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Article

Risky main stems are a poorly understood constraint on salmon recovery in coastal California rivers

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ABSTRACT

Objective: Investment in salmon habitat restoration often focuses on natal streams, with a goal of improving access for spawning fish and increasing early life survival of juveniles. This work is justified by a large body of research; however, return on investment in natal streams (at least in terms of increased adult abundance) has, so far, been marginally successful at best. The factors that constrain salmon populations may shift in space and time, and accurately tracking these constraints requires monitoring the full spatial and temporal scope of the salmon life cycle. In particular, juvenile salmon emigration through main-stem rivers to the ocean is not well studied and is poorly understood. Low emigration survival can prevent successful upstream habitat restoration from being realized as increased adult recruitment.

Methods: We present acoustic telemetry studies from two coastal California rivers to estimate seaward emigration survival of Coho Salmon *Oncorhynchus kisutch* from their natal streams. We contrast emigration survival with other life stages and with relative restoration investment in main-stem rivers.

Results: In both watersheds, survival was low and highly variable across years. Main-stem river segments had the lowest survival, and survival was lower for migrants that traveled greater lengths in risky main stems. Main-stem emigration occurred over a very short time span, yet survival was similar to or lower than that of other juvenile freshwater life stages (e.g., oversummer and overwinter survival), which occur over much longer time spans. We also found that later emigrants had lower survival than earlier emigrants in both rivers. A summary of restoration investment in both watersheds indicates that much less planning and restoration implementation is occurring in main-stem rivers than in small natal streams.

Conclusions: Taken together, our results suggest that juvenile emigration success is likely an important constraint on salmon population recovery. Greater understanding of and greater investment in main-stem rivers are sorely needed.

KEYWORDS: acoustic telemetry, animal migration, life cycle modeling, salmon recovery, salmon survival, watershed restoration

LAY SUMMARY

We observed low and variable main-stem emigration survival of acoustically tagged juvenile Coho Salmon in two California rivers. This highlights the importance of identifying and understanding the drivers of mortality in main-stem rivers during this brief yet vulnerable period in the life of anadromous salmonids.

INTRODUCTION

Over the past century and a half, populations of Pacific salmon *Oncorhynchus* spp. have been depleted across almost their entire range. The social, cultural, and economic values of salmon have facilitated an unprecedented movement to recover their imperiled populations—starting in the late 1800s but significantly

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increasing in economic scope since the 1980s (e.g., Jaeger & Scheuerell, 2023; National Marine Fisheries Service [NMFS], 2023). Salmon recovery has become a major enterprise, with billions of dollars invested over the past few decades (U.S. Senate Committee on Commerce, Science, and Transportation, 2023). Although removal of barriers to upstream passage has been successful in increasing adult recruitment of Pacific salmon in some cases (e.g., Duda et al., 2021), clear linkages between other types of habitat restoration and adult recruitment are rare (although see Hyatt & Stockwell, 2019). In practice, both salmon monitoring and restoration efforts tend to focus on parts of the life cycle and habitats that are most feasible to survey and restore. For example, Roni et al. (2014) listed several peer-reviewed habitat enhancement efforts that successfully increased survival, abundance, and distribution of juvenile salmonids. Notably, most of the successes occurred in smaller streams, which reflects a bias in both monitoring and restoration. In their review paper of salmon habitat restoration, Bilby et al. (2024) noted that the failure to accurately identify the key elements constraining salmon populations is a major factor contributing to the lack of progress in salmon recovery. Identifying the complete spectrum of constraints on salmon populations requires monitoring the full spatial and temporal scope of the salmon life cycle—something that is rarely, if ever, done.

Often, the trajectory of salmon recovery efforts reflects a hierarchy of perceived needs given limited knowledge about the factors that constrain fish production. For example, when salmon are entirely absent upstream of a human-caused barrier, fish passage may be prioritized over improving the quality and quantity of spawning and rearing habitat in currently inaccessible areas. In these cases, the implementation of a recovery action (e.g., barrier removal) might successfully increase access to spawning habitat and early life stage production but may not result in greater adult abundance in the next generation because of low-quality spawning and/or rearing habitat upstream of the barrier. Rather, these successful restoration actions may unveil a previously masked population constraint, causing low-quality habitat in the newly available stream reach to become the new population bottleneck. Shifts in bottlenecks may occur in other locations and life stages as well. Consider cases where the quality of natal rearing habitat is improved but juvenile fish are unsuccessful at emigrating to the ocean because riverine or estuarine habitat is in poor condition or presents an elevated predation risk. In these cases, a successful and necessary restoration action (e.g., improved natal stream habitat quality) may not result in increased adult recruitment due to the constraints as fish migrate downstream.

Coastal watersheds in northern California illustrate the relationship between restoration priorities and imperfect knowledge of the changing factors that limit fish production. North of San Francisco Bay (37.85°N) and south of the Klamath River (41.53°N), there are dozens of salmon-bearing streams that drain directly into the Pacific Ocean and provide critical habitat for Chinook Salmon *O. tshawytscha*, Coho Salmon *O. kisutch*, steelhead *O. mykiss* (anadromous Rainbow Trout), and Coastal Cutthroat Trout *O. clarkii* (NMFS, 2016). Over the past three decades, restoration efforts in many of these watersheds have emphasized projects that restore access to or improve habitat quality in small natal streams, primarily for Coho Salmon and steelhead. This focus is grounded in extensive documentation of fish passage needs (e.g., Goslin, 2005) and California and federal recovery planning documents (California Department of Fish and Game, 2002; NMFS, 2014, 2016). An entire field devoted to improving fish passage (Katopodis & Williams, 2012)—as well as recognition that habitat degradation and flow impairment can limit salmon carrying capacity in natal streams (Grantham et al., 2012; Kastl et al., 2022; Obedzinski et al., 2018; Roni, 2019)—has led to successful projects in tributary streams of California and the Pacific Northwest. Although significant and justifiable investment in recovery of natal streams has occurred (Hampton et al., 2021; Roni, 2019), there has been only a marginal effect on adult recruitment (e.g., NMFS, 2024). Beyond California's north coast, there is growing recognition that poor survival in larger main-stem rivers (e.g., Chittenden et al., 2010; Michel, 2018), poor estuarine habitat quality (e.g., Hodgson et al., 2020; Nobriga et al., 2021), and low near-marine survival (e.g., Beamish et al., 2010; Pearcy, 1992) may prevent juvenile salmon production in natal streams from being realized as increased adult salmon abundance. In recent years, the restoration community has focused more attention on these nonnatal habitats. Nevertheless, research on and investment in main-stem, estuarine, and near-marine salmon habitats still lag far behind work in smaller natal streams.

To improve our understanding of population constraints beyond the natal stream environment, we tracked yearling Coho Salmon during their downstream migration through river and estuary habitats in two northern California rivers during the spring season. This stage of the salmonid life history (main-stem emigration of juveniles) has been poorly described in California coastal streams, in part because until recently, methodological constraints had made it difficult to estimate the survival of migrating juvenile salmonids in larger main-stem rivers. In the past 15 years, acoustic telemetry has emerged as a technology that allows researchers to track movement and estimate survival of juvenile salmonids. It has proven particularly useful for life stages that travel long distances from natal streams to the ocean in habitats that are challenging to monitor with other methods, such as PIT tags (McMichael et al., 2010; Michel, 2018). Acoustic telemetry can also reveal habitat-specific survival and identify mortality hot spots, thus helping managers to more effectively develop, prioritize, and target meaningful restoration actions. Although acoustic telemetry has been used extensively throughout the Pacific Northwest and in California's Sacramento–San Joaquin River system (e.g., Goertler et al., 2024; Michel, 2018) and the Klamath River (e.g., Beeman et al., 2012), our work is among the first to use the technology to study freshwater survival in coastal California rivers (south of the Klamath River).

Our goal was to evaluate whether relative investments in habitat restoration across different freshwater habitats align with the magnitudes of life-stage-specific and habitat-specific survival of juvenile Coho Salmon. Specifically, we were interested in whether main-stem migratory survival was a significant constraint on juvenile Coho Salmon populations and how restoration investment in main-stem river habitats compared

Figure 1. Survival gate (i.e., acoustic receiver) locations along the migration route of Coho Salmon juveniles in the Russian River, California, 2021–2024. Note that not all gates were deployed each year. Tributaries depict locations of intensively monitored watersheds, and numbers represent distance (km) from the ocean.

with investment in other freshwater habitat types (e.g., small tributaries, floodplains, and estuaries). We conducted survival studies in the Russian River and the South Fork Eel River—two coastal rivers in California that are situated north of San Francisco Bay and south of the Klamath River. We used acoustic telemetry to obtain spatially explicit estimates of Coho Salmon emigration survival along the migration pathway between natal streams and the ocean or estuary (Figures 1 and 2). We then compared emigration survival to other life-stage-specific survival estimates from nearby life cycle monitoring stations. Finally, we compiled restoration investment data (planning and implementation) in both watersheds by habitat type and contrasted main-stem emigration survival of juvenile Coho Salmon with the relative investment in main-stem rivers.

Study site

Russian River

The Russian River in northern California drains approximately 3,800 km^2 and flows 177 km from its headwaters in Mendocino County to its mouth at the Pacific Ocean in Sonoma County. Flow is regulated by releases from two dams. Historical estimates suggest that tens of thousands of Coho Salmon, Chinook Salmon, and steelhead inhabited the Russian River in the early to mid-20th century (NMFS, 2008). The Russian River includes over 200 tributaries that provide habitat for these species and have been the focus of intensive salmon recovery efforts for decades (NMFS, 2012). Historically, Coho Salmon existed throughout the Russian River basin, but habitat quality and fish passage have been

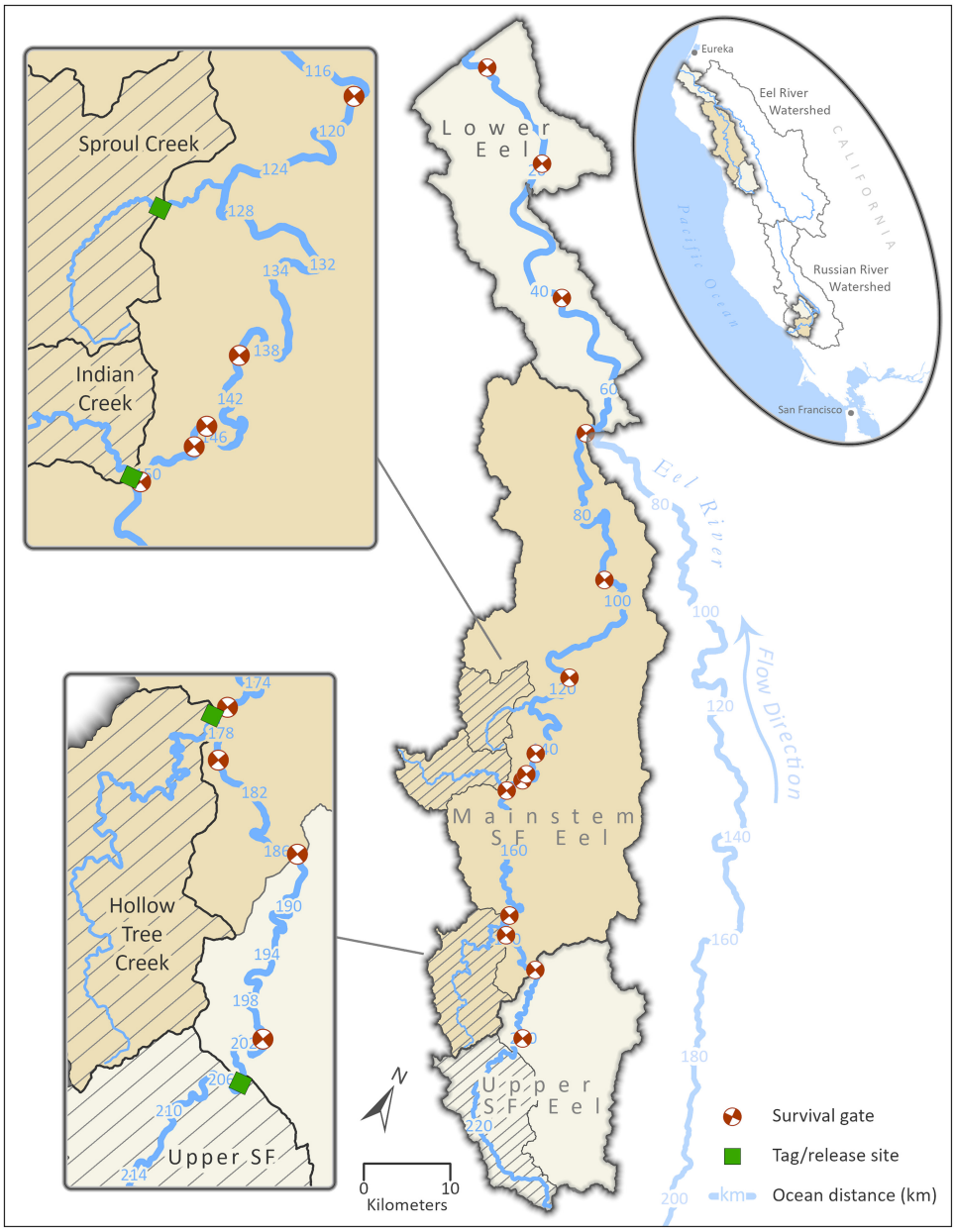

Figure 2. Survival gate (i.e., acoustic receiver) locations along the migration route of Coho Salmon juveniles in the South Fork Eel River and lower main-stem Eel River, California, 2023 and 2024. Note that not all gates were deployed each year. Shaded watersheds depict sampling areas of downstream migrant traps, and numbers represent distance (km) from the ocean. Abbreviation is as follows: SF = South Fork.

degraded to a point that abundance has declined substantially and distribution is currently restricted to tributaries in the lower third of the watershed, resulting in state and federal endangered status (California Department of Fish and Game, 2002; U.S. Office of the Federal Register, 2005). In 2001, a conservation hatchery program was initiated to prevent extirpation of Coho Salmon from the Russian River by re-establishing self-sustaining runs in its tributaries (NMFS, 2008). At Don Clausen Warm Springs Fish Hatchery at Warm Springs Dam, offspring of natural-origin Coho Salmon are reared to the adult stage and spawned. Progeny are released as juveniles into tributaries in their historical range with the expectation that a portion of them will return to reproduce naturally. Thus far, hatchery intervention has prevented extirpation of Russian River Coho Salmon, but the population remains highly imperiled, with fewer than 1,000 fish returning each year to spawn (California Sea Grant & Sonoma Water, 2024).

