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Navigating Shallow Streams: Effects of Changing Stream Water Depths on Outmigration of Endangered Coho Salmon

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ABSTRACT

Declining streamflow from water management and climate change threatens fish migration. In coastal California, USA, we evaluated the effects of receding streamflow on the seaward migration of juvenile Coho Salmon (*Oncorhynchus kisutch*) in four streams over 10 years (2010–2020). We monitored the movement of juveniles tagged with passive integrated transponders and measured depths at riffle crest thalwegs (RCTs), the shallowest channel feature that fish must navigate. Each stream exhibited a unique relationship between RCT depth and flow, relating to its geomorphic characteristics, producing distinct ranges of water depths among streams. During the peak migration period, juveniles moved over a wide range of depths (interquartile range 5.8–19.2 cm), with greater depths occurring in wet years than in dry years. However, the depths at which fish were detected were significantly deeper than continuous, observed depth measurements during the same period. We found the greatest differences between depth-at-movement and observed depths when streams were shallowest (< 10th percentile of observed depths). The timing at which stream depths fell below a regional fish passage criterion (9.1 cm) was also significantly correlated with the end of juvenile migration. In dry years, we observed greater variation in migration timing among streams, highlighting stream-specific variation in the timing at which depths limit fish movement. Collectively, our study indicates that shallow depths impair salmon outmigration and that flow-RCT depth relationships can be used to assess flow needs for fish migration and to guide streamflow restoration.

1 | Introduction

Water scarcity is increasing in many regions of the world, due to growing human population pressures and climate change (Vörösmarty et al. 2000). In the western United States, record-low streamflow and reservoir levels in recent decades have had major impacts on water supplies for agriculture, industry, and municipalities (Wahl et al. 2022). Streamflow depletion has also had significant ecological effects, pushing many aquatic species to the brink of extinction (Closs et al. 2016). Periods of extreme low flow have been shown to reduce access to suitable habitats (Jaeger et al. 2014; Thorstad et al. 2003), increase water temperatures, increase susceptibility of organisms to predation (Nobriga et al. 2021; Lonzarich and Quinn 1995), limit hydrologic connectivity, and disrupt migration pathways (Magoulick and Kobza 2003).

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California's Pacific salmon are particularly vulnerable to declining streamflow. Occurring at the southern end of their range, Pacific salmon in California experience a more intense dry season than populations farther north and may be particularly vulnerable to low-flow stressors. Previous studies have shown that over-summer survival of juvenile Coho Salmon is lowest in drought years, when naturally limited water supplies, coupled with high human demands, increase the risk of flow depletion (Deitch and Dolman 2017). Low flow is now recognized as an important limiting factor to juvenile salmon rearing in many coastal California streams (Grantham et al. 2012; Obedzinski et al. 2018).

Low streamflow also threatens the spring seaward migration (outmigration) of juvenile salmon (smolts) in California (Sturrock et al. 2020; Sykes et al. 2009). Unlike in the northern, temperate-climate region of their range, coastal streams in Mediterranean-climate California experience a predictable flow recession throughout the spring that reaches zero or near-zero values by summer (Deitch and Dolman 2017). This transition between wet and dry seasons is accelerated in drought years, and in coastal streams an earlier flow recession is associated with an earlier end of migration for Coho Salmon smolts (Kastl et al. 2022; Osterback et al. 2018). This suggests that low streamflow during spring may be an important limiting factor to smolt migration. While previous research has shown that juvenile passage through fishways can be limited by insufficient water depths, barriers, biological conditions, and physical habitat features https://www.zotero.org/google-docs/?broken=rhcqpK (Reiser and Bjornn 1979; Powers and Orsborn 1985; ODFW 2004; R2 Resource Consultants and Stetson Engineers 2007; Ohms et al. 2022), gaps remain in the understanding of the effects of shallow water depths on outmigration through natural stream channels. Moreover, most studies of salmon passage suitability estimate the flow (or depth) of water required to submerge the standard body depth of salmon at different life stages (e.g., 9.1 cm for salmon smolts; CDFW 2017). Studies that directly measure the depths of water navigated by salmon in natural stream channels are limited. A better understanding of passage flow requirements for Coho Salmon smolts in coastal California is particularly important because of their highly imperiled population and the growing risk of streamflow depletion in the spring from both human water withdrawals (Deitch et al. 2009) and climate change (Grantham et al. 2018).

