C).

The maximum combined effect size of E (i.e., baseline flow and daily flow change) on Y_m was equivalent to that of T_p (i.e., it was 1.00- and 1.03-fold greater in fry and smolts, respectively). This suggests that E could massively increase Y_m if applied at the appropriate T_p. During Y_m peaks, large batches of migration-ready individuals were especially responsive to daily flow changes (Figure 7D–G). For example, at the height of the first fry peak and second smolt peak, moderate flow increases (e.g., +200 $m^3 s^{-1}$ [7063 $ft^3 s^{-1}$]) were associated with Y_m of 5%–23% and 5%–10% of the median total annual Y_m of fry and smolts, respectively (Figure 7E,F). Even at the smaller peaks, similar conditions could initiate 4%–6% of the median total annual Y_m of each lifestage (Figure 7D,G).

Facilitated migration efficacy

Facilitated migration was predicted to increase the number of surviving migrants (Y_{ms}) for natural-origin spring- and fall-run smolts over the "status quo" scenario, and this effect was considerably amplified with concomitant passage protection. If initiated at the most optimal time while keeping all other factors constant (Figure 8, scenario 1), advancing migrations by 25 days could allow for an additional (uncertainty, δ, range) 944 (−1209 to 4761) spring-run and 985 (−1231 to 4913) fall-run smolts to successfully migrate over the status quo. The 15-day average temperature required for this shift was 8.49 (6.79–9.99°C) in spring-run and 9.75 (5.89–13.4°C) in fall-run. If initiated within the normal migration timeframe, passage protection (i.e., increased flow) alone (Figure 8, scenario 2) could allow for an additional 10,084 (2040–24,231) spring-run and 10,298 (2114–24,640) fall-run successful migrants over the status quo. The 15-day average temperature associated with the normal migration timeframe (i.e., median 10% initiation threshold) was 10.4 (9.55–11.3°C) in spring-run and 13.6 (11.6–15.6°C) in fall-run. Finally, advanced migration combined with passage protection (Figure 8, scenario 3) could allow for an additional 16,945 (4689–38,537) spring-run and 17,452 (4855–39,684) fall-run successful migrants over the status quo.

In context, facilitated migration could have a substantial impact on natural-origin Chinook salmon populations in California. In 2014 and 2007, the water years when the most natural-origin spring- (363,953) and fall-run (4,099,066) smolts were respectively estimated to have initiated migration, may have seen as few as 3444–10,663 spring-run and 34,569–45,227 fall-run successfully migrate to the estuary exit. Had facilitated migration scenarios 1–3 been implemented, Y_{ms} could have respectively been boosted by (δ range): 25% (−32% to 126%), 293% (59%–704%), and 479% (133%–1090%) for spring-run, and 2% (−3% to 11%), 27% (6%–65%), and 43% (12%–98%) for fall-run.

In our efficacy analysis, we used 95% CIs to propagate the δ of ϕ_s and Y_m estimates ($\delta\phi_s$ and δY_m, respectively). For the "status quo" scenario, scenario 1, scenario 2, and scenario 3, average (±1 SD) fractional $\delta\phi_s$—that is, $\delta\phi_s$ relative to ϕ_s (Equation 12)—was 0.22 ± 0.12, 0.18 ± 0.03, 0.20 ± 0.10, and 0.15 ± 0.04, respectively. In all scenarios, the average fractional δY_m was 0.70 ± 0.22 because the same flow pulse was used to initiate migrants given that it conferred the largest Y_m across evaluated scenarios. Relative to the full range of possible flow changes, this fractional δY_m was below average; thus, δY_m was generally larger than $\delta\phi_s$ in our study.

DISCUSSION

Informing expectations across study systems

Given the ecological (Bauer & Hoye, 2014), economic (Munsch et al., 2022), and cultural (Blanchet et al., 2021) importance of migratory species, it is paramount that we reduce the risk associated with migrations in order to support relevant populations. Anthropogenic habitat alteration can outpace the adaptive capacity of migratory taxa (McNamara et al., 2011; Stenseth & Mysterud, 2002) and thereby make an already risky life history strategy more treacherous. Facilitated migration is a management framework intended to leverage anthropogenic alterations to benefit migratory species conservation. Whereas assisted migration, also referred to as assisted colonization or managed relocation, involves the active transport of species by humans beyond known ranges to prevent extinction (Hoegh-Guldberg et al., 2008), facilitated migration

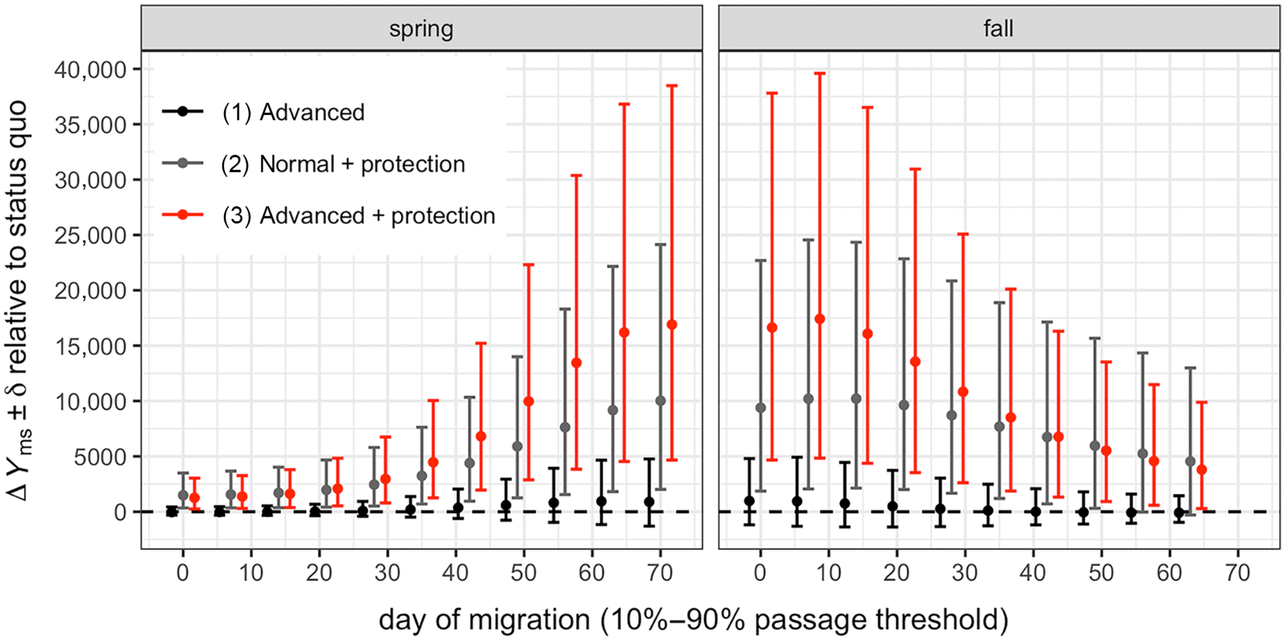


FIGURE 8 Facilitated migration could allow thousands of additional juvenile Chinook salmon to migrate successfully. Plot shows how three different facilitated migration scenarios compared to a "status quo" management scenario (i.e., Figure 2A), or the normal migration timeframe with mean upper river baseline flow (264 $m^3\ s^{-1}$ [9340 $ft^3\ s^{-1}$]) sustained to the freshwater estuary for spring-run (left) and fall-run (right) smolts. Examined is each scenario's impact on the change in surviving migrants (ΔY_{ms}), or the change in the number of fish initiating migration that survived to the estuary exit. Each pairing of points and error bars (δ = uncertainty around ΔY_{ms}) is a potential time to execute one of the following scenarios. (1) Black shows the effect of shifting migrants to a safer migration timeframe (i.e., Figure 2F), where migrations were advanced by 25 days, while maintaining average flow. (2) Gray shows the effect of passage protection (i.e., Figure 2E), or increased flow (722 $m^3\ s^{-1}$ [25,527 $ft^3\ s^{-1}$]), the sum of the mean baseline flow and the flow pulse that initiated the maximum number of migrants (458 $m^3\ s^{-1}$ [16,187 $ft^3\ s^{-1}$]), during the normal migration timeframe. (3) Red shows the effect of a safer passage timeframe combined with passage protection (i.e., Figure 2G). Day of migration is the normalized (min = 0, max = max − min) day of water year between median 10% and 90% initiation thresholds, which were 140 (February 17) to 211 (April 29) and 203 (April 21) to 272 (June 29) in spring- and fall-run smolts, respectively, under the normal migration timeframe (Figure 4).