South Fork Eel River

The South Fork Eel River is an unregulated watershed that drains 1,785 km^2 of the Eel River's 9,541 km^2 from its headwaters in the coastal mountains of Mendocino County to its confluence with the main-stem Eel River in Humboldt County. The South Fork Eel River is a priority conservation watershed for Coho Salmon, Chinook Salmon, and steelhead (Hayes et al., 2016; NMFS, 2014). Coho Salmon in the South Fork Eel River

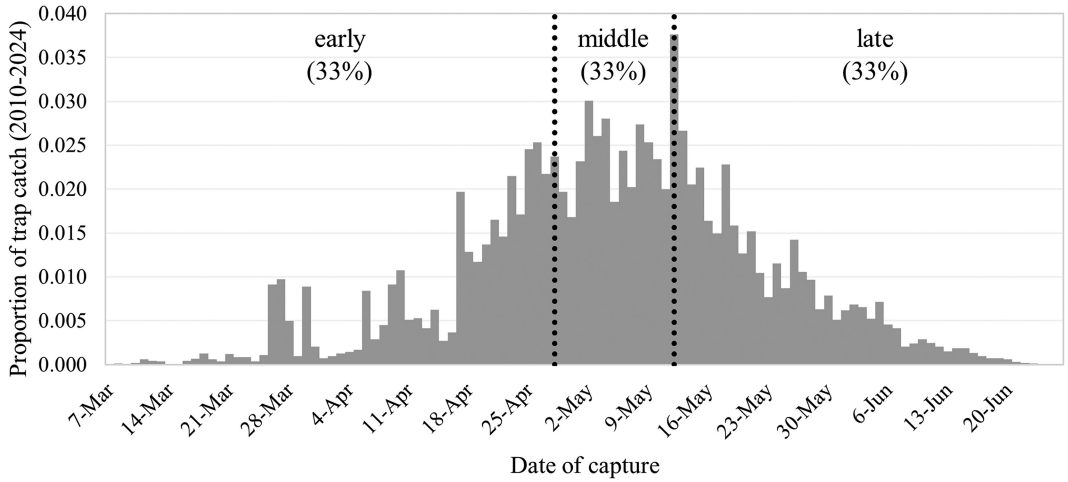

Figure 3. Frequency distribution of the date of capture for Coho Salmon smolts in downstream migrant traps on four intensively monitored subwatersheds of the Russian River watershed (Willow, Dutch Bill, Green Valley, and Mill creeks; see Figure 1 for tributary locations), 2010–2024.

watershed are listed as threatened under both the federal and state Endangered Species Acts (California Department of Fish and Game, 2002; U.S. Office of the Federal Register, 2005). Historical counts of adult Coho Salmon in the upper two-thirds of the South Fork Eel River ranged from approximately 7,000 to 25,000 in the late 1930s and 1940s—after these populations were already severely depressed from overfishing (California Trout et al., 2024). More recently, the Coho Salmon spawning population in the South Fork Eel River has ranged from approximately 150 to 4,000 individuals based on redd estimates from the period 2010–2020 (Guczek et al., 2020) and unpublished sonar data (2018–2024; California Trout, unpublished data). A notable change in the South Fork Eel River fish assemblage was the introduction of Sacramento Pikeminnow *Ptychocheilus grandis* in 1979 (Georgakakos et al., 2023). The river previously had no other large piscivorous fish except native Rainbow Trout. Today, the Sacramento Pikeminnow is the most numerous predatory fish in the basin, one of the most abundant fish overall, and a significant restoration concern in native fish recovery plans (California Trout et al., 2024; NMFS, 2014, 2024).

METHODS

To estimate yearling Coho Salmon emigration survival along their migration route in spring, we conducted acoustic telemetry studies in the Russian and Eel River watersheds. In the spring of each study year, acoustic tags were surgically implanted into individual fish at Don Clausen Warm Springs Fish Hatchery on a tributary of the Russian River (Figure 1) and at trapping sites in tributaries to the South Fork Eel River (Figure 2). The tags transmitted a low-frequency signal at a set rate, which uniquely identified each individual. We assumed that all tagged individuals would exhibit downstream migration behavior consistent with smoltification (Supplement A [see online Supplementary Material]). Acoustic receivers were deployed along the downstream migration paths, enabling us to detect tagged fish as they moved past stationary receivers that were continuously "listening" for tags. When a signal was identified, the tag's unique identification code was saved along with the date and time.

In both streams, the date of receiver deployment varied depending on stream discharge (which dictated personnel safety) but generally targeted early to mid-April before the peak migration season (Figure 3). Receiver retrieval occurred in summer or fall after the migration season. Receivers were deployed at selected locations ("survival gates") to provide spatially explicit survival estimates through the stream length between the release location and the first survival gate downstream or between successive survival gates ("reaches"; Figures 1 and 2). We deployed multiple receivers per gate at most sites to bolster detection probability by increasing detection range across the channel width and providing receiver redundancy within a gate in case a receiver failed. The total number and location of gates varied depending upon site conditions in each year (Table 1). Receivers were tethered to an anchor so that they maintained a vertical position in the water column.

We divided the migration route in both systems into broad habitat segments to better understand habitat-specific survival and migration behavior. "Habitat segments" were defined as long reaches (10–100 km) or entire tributaries that shared similar geomorphic and hydrologic characteristics (Frissell et al., 1986). Note that the concept of habitat segment (Frissell et al., 1986) is distinct from the concept of reach in this article and that most habitat segments contained multiple reaches. The Russian River was divided into three habitat segments: Dry Creek, main-stem Russian River, and estuary (Figure 1). The Eel River was also divided into three habitat segments: upper South Fork Eel River (hereafter, "upper SF"), main-stem South Fork Eel River (hereafter, "main-stem SF"), and lower main-stem Eel River (Figure 2). Hereafter, we shall refer to the "South Fork Eel River study," but it should be remembered that the South Fork Eel River is a tributary to the Eel River and our study included survival estimates in the lower main-stem Eel River. There was not perfect parity between the Russian River and South Fork Eel River habitat segments, although the main-stem SF and main-stem Russian River segments share a similar

Table 1. Study details related to receiver deployment, Coho Salmon releases, and Coho Salmon body size (fork length [FL]) in the Russian and South Fork Eel River watersheds, California.

Watershed	Year	Receiver deployment	Receiver retrieval	Number of gates (receivers)	Number of reaches	Release date	Number released	Mean (SD) FL (mm)
Russian River	2021	Apr 26–29	Jun 7–23	9 (19)	8	Apr 21	49[a]	130.8 (10.3)
		–	–	–	–	May 21	51	132.8 (10.3)
	2022	Apr 11–19	May 31–Jun 15	11 (22)	10	Apr 22	70[b]	132.2 (4.2)
		–	–	–	–	Apr 22	70	130.6 (3.2)
		–	–	–	–	May 22	70	136.6 (6.3)
		–	–	–	–	May 22	70	130.7 (2.9)
	2023	Apr 24–May 2	Jun 27–29	8 (16)	7	Apr 23	100	131.6 (2.6)
		–	–	–	–	May 23	100	131.6 (2.4)
		–	–	–	–	May 23	100	132.5 (2.4)
		–	–	–	–	May 23	100	132.8 (2.9)
	2024	Apr 10–29	Jul 2–17	10 (20)	9	Apr 24	100	130.3 (4.2)
		–	–	–	–	May 24	100	130.4 (4.1)
		–	–	–	–	May 24	100	131.1 (4.0)
		–	–	–	–	May 24	100	131.9 (3.8)
		–	–	–	–	May 24	50	132.4 (4.4)
						Total	1,230	131.8 (4.8)
South Fork Eel River[c]	2023	Apr 19–22	Jul 5	10 (19)	10	Apr 19–22	69	91.6 (6.1)
		–	–	–	–	May 2–12	192	91.9 (7.3)
		–	–	–	–	May 13–24	144	91 (5.7)
	2024	Apr 5–25	Sep 20	13 (32)	13	Apr 20–24	135	96.3 (8.3)
		–	–	–	–	May 7–10	185	94.4 (9.5)
		–	–	–	–	May 21–23	77	92.8 (8.4)
						Total	802	93.1 (8.0)

[a]One fish from group 1 died 2–3 d after tagging. That individual's tag was used to tag a different fish, which was released in group 2.
[b]One fish died when it jumped out of the hatchery tank after tagging. A replacement fish was tagged on April 14 and released on the same date as other fish in the group (April 19).
[c]Note that there were three tagging sites each year in the South Fork Eel River (Figure 2). "Number released" aggregates across these sites.

habitat scale and geomorphic setting; however, Dry Creek, a flow-controlled tributary stream with higher velocity (and lower predator density), does not have a corollary in the South Fork Eel River. The lower main-stem Eel River is a large river system (nearly three times the drainage area of the Russian River), which flows 63 km to the Pacific Ocean.

To the extent possible, we timed releases to encompass the peak of the spring yearling Coho Salmon emigration season based on a 15-year data set of downstream migrant trapping in four intensively monitored subwatersheds within the Russian River watershed (Figure 3). The limited historical data on juvenile emigration from the South Fork Eel River suggest a similar temporal pattern (California Trout et al., 2024). To define periods for run timing, we divided the date frequency distribution into thirds, resulting in dates earlier than April 28 defined as "early," dates later than May 12 defined as "late," and dates between April 28 and May 12, inclusive, defined as "middle." We applied these run timing categories for both studies. From detections of tagged individuals on receivers at gates, we constructed detection histories to facilitate survival estimation using the Cormack–Jolly–Seber (CJS) model (Lebreton et al., 1992). In the CJS open-population model, sampling occasions generally represent discrete sampling events that are separated by a discrete amount of time between events and where each digit in an individual's encounter history represents capture (1) or noncapture (0) on each sampling event. However, we assumed that the individual Coho Salmon in our studies were exhibiting directed downstream migration, meaning that instead, each digit in an individual's encounter history is either a detection (1) or nondetection (0) on each successive receiver along the migration route (i.e., we substituted space for time).

Russian River telemetry study

Acoustic telemetry studies were conducted each spring from 2021 to 2024 to track hatchery-origin juvenile Coho Salmon emigrants in the Russian River. We used Innovasea 307-kHz HR3 acoustic receivers and 307-kHz V3 acoustic transmitters (15-mm length; 4-mm diameter; 0.15 g in water; 0.30 g in air). Tag transmission frequency (ping rate) was approximately 5 s in all four study years. During the first year of study (2021), we used pulse interval (i.e., HTI) tag encoding, but in subsequent years, we used high-residency (HR) tag encoding. Regardless of tag coding, the tag size and shape were identical in all 4 years of the study. We made the switch from pulse interval to HR coding based on results from a field evaluation conducted in 2022, which suggested that HR was preferable because of simpler data processing, with no difference in detection efficiency in our study (Sonoma Water, unpublished data). Acoustic tag battery life was 47 d in 2021 and 2022, 118 d in 2023, and 121 d in 2024. We think that this was sufficient to encompass the time necessary for fish to exit the study area because based on a 13-year data set, previous PIT monitoring of Coho Salmon travel time from an upstream detection site in the Russian River to a site 41 km downstream in the estuary indicated a 13-year median travel time of 6.5 d at 6.3 km/d. The maximum distance between receiver gates was 24 km.