In this study, we characterized Coho Salmon smolt movement patterns in relation to flow and water depths encountered during spring outmigration. Specifically, we asked (1) What are the water depths that juvenile Coho Salmon navigate during their outmigration, and how do these vary among years and streams? (2) How does the occurrence of shallow water depths affect outmigration? And (3) do dry years lead to greater variability in outmigration timing and depth, due to greater variability in the timing of drying among streams? To address these questions, we tracked the movement of fish individually marked with passive integrated transponder (PIT) tags and monitored flow and water depths at riffle crests—the shallowest section of repeating pool-riffle habitat units—during the outmigration period at four study streams within the Russian River watershed in northern California, USA over 10 years (2010–2020, excluding 2015). We compared water depths recorded during smolt movement detections to depths observed continuously during the outmigration period. We hypothesized (H1) that smolts avoid navigating shallow water depths. We also hypothesized (H2) that shallow water depths truncate the outmigration season. Finally, we predicted (H3) that dry years would correspond to greater inter-stream variability in outmigration timing. Overall, this work advances understanding of environmental controls on salmon outmigration and highlights that management interventions, including stream-specific flow protections that correspond to minimum water depths, can be designed to protect the movement of migratory fish in a changing climate.

2 | Materials and Methods

2.1 | Study Area

The study area includes four tributaries to the Russian River, in Sonoma County, California (Figure 1). The region has a distinct winter rainfall regime (November–April) with streams experiencing flashy, high flows during winter storms, followed by a flow recession in spring and through the summer dry season. During most years, streamflow in the study streams fell to less than 0.003 m^3s^{-1} (0.1 cubic foot per second [cfs]) by 1 August, often as early as 1 May in dry years. Mean annual precipitation over the study period (2010–2020) at the Sonoma County Airport in Santa Rosa, California was 80.3 cm (range = 37.8–153.4 cm, CV = 0.42). The study watersheds include Willow, Dutch Bill, Porter, and Mill creeks (Figure 1), which have drainage areas between 9.8 and 30.2 km^2 (Table 1), and support oak woodlands, grassland, mixed coniferous forest, and redwood forest. The watersheds also support extensive vineyard agriculture and rural residential development that rely on stream diversions or shallow wells to satisfy water demands (Deitch et al. 2009). Methods used to characterize the geomorphology of the study stream reaches are provided in Appendix S1.

2.2 | Study Population

The Russian River historically supported large runs of Coho Salmon that were fished for subsistence by local tribes for thousands of years and, after European settlement, supported a commercial fishery through the 1950s (Steiner 1996). However, dam construction, flow and temperature changes, invasive species, habitat modification and loss, and hatchery impacts drove the population to near extinction by the late 1990s (Steiner 1996). The Central California Coast Coho Salmon Evolutionary Significant Unit (Waples 1991) was listed as threatened under the Federal Endangered Species Act (70 FR 37160) in 1996 and was endangered in 2005 (70 FR 37159). The streams in this study have all been identified as priorities for Coho Salmon recovery (National Marine Fisheries Service 2012).

Efforts to restore Coho Salmon in the Russian River have included physical habitat restoration and instream flow enhancement projects. In 2001, a conservation hatchery program was established to accelerate population recovery (Pregler et al. 2023). During the study period, approximately 43,000 hatchery, age-0 juvenile Coho Salmon were released in the study