leverages environmental manipulations to elicit and protect natural migrations in anthropogenically altered ecosystems (Figure 1) so that migratory species may continue to persist in their native range.

Conceptually, the goal of facilitated migration is to increase the number of successful migrants (Y_{ms}) by simultaneously increasing successful passage probability (ϕ_s) and the number of individuals that initiate migration (Y_m). Increasing ϕ_s could occur by (1) temporally shifting migration phenology to take advantage of naturally higher ϕ_s, (2) temporarily manipulating environmental factors (E–e.g., flow) to protect migrant passage, or (3) both. While strategy 2 had a larger effect size than strategy 1 in our study system, strategy 3 had the greatest possible effect size—passage protection may therefore be more efficient than phenology shifting at increasing ϕ_s, but the most efficient strategy would be to simultaneously implement both. E could also be manipulated to increase Y_m, with or without shifting the timing of migration preparation (T_p). In our study system, where managed conditions vastly differ from historical conditions to which migrations have evolved, E and T_p had comparable maximum effects on Y_m. Furthermore, few populations exhibited readily controllable T_p, but most had relatively large windows over which T_p naturally occurred—therefore, using E to precisely initiate large batches of migration-ready individuals is probably the more efficient route toward increasing Y_m. However, it is important to note that most uncertainty in our efficacy analysis arose from estimating Y_m; one option to constrain this uncertainty would be to update the fit of our Y_m model once the study system experienced additional variability in E (i.e., larger and more seasonally dispersed flow pulses). Nevertheless, our results suggest that a promising facilitated migration strategy in our study system would be to use E to increase Y_m when ϕ_s was highest within the natural migration timeframe, at which point E should be used to further increase ϕ_s via passage protection.

The synergistic effects of time and E on Y_m and ϕ_s underpinned the high potential efficacy of facilitated migration in our study system (Figure 8), but density-dependence may also play a key role in this pattern. We explicitly accounted for autocorrelation in Y_m (i.e., that migration initiation in some members of a population encouraged others to begin migration); however, density-dependence was not considered in evaluating ϕ_s. While higher conspecific densities can reduce the availability of high-quality reproductive or rearing habitat (Dudley, 2019), higher conspecific densities have been shown to benefit migrations through predator swamping (Furey et al., 2021) and more efficient navigation (Okasaki et al., 2020). It is important to recognize that density-dependent detriments and benefits could both occur when implementing facilitated migration, and depending on the system, a more explicit and rigorous quantification of their potential impacts might be warranted.

Also deserving the attention of future research is an explicit examination of whether artificially manipulating migration phenology could lead to fundamental changes in how migrants respond to their surroundings. Could, for example, artificially expedited migration cause a migratory population to reduce its responsiveness to (or switch) initiation cues? It is important to note that, for migratory populations where facilitated migration is potentially appropriate—that is, those that inhabit anthropogenically altered ecosystems with near-irreversible land use changes and fundamentally altered environmental regimes—artificial selection is already occurring, but not in a manner nor at a pace that might confer benefits for migratory populations into the future.

Synchrony, which can be defined as the spatiotemporal overlap of individuals exhibiting a life history event like migration (Hulthén et al., 2022), is likely a major underlying biological phenomenon our models described. In addition to any effects of density-dependence (Gil et al., 2018), synchronous migration involves a shared preparatory and initiation response to common environmental conditions that have evolved to optimize phenological matching (McNamara et al., 2011). If the risks associated with phenological mismatch are especially high, then selection can favor higher degrees of synchrony in migrations. Migratory birds are a prominent example, as they generally exhibit greater synchrony of pre-breeding migration compared to post-breeding migration because mistiming the pre-breeding migration could uniquely impact the number and condition of surviving offspring (e.g., Nilsson et al., 2013). However, if the likelihood of phenological mismatch itself is especially high, then selection can favor risk-spreading through asynchronous migration. For example, in western North America, which exhibits considerable year-to-year variability in precipitation (Diffenbaugh et al., 2015; Swain et al., 2018) and ocean conditions (Checkley & Barth, 2009), Chinook salmon that spawn and rear within the same watershed have diversified into populations that exhibit uniquely timed migrations to and from the ocean (e.g., Fisher, 1994; Munsch et al., 2022).

Given that facilitated migration acts to synchronize migration, the nuances of phenological matching and mismatching are key to its success or failure. Our case study system presents a unique challenge, as both high risks to phenological mismatch (favoring synchrony) and exceptionally variable environments (favoring asynchrony) are at play. The oceanward migration of juvenile Chinook salmon is the largest population bottleneck to California populations originating from the Sacramento River watershed, especially during drought years (Michel, 2019). Artificially synchronizing this migration to occur under suitable river conditions could therefore make ecological sense. However, the California Current, which is the destination ecosystem of this migration, exhibits high degrees of seasonal variation and interannual variability (Checkley & Barth, 2009), and this can have massive impacts on Chinook salmon populations (Lindley et al., 2009). Ocean entry that coincides with seasonal upwelling, and therefore higher productivity, is associated with higher rates of marine growth and survival for juvenile Chinook salmon (Satterthwaite et al., 2014; Wells et al., 2012). However, growth and survival decline drastically when ocean entry coincides with periods of reduced upwelling, likely due to decreased food availability and increased vulnerability to predation (Wells et al., 2017). From a seasonal variation perspective, one specific challenge to reconcile in our study system is that oceanward migrations were most successful in late winter, which is generally the onset of net upwelling, but success rapidly diminished thereafter (Figure 4). In contrast, early ocean survival is lowest if ocean entry occurs shortly after the onset of net upwelling, but increases if entry occurs later into spring as upwelling progresses (Satterthwaite et al., 2014).

In fluctuating environments, facilitated migration could be a high-risk, high-reward strategy at present. However, we see two ways to mitigate the relevant risks. First, uncertainty could be constrained by improved monitoring, understanding, and forecasting of the study system. Among other consequences, a mistimed facilitation event (e.g., one which encourages ocean entry before sufficient upwelling has occurred) could cause juvenile Chinook salmon to enter the ocean during unproductive periods or at small body sizes when they are most vulnerable to gape-limited predators (Wells et al., 2017). However, forecasts of relevant ocean conditions are becoming increasingly skilled (e.g., Jacox et al., 2024), as are models of early ocean survival and growth that can incorporate forecasted conditions (e.g., Vasbinder et al., 2024). Thus, when tailored to destination ecosystem forecasts, facilitated migration could have a powerful role in the recovery of imperiled migratory populations. Intentional risk-spreading (i.e., explicit incorporation of migration asynchrony) is a second option to mitigate risks associated with fluctuating environments, and this could be accomplished within the facilitation framework simply by implementing multiple events per migratory population. Whether uncertainty reduction, risk-spreading, or both are used to wield the double-edged sword of synchrony more dexterously, a single recommendation for implementing facilitated migration emerges: rather than trickle out sub-par management actions across the full migration phenology, limited resources should be directed at providing fewer high-quality events with the greatest situational awareness possible.