All fish were tagged as age-1 juveniles at Don Clausen Warm Springs Fish Hatchery (hereafter, "fish hatchery"). To

evaluate potential differences in migration survival due to differences in environmental conditions (e.g., turbidity, flow, and temperature), multiple batches of fish were released each year across the early, middle, and late distribution of the yearling spring emigration season (Figure 3). Because we were trying to make inferences about survival of hatchery-released fish in the Russian River (objectives that were outside of this study), we targeted average body size at tagging (Table 1) to match the long-term average size of smolts released from the fish hatchery (mean ± SD = 130.0 ± 13.6 mm) rather than the body size of smolts captured at downstream migrant traps in the watershed (114.0 ± 13.6 mm).

Tagging consisted of making a small (~5-mm-long) incision on the ventral side of the fish, just off the midline, approximately equidistant between the insertion points of the pelvic and pectoral fins. We did not suture the incision closed. To look for short-term effects of tag loss, tagging mortality, and tag failure, we held the fish at the fish hatchery prior to release for 7 d after tagging, and all fish were scanned for the presence of a functioning tag on the day of release. Of the 1,230 fish tagged over the four seasons of study, all retained their tags during the 7-d holding period. Only one fish died from what could have been delayed effects from tagging. Fish were released during daylight hours. The number of fish tagged during each year varied from a total of 100 divided into two groups (2021) to a total of 450 divided into five groups (2024), and all fish were released into Dry Creek immediately downstream of the fish hatchery (73 km from the ocean; Figure 1). Detection data from acoustic receivers at the mouth of Dry Creek approximately 21 km downstream of the release site supported the conclusion that initial survival after release was high (median estimated survival for all years and groups combined was 0.96; see Supplement B for annual estimates).

South Fork Eel River telemetry study

Acoustic telemetry studies were conducted each spring in 2023 and 2024 to track wild-origin juvenile Coho Salmon emigrants through sections of the South Fork Eel River and lower main-stem Eel River. We used LOTEK WHS 4350L acoustic receivers and ATS SS400 acoustic transmitters at 416.7 kHz (0.216-g dry weight; 15.00 × 3.38 mm). Tag transmission frequency (ping rate) was set to 8 s in 2023 and to 5 or 8 s in 2024. No independent data on travel time of Coho Salmon smolts through the main-stem SF were available, so we relied on unpublished data from the Russian River (see *Russian River telemetry study* section) to estimate the battery life needed to detect yearling fish throughout the spring migration window. Although the travel distance through the main-stem SF was longer (up to 140 km depending on the release tributary) than it was in the Russian River study (73 km), we assumed that the travel rate would be similar, meaning that the battery life (71 d at a 5-s ping rate) was sufficient to encompass the time necessary for fish to exit the study area. In 2023, 19 receivers were deployed at 10 survival gates in the main-stem SF only. In 2024, 20 receivers were deployed at 10 survival gates in the main-stem SF, and an additional nine receivers were deployed at three gates in the lower main-stem Eel River downstream of the South Fork Eel River. The maximum distance between receiver gates was 28 km.

Wild-origin juvenile Coho Salmon were captured, tagged, and released in four locations distributed throughout the South Fork Eel River watershed, although tagging tributaries varied between years (Figure 2; Table 1). To evaluate potential differences in migration survival due to release location and release date, we attempted to conduct three tagging events in three tributaries during each year (Figure 2; Table 1). All trapping was conducted using channel-spanning fyke nets and trap boxes. Captured individuals were anesthetized using tricaine methanesulfonate (MS-222) before and during tagging. Tagging followed the methods described for the Russian River study, except that the incisions were closed with a single suture. Fish were held in an instream live-box and were released at least 12 h after tagging. Among the 802 fish tagged over the 2 years of study, no tag losses or posttagging mortalities occurred during the holding period.

Mark–recapture model

Prior to conducting survival estimates, we first selected raw detections of active tag identification codes that met a threshold "quality" and showed feasible detection patterns on other receivers and gates in the study (Supplement C). We then filtered out false-positive detections, which can originate from several sources and can severely bias estimates. After data filtering, we constructed encounter histories for each tagged and released individual (where 1 = detection and 0 = nondetection) on each receiver and used these as input for mark–recapture modeling to estimate reach-specific survival probabilities for each release group by study year and study basin. For both studies, we used CJS models to obtain estimates of true survival between survival gates (see justification for true survival vs. apparent survival in Supplement A). Data from each basin were analyzed separately using program MARK (White & Burnham, 1999). For the Russian River data, we used standalone MARK; for the Eel River data, we used the RMark package in R (Laake, 2013; R Core Team, 2024).

For each basin and year, we ran a separate CJS model that allowed survival to vary by reach (i.e., between successive survival gates), resulting in six separate models: one model for each of the 4 years of the Russian River study (i.e., 2021, 2022, 2023, and 2024 models) and one model for each of the 2 years of the South Fork Eel River study (2023 and 2024 models). Because the longitudinal distance between receivers within a gate was less than 50 m, we assumed that survival between receivers within a survival gate was 1.0. However, we estimated detection probability for each receiver irrespective of where the receiver was located. For example, in a 10-gate study consisting of 20 receivers, model construction allowed estimation of nine reach-specific survival probabilities and 20 detection probabilities. Goodness of fit was evaluated for each of the six models, and none showed a significant lack of fit. We used reach-specific survival estimates from these six models as the basis for habitat segment survival estimation (i.e., Dry Creek, upper SF, main stem, lower main stem, estuary) and overall survival estimation (i.e., from release to the downstream-most survival gate).

In addition to reach-specific survival estimates, which were directly output from the mark–recapture models, we

summarized survival in the following ways. First, the product of the appropriate reach-specific survival estimates in each habitat segment was used to represent segment-specific survival probability. Second, estimated overall annual survival for each basin was calculated as the product of all reach-specific survival probability estimates within each year regardless of habitat segment. For both segment-specific and overall survival probability estimates, we used the delta method to approximate the sampling variance (Williams et al., 2002). To summarize segment-specific and overall survival probabilities across all years and release groups within each basin, we calculated the median segment-specific survival and the median overall survival. Finally, we compared survival over a standard distance (10 km) within each habitat segment by raising the estimated habitat segment survival probability to the quotient of 10 km and segment length. We refer to this third metric as the "scaled survival rate."

Finally, we constructed two linear models to evaluate the effect of departure date (from the natal stream) on survival for each study stream. The model regressed cumulative_*S* against release date, where cumulative_*S* is the survival probability from the mark–recapture model for each release date (Table 1) from the natal stream to the downstream-most gate. The model was run using the LM command in R version 3.5.1 (R Core Team, 2024).

Migration rate

In addition to survival, we considered how migration rate varied among release groups and between habitat segments and whether migration rate may be related to survival. To do this, we identified the first detection of each individual at each gate, which we defined as a "detection event." Because many fish were not detected or did not survive through an entire segment, we calculated the migration time for each individual in each segment as the difference in the number of days between the furthest upstream detection event in the segment and the furthest downstream detection event in the same segment. Because this approach could result in a biased representation of migration, especially if mortality within the habitat segment or detection probability was low, we standardized estimates by also calculating the distance (km) between these same two gates and dividing that migration distance by migration time for each individual to calculate migration rate (km/d). These individual values were then summarized as medians and quartiles (25th and 75th) across all individuals by year, by habitat segment, and overall.

RESULTS

Detection probability and survival of juvenile Coho Salmon

Across all years of study, gate-specific detection probability estimates ranged from 0.76 to 1.00 in the Russian River and from 0.53 to 0.96 in the South Fork Eel River (except for one estimate of 0.16 in 2023 for the South Fork Eel River). We did not summarize detection probability estimates either by habitat segment or overall as we did with survival probability estimates. Median unscaled overall survival probability across all years and release times from the Dry Creek release site to the downstream-most gate in the Russian River estuary at river kilometer (rkm) 2.3 was 0.40 (range = 0.14–0.61). River kilometer 0 was set at the river mouth in both systems. In the South Fork Eel River, median overall survival probability from release sites to rkm 19.1 near the downstream end of the lower main-stem Eel River across years, migration timing, and tagging locations was 0.06 (range = 0.00–0.23). Survival in the main-stem Russian River and main-stem SF habitat segments was lower and more variable compared with other habitat segments in both studies (Figure 4). The estimated median survival probability for all groups and years combined was 0.44 (range = 0.14–0.73) in the main-stem Russian River and 0.11 (range = 0.00–0.45) in the main-stem SF. However, the scaled survival probabilities in these two main-stem segments were similar between watersheds (0.82 and 0.83 per 10 km, respectively).

In 3 of 4 years for the Russian River study and in both years for the South Fork Eel River study, survival was generally lower for groups that were released later in the migration season (Figure 5). The linear regression of cumulative survival and release date (Table 2) showed a 0.7% decline in survival for each day later in the year from the point of the first release group (Russian River; $P < 0.005$, adjusted $r^2 = 0.219$) and a 1.1% decline in survival per day for the South Fork Eel River ($P < 0.005$, adjusted $r^2 = 0.682$). For the Russian River study, overall survival was extremely low for both release groups in 2021 (0.18 and 0.14) and the latter two release groups in 2022 (0.28 and 0.14). For all release groups during both years in the South Fork Eel River, median survival from release to the downstream end of the main-stem SF was lower (0.07 in 2023; 0.11 in 2024) than the lowest survival from release to the downstream end of the main-stem Russian River (0.14). Notably, in both studies, even releases that occurred during the historical peak of the spring Coho Salmon smolt migration experienced low survival through their respective main stems (range = 0.14–0.64 for the Russian River study; range = 0.00–0.36 for the South Fork Eel River study).

We also observed reach-specific variation in survival along the course of each main-stem habitat segment, suggesting the presence of mortality hot-spots (note the steep drops in survival estimates in Figures 6 and 7). In the main-stem Russian River, the 1.0-km reach immediately downstream of the mouth of Dry Creek (rkm 51.6–50.6) and the 4.9-km reach from rkm 44.2 to rkm 39.3 in the main-stem Russian River exhibited high mortality in most years. In the South Fork Eel River, mortality hot spots corresponded to the 1.1-km reach from rkm 147.2 to rkm 146.1 and the 27.6-km reach from rkm 146.1 to rkm 118.5. In 2024, there was also evidence of high mortality between the Sproul Creek tagging site and rkm 95.2. However, because of the arrangement of survival gates, it is unclear how much of that mortality occurred in the 3.3-km distance fish had to traverse through Sproul Creek to reach the main-stem SF as compared to the 7.7 km between the Sproul Creek confluence and the next gate downstream in the main-stem SF (Figure 2).