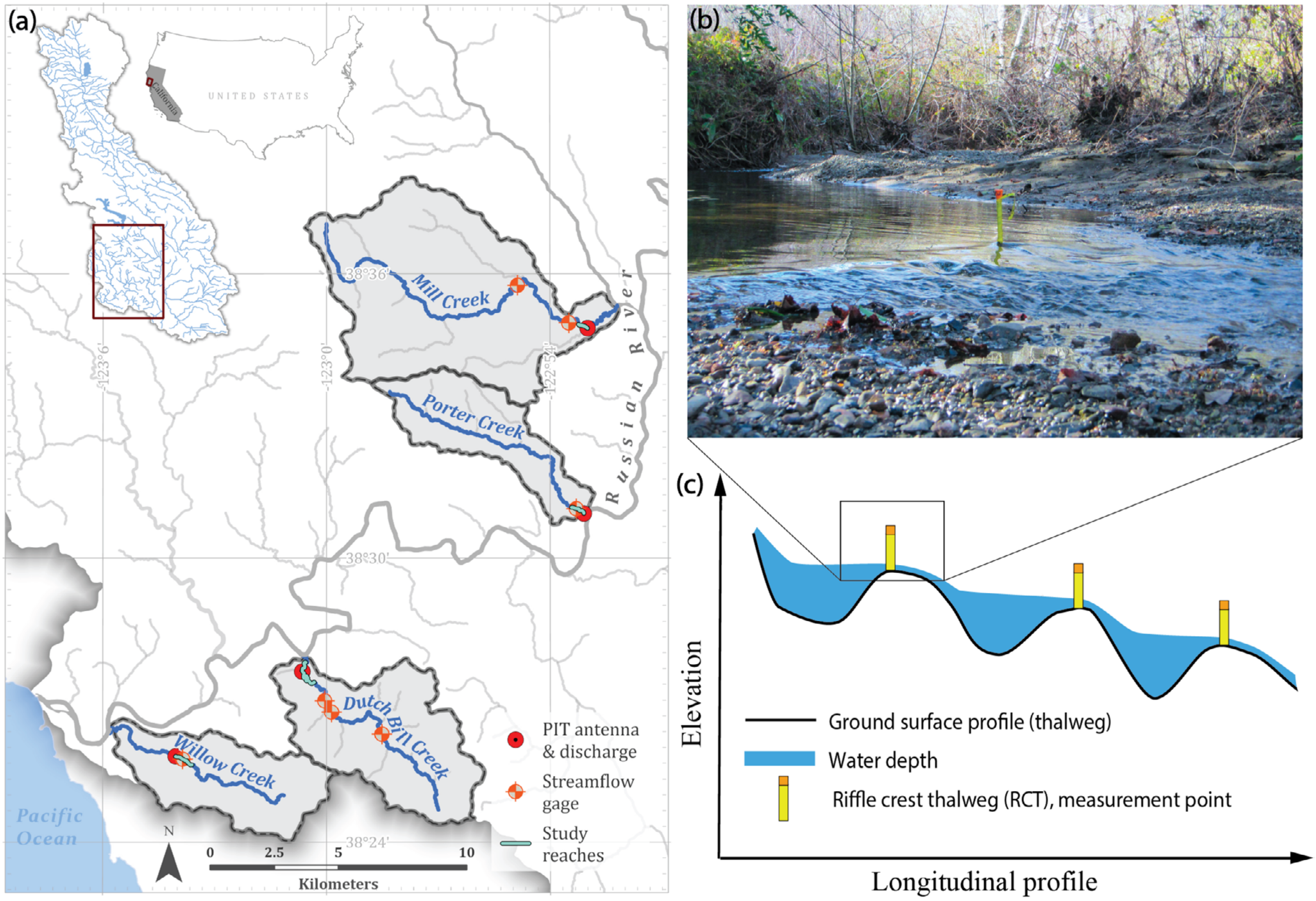

FIGURE 1 | (a) Study streams and monitoring locations in the Russian River basin, northern California. (b) Example of riffle crest thalweg (RCT) field measurement location, marked by rebar. (c) Pool-riffle sequence (vertical exaggeration) and RCTs (adapted from Rossi et al. 2021). [Color figure can be viewed at wileyonlinelibrary.com]

TABLE 1 | Study stream characteristics and geomorphic attributes.

Stream	Study length (m)	Catchment area (km^2)	Geomorphology	Slope (%)	Substrate (mm)	Width: depth	Flow m^{3}s^{-1} (cfs) at 9.1 cm	75th pctl RCT$_d$
Dutch Bill	2.0	30.2	Pool-riffle	0.4	54.0	18.5	0.11 (3.9)	6.2
Mill	0.5	9.8	Step-pool	0.6	61.5	12.5	0.02 (0.7)	11.0
Porter	0.8	19.2	Pool-riffle	0.5	40.8	21.0	0.06 (2.1)	4.8
Willow	0.9	18.5	Pool-riffle	0.6	18.7	18.5	0.1 (3.5)	2.8

Note: Slope, substrate, and width-to-depth ratio are based on the means of field measurements made at five locations before and five locations within each study reach after the > 50-year flood in 2019 (geomorphic data collection methods described in Appendix S1). Substrate size represents the 84th percentile of the intermediate axis. The 75th percentile RCT$_d$ represents the riffle crest thalweg depth below which 75% of continuously measured depths 1 March–3 July were observed. Methods are described in Appendix S1.

streams each fall prior to outmigration, as smolts the following spring (March–June). Approximately 15% of the hatchery fish were implanted with PIT tags and held for up to 2 weeks prior to release into the streams. Mortality during this window of time was < 0.2%. PIT antenna arrays, composed of channel-spanning upstream and downstream antennas placed 5–10 m apart, were installed in the study streams to document outmigration timing. Detection efficiencies of the combined upper and lower antennas on each stream averaged 0.97 (SD 0.11) across all streams and years.