It is widely recognized that the restoration of natural environmental regimes, to which native organisms are adapted, could have major benefits for anthropogenically altered ecosystems (e.g., Baruch et al., 2024; Kendy et al., 2017; Kiernan et al., 2012; Poff & Zimmerman, 2010; Yarnell et al., 2015). However, especially in ecosystems where managers face competing demands for resources between humans and wildlife, restoration actions are often prioritized based upon specific, defensible benefits for imperiled species (e.g., NMFS, 1994, 1999). We therefore see a potential role of facilitated migration in regime restoration as one of political expediency. If migrations of imperiled taxa are adapted to take advantage of specific features of natural regimes, as appears to be true in our case study, then implementation of the feature within the facilitated migration framework could ultimately supply co-benefits for other ecosystem constituents more rapidly than advocating for the restoration of the feature itself. For example, in highly regulated rivers like our study system, there has been a decades-long push to move beyond management based on minimum instream flow requirements toward flow schedules that recreate important aspects of natural flow regimes (Kiernan et al., 2012; Poff & Zimmerman, 2010). This so-called "functional flows" concept specifically recommends that, when recreating features of natural flow regimes (e.g., wet-season initiation flows, peak magnitude flows, spring recession flows, and dry-season low flows), the timing, rate of change, magnitude, and duration of flow events are all important considerations if the goal is to restore self-sustaining ecosystems (Baruch et al., 2024; Yarnell et al., 2015). As it relates to this paradigm, the models from our case study are currently capable of estimating the increased number of threatened and endangered natural-origin Chinook salmon that would successfully migrate by implementing facilitated migration in the form of natural flow regime features versus status quo flow management—biological outcomes that could justify the water use of regime restoration.

Guiding salmon recovery in our study system

By blocking reproductive areas (Yoshiyama et al., 2001) and rearing habitat (Whipple et al., 2012) while reducing and homogenizing the flow regimes of migratory corridors (Buer et al., 1990), humans have drastically reduced the size and diversity of Chinook salmon populations in California (Munsch et al., 2022; Sturrock et al., 2020). Here, dams are mainly used to regulate the release of water from storage reservoirs for flood control, agricultural, and municipal uses (Munsch et al., 2022). However, reservoir releases and climatological conditions have predictable effects on downstream flow and temperature (Daniels & Danner, 2020; Michel et al., 2023; Pike et al., 2013), two variables with substantial effects on the life history of migratory aquatic species, including Chinook salmon (Quinn, 2018). In our case study, we found that relatively simple temperature and flow manipulations could be leveraged to prepare, initiate, and protect downstream movements and oceanward migrations of juvenile Chinook salmon, which are the major population bottlenecks hampering the recovery of this imperiled taxon in California (Michel, 2019; Munsch et al., 2022; Sturrock et al., 2020). Our estimates suggest that, depending on the population evaluated, a single, comprehensive facilitation event, including thermally shifted preparation, flow pulse-mediated initiation, and passage protection via increased flow (i.e., Figure 2G), could increase the size of natural-origin populations at ocean entry by 43%–479% compared to the status quo scenario (Figure 8, scenario 3).

Some system-specific aspects of our results must be highlighted. We found strong seasonality in successful migrant passage, such that migrations were relatively successful during winter but became increasingly unsuccessful from early March until mid-May (Figure 4). At least in our data, few natural-origin smolts from any population initiated their migration during the relatively successful winter migration period; instead, this time of year was characterized by fry downstream movement. However, winter not only coincides with reduced sampling abilities due to storm events and high flows but also the migration of spring-run yearlings from tributaries downstream of RBDD (thus not enumerated in our data), which have outsized contributions to adult returns in some drought years (Cordoleani et al., 2021). Winter-run are currently the only population of the four listed as endangered (NMFS, 1994), yet their natural migrations, which occur from late summer through fall, fell mostly outside the period monitored with telemetry. In addition to adverse conditions during incubation and rearing (Dudley, 2019; Martin et al., 2017), it is plausible that the recovery of natural winter-run populations is limited by adverse conditions during migration. Fall- and spring-run smolts were found to initiate their migration during the spring—a period of rapidly declining migration success. This would suggest that, assuming suitable ocean conditions, relatively small advances in migration initiation during the spring could yield disproportionately large population gains. Furthermore, the boost in migration success per unit flow addition increased when migrations began earlier in spring, further amplifying the benefits of advanced initiation.

Increased flows for the duration of migration, which on average ranged from 7.70 to 37.9 days depending on the population and release location, drastically improved the successful passage probability of juvenile Chinook salmon in our study system (Figures 4 and 5). Similar to some studies (Antonsson & Gudjonsson, 2002; Quinn, 2018; Raymond, 1979; Sturrock et al., 2020; Sykes et al., 2009; Whalen et al., 1999), we found that fish were exceptionally responsive to flow changes, with flow pulses readily triggering fry downstream movement and smolt migration in large batches of ready individuals under typical conditions (Figure 7). Taken together, we found that, depending on the population evaluated, a single facilitation event that only included precise initiation via flow pulse and passage protection via increased flow (i.e., Figure 2E) could increase the size of natural-origin populations at ocean entry by 27%–293% compared to the status quo scenario (Figure 8, scenario 2).

While temperature showed population-specific associations with migration preparation, the direction of this relationship was unexpected. In *Oncorhynchus* spp., increased temperature typically leads to earlier migration (Kovach et al., 2013; Otero et al., 2014). Conversely, for spring- and fall-run Chinook salmon populations in our system, the opposite association was found under typical flows (Figure 6). While warmer temperatures should expedite smoltification (Bourret et al., 2016; Hoar, 1976; Muir et al., 1994), it is possible that the unusually low and homogenous flows in this system compared to the historical hydrograph (Buer et al., 1990) reduced the discernable effect of temperature because fish were so eager to respond to any flow increase. Only under exceptionally high flows did we find that temperature increases resulted in advanced migrations. In addition, temperature is tightly regulated in the main stem Sacramento River downstream of Keswick Dam (Daniels & Danner, 2020; Michel et al., 2023; Pike et al., 2013); thus, evaluated populations likely experienced a suppressed temperature regime compared to the unmanaged conditions that occurred historically.

A lack of association between migration preparation and temperature in late-fall and winter-run populations could be explained by sampling methodology, life history, or both. RSTs are less efficient at capturing late-fall-run smolts given that this population typically migrates at larger size and older age than the other runs, allowing them to evade RSTs more easily (Pilger et al., 2019; Quinn, 2018). For winter-run, it is possible that their unique life history, which historically involved spawning and rearing in consistently cold, spring-fed tributaries to the Sacramento River (NMFS, 1994; Yoshiyama et al., 2001), could have reduced the relevance of temperature as a smoltification trigger during their evolution. While temperature regulation could be used as a tool to help salmon populations access safer passage timeframes for migration, the efficacy of this strategy without any passage protection seems limited. Our estimates suggested that, depending on the population evaluated, a single facilitation event that only included thermally shifted phenology and precise initiation (i.e., Figure 2F) could increase the size of natural-origin populations at ocean entry by 2%–25% compared to the status quo scenario (Figure 8, scenario 1).