Migration rate of juvenile Coho Salmon

When compared to other habitat segments in the same watershed, the migration rate was slower in the main-stem Russian

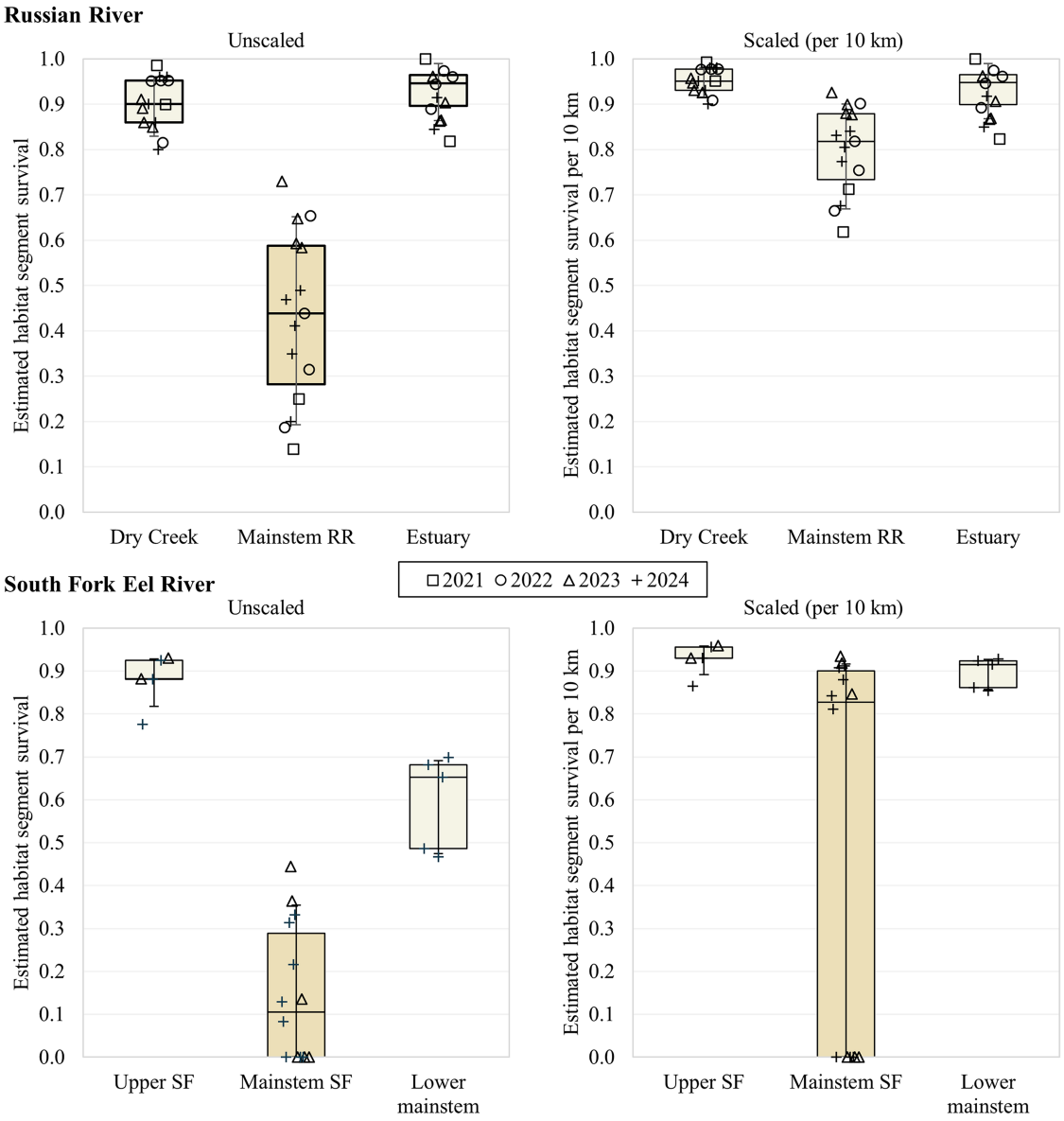

Figure 4. Habitat segment survival estimates by year for the Russian River (RR) and the South Fork Eel River (SF) studies. Points represent survival estimates for each release group. Scaled survival rate is survival from the upstream end to the downstream end of each habitat segment, standardized per 10 km. The line within each box represents the median, the ends of each box represent the 25th and 75th percentiles, and the ends of the whiskers represent the 10th and 90th percentiles.

River (10.6 km/d) compared to the main-stem SF (12.9 km/d; Table 3). The variability in migration rate between habitat segments (and across years) was greater in the South Fork Eel River study than in the Russian River study. In particular, the upper SF had relatively slow migration rates (median across years = 3.3 km/d), and juvenile Coho Salmon increased their migration rate after they entered the main-stem SF. Tagged Coho Salmon in the upper SF migrated slower and survived at higher rates than anywhere else in the basin. However, more work is needed to understand whether there is any causal relationship between migration rate and survival. In addition, juveniles in the main-stem SF migrated nearly twice as fast in 2023 when compared to 2024. In the Russian River, among-year variability was high, with the overall migration rate from the point of release to the ocean ranging from 9.7 km/d in 2021 to 20.2 km/d in 2024. There was no apparent relationship between survival and migration rate in the Russian River.

DISCUSSION

Major findings from the survival studies

We found that the overall survival of yearling Coho Salmon emigrants from their natal streams to the estuary in spring was low but also highly variable across habitat segments, years, and release groups within years: 0.40 (range = 0.14–0.61) in the Russian River study and 0.06 (range = 0.00–0.23) in the South Fork Eel River study. Although overall survival was higher in the Russian River, when scaled by distance across main-stem habitat segments, survival was remarkably similar between the two studies (0.82 per 10 km for the Russian River and 0.83 per

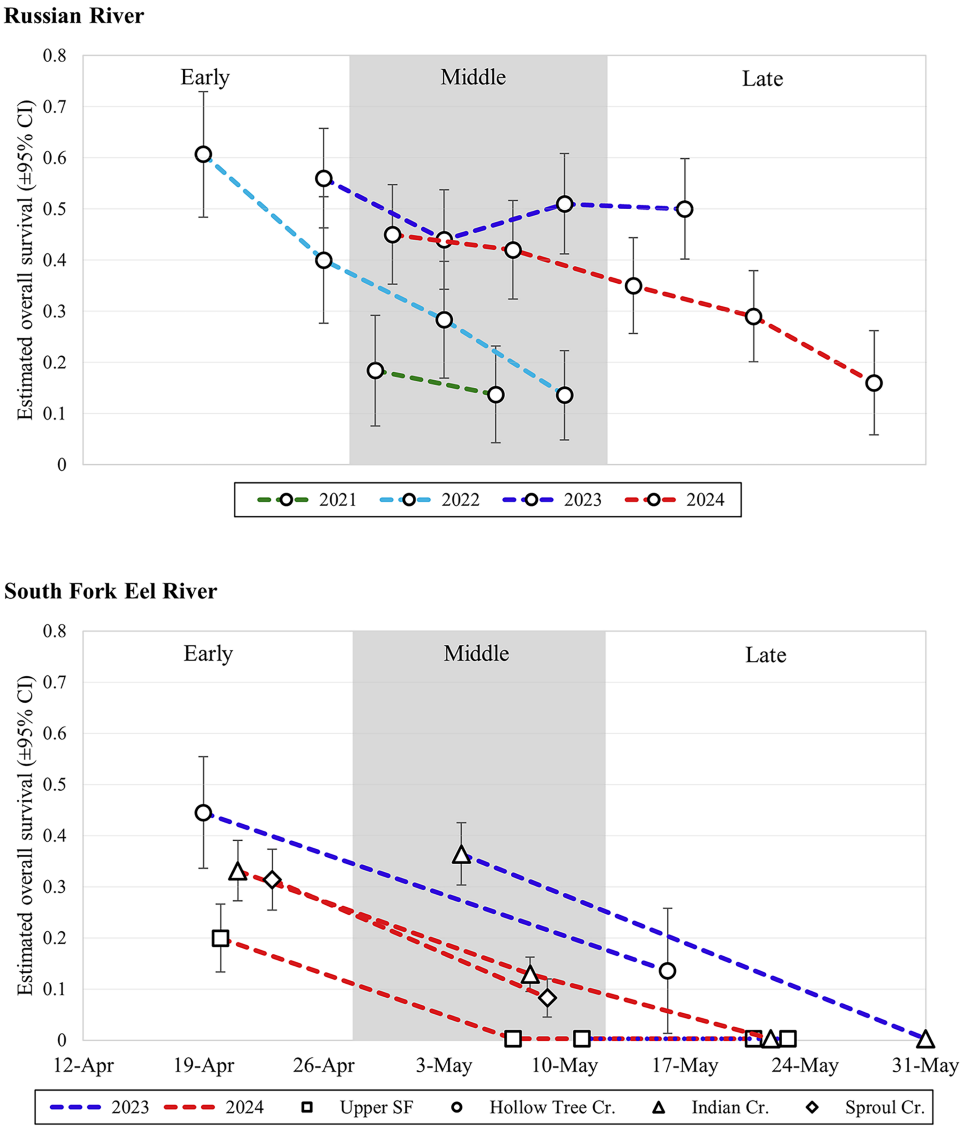

Figure 5. Estimated overall survival by release date (group) from Dry Creek (Cr.) to the downstream-most gate in the Russian River estuary (top panel) and from four release locations in the South Fork Eel River (SF) watershed to the downstream-most gate in the main-stem SF (bottom panel). Color represents year, and point type represents release location. Error bars represent 95% CIs.

Table 2. Linear model results for Coho Salmon survival as a function of the day of release (0–365). Note that for the Russian River, survival was estimated from the release site on Dry Creek to the estuary; for the South Fork Eel River, survival was estimated from the release site to the downstream end of the South Fork Eel River.

Stream	Estimate	SE	*P*-value
Russian River	−0.007676	0.002537	0.005263
South Fork Eel River	−0.010629	0.001905	8.94×10^{-5}

10 km for the South Fork Eel River). This finding suggests that the length of risky main stem that must be traversed by emigrating salmonids plays an important role in their survival. Survival was lowest in the main-stem SF and main-stem Russian River habitat segments, and survival increased in the lower main-stem Eel River and the Russian River estuary, both of which are larger, less confined habitats. Both studies indicated that earlier migrants survived at significantly higher rates than later migrants (Table 2). Finally, in contrast to other common life-stage-specific survival estimates (Table 4), the emigration mortality that we documented occurred over a very short period. For example, by extrapolating the median migration rates listed in Table 3 over the length of main-stem channel, the expected time spent in the Russian River by yearling Coho Salmon during spring emigration was 3.9 d (25th–75th percentiles = 3.0–5.8 d) and the expected time spent in the main-stem SF was 9.3 d (25th–75th percentiles = 5.9–17.6 d). In contrast, summer and winter juvenile survival estimates for Coho Salmon can range from 0.25 to 0.52 but occur over an interval of 100 d to more than 200 d (Table 4). Collectively, these results suggest that (1) main-stem rivers can be high-risk environments for juvenile salmonids; (2) risk differs significantly across years; (3) for yearling Coho Salmon, risk increases as the spring emigration season progresses, and high mortality may disproportionately impact late-spring or early summer emigrant

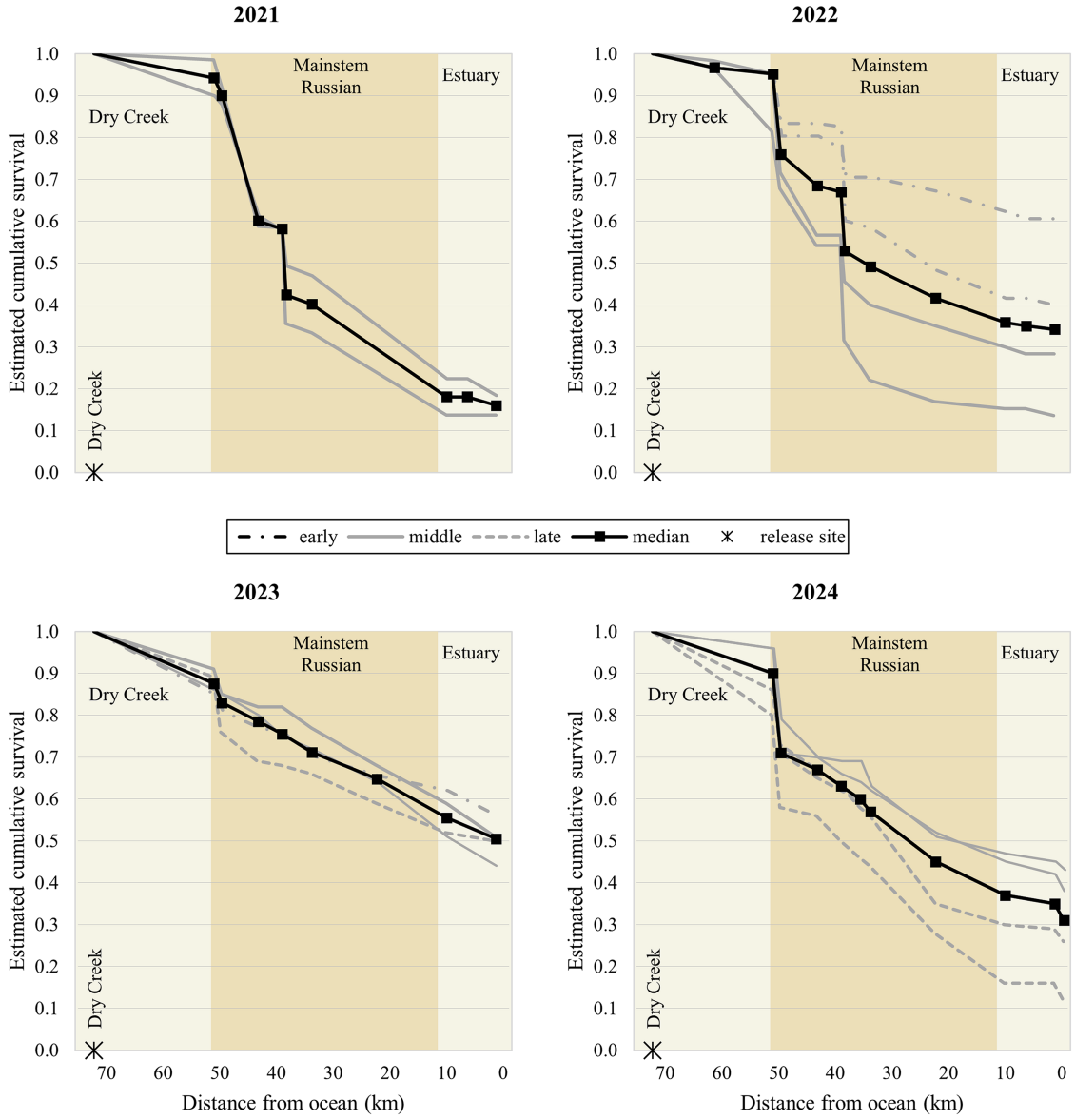

Figure 6. Estimated cumulative survival by release time (early, middle, and late) from release in Dry Creek to each gate in the Russian River. Note that cumulative survival to a given gate (i.e., distance from the ocean) is the product of upstream reach-specific survivals. The median survival at each gate is the median of the cumulative survivals of all release groups.