Our case study focused on populations produced upstream of RBDD in the main stem Sacramento River, but it is important to note that natural-origin juveniles rear outside of this reach. For example, most spring-run populations are typically found in high elevation tributaries of the Sacramento River (Cordoleani et al., 2018; Cordoleani et al., 2021; NMFS, 1999; Notch et al., 2020). Nevertheless, water management below Keswick Dam can still impart benefits to the early life history of the overall population, as fry moving downstream from tributaries may rear in the lower Sacramento River during the winter and early spring, and the passage of smolts migrating in late spring (Cordoleani et al., 2018; Notch et al., 2020) and yearlings in early winter (Cordoleani et al., 2021) will benefit from flow pulses. As a result of delayed incubation, rearing, and migration from high elevation habitat, tributary spring-run typically experience relatively low flows and high water temperatures in the Sacramento River as agricultural diversion rates increase in late spring (Cordoleani et al., 2018; Notch et al., 2020). Incorporating management actions for these tributary populations, as outlined in this study, is therefore an important consideration for recovery. Likewise, these populations and the environment they inhabit provide a more natural system that could be studied and mimicked to better prepare populations in the main stem of the Sacramento River for migration.

Given a drastically reduced life history diversity in response to ~175 years of intensive anthropogenic habitat alteration, salmon populations in California now tend to be one season of anomalous conditions or mismanagement away from collapse (Lindley et al., 2009). We found that, on average, around 6.0% of juvenile salmon in the Sacramento River watershed survive the migration to the estuary exit. Thus, if natural-origin populations are to continue existing, a focus point should be the oceanward migration survival bottleneck (Michel, 2019). In alignment with a growing body of literature (Buchanan et al., 2018; Crozier &

Zabel, 2006; Michel, 2019; Michel et al., 2015, 2021; Sturrock et al., 2020), our results clearly demonstrate that more water would drastically benefit Chinook salmon populations. We acknowledge that this is not a simple task, as increasing precipitation volatility and drought risk (Diffenbaugh et al., 2015; Swain et al., 2018) are sure to make the balance of water allocation for humans and wildlife more difficult in the future (Lund et al., 2018). However, our results also demonstrate that the timing of water allocation for wildlife is key—even with existing data limitations, facilitated migration that, at a minimum, synchronizes migration initiation with passage protection could effectively increase the number of successful migrants per unit water allocated. Thus, relatively small but properly timed pulse flows could not only help revive ecosystems (Kendy et al., 2017) but also help recover imperiled populations.

In our case study, we identified three major data gaps that should be filled by future research efforts. First, the temporal scope of successful passage probability should be expanded to encompass the entirety of the water year, given that natural-origin fish migrate year-round (Figure 4). The priority would be to evaluate fall and early winter, when the endangered winter-run populations tend to migrate. Second, the scope of flows and flow pulses that juvenile salmon experience in this system should be expanded in order to further resolve associations. Specifically, both have skewed distributions, with many observations at small values and far fewer at moderate or high values. Third, telemetry efforts should be conducted for the fry downstream movements, comparable to current efforts with smolts. This is currently a technological hurdle and requires further miniaturization of acoustic tags or alternative methods for estimating survival.

CONCLUSION

Our goal was to lay out a framework to enhance migratory species conservation and management. While we believe it could have utility in other study systems, experts in those systems would be better equipped to assess its relevance now and in the future. We hazard a grim guess that more ecosystems will become anthropogenically altered to the extent that facilitated migration becomes feasible, even necessary. At its core, facilitated migration not only forces scientists and managers to critically evaluate how a species migration can be supported, but also how it can be manipulated. In doing so, opportunities and knowledge gaps become readily apparent. Resolving knowledge gaps concerning how environmental conditions prepare, initiate, and safeguard migrants is only feasible while natural migrations exist.

AUTHOR CONTRIBUTIONS

Conceptualization: Benjamin P. Burford and Cyril J. Michel. *Data curation*: Benjamin P. Burford, Jeremy J. Notch, William R. Poytress, and Cyril J. Michel. *Formal analysis*: Benjamin P. Burford and Cyril J. Michel. *Funding acquisition*: Cyril J. Michel. *Investigation*: Benjamin P. Burford, Jeremy J. Notch, William R. Poytress, and Cyril J. Michel. *Methodology*: Benjamin P. Burford, Jeremy J. Notch, William R. Poytress, and Cyril J. Michel. *Project administration*: Benjamin P. Burford and Cyril J. Michel. *Resources*: Jeremy J. Notch and Cyril J. Michel. *Supervision*: Jeremy J. Notch and Cyril J. Michel. *Validation*: Benjamin P. Burford. *Visualization*: Benjamin P. Burford. *Writing—original draft*: Benjamin P. Burford. *Writing—review and editing*: Benjamin P. Burford, Jeremy J. Notch, William R. Poytress, and Cyril J. Michel.

ACKNOWLEDGMENTS

We thank Peter Dudley, Eric Danner, and two anonymous reviewers for providing insightful feedback that improved the manuscript. We are grateful to the people and agencies who contributed to the publicly available datasets used in this study (ITAG, 2024; USGS, 2024; Voss, 2024). We are especially grateful to Arnold Ammann for acoustic telemetry coordination, logistical support, and data management. Lastly, we extend a special thanks to Kevin Niemela, Robert Null, Kaitlin Dunham, Brett Galyean, and the helpful staff of Livingston Stone and Coleman National Fish Hatcheries.

CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Data (Burford, 2024a) are available in Dryad at https://doi.org/10.5061/dryad.xksn02vpx. Code (Burford, 2024b) is available in Zenodo at https://doi.org/10.5281/zenodo.11246542. Raw data utilized for this research are available via (a) the Interagency Telemetry Advisory Group (ITAG), Central Valley Enhanced Acoustic Tagging Project (2024) at https://oceanview.pfeg.noaa.gov/erddap/tabledap/FED_JSATS_detects.html; (b) the United States Fish and Wildlife Service (USFWS) Red Bluff Diversion Dam Rotary Screw Trap Juvenile Fish Monitoring Database, Environmental Data Initiative (Voss, 2024) at https://doi.org/10.6073/pasta/3534f98e531d7238dca001bfd8e55dcf; (c) the United States Geological Survey (USGS) National Water Information System, Water Data for California (2024) at https://nwis.waterdata.usgs.gov/ca/nwis.

ORCID

Benjamin P. Burford https://orcid.org/0000-0002-2120-3769

Cyril J. Michel https://orcid.org/0000-0002-1198-3837

REFERENCES

Adamczewska, A. M., and S. Morris. 2001. “Ecology and Behavior of *Gecarcoidea natalis*, the Christmas Island Red Crab, during the Annual Breeding Migration.” *The Biological Bulletin* 200(3): 305–320.

Aldvén, D., E. Degerman, and J. Höjesjö. 2015. “Environmental Cues and Downstream Migration of Anadromous Brown Trout (*Salmo trutta*) and Atlantic Salmon (*Salmo salar*) Smolts.” *Boreal Environment Research* 20: 35–44.

Allen, A. M., and N. J. Singh. 2016. “Linking Movement Ecology with Wildlife Management and Conservation.” *Frontiers in Ecology and Evolution* 3: 155.

Antonsson, T., and S. Gudjonsson. 2002. “Variability in Timing and Characteristics of Atlantic Salmon Smolt in Icelandic Rivers.” *Transactions of the American Fisheries Society* 131(4): 643–655.

Baruch, E. M., S. M. Yarnell, T. E. Grantham, J. R. Ayers, A. L. Rypel, and R. A. Lusardi. 2024. “Mimicking Functional Elements of the Natural Flow Regime Promotes Native Fish Recovery in a Regulated River.” *Ecological Applications* 34(6): e3013.

Bauer, S., and B. J. Hoye. 2014. “Migratory Animals Couple Biodiversity and Ecosystem Functioning Worldwide.” *Science* 344(6179): 1242552.

Blanchet, R., M. Batal, L. Johnson-Down, S. Johnson, Okanagan Nation Salmon Reintroduction Initiatives Colette Louie Eliza Terbasket Pauline Terbasket Howie Wright, and N. Willows. 2021. “An Indigenous Food Sovereignty Initiative Is Positively Associated with Well-Being and Cultural Connectedness in a Survey of Syilx Okanagan Adults in British Columbia, Canada.” *BMC Public Health* 21: 1–12.

Bourret, S. L., C. C. Caudill, and M. L. Keefer. 2016. “Diversity of Juvenile Chinook Salmon Life History Pathways.” *Reviews in Fish Biology and Fisheries* 26(3): 375–403.

Buchanan, R. A., P. L. Brandes, and J. R. Skalski. 2018. “Survival of Juvenile Fall-Run Chinook Salmon through the San Joaquin River Delta, California, 2010–2015.” *North American Journal of Fisheries Management* 38(3): 663–679.

Buer, K., D. Forwalter, M. Kissel, and B. Stohler. 1990. “Ecological Processes along a Meandering River.” In *Protection, Management, and Restoration for the 1990’s: Proceedings of the California Riparian Systems Conference, September 22–24, 1988, Davis, California*, 110. 22 pp. Pacific Southwest Forest and Range Experiment Station.

Burford, B. 2024a. “Facilitated Migration Could Bolster Migrant Passage through Anthropogenically Altered Ecosystems.” Dryad. https://doi.org/10.5061/dryad.xksn02vpx.

Burford, B. 2024b. “Facilitated Migration Could Bolster Migrant Passage through Anthropogenically Altered Ecosystems.” Zenodo. https://doi.org/10.5281/zenodo.11246542.

California Department of Water Resources (DWR). 2022. “Water Plan Balance Data.” https://water.ca.gov/Programs/California-Water-Plan/Water-Portfolios.

Checkley, D. M., Jr., and J. A. Barth. 2009. “Patterns and Processes in the California Current System.” *Progress in Oceanography* 83(1–4): 49–64.

Cooke, S. J., C. M. Woodley, M. Brad Eppard, R. S. Brown, and J. L. Nielsen. 2011. “Advancing the Surgical Implantation of Electronic Tags in Fish: A Gap Analysis and Research Agenda Based on a Review of Trends in Intracoelomic Tagging Effects Studies.” *Reviews in Fish Biology and Fisheries* 21: 127–151.

Cordoleani, F., C. C. Phillis, A. M. Sturrock, A. M. FitzGerald, A. Malkassian, G. E. Whitman, P. K. Weber, and R. C. Johnson. 2021. “Threatened Salmon Rely on a Rare Life History Strategy in a Warming Landscape.” *Nature Climate Change* 11(11): 982–88.

Cordoleani, F., J. Notch, A. S. McHuron, A. J. Ammann, and C. J. Michel. 2018. “Movement and Survival of Wild Chinook Salmon Smolts from Butte Creek during their out-Migration to the Ocean: Comparison of a Dry Year Versus a Wet Year.” *Transactions of the American Fisheries Society* 147(1): 171–184.

Crozier, L., and R. W. Zabel. 2006. “Climate Impacts at Multiple Scales: Evidence for Differential Population Responses in Juvenile Chinook Salmon.” *Journal of Animal Ecology* 75: 1100–1109.

Daniels, M. E., and E. M. Danner. 2020. “The Drivers of River Temperatures below a Large Dam.” *Water Resources Research* 56(5): e2019WR026751.

Diffenbaugh, N. S., D. L. Swain, and D. Touma. 2015. “Anthropogenic Warming Has Increased Drought Risk in California.” *Proceedings of the National Academy of Sciences of the United States of America* 112(13): 3931–36.

Dingle, H. 2014. *Migration: The Biology of Life on the Move*. Oxford: Oxford University Press.

Dudley, P. N. 2019. “Insights from an Individual Based Model of a Fish Population on a Large Regulated River.” *Environmental Biology of Fishes* 102(8): 1069–95.

Eliason, E. J., T. D. Clark, M. J. Hague, L. M. Hanson, Z. S. Gallagher, K. M. Jeffries, M. K. Gale, D. A. Patterson, S. G. Hinch, and A. P. Farrell. 2011. “Differences in Thermal Tolerance among Sockeye Salmon Populations.” *Science* 332(6025): 109–112.

Fisher, F. W. 1994. “Past and Present Status of Central Valley Chinook Salmon.” *Conservation Biology* 8(3): 870–73.

Folmar, L. C., and W. W. Dickhoff. 1980. “The Parr—Smolt Transformation (Smoltification) and Seawater Adaptation in Salmonids: A Review of Selected Literature.” *Aquaculture* 21(1): 1–37.

Fraser, K. C., K. T. Davies, C. M. Davy, A. T. Ford, D. T. Flockhart, and E. G. Martins. 2018. “Tracking the Conservation Promise of Movement Ecology.” *Frontiers in Ecology and Evolution* 6: 150.

Frechette, D. M., J. P. Hawkes, and J. F. Kocik. 2023. “Managing for Atlantic Salmon Smolt Run Timing Variability in a Changing Climate.” *North American Journal of Fisheries Management* 43(2): 517–538.

Fryer, J. L., and K. S. Pilcher. 1974. *Effects of Temperature on Diseases of Salmonid Fishes*. Washington, DC: Office of Research and Development U.S. Environmental Protection Agency.

Furey, N. B., E. G. Martins, and S. G. Hinch. 2021. “Migratory Salmon Smolts Exhibit Consistent Interannual Depensatory Predator Swamping: Effects on Telemetry-Based Survival Estimates.” *Ecology of Freshwater Fish* 30(1): 18–30.

Gaines, P. D., and C. D. Martin. 2002. *Abundance and Seasonal, Spatial and Diel Distribution Patterns of Juvenile Salmonids Passing the Red Bluff Diversion Dam, Sacramento River*. Red Bluff Research Pumping Plant Report Series, Vol. 14. Red Bluff, CA: U.S. Fish and Wildlife Service.

Gartrell, G., J. Mount, E. Hanak, and B. Gray. 2017. *A New Approach to Accounting for Environmental Water: Insights from the Sacramento–San Joaquin Delta*. San Francisco, CA: Public Policy Institute of California. 22 pp.

Gil, M. A., A. M. Hein, O. Spiegel, M. L. Baskett, and A. Sih. 2018. “Social Information Links Individual Behavior to Population and Community Dynamics." *Trends in Ecology & Evolution* 33 (7): 535–548.

Golet, G. H., C. Low, S. Avery, K. Andrews, C. J. McColl, R. Laney, and M. D. Reynolds. 2018. "Using Ricelands to Provide Temporary Shorebird Habitat during Migration." *Ecological Applications* 28(2): 409–426.

Grant, R. A., E. A. Chadwick, and T. Halliday. 2009. "The Lunar Cycle: A Cue for Amphibian Reproductive Phenology?" *Animal Behaviour* 78(2): 349–357.

Hartig, F. 2022. "DHARMa: Residual Diagnostics for Hierarchical (Multi-Level/Mixed) Regression Models." R Package Version 0.4.6. https://CRAN.R-project.org/package=DHARMa.