Table 3. Median migration rate (km/d) for Coho Salmon by habitat segment from the release site to the ocean for each study year and overall. Numbers in parentheses for each year indicate the lower (25th) and upper (75th) quartiles, respectively. The overall migration rate for each habitat segment is the average of the yearly medians and the average of the yearly quartiles. Migration rate from the release site to the ocean was not calculated for the South Fork Eel River because fish were released from multiple locations; NA = not applicable.

Watershed	Habitat segment	2021	2022	2023	2024	Overall
Russian River	Dry Creek	14.8 (13.3, 21.3)	9.7 (8.1, 12.6)	11.9 (7.2, 19.8)	14.1 (7.9, 18.1)	12.6 (9.1, 17.9)
	Main-stem Russian River	6.7 (4.4, 7.9)	11.7 (8.0, 12.8)	15.9 (12.6, 20.8)	8.1 (3.7, 13.8)	10.6 (7.1, 13.8)
	Estuary	16.1 (6.1, 25.8)	11.3 (7.2, 16.8)	12.0 (0.8, 14.0)	13.7 (6.3, 20.3)	13.3 (5.1, 19.2)
	Release to ocean	9.7 (8.1, 12.6)	15.9 (12.6, 20.8)	13.7 (6.3, 20.3)	20.2 (13.2, 27.0)	14.9 (10.1, 20.2)
South Fork Eel River	Upper South Fork Eel River			4.1 (2, 4.9)	2.4 (1.3, 3.2)	3.3 (1.7, 4.0)
	Main-stem South Fork Eel River			16.2 (8.9, 25.1)	9.5 (4.7, 15.4)	12.9 (6.8, 20.2)
	Lower main-stem Eel River			NA	4.7 (2.3, 11.3)	4.7 (2.3, 11.3)

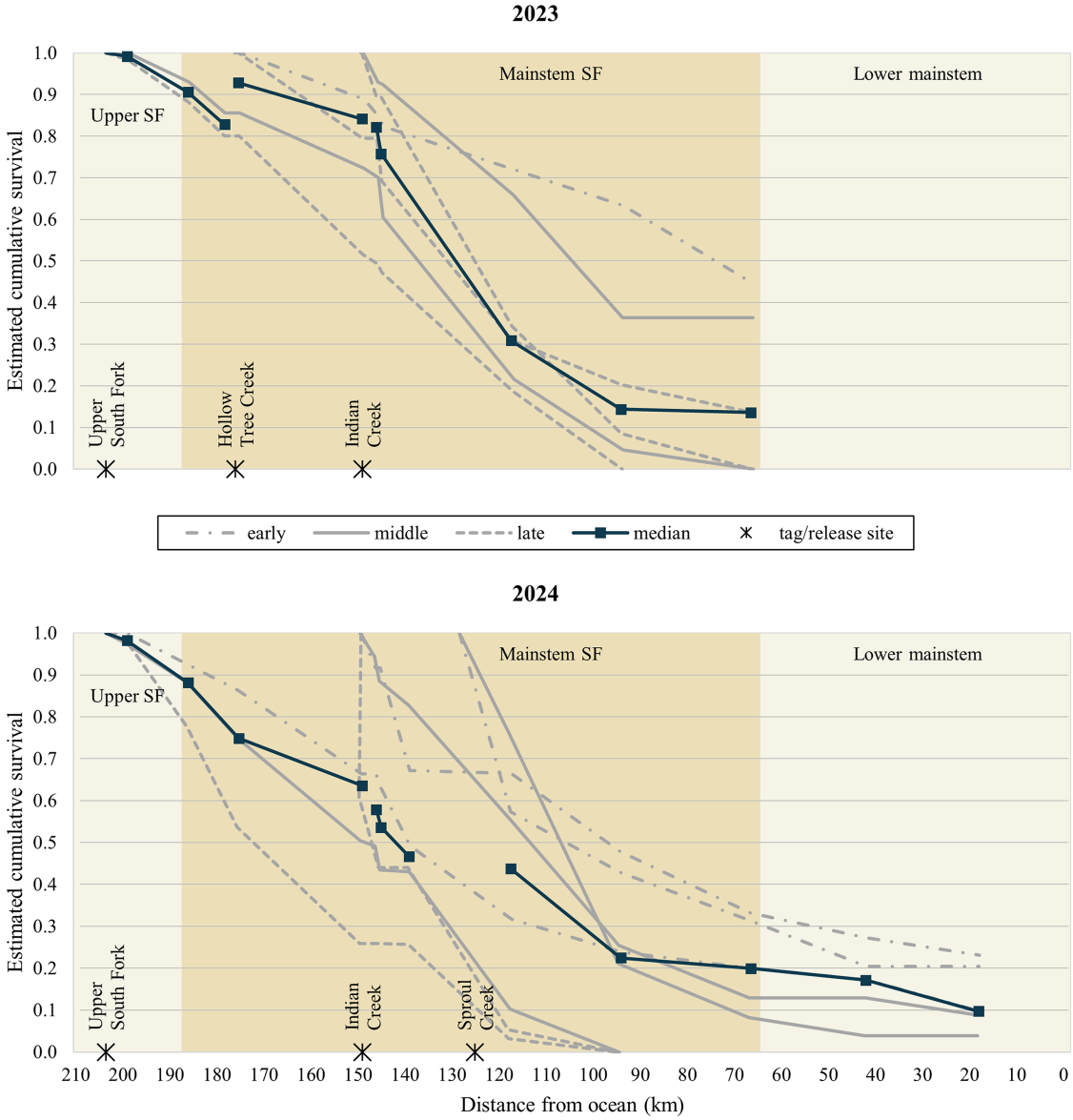

Figure 7. Estimated cumulative survival by release time (early, middle, and late) from the tag/release site (upper South Fork Eel River [upper SF] and Hollow Tree, Indian, and Sproul creeks) to each gate in the Eel River. Note that cumulative survival to a given gate (i.e., distance from the ocean) is the product of upstream reach-specific survivals. The median survival (black line) is the median of the cumulative survivals of all release groups. Breaks in the median survival line represent reaches where newly tagged fish entered the main stem.

life histories; and (4) this short but critical time period may pose a population bottleneck, especially in river systems with impaired main-stem habitats.

Comparison between the Russian River and South Fork Eel River

Given many differences between the two studies in habitat, fish size, development state, and origin (hatchery vs. wild), the similar patterns of low reach-scaled survival in main-stem rivers and declining survival with migration date are striking. The Russian and South Fork Eel rivers have distinct hydrogeologic settings, riverine species assemblages, watershed development, and degrees of anthropogenic flow alteration. Streamflow in the Russian River is influenced by releases from the two major reservoirs, whereas the South Fork Eel River is an unregulated stream with decentralized, small-scale diversions. Coho Salmon from the Russian River were hatchery origin and tagged as age-1 smolts, whereas fish from the South Fork Eel River were wild origin and captured as they departed from different natal streams. Consequently, emigrants in the South Fork Eel River study displayed a range of characteristics along the smoltification trajectory: from parr with minimal visual evidence of smolting to fish with evidence of more advanced smoltification. Hatchery-origin smolts in the Russian River were released at larger sizes (mean across years = 130–137 mm) than wild-origin South Fork Eel River fish (mean across years = 91–96 mm), and they were held in a hatchery environment for 7 d before release versus 12 h or

more in the South Fork Eel River. Despite these differences, main-stem habitat segments in both rivers share similar characteristics in terms of channel geometry, spring streamflow recession dynamics, and predator densities, which may drive the similar scaled survival estimates (see *Causes of risky main stems* section below).

Comparison to migratory survival in other systems

Chittenden et al. (2010) evaluated the survival of wild-origin Coho Salmon during their emigration from tributaries of the Thompson River to the Fraser River, British Columbia, over a 3-year period (distances ranging from 381 to 410 km), and those authors found extreme interannual variation. During two of the years, cumulative survival was very low (0.00–0.07; SE = 0.00–0.09), but survival in the final year was much higher (0.51; SE = 0.19). Chittenden et al. (2010) could not determine the drivers of this variability but hypothesized that predation, competition, and pollution levels in each river system contributed to the differences. They concluded that mortality during the freshwater emigration phase is a major factor in the population success of endangered Thompson River Coho Salmon.

The suggestion that freshwater migratory survival is a major population bottleneck was also posed by Michel (2018), who used acoustic telemetry to decouple marine and freshwater migratory survival over 5 years for Chinook Salmon in the Sacramento River, California. Michel (2018) found that freshwater emigration survival of juvenile Chinook Salmon ranged from 2.6% to 17%, while marine survival ranged from 4.2% to 22.8% for those cohorts. The author determined that contrary to convention, interannual fluctuations in smolt-to-adult returns were generally explained by freshwater emigration survival (rather than marine survival) unless abnormally poor marine conditions were present.

A 3-year radiotelemetry study of hatchery-origin Coho Salmon in the Klamath River, California, showed higher survival of main-stem emigrants than our studies. Beeman et al. (2012) found that over 4 years (2006–2009), apparent survival of hatchery fish through 276 km of the Klamath River (Iron Gate Dam to the upstream end of the estuary) ranged from 0.41 (SE = 0.048) to 0.648 (SE = 0.07), depending on the year, and averaged 0.79 per 100 km traveled. Scaled to survival per 10 km (as in Figure 4), this represented a survival rate of 0.98 per 10 km traveled. These results suggest much higher scaled survival than was observed in the Russian River (0.82 per 10 km), the South Fork Eel River (0.83 per 10 km), and 2 of 3 years for the Thompson River studies (Chittenden et al., 2010).

A telemetry study in the Trinity River, California, was conducted in 2022 and 2023 using wild-captured and hatchery-reared juvenile Chinook Salmon (Martel et al., 2024). Overall cumulative survival during spring out-migration from the upper Trinity River to the lower Klamath River differed drastically over the first 2 years of the study, with survival rates of 0.61 (SE = 0.15) in 2022 and 0.27 (SE = 0.08) in 2023. However, the overall length of the study design in 2023 was about 62 km longer than that in 2022. Survival scaled per 10 km of river was 0.95 in 2022 and 0.88 in 2023. Again, these survival rates are all higher than what we observed in the Russian and South Fork Eel rivers. The authors also noted high spatial heterogeneity in survival (Martel et al., 2024); however, unlike our studies of the Russian and South Fork Eel rivers, the uppermost reach of the Trinity River had the poorest survival rate of approximately 0.22 per 10 km. This segment of the Trinity River is the tailwater of a reservoir system where piscivorous animals, including resident Rainbow Trout, Brown Trout *Salmo trutta*, and a variety of birds, are known to congregate. Interestingly, this is also a segment of the river that has received a substantial investment in large-scale restoration projects; however, the natural hydrograph and temperature regime are still largely impacted by the reservoir systems. With the inclusion of this upper reach in 2023, overall and scaled survival rates more closely matched what we observed in the South Fork Eel and Russian rivers.

Contrasting yearling spring emigration survival with other life-stage-specific survival of Coho Salmon

Although estimates of life-stage-specific survival of juvenile salmonids in California are largely unpublished (although see Rebenack et al., 2015; Scheer, 2017), we were able to compare our estimates of juvenile emigration survival to estimates of

Table 4. Life-stage-specific survival estimates for Coho Salmon from three California streams. Abbreviations are as follows: min = minimum, max = maximum, and est. = estimate.