Harvey, B. N., D. P. Jacobson, and M. A. Banks. 2014. "Quantifying the Uncertainty of a Juvenile Chinook Salmon Race Identification Method for a Mixed-Race Stock." *North American Journal of Fisheries Management* 34(6): 1177–86.

Hassrick, J. L., A. J. Ammann, R. W. Perry, S. N. John, and M. E. Daniels. 2022. "Factors Affecting Spatiotemporal Variation in Survival of Endangered Winter-Run Chinook Salmon Out-Migrating from the Sacramento River." *North American Journal of Fisheries Management* 42(2): 375–395.

Hausner, A., J. F. Samhouri, E. L. Hazen, D. Delgerjargal, and B. Abrahms. 2021. "Dynamic Strategies Offer Potential to Reduce Lethal Ship Collisions with Large Whales under Changing Climate Conditions." *Marine Policy* 130: 104565.

Hazen, E. L., D. M. Palacios, K. A. Forney, E. A. Howell, E. Becker, A. L. Hoover, L. Irvine, et al. 2017. "WhaleWatch: A Dynamic Management Tool for Predicting Blue Whale Density in the California Current." *Journal of Applied Ecology* 54(5): 1415–28.

Henderson, M. J., I. S. Iglesias, C. J. Michel, A. J. Ammann, and D. D. Huff. 2019. "Estimating Spatial–Temporal Differences in Chinook Salmon Outmigration Survival with Habitat-and Predation-Related Covariates." *Canadian Journal of Fisheries and Aquatic Sciences* 76(9): 1549–61.

Hoar, W. S. 1976. "Smolt Transformation: Evolution, Behavior, and Physiology." *Journal of the Fisheries Research Board of Canada* 33(5): 1233–52.

Hoegh-Guldberg, O., L. Hughes, S. McIntyre, D. B. Lindenmayer, C. Parmesan, H. P. Possingham, and C. D. Thomas. 2008. "Assisted Colonization and Rapid Climate Change." *Science* 321(5887): 345–46.

Hulthén, K., B. B. Chapman, P. A. Nilsson, L. A. Hansson, C. Skov, J. Brodersen, and C. Brönmark. 2022. "Timing and Synchrony of Migration in a Freshwater Fish: Consequences for Survival." *Journal of Animal Ecology* 91(10): 2103–12.

ITAG (Interagency Telemetry Advisory Group). 2024. "Central Valley Enhanced Acoustic Tagging Project." Accessed at NOAA Environmental Research Division's Data Access Program. https://oceanview.pfeg.noaa.gov/erddap/tabledap/FED_JSATS_detects.html.

Jacox, M. G., S. J. Bograd, J. Fiechter, M. Pozo Buil, M. Alexander, D. Amaya, N. Cordero Quiros, H. Ding, and R. R. Rykaczewski. 2024. "Linking Upwelling Dynamics and Subsurface Nutrients to Projected Productivity Changes in the California Current System." *Geophysical Research Letters* 51(10): e2023GL108096.

Jonsson, B., and J. Ruud-Hansen. 1985. "Water Temperature as the Primary Influence on Timing of Seaward Migrations of Atlantic Salmon (*Salmo salar*) Smolts." *Canadian Journal of Fisheries and Aquatic Sciences* 42(3): 593–95.

Kendy, E., K. W. Flessa, K. J. Schlatter, C. A. de la Parra, O. M. H. Huerta, Y. K. Carrillo-Guerrero, and E. Guillen. 2017. "Leveraging Environmental Flows to Reform Water Management Policy: Lessons Learned from the 2014 Colorado River Delta Pulse Flow." *Ecological Engineering* 106: 683–694.

Kiernan, J. D., P. B. Moyle, and P. K. Crain. 2012. "Restoring Native Fish Assemblages to a Regulated California Stream Using the Natural Flow Regime Concept." *Ecological Applications* 22(5): 1472–82.

Kovach, R. P., J. E. Joyce, J. D. Echave, M. S. Lindberg, and D. A. Tallmon. 2013. "Earlier Migration Timing, Decreasing Phenotypic Variation, and Biocomplexity in Multiple Salmonid Species." *PLoS One* 8(1): e53807.

Lindley, S. T., C. B. Grimes, M. S. Mohr, W. T. Peterson, J. E. Stein, J. J. Anderson, J. T. Botsford, et al. 2009. *What Caused the Sacramento River fall Chinook Stock Collapse?* National Oceanic and Atmospheric Administration (NOAA) National Marine Fisheries Service Technical Memorandum NOAA-TM-NMFS-SWFSC-447 (Tech Memo NMFS-SWFSC 447). Santa Cruz, CA: NOAA.

Lund, J., J. Medellin-Azuara, J. Durand, and K. Stone. 2018. "Lessons from California's 2012–2016 Drought." *Journal of Water Resources Planning and Management* 144(10): 04018067.

Macdonald, J. S., J. Morrison, and D. A. Patterson. 2012. "The Efficacy of Reservoir Flow Regulation for Cooling Migration Temperature for Sockeye Salmon in the Nechako River Watershed of British Columbia." *North American Journal of Fisheries Management* 32(3): 415–427.

Marschall, E. A., M. E. Mather, D. L. Parrish, G. W. Allison, and J. R. McMenemy. 2011. "Migration Delays Caused by Anthropogenic Barriers: Modeling Dams, Temperature, and Success of Migrating Salmon Smolts." *Ecological Applications* 21(8): 3014–31.

Martin, B. T., A. Pike, S. N. John, N. Hamda, J. Roberts, S. T. Lindley, and E. M. Danner. 2017. "Phenomenological Vs. Biophysical Models of Thermal Stress in Aquatic Eggs." *Ecology Letters* 20(1): 50–59.

Martin, C. D., P. D. Gaines, and R. R. Johnson. 2001. *Estimating the Abundance of Sacramento River Juvenile Winter Chinook Salmon with Comparisons to Adult Escapement.* Red Bluff Research Pumping Plant Report Series, Vol. 5. Red Bluff, CA: U.S. Fish and Wildlife Service.

McCormick, S. D., R. A. Cunjak, B. Dempson, M. F. O'Dea, and J. B. Carey. 1999. "Temperature-Related Loss of Smolt Characteristics in Atlantic Salmon (*Salmo salar*) in the Wild." *Canadian Journal of Fisheries and Aquatic Sciences* 56(9): 1649–67.

McInturf, A. G., K. W. Zillig, K. Cook, J. Fukumoto, A. Jones, E. Patterson, D. E. Cocherell, C. J. Michel, D. Caillaud, and N. A. Fangue. 2022. "In Hot Water? Assessing the Link between Fundamental Thermal Physiology and Predation of Juvenile Chinook Salmon." *Ecosphere* 13(11): e4264.

McNamara, J. M., Z. Barta, M. Klaassen, and S. Bauer. 2011. "Cues and the Optimal Timing of Activities under Environmental Changes." *Ecology Letters* 14(12): 1183–90.

Michel, C. J. 2019. "Decoupling Outmigration from Marine Survival Indicates Outsized Influence of Streamflow on Cohort Success for California's Chinook Salmon Populations." *Canadian Journal of Fisheries and Aquatic Sciences* 76(8): 1398–1410.

Michel, C. J., A. J. Ammann, S. T. Lindley, P. T. Sandstrom, E. D. Chapman, M. J. Thomas, G. P. Singer, A. P. Klimley, and R. B.

MacFarlane. 2015. "Chinook Salmon Outmigration Survival in Wet and Dry Years in California's Sacramento River." *Canadian Journal of Fisheries and Aquatic Sciences* 72(11): 1749–59.

Michel, C. J., J. J. Notch, F. Cordoleani, A. J. Ammann, and E. M. Danner. 2021. "Nonlinear Survival of Imperiled Fish Informs Managed Flows in a Highly Modified River." *Ecosphere* 12(5): e03498.

Michel, C. J., M. E. Daniels, and E. M. Danner. 2023. "Discharge-Mediated Temperature Management in a Large, Regulated River, with Implications for Management of Endangered Fish." *Water Resources Research* 59(9): e2023WR035077.

Michel, C. J., M. J. Henderson, C. M. Loomis, J. M. Smith, N. J. Demetras, I. S. Iglesias, B. M. Lehman, and D. D. Huff. 2020. "Fish Predation on a Landscape Scale." *Ecosphere* 11(6): e03168.

Mount, J., B. Gray, C. Chappelle, G. Gartrell, T. Grantham, P. Moyle, N. Seavy, L. Szeptycki, and B. Thompson. 2017. *Managing California's Freshwater Ecosystems: Lessons from the 2012–2016 Drought*. San Francisco, CA: Public Policy Institute of California. 52 pp.

Muir, W. D., W. S. Zaugg, A. E. Giorgi, and S. McCutcheon. 1994. "Accelerating Smolt Development and Downstream Movement in Yearling Chinook Salmon with Advanced Photoperiod and Increased Temperature." *Aquaculture* 123(3–4): 387–399.

Munsch, S. H., C. M. Greene, N. J. Mantua, and W. H. Satterthwaite. 2022. "One Hundred-Seventy Years of Stressors Erode Salmon Fishery Climate Resilience in California's Warming Landscape." *Global Change Biology* 28(7): 2183–2201.

National Marine Fisheries Service (NMFS). 1994. "Endangered and Threatened Species; Status of Sacramento River Winter-Run Chinook Salmon; Final Rule." *Federal Register* 59(2): 440–450.

National Marine Fisheries Service (NMFS). 1999. "Endangered and Threatened Species; Threatened Status for Two Chinook Salmon Evolutionarily Significant Units (ESUs) in California; Final Rule." *Federal Register* 64(179): 50394–415.

Nilsson, C., R. H. Klaassen, and T. Alerstam. 2013. "Differences in Speed and Duration of Bird Migration between Spring and Autumn." *The American Naturalist* 181(6): 837–845.

Northwest Power and Conservation Council (NPCC). 2014. "Columbia River Basin Fish and Wildlife Program." 334 pp. https://www.nwcouncil.org/sites/default/files/2014-12_1.pdf.

Notch, J. J., A. S. McHuron, C. J. Michel, F. Cordoleani, M. Johnson, M. J. Henderson, and A. J. Ammann. 2020. "Outmigration Survival of Wild Chinook Salmon Smolts through the Sacramento River during Historic Drought and High Water Conditions." *Environmental Biology of Fishes* 103: 561–576.

Oestreich, W. K., M. S. Chapman, and L. B. Crowder. 2020. "A Comparative Analysis of Dynamic Management in Marine and Terrestrial Systems." *Frontiers in Ecology and the Environment* 18(9): 496–504.

Okasaki, C., M. L. Keefer, P. A. Westley, and A. M. Berdahl. 2020. "Collective Navigation Can Facilitate Passage through Human-Made Barriers by Homeward Migrating Pacific Salmon." *Proceedings of the Royal Society B: Biological Sciences* 287(1937): 20202137.

Olivetti, S., M. A. Gil, V. K. Sridharan, and A. M. Hein. 2021. "Merging Computational Fluid Dynamics and Machine Learning to Reveal Animal Migration Strategies." *Methods in Ecology and Evolution* 12(7): 1186–1200.

Otero, J., J. H. L'Abée-Lund, T. Castro-Santos, K. Leonardsson, G. O. Storvik, B. Jonsson, B. Dempson, et al. 2014. "Basin-Scale Phenology and Effects of Climate Variability on Global Timing of Initial Seaward Migration of Atlantic Salmon (*Salmo salar*)." *Global Change Biology* 20(1): 61–75.

Pedgley, D. E., D. R. Reynolds, G. M. Tatchell, V. A. Drake, and A. G. Gatehouse. 1995. "Long-Range Insect Migration in Relation to Climate and Weather: Africa and Europe." In *Insect Migration: Tracking Resources through Space and Time*, edited by V. A. Drake and A. G. Gatehouse. Cambridge: Cambridge University Press. 3–29.

Perry, R. W., A. C. Pope, J. G. Romine, P. L. Brandes, J. R. Burau, A. R. Blake, A. J. Ammann, and C. J. Michel. 2018. "Flow-Mediated Effects on Travel Time, Routing, and Survival of Juvenile Chinook Salmon in a Spatially Complex, Tidally Forced River Delta." *Canadian Journal of Fisheries and Aquatic Sciences* 75(11): 1886–1901.

Phillis, C. C., A. M. Sturrock, R. C. Johnson, and P. K. Weber. 2018. "Endangered Winter-Run Chinook Salmon Rely on Diverse Rearing Habitats in a Highly Altered Landscape." *Biological Conservation* 217: 358–362.

Pike, A., E. Danner, D. Boughton, F. Melton, R. Nemani, B. Rajagopalan, and S. Lindley. 2013. "Forecasting River Temperatures in Real Time Using a Stochastic Dynamics Approach." *Water Resources Research* 49(9): 5168–82.

Pilger, T. J., M. L. Peterson, D. Lee, A. Fuller, and D. Demko. 2019. "Evaluation of Long-Term Mark-Recapture Data for Estimating Abundance of Juvenile Fall-Run Chinook Salmon on the Stanislaus River from 1996 to 2017." *San Francisco Estuary and Watershed Science* 17(1): 1–21.

Poff, N. L., and J. K. Zimmerman. 2010. "Ecological Responses to Altered Flow Regimes: A Literature Review to Inform the Science and Management of Environmental Flows." *Freshwater Biology* 55(1): 194–205.

Quinn, T. P. 2018. *The Behavior and Ecology of Pacific Salmon and Trout*. Seattle, WA: University of Washington press.

R Core Team. 2021. *R: A Language and Environment for Statistical Computing*. Vienna: R Foundation for Statistical Computing.

Ramenofsky, M., and J. C. Wingfield. 2007. "Regulation of Migration." *BioScience* 57(2): 135–143.

Raymond, H. L. 1979. "Effects of Dams and Impoundments on Migrations of Juvenile Chinook Salmon and Steelhead from the Snake River, 1966 to 1975." *Transactions of the American Fisheries Society* 108(6): 505–529.

Reis, G. J., J. K. Howard, and J. A. Rosenfield. 2019. "Clarifying Effects of Environmental Protections on Freshwater Flows To—And Water Exports From—The San Francisco Bay Estuary." *San Francisco Estuary and Watershed Science* 17(1): 1–22.

Reynolds, M. D., B. L. Sullivan, E. Hallstein, S. Matsumoto, S. Kelling, M. Merrifield, D. Fink, et al. 2017. "Dynamic Conservation for Migratory Species." *Science Advances* 3(8): e1700707.

Satterthwaite, W. H., S. M. Carlson, S. D. Allen-Moran, S. Vincenzi, S. J. Bograd, and B. K. Wells. 2014. "Match-Mismatch Dynamics and the Relationship between Ocean-Entry Timing and Relative Ocean Recoveries of Central Valley Fall Run Chinook Salmon." *Marine Ecology Progress Series* 511: 237–248.