Description	Site	Mean	Min	Max	SD	Interval (d)	Source
Survival from emergence until fall	Freshwater Creek	0.57	0.09	1.00	0.11	(>150 d)	Scheer (2017)
Juvenile oversummer survival	Russian River tributaries	0.52	0.00	0.90	0.25	Jun 15–Oct 15 (122 d)	California Sea Grant (unpublished data; mean of 39 estimates from three streams over 8 years)
Juvenile overwinter survival	Freshwater Creek	0.27	0.22	0.33		Sep 15–May 30 or less (≤260 d)	Scheer (2017)
Juvenile overwinter survival	Russian River tributaries	0.25	0.04	0.54	0.13	Nov 30–Jun 15 (198 d)	California Sea Grant (unpublished data; mean of 40 estimates from four streams over 11 years)
Emigration survival in main-stem river	Russian River	0.44	0.14	0.73		Apr–May (est.: 3.9 d)	Present study
Emigration survival in main-stem river	South Fork Eel River	0.11	0.00	0.44		Apr–May (est.: 9.3 d)	Present study

juvenile oversummer and overwinter survival in Freshwater Creek (Scheer, 2017; Table 4) and tributaries of the Russian River (California Sea Grant, unpublished data; Table 4). Estimates for yearling spring emigration survival from our acoustic telemetry studies were lower than mean emergence-to-fall survival in Freshwater Creek and oversummer survival in the Russian River (although within the range of variance) and were similar to or lower than the mean overwinter survival. However, the mortality that we observed during emigration occurred over a much shorter time span and at an older age (fish > 1 year old). More published data on life-stage-specific survival would greatly enhance our ability to understand the relative importance of survival at different life stages and the factors constraining population recovery (Bilby et al., 2024).

A growing number of studies have highlighted the importance of alternative juvenile Coho Salmon emigration strategies in which fish leave their natal streams prior to their age-1 spring (Jones et al., 2014; Koski, 2009; Roni et al., 2012). Fish expressing these earlier emigration strategies contribute to adult returns (Bennett et al., 2015; Jones et al., 2021) and increase population stability (Baker et al., 2025). Due to limitations on sampling feasibility (prohibitively high winter flows and size thresholds for tagging), our study focused on estimating emigration survival of yearling Coho Salmon during the spring migration window. We were unable to estimate survival for these earlier emigrating life history strategies. We observed a range of ages and sizes at departure from natal streams, including fry migration, in our downstream migrant traps (Supplement D). However, because spring migration of yearling Coho Salmon is currently the most prevalent life history strategy in these systems (California Sea Grant, unpublished data), we think that emigration survival of this group has an outsized effect on population dynamics. Further work is needed to understand the contribution of earlier emigrants, particularly in years when yearling spring emigrant survival is extremely low.

Causes of risky main stems

Several possible factors may have contributed to mortality of juvenile Coho Salmon emigrants in both systems within and between years. Predation and metabolic stress are both proximate causes of mortality that are modulated by environmental factors like discharge, temperature, and turbidity (Gregory & Levings, 1998; Lawrence et al., 2023). Predation is likely a primary cause of mortality in main-stem reaches from both rivers, where emigrating salmonids encounter a high density of piscivorous fishes (Georgakakos et al., 2023; NMFS, 2024). The Russian River watershed contains native Sacramento Pikeminnow as well as nonnative black bass *Micropterus* spp., catfishes (*Ameiurus* spp. and *Ictalurus* spp.), and Striped Bass *Morone saxatilis*. Although there are no published studies documenting predation by these species on salmonid smolts in the Russian River, all have been documented as preying on salmonid smolts elsewhere, including the neighboring Sacramento River watershed (Michel, 2018; Peterson et al., 2023). Anthropogenic moderation of the Russian River's flow regime (e.g., decreased storm events and increased summer base flows) and creation of potential knickpoints (through infrastructure or by altering river morphology) could both stabilize habitat for nonnative fishes and funnel out-migrating salmonids through narrow zones of high potential predation. The Eel River, which historically did not have piscivorous fishes capable of consuming juvenile salmonids other than resident Rainbow Trout, currently has an abundant population of invasive Sacramento Pikeminnow (Georgakakos et al., 2023; NMFS, 2024). Juvenile salmonids have been found in the stomachs of these nonnative predators during the out-migration season (Wiyot Tribe, unpublished data). Working in the Eel River, Nakamoto and Harvey (2003) reported that the summer diets of Sacramento Pikeminnow larger than 250 mm were on average composed of nearly 70% fish species, with steelhead, Sacramento Sucker *Catostomus occidentalis*, Sacramento Pikeminnow, and California Roach *Hesperoleucus symmetricus* being the most common prey species. Sacramento Pikeminnow are concentrated in the confined South Fork Eel River main stem, where their habitat and foraging conditions are advantageous compared to the colder natal streams used by salmonids or the very large lower main-stem rivers and estuaries.

Additionally, avian predators (e.g., common merganser *Mergus merganser*, belted kingfisher *Megaceryle alcyon*, and herons *Ardea* spp.) and mammalian predators (e.g., river otter *Lontra canadensis*) inhabit both watersheds. Because many of the predators in these systems are gape-limited, larger salmonid emigrants are likely less vulnerable to some of these threats. The larger size of hatchery-origin Coho Salmon smolts in the Russian River study (mean of 132 mm compared to 93 mm for fish in the South Fork Eel River) might explain their higher survival (e.g., lower predation risk) relative to South Fork Eel River emigrants (Vasbinder et al., 2024). However, naïve fish, such as those reared in hatcheries, may also have a higher likelihood of being consumed by predators (Healey & Reinhardt, 1995). Smaller salmonids are vulnerable to a broader array of predators, but when they occur at very high densities (such as during fry migration), they may cause a prey swamping effect, thereby reducing individual predation risk (Holling, 1959). Our study was unable to evaluate the survival of smaller Coho Salmon or the effects of salmonid density on predation risk. More work is needed to understand the relationship between Coho Salmon vulnerability to predation and their size, origin, density, and life history expression.

Streamflow-driven effects on turbidity and water temperature may also play a role in predation risk (e.g., Cordoleani et al., 2018; Gregory & Levings, 1998; Ward et al., 2016). Although we do not have survival data for the South Fork Eel River during the extremely low flow years of 2021 and 2022, the extremely low flows in the Russian River during those years (U.S. Geological Survey gauge 11467000; 1940–2024) correspond to the lowest survival values observed during the 4 years of study. Relatively high flows during the 2023 and 2024 migration seasons in the Russian River may help to explain the higher survival observed in those years (i.e., Cordoleani et al., 2018). However, relationships between juvenile salmon survival and flow, turbidity, and temperature are complex. For example, while turbidity may reduce predation on salmonid emigrants, it also reduces their ability to forage and navigate complex habitat (Gregory & Levings, 1998; Ward et al., 2016). Temperature may also influence juvenile survival and fish responses along the emigration route, although there are numerous factors mediating these relationships (e.g., Armstrong & Schindler, 2013; McInturf et al., 2022). Over the course of both studies, temperatures in

main-stem habitat segments, which exceeded 20°C as early as mid-May in both systems, often exceeded established thresholds of suitability for juvenile Coho Salmon growth, swimming performance, and immune responses, but the timing of temperature increases varied across years (although fish emigrating in April experienced suitable temperatures across all years). More work is needed to understand how the interactions between flow, turbidity, water temperature, and predation risk influence the survival of emigrating juveniles.

Restoration investment across freshwater salmon habitats

Bilby et al. (2024) argued that a primary cause for the failure to see a return on investment in salmon recovery is that we are "not doing the right things in the right places at the right times." For many coastal river basins in California and throughout the Pacific Northwest, restoration investment in main-stem habitats lags significantly behind the restoration of spawning and rearing tributaries, yet our case studies show that main-stem migration survival for spring yearlings may be as limiting as (or more limiting than) early (e.g., age-0 summer, winter) survival in natal streams (Table 4). To explore whether restoration effort is concordant with the spatial and temporal constraints on salmon population recovery, we compared investment in stream habitat restoration planning and implementation across different stream habitats in the Russian and Eel River watersheds. Investment in stream restoration planning and implementation (in coastal California) comes largely from the following sources: the California Department of Fish and Wildlife's (CDFW) Watershed Restoration Grants Branch, the California Coastal Conservancy, the California Wildlife Conservation Board, significant federal investment (primarily the National Oceanic and Atmospheric Administration [NOAA] but also the Bureau of Land Management and U.S. Fish and Wildlife Service), and tribal and private sources. Although a complete assessment of each source is beyond the scope of this study, we obtained public records for Watershed Restoration Grants Branch (state-sourced) and NOAA Restoration Center (federally sourced) funding of salmonid-related projects in the Russian and Eel rivers for the period 2012–2024. To evaluate how restoration funding is being distributed across habitat types, we classified funded projects by type (design/planning or restoration) and we classified habitats targeted by restoration (estuary, floodplain, main-stem river, tributary, and upland). We excluded projects on lake ecosystems and funding types such as acquisition, scientific research, monitoring, and public outreach, which made up a small portion of overall investment.

In both the Russian and Eel River watersheds, the majority of design/planning (67% and 64%, respectively) as well as restoration (86% and 58%) work was focused on tributaries (Figure 8). This contrasts with a very small proportion of effort on main-stem rivers for design/planning (14% and 9%) and for restoration (10% and 5%). There are many reasons why main-stem river restoration investment lags behind tributary work, including the high need in some tributary habitats because of their degraded state and the fact that main-stem rivers are larger and more difficult environments in which to implement habitat restoration actions. The feasibility, cost, and jurisdictional and regulatory complications of restoration work are also typically greater in main-stem rivers (Bouska et al., 2023). Further, the difficulty in achieving and evaluating the success of objectives is greater in main-stem environments (Healy et al., 2024). A broader synthesis (beyond northern California) of efforts to understand and manage the mortality of emigrating salmonids in main-stem rivers is needed. Nevertheless, our studies and data analyses suggest that migration survival through main-stem rivers may be an overlooked constraint on salmonid population recovery in California coastal river systems.

Implications for population recovery and restoration prioritization

What should we do with this information? There are several aspects of our findings that could guide approaches to restoring depleted populations in other watersheds where juvenile emigration mortality is a concern. In our studies, certain main-stem reaches were particularly risky for juvenile Coho Salmon emigrants (Figure 6). Data suggest that the riskiest South Fork Eel River reaches are associated with higher Sacramento Pikeminnow density (Wiyot Tribe Natural Resources Department, 2024). In both rivers, there were indications that at least some tributary confluences are mortality hot spots, suggesting that efforts focused on quantifying and increasing survival at such locations may be warranted. We are beginning to reveal strong relationships between survival and environmental factors, including temperature, flow, and turbidity, which leads us to speculate that predation may be an important source of mortality in our study watersheds (Sonoma Water, unpublished data). We speculate that predatory fish focus on natal stream–main-stem confluences where juvenile salmonids transition from cooler tributaries into warmer main stems. It is well documented that temperatures preferable for warmwater fish predators, such as Sacramento Pikeminnow and black bass (≥20°C), are stressful to Coho Salmon (e.g., Nakano et al., 2014), and Olla et al. (1992) showed that stress hindered predator avoidance by Coho Salmon. Additionally, work by McInturf et al. (2022) confirmed that predators that are thermally adapted to higher temperatures will consume salmon with an increasing frequency as waters warm; therefore, fish that emigrate later in the season when water temperatures are warmer are at higher risk of predation. Turbidity may also play a role in moderating predation by providing juvenile escape cover (Ward et al., 2016), and faster migration rates that are facilitated by higher flow (Cordoleani et al., 2018) likely result in shorter periods of predation risk and lower concentrations of prey for predators to focus on. If this speculation is valid, creating shelter at tributary confluences to allow juveniles time to acclimate may be beneficial, especially during years with low turbidity and low flow. However, we caution that providing shelter for juveniles may also provide ambush habitat for predators. More research and experimentation are needed on this topic. Risky main stems may also be candidates for invasive predator suppression programs (California Trout et al., 2024), but suppression should only be considered in the context of well-designed, supported, and planned programs with clear objectives and based on testable hypotheses (Klein et al., 2022).