Smircich, M. G., and J. T. Kelly. 2014. "Extending the 2% Rule: The Effects of Heavy Internal Tags on Stress Physiology, Swimming Performance, and Growth in Brook Trout." *Animal Biotelemetry* 2(1): 1–7.

Stenseth, N. C., and A. Mysterud. 2002. “Climate, Changing Phenology, and Other Life History Traits: Nonlinearity and Match–Mismatch to the Environment.” *Proceedings of the National Academy of Sciences of the United States of America* 99(21): 13379–81.

Stich, D. S., M. T. Kinnison, J. F. Kocik, and J. D. Zydlewski. 2015. “Initiation of Migration and Movement Rates of Atlantic Salmon Smolts in Fresh Water.” *Canadian Journal of Fisheries and Aquatic Sciences* 72(9): 1339–51.

Sturrock, A. M., S. M. Carlson, J. D. Wikert, T. Heyne, S. Nusslé, J. E. Merz, H. J. W. Sturrock, and R. C. Johnson. 2020. “Unnatural Selection of Salmon Life Histories in a Modified Riverscape.” *Global Change Biology* 26: 1235–47.

Swain, D. L., B. Langenbrunner, J. D. Neelin, and A. Hall. 2018. “Increasing Precipitation Volatility in Twenty-First-Century California.” *Nature Climate Change* 8(5): 427–433.

Sykes, G. E., C. J. Johnson, and J. M. Shrimpton. 2009. “Temperature and Flow Effects on Migration Timing of Chinook Salmon Smolts.” *Transactions of the American Fisheries Society* 138(6): 1252–65.

Taylor, J. R. 1997. *An Introduction to Error Analysis*, 2nd ed. Sausalito, CA: University Science Books.

Teichert, N., J. P. Benitez, A. Dierckx, S. Tétard, E. De Oliveira, T. Trancart, E. Feunteun, and M. Ovidio. 2020. “Development of an Accurate Model to Predict the Phenology of Atlantic Salmon Smolt Spring Migration.” *Aquatic Conservation: Marine and Freshwater Ecosystems* 30(8): 1552–65.

Tsukamoto, K., T. Otake, N. Mochioka, T. W. Lee, H. Fricke, T. Inagaki, J. Aoyama, et al. 2003. “Seamounts, New Moon and Eel Spawning: The Search for the Spawning Site of the Japanese Eel.” *Environmental Biology of Fishes* 66: 221–29.

USGS (U. S. Geological Survey) National Water Information System. 2024. “USGS Water Data for California.” USGS. https://nwis.waterdata.usgs.gov/ca/nwis.

Vasbinder, K., J. Fiechter, J. A. Santora, J. J. Anderson, N. Mantua, S. T. Lindley, D. D. Huff, and B. K. Wells. 2024. “Size-Selective Predation Effects on Juvenile Chinook Salmon Cohort Survival off Central California Evaluated with an Individual-Based Model.” *Fisheries Oceanography* 33(1): e12654.

Voss, S. 2024. “USFWS Red Bluff Diversion Dam Rotary Screw Trap Juvenile Fish Monitoring Database Version 10.” Environmental Data Initiative. https://doi.org/10.6073/pasta/3534f98e531d7238dca001bfd8e55dcf.

Voss, S. D., and W. R. Poytress. 2022. *2019 Red Bluff Diversion Dam Rotary Trap Juvenile Anadromous Fish Abundance Estimates*. Report of U.S. Fish and Wildlife Service to U.S. Bureau of Reclamation, Sacramento, CA. Red Bluff, CA: U.S. Fish and Wildlife Service.

Ward, D. L., and R. Morton-Starner. 2015. “Effects of Water Temperature and Fish Size on Predation Vulnerability of Juvenile Humpback Chub to Rainbow Trout and Brown Trout.” *Transactions of the American Fisheries Society* 144(6): 1184–91.

Wells, B. K., J. A. Santora, J. C. Field, R. B. MacFarlane, B. B. Marinovic, and W. J. Sydeman. 2012. “Population Dynamics of Chinook Salmon *Oncorhynchus tshawytscha* Relative to Prey Availability in the Central California Coastal Region.” *Marine Ecology Progress Series* 457: 125–137.

Wells, B. K., J. A. Santora, M. J. Henderson, P. Warzybok, J. Jahncke, R. W. Bradley, D. D. Huff, et al. 2017. “Environmental Conditions and Prey-Switching by a Seabird Predator Impact Juvenile Salmon Survival.” *Journal of Marine Systems* 174: 54–63.

Whalen, K. G., D. L. Parrish, and S. D. McCormick. 1999. “Migration Timing of Atlantic Salmon Smolts Relative to Environmental and Physiological Factors.” *Transactions of the American Fisheries Society* 128(2): 289–301.

Whipple, A. A., R. M. Grossinger, D. Rankin, B. Stanford, and R. Askevold. 2012. *Sacramento-San Joaquin Delta Historical Ecology Investigation: Exploring Pattern and Process*. Richmond, CA: San Francisco Estuary Institute-Aquatic Science Center.

Wood, S. N. 2011. “Fast Stable Restricted Maximum Likelihood and Marginal Likelihood Estimation of Semiparametric Generalized Linear Models.” *Journal of the Royal Statistical Society. Series B, Statistical Methodology* 73(1): 3–36.

Wood, S. N. 2017. *Generalized Additive Models: An Introduction with R*, 2nd ed. Boca Raton, FL: Chapman and Hall/CRC.

Yarnell, S. M., G. E. Petts, J. C. Schmidt, A. A. Whipple, E. E. Beller, C. N. Dahm, P. Goodwin, and J. H. Viers. 2015. “Functional Flows in Modified Riverscapes: Hydrographs, Habitats and Opportunities.” *BioScience* 65(10): 963–972.

Yoshiyama, R. M., E. R. Gerstung, F. W. Fisher, and P. B. Moyle. 2001. “Historical and Present Distribution of Chinook Salmon in the Central Valley Drainage of California.” *Fish Bulletin* 179(1): 71–176.

Zarri, L. J., E. M. Danner, M. E. Daniels, and E. P. Palkovacs. 2019. “Managing Hydropower Dam Releases for Water Users and Imperiled Fishes with Contrasting Thermal Habitat Requirements.” *Journal of Applied Ecology* 56(11): 2423–30.

Zeug, S. C., K. Sellheim, C. Watry, J. D. Wikert, and J. Merz. 2014. “Response of Juvenile Chinook Salmon to Managed Flow: Lessons Learned from a Population at the Southern Extent of their Range in North America.” *Fisheries Management and Ecology* 21(2): 155–168.

Zillig, K. W., R. A. Lusardi, D. E. Cocherell, and N. A. Fangue. 2023. “Interpopulation Variation in Thermal Physiology among Seasonal Runs of Chinook Salmon.” *Canadian Journal of Fisheries and Aquatic Sciences* 80(1): 1–13.

Zydlewski, G. B., A. Haro, and S. D. McCormick. 2005. “Evidence for Cumulative Temperature as an Initiating and Terminating Factor in Downstream Migratory Behavior of Atlantic Salmon (*Salmo salar*) Smolts.” *Canadian Journal of Fisheries and Aquatic Sciences* 62(1): 68–78.

SUPPORTING INFORMATION

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

How to cite this article: Burford, Benjamin P., Jeremy J. Notch, William R. Poytress, and Cyril J. Michel. 2025. “Facilitated Migration Could Bolster Migrant Passage through Anthropogenically Altered Ecosystems.” *Ecological Applications* 35(5): e70070. https://doi.org/10.1002/eap.70070