Another important reason to consider juvenile emigration survival is to improve population models and their application to recovery actions. There are many published studies that combine stage-specific salmonid survival estimates to approximate production of various life stages. However, survival during the short but critical period of freshwater emigration is often

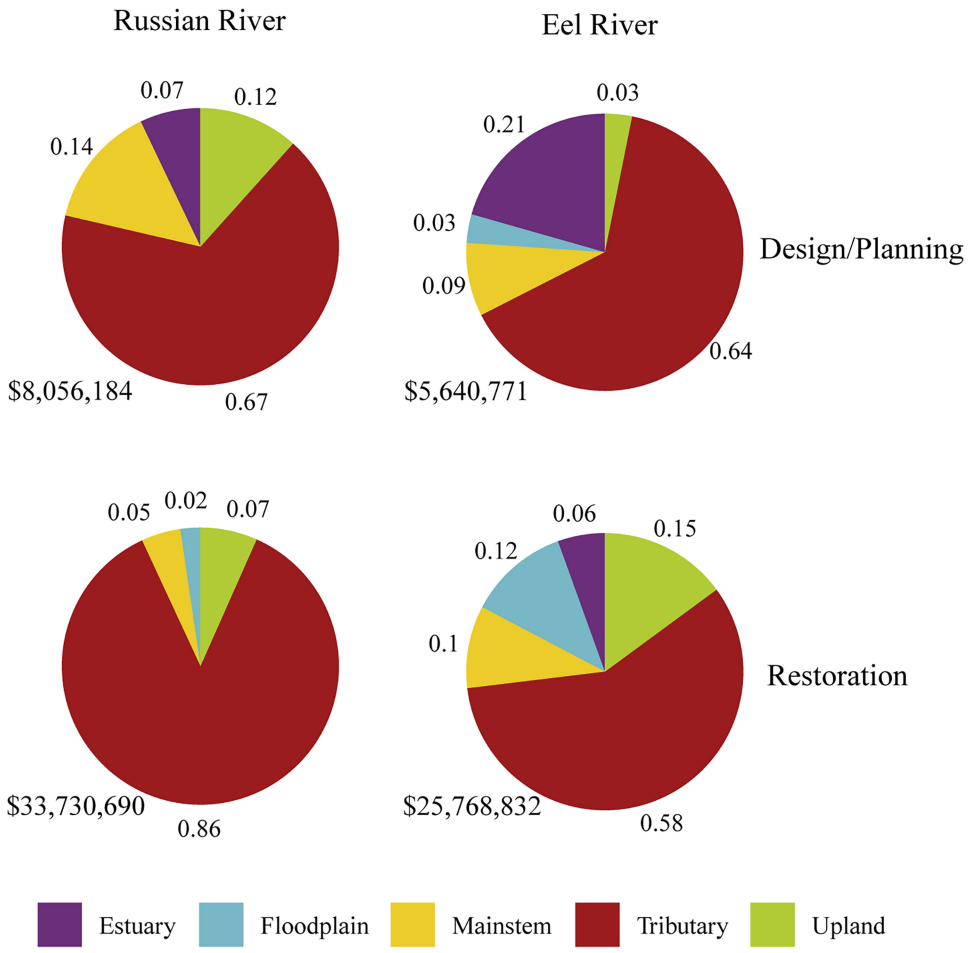

Figure 8. Grant investment in design/planning (top row) and restoration (bottom row) projects in the Russian River watershed (left column) and the Eel River watershed (right column) between 2012 and 2024. Total dollar values (US$) are provided for each stream and investment type, and the proportion of those values spent in different habitat types (e.g., estuary, floodplain, main-stem river, tributary, and upland) is shown by color in each chart.

not explicitly incorporated into these models. Consequently, estimates of smolt-to-adult returns may be seriously biased and difficult to interpret because freshwater, estuarine, and marine survival remain confounded (Chittenden et al., 2010; Michel, 2018). This type of bias impacts how limiting factors are assessed in population or life cycle models and consequently influences how recovery efforts are allocated based on these models. An important factor affecting the degree of that bias is the distribution of juvenile emigrant production within the watershed. Scaled survival estimates suggest that tributaries entering further downstream in main-stem rivers (or estuaries) would have much higher emigration survival than upper main-stem tributaries (although this pattern likely varies across water years). This information can be used to inform how smolt-to-adult returns are computed (decoupling freshwater and marine survival) and to guide salmon management and restoration priorities. Although fish emigrating from streams that enter risky main stems further upstream may experience higher emigration mortality, that difference may be offset by higher survival and growth at other life stages (e.g., Ebersole et al., 2006), making it an important consideration in population models. The intrinsic expression of life history diversity within salmon populations (and within watersheds) must be considered and ideally protected—even if some of those life histories are inherently risky (Carlson & Satterthwaite, 2011; Schindler et al., 2010).

Conclusions

Our work clearly highlights the importance of accounting for emigration survival when developing and evaluating salmonid protection and recovery strategies. Estimates of juvenile Coho Salmon emigration survival in other watersheds are also low and variable (e.g., Beeman et al., 2012; Chittenden et al., 2010), suggesting that the issue of high emigration mortality may be quite prevalent across their range. However, we know little about survival during this period in unimpaired systems. Beyond the population effects of mortality due to predation or other causes, risky main stems may also have indirect effects on salmon populations. For example, contemporary salmon conservation science emphasizes the importance of salmon life history diversity in maintaining the abundance and resilience of populations (Carlson & Satterthwaite, 2011; Schindler et al., 2010). Juvenile salmon populations often depend on rearing opportunities that may include time spent in the main stem and other nonnatal habitats for rearing or as stopover sites (i.e., nonnatal rearing life histories; Flitcroft et al., 2016). The ability of fish to access a mosaic of connected habitats distributed in

space provides the raw potential for the expression of life history diversity, which both increases population resilience and drives greater overall abundance (Baker et al., 2025; Rossi et al., 2024). The small size of most natal streams limits their carrying capacity. Thus, when juvenile fish can spread out across the watershed and use diverse nonnatal habitats (e.g., river main stems, floodplains, and estuaries), the watershed's overall rearing habitat area and associated carrying capacity increase, which in turn increases population abundance and resilience. Therefore, the poor survival that we documented during Coho Salmon emigration in main-stem rivers not only limits production of future life stages but may also truncate the expression of critical life history diversity in salmon populations.

SUPPLEMENTARY MATERIAL

Supplementary material is available at *North American Journal of Fisheries Management* online.

DATA AVAILABILITY

The data associated with this study are available from the corresponding author upon reasonable request.

ETHICS STATEMENT

The handling of all fish that were captured for this study was in accordance with California Endangered Species Act and federal Endangered Species Act permits.

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CONFLICTS OF INTEREST

The authors declare no conflicts of interest.

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REFERENCES

Armstrong, J. B., & Schindler, D. E. (2013). Going with the flow: Spatial distributions of juvenile Coho Salmon track an annually shifting mosaic of water temperature. *Ecosystems, 16*, 1429–1441. https://doi.org/10.1007/s10021-013-9693-9

Baker, H. K., Obedzinski, M., Grantham, T. E., & Carlson, S. M. (2025). Variation in salmon migration phenology bolsters population stability but is threatened by drought. *Ecology Letters, 28*, Article e70081. https://doi.org/10.1111/ele.70081

Beamish, R. J., Sweeting, R. M., Lange, K. L., Noakes, D. J., Preikshot, D., & Neville, C. M. (2010). Early marine survival of Coho Salmon in the Strait of Georgia declines to very low levels. *Marine and Coastal Fisheries: Dynamics, Management, and Ecosystem Science, 2*, 424–439. https://doi.org/10.1577/C09-040.1

Beeman, J., Juhnke, S., Stutzer, G., & Wright, K. (2012). *Effects of Iron Gate Dam discharge and other factors on the survival and migration of juvenile Coho Salmon in the lower Klamath River, northern California, 2006–09* (Open-File Report 2012-1067). U.S. Geological Survey.

Bennett, T., Roni, P., Denton, K., Mchenry, M., & Moses, R. (2015). Nomads no more: Early juvenile Coho Salmon migrants contribute to the adult return. *Ecology of Freshwater Fish, 24*, 264–275. https://doi.org/10.1111/eff.12144

Bilby, R. E., Currens, K. P., Fresh, K. L., Booth, D. B., Fuerstenberg, R. R., & Lucchetti, G. L. (2024). Why aren't salmon responding to habitat restoration in the Pacific Northwest? *Fisheries, 49*, 16–27. https://doi.org/10.1002/fsh.10991

Bouska, K. L., Healy, B. D., Moore, M. J., Dunn, C. G., Spurgeon, J. J., & Paukert, C. P. (2023). Diverse portfolios: Investing in tributaries for restoration of large river fishes in the Anthropocene. *Frontiers in Environmental Science, 11*, Article 1151315. https://doi.org/10.3389/fenvs.2023.1151315

California Department of Fish and Game. (2002). *Status review of California Coho Salmon north of San Francisco*. https://cawaterlibrary.net/wp-content/uploads/2017/10/SAL_Coho_StatusNorth_2002.pdf

California Sea Grant, & Sonoma Water. (2024). *Coho Salmon and steelhead monitoring report: Winter 2023/24*. University of California.

California Trout, Stillwater Sciences, Applied River Sciences, & University of California Berkeley. (2024). *Eel River restoration and conservation plan—Phase 1: Planning—of the Eel River Watershed Restoration and Conservation Program*. California Trout.

Carlson, S. M., & Satterthwaite, W. H. (2011). Weakened portfolio effect in a collapsed salmon population complex. *Canadian Journal of Fisheries and Aquatic Sciences: Journal Canadien des Sciences Halieutiques et Aquatiques, 68*, 1579–1589. https://doi.org/10.1139/F2011-084

Chittenden, C. M., Melnychuk, M. C., Welch, D. W., & McKinley, R. S. (2010). An investigation into the poor survival of an endangered Coho Salmon population. *PLoS One, 5*, Article e10869. https://doi.org/10.1371/journal.pone.0010869

Cordoleani, F., Notch, J., McHuron, A. S., Ammann, A. J., & Michel, C. J. (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, 171–184. https://doi.org/10.1002/tafs.10008

Duda, J. J., Torgersen, C. E., Brenkman, S. J., Peters, R. J., Sutton, K. T., Connor, H. A., Kennedy, P., Corbett, S. C., Welty, E. Z., Geffre, A., Geffre, J., Crain, P., Shreffler, D., McMillan, J. R., McHenry, M., & Pess, G. R. (2021). Reconnecting the Elwha River: Spatial patterns of fish response to dam removal. *Frontiers in Ecology and Evolution, 9*, Article 765488. https://doi.org/10.3389/fevo.2021.765488

Ebersole, J. L., Wigington, P. J., Baker, J. P., Cairns, M. A., Church, M. R., Hansen, B. P., Miller, B. A., Lavigne, H. R., Compton, J. E., & Leibowitz, S. G. (2006). Juvenile Coho Salmon growth and survival across stream network seasonal habitats. *Transactions of the American Fisheries Society, 135*, 1681–1697. https://doi.org/10.1577/T05-144.1

Flitcroft, R. L., Lewis, S. L., Arismendi, I., LovellFord, R., Santelmann, M. V., Safeeq, M., & Grant, G. (2016). Linking hydroclimate to fish phenology and habitat use with ichthyographs. *PLoS One, 11*, Article e0168831. https://doi.org/10.1371/journal.pone.0168831

Frissell, C. A., Liss, W. J., Warren, C. E., & Hurley, M. D. (1986). A hierarchical framework for stream habitat classification: Viewing streams in a watershed context. *Environmental Management, 10*, 199–214. https://doi.org/10.1007/BF01867358

Georgakakos, P. B., Dralle, D. N., & Power, M. E. (2023). Spring temperature predicts upstream migration timing of invasive Sacramento Pikeminnow within its introduced range. *Environmental Biology of Fishes, 106*, 2069–2082. https://doi.org/10.1007/s10641-023-01486-y

Goertler, P. A. L., Johnston, M., Michel, C. J., Grimes, T., Singer, G., Notch, J., & Sommer, T. (2024). Use of telemetry data to quantify life history diversity in migrating juvenile Chinook Salmon (*Oncorhynchus tshawytscha*). *Water, 16*, Article 2529. https://doi.org/10.3390/w16172529

Goslin, M. (2005). *Creating a comprehensive dam dataset for assessing anadromous fish passage in California* (Technical Memorandum NMFS-SWFSC-376). National Oceanic and Atmospheric Administration.

Grantham, T. E., Newburn, D. A., McCarthy, M. A., & Merenlender, A. M. (2012). The role of streamflow and land use in limiting oversummer survival of juvenile steelhead in California streams. *Transactions of the American Fisheries Society, 141*, 585–598. https://doi.org/10.1080/00028487.2012.683472

Gregory, R. S., & Levings, C. D. (1998). Turbidity reduces predation on migrating juvenile Pacific salmon. *Transactions of the American Fisheries Society, 127*, 275–285. https://doi.org/10.1577/1548-8659(1998)127<0275:TRPOMJ>2.0.CO;2

Guczek, J., Powers, S., & Larson, M. (2020). *Results of regional spawning ground surveys and estimates of salmonid redd abundance in the South Fork Eel River, Humboldt and Mendocino counties, California, 2019–2020* (Annual Report). California Department of Fish and Wildlife.

Hampton, A., Lindley, C., Loomis, C., & Olswang, M. (2021). *Assessment of restoration projects funded from 2004 to 2018 supporting Coho Salmon recovery in four focus areas along California's north coast*. California Department of Fish and Wildlife. https://nrm.dfg.ca.gov/FileHandler.ashx?DocumentID=193854&inline

Hayes, J. W., Goodwin, E., Shearer, K. A., Hay, J., & Kelly, L. (2016). Can weighted useable area predict flow requirements of drift-feeding salmonids? Comparison with a net rate of energy intake model incorporating drift-flow processes. *Transactions of the American Fisheries Society, 145*, 589–609. https://doi.org/10.1080/00028487.2015.1121923

Healey, M. C., & Reinhardt, U. (1995). Predator avoidance in naive and experienced juvenile Chinook and Coho salmon. *Canadian Journal of Fisheries and Aquatic Sciences: Journal Canadien des Sciences Halieutiques et Aquatiques, 52*, 614–622. https://doi.org/10.1139/f95-061

Healy, B. D., Runge, M. C., Beakes, M., Phillis, C. C., Jensen, A. J., & Israel, J. A. (2024). The value of information is context dependent: A demonstration of decision tools to address multispecies river temperature management under uncertainty. *Fisheries, 49*, 508–523. https://doi.org/10.1002/fsh.11174

Hodgson, E. E., Wilson, S. M., & Moore, J. W. (2020). Changing estuaries and impacts on juvenile salmon: A systematic review. *Global Change Biology, 26*, 1986–2001. https://doi.org/10.1111/gcb.14997

Holling, C. S. (1959). Some characteristics of simple types of predation and parasitism. *The Canadian Entomologist, 91*, 385–398. https://doi.org/10.4039/Ent91385-7

Hyatt, K. D., & Stockwell, M. M. (2019). Chasing an illusion? Successful restoration of Okanagan River Sockeye Salmon in a sea of uncertainty. In C. C. Krueger, W. W. Taylor, & S. Youn (Eds.), *From catastrophe to recovery: Stories of fish management success* (pp. 65–100). American Fisheries Society. https://doi.org/10.47886/9781934874554.ch4

Jaeger, W. K., & Scheuerell, M. D. (2023). Return(s) on investment: Restoration spending in the Columbia River basin and increased abundance of salmon and steelhead. *PLoS One, 18*, Article e0289246. https://doi.org/10.1371/journal.pone.0289246

Jones, K. K., Cornwell, T. J., Bottom, D. L., Campbell, L. A., & Stein, S. (2014). The contribution of estuary-resident life histories to the return of adult *Oncorhynchus kisutch*. *Journal of Fish Biology, 85*, 52–80. https://doi.org/10.1111/jfb.12380

Jones, K. K., Cornwell, T. J., Bottom, D. L., Stein, S., & Starcevich, S. (2021). Interannual variability in life-stage specific survival and life history diversity of Coho Salmon in a coastal Oregon basin. *Canadian Journal of Fisheries and Aquatic Sciences, 78*, 1887–1899. https://doi.org/10.1139/cjfas-2020-0306

Kastl, B., Obedzinski, M., Carlson, S. M., Boucher, W. T., & Grantham, T. E. (2022). Migration in drought: Receding streams contract the seaward migration window of endangered salmon. *Ecosphere, 13*, Article e4295. https://doi.org/10.1002/ecs2.4295

Katopodis, C., & Williams, J. G. (2012). The development of fish passage research in a historical context. *Ecological Engineering, 48*, 8–18. https://doi.org/10.1016/j.ecoleng.2011.07.004

Klein, Z. B., Quist, M. C., & Guy, C. S. (2022). Suppression of invasive fish in the west: Synthesis and suggestions for improvement. *North American Journal of Fisheries Management, 43*, 369–383. https://doi.org/10.1002/nafm.10827

Koski, K. V. (2009). The fate of Coho Salmon nomads: The story of an estuarine-rearing strategy promoting resilience. *Ecology and Society, 14*, Article 4.

Laake, J. L. (2013). *RMark: an R interface for analysis of capture–recapture data with MARK* (AFSC Processed Report 2013-01). National Marine Fisheries Service, Alaska Fisheries Science Center.

Lawrence, M. J., Prystay, T. S., Dick, M., Eliason, E. J., Elvidge, C. K., Hinch, S. G., Patterson, D. A., Lotto, A. G., & Cooke, S. J. (2023). Metabolic constraints and individual variation shape the trade-off between physiological recovery and anti-predator responses in adult Sockeye Salmon. *Journal of Fish Biology, 103*, 280–291. https://doi.org/10.1111/jfb.15420

Lebreton, J.-D., Burnham, K. P., Clobert, J., & Anderson, D. R. (1992). Modeling survival and testing biological hypotheses using marked animals: A unified approach with case studies. *Ecological Monographs, 62*, 67–118. https://doi.org/10.2307/2937171

Martel, C., Alvarez, J., & Reinstein, Z. (2024). *Chinook survival and migration on the Trinity River* [Presentation]. 2024 Science Symposium, Trinity River Restoration Program, Weaverville, California. https://www.trrp.net/2024-science-symposium/

McInturf, A. G., Zillig, K. W., Cook, K., Fukumoto, J., Jones, A., Patterson, E., Cocherell, D. E., Michel, C. J., Caillaud, D., & Fangue, N. A. (2022). In hot water? Assessing the link between fundamental thermal physiology and predation of juvenile Chinook Salmon. *Ecosphere, 13*, Article e4264. https://doi.org/10.1002/ecs2.4264

McMichael, G. A., Eppard, M. B., Carlson, T. J., Carter, J. A., Ebberts, B. D., Brown, R. S., Weiland, M., Ploskey, G. R., Harnish, R. A., & Deng, Z. D. (2010). The Juvenile Salmon Acoustic Telemetry System: A new tool. *Fisheries, 35*, 9–22. https://doi.org/10.1577/1548-8446-35.1.9

Michel, C. J. (2018). 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: Journal Canadien des Sciences Halieutiques et Aquatiques*, *76*, 1398–1410. https://doi.org/10.1139/cjfas-2018-0140

Nakamoto, R. J., & Harvey, B. C. (2003). Spatial, seasonal, and size-dependent variation in the diet of Sacramento Pikeminnow in the Eel River, northwestern California. *California Fish and Game Journal*, *89*, 30–45.

Nakano, T., Kameda, M., Shoji, Y., Hayashi, S., Yamaguchi, T., & Sato, M. (2014). Effect of severe environmental thermal stress on redox state in salmon. *Redox Biology*, *2*, 772–776. https://doi.org/10.1016/j.redox.2014.05.007

National Marine Fisheries Service. (2008). *Biological opinion for water supply, flood control operations, and channel maintenance conducted by the U.S. Army Corps of Engineers, the Sonoma County Water Agency, and the Mendocino County Russian River Flood Control and Water Conservation Improvement District in the Russian River watershed*.

National Marine Fisheries Service. (2012). *Final recovery plan for central California coast Coho Salmon evolutionarily significant unit*. National Marine Fisheries Service, Southwest Region.

National Marine Fisheries Service. (2014). *Final recovery plan for the southern Oregon/northern California coast evolutionarily significant unit of Coho Salmon* (Oncorhynchus kisutch). National Oceanic and Atmospheric Administration.

National Marine Fisheries Service. (2016). *Coastal multispecies recovery plan: California coastal Chinook Salmon ESU, northern California steelhead DPS, and central California coast steelhead DPS*. National Oceanic and Atmospheric Administration.

National Marine Fisheries Service. (2023). *FY22 Pacific Coastal Salmon Recovery Fund report to Congress, May 9, 2023*. National Oceanic and Atmospheric Administration. https://storymaps.arcgis.com/stories/9385da2091964a37bbd53971cf6e9e03.

National Marine Fisheries Service. (2024). *2024 5-year review: Summary and evaluation of southern Oregon/northern California coast Coho Salmon*. National Oceanic and Atmospheric Administration. https://www.fisheries.noaa.gov/s3//2024-12/soncc-coho-5yr-review.pdf.

Nobriga, M. L., Michel, C. J., Johnson, R. C., & Wikert, J. D. (2021). Coldwater fish in a warm water world: Implications for predation of salmon smolts during estuary transit. *Ecology and Evolution*, *11*, 10381–10395. https://doi.org/10.1002/ece3.7840

Obedzinski, M., Nossaman Pierce, S., Horton, G. E., & Deitch, M. J. (2018). Effects of flow-related variables on oversummer survival of juvenile Coho Salmon in intermittent streams. *Transactions of the American Fisheries Society*, *147*, 588–605. https://doi.org/10.1002/tafs.10057

Olla, B. L., Davis, M. W., & Schreck, C. B. (1992). Notes: Comparison of predator avoidance capabilities with corticosteroid levels induced by stress in juvenile Coho Salmon. *Transactions of the American Fisheries Society*, *121*, 544–547. https://doi.org/10.1577/1548-8659(1992)121<0544:NCOPAC>2.3.CO;2

Pearcy, W. G. (1992). *Ocean ecology of North Pacific salmonids*. University of Washington Press.

Peterson, M. L., Pilger, T. J., Guignard, J., Fuller, A., & Demko, D. (2023). Diets of native and non-native piscivores in the Stanislaus River, California, under contrasting hydrologic conditions. *San Francisco Estuary and Watershed Science*, *21*, Article 1. https://doi.org/10.15447/sfews.2023v21iss4art4

R Core Team. (2024). *R: A language and environment for statistical computing*. R Foundation for Statistical Computing.

Rebenack, J. J., Ricker, S., Anderson, C., Wallace, M., & Ward, D. M. (2015). Early emigration of juvenile Coho Salmon: Implications for population monitoring. *Transactions of the American Fisheries Society*, *144*, 163–172. https://doi.org/10.1080/00028487.2014.982258

Roni, P. (2019). Does river restoration increase fish abundance and survival or concentrate fish? The effects of project scale, location, and fish life history. *Fisheries*, *44*, 7–19. https://doi.org/10.1002/fsh.10180

Roni, P., Bennett, T., Holland, R., Pess, G., Hanson, K., Moses, R., Mchenry, M., Ehinger, W., & Walter, J. (2012). Factors affecting migration timing, growth, and survival of juvenile Coho Salmon in two coastal Washington watersheds. *Transactions of the American Fisheries Society*, *141*, 890–906. https://doi.org/10.1080/00028487.2012.675895

Roni, P., Pess, G. R., Beechie, T. J., & Hanson, K. M. (2014). *Fish–habitat relationships and the effectiveness of habitat restoration* (Technical Memorandum NMFS-NWFSC-127). National Oceanic and Atmospheric Administration.

Rossi, G. J., Bellmore, J. R., Armstrong, J. B., Jeffres, C., Naman, S. M., Carlson, S. M., Grantham, T. E., Kaylor, J. M., White, S., Katz, J., & Power, M. E. (2024). Foodscapes for salmon and other mobile consumers in river networks. *Bioscience*, *74*, 586–600. https://doi.org/10.1093/biosci/biae064

Scheer, G. (2017). *A population model for Coho Salmon* (Oncorhynchus kisutch) *in Freshwater Creek: Evaluating the effects of life history variation and habitat restoration* [Master's thesis, Cal Poly Humboldt]. Cal Poly Humboldt Digital Commons. https://digitalcommons.humboldt.edu/etd/105.

Schindler, D. E., Hilborn, R., Chasco, B., Boatright, C. P., Quinn, T. P., Rogers, L. A., & Webster, M. S. (2010). Population diversity and the portfolio effect in an exploited species. *Nature*, *465*, 609–612. https://doi.org/10.1038/nature09060

U.S. Office of the Federal Register. (2005). Endangered and threatened species: Final listing determinations for 16 ESUs of West Coast salmon, and final 4(d) protective regulations for threatened salmonid ESUs, final rule. *Federal Register* 70:123:(28 June 2005): 37160–37204.

U.S. Senate Committee on Commerce, Science, and Transportation. (2023). *NOAA announces $3.31 billion investment in coastal resilience, salmon recovery, and infrastructure—Largest in agency's history* (Press release). https://www.commerce.senate.gov/2023/6/noaa-announces-3-31-billion-investment-in-coastal-resilience-salmon-recovery-and-infrastructure-largest-in-agency-s-history

Vasbinder, K., Fiechter, J., Santora, J. A., Anderson, J. J., Mantua, N., Lindley, S. T., Huff, D. D., & Wells, B. K. (2024). Size-selective predation effects on juvenile Chinook Salmon cohort survival off central California evaluated with an individual-based model. *Fisheries Oceanography*, *33*, Article e12654. https://doi.org/10.1111/fog.12654

Ward, D. L., Morton-Starner, R., & Vaage, B. (2016). Effects of turbidity on predation vulnerability of juvenile Humpback Chub to Rainbow Trout and Brown Trout. *Journal of Fish and Wildlife Management*, *7*, 205–212. https://doi.org/10.3996/102015-JFWM-101

White, G. C., & Burnham, K. P. (1999). Program MARK: Survival estimation from populations of marked animals. *Bird Study*, *46*, S120–S139. https://doi.org/10.1080/00063659909477239

Williams, B. K., Nichols, J. D., & Conroy, M. J. (2002). *Analysis and management of animal populations*. Academic Press.

Wiyot Tribe Natural Resources Department. (2024). *Lhou'lhaqh (South Fork Eel River) Sacramento Pikeminnow management plan*.