2.3 | Measuring Flow and Continuous Water Depths

To estimate water depths during the Coho Salmon outmigration period, we used real-time hydraulic measurements, long-term discharge datasets, and values estimated from depth-discharge relationships. In each stream, we established a 0.5–2 km study reach in proximity to the PIT antenna nearest the confluence with the Russian River (Figure 1). During the outmigration season in 2018 and 2019, we measured the depth of water within the channel across a range of flow conditions using a stadia rod. Specifically, we measured water depths at the riffle crest thalweg (RCT), which is the deepest point of the channel (thalweg) at the riffle crest (Rossi et al. 2021). The riffle crest occurs immediately downstream of the pool tail and is the shallowest depth in the longitudinal profile of riffle-pool sequences. The RCT therefore represents the shallowest point in the deepest path of the stream that out-migrating juvenile salmon must pass as water levels recede. We measured 9–15 RCT depths per stream during each site visit, and each site was visited 15–18 times over the 2-year study period, resulting in over 1300 RCT depth measurements. During each site visit, discharge (flow) was also measured with a Sontek FlowTracker2 handheld acoustic doppler velocimeter within 100 m of antenna arrays, following standard measurement protocols (Rantz 1982). In situ pressure transducers in pools of each study stream near antenna arrays continuously measured water depth (stage) in 15-min intervals (stage measurement details in Appendix S1). We transformed these depths to flow using power-law relationships derived from flow measurements collected at each site across a range of flows (Harrelson et al. 1994).

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

$$Q = a\left(RCT_d\right)^b$$

where Q is the volumetric flow rate (m^3s^{-1}), RCT_d is the riffle crest thalweg depth (cm), and a and b are empirically determined values. We fit nonlinear (weighted) least-squares models to each stream, using 12–15 points that represent the median RCT depth and a flow measurement per stream, producing a unique power-law equation for each stream. Then the power-law equations were used to convert previous years of continuous streamflow data into continuous RCT depth data. Since we were interested in applying rating curve equations to 10 years of stream data, we checked whether rating curves were consistent among years, using the flow and RCT depth measurements collected in 2018 and 2019. All 2019 flow and RCT depth measurements were made after a > 50-year flood event in late February 2019, which induced greater channel geomorphic change than any other period of the study, allowing us to assess the stability of RCT rating curves over time.

2.4 | Assessing Depths During Outmigration Detections

To estimate the depths that occurred at the timing of fish outmigration, we analyzed PIT antenna detections of 1-year-old smolts during each smolt outmigration season from 2010 to 2020. We matched the timing of the first detection for each marked individual with the closest 15-min time interval at which median RCT depth in the study reach was estimated. In the Russian River basin, the historical outmigration start date is early March, and the latest detection date during our study period was 3 July. We first assessed fish movement depths during the peak outmigration period, which we defined as the average duration (25.2 days) of the interquartile range of smolt outmigration timing since 1 March among stream-years, centered around the median outmigration date for each stream-year. This data filtering yielded 17 stream-years in our analyses (2 Dutch Bill Creek years, 6 Mill Creek years, 3 Porter Creek years, and 6 Willow Creek years). Second, we evaluated fish movement depths during the late-season migration period, defined as 1 May–3 July, which included 26 stream-years of observations.

To characterize the fish movement depths during peak migration, we compared the distribution of depths when fish were detected with the distribution of continuous, observed depths occurring during the same period. To test if there was a statistically significant difference between the two distributions, we applied the non-parametric Kruskal-Wallis test, using the functions *kruskal_test* and *kruskal_effsize* of the *rstatix* package (version 0.7.2; Kassambara 2023). The *eta²*, based on the H-statistic, was used as the measure of the Kruskal-Wallis test effect size:

$$\text{eta}^2[H] = (H - k + 1)/(n - k)$$

where H is the value obtained in the Kruskal-Wallis test, k is the number of groups, and n is the total number of observations (Tomczak and Tomczak 2014). The eta^2 estimate is scaled from 0 to 1 (> 0.14: "large", > 0.06 "moderate", > 0.01 "small") and when multiplied by 100 indicates the percentage of variance (Tomczak and Tomczak 2014). We conducted Kruskal-Wallis tests collectively for all stream-years, as well as for each stream. To evaluate movement behavior during the shallowest depths observed in our streams during peak migration, we conducted additional Kruskal-Wallis tests on the lowest 10th percentile of movement detection depths against the lowest 10th percentile of continuous depths occurring over the same period.

We next evaluated fish movement depths at the end of the outmigration period by determining how the timing of declining water depths affected the timing of movement to test our hypothesis that shallow water depths truncate the outmigration season. Specifically, we used linear mixed-effects models to explore how outmigration end date was influenced by the timing of riffle depths (Thompson 1972) falling below 9.1 cm (0.3 ft.). This passage depth threshold for juvenile salmonids is used by the California Department of Fish & Wildlife (CDFW 2017) and other management agencies, based on a 3.0 cm (0.1 ft.) passage clearance above the average body depth of salmon smolts (R2 Resources 2008). Outmigration end date was calculated for each stream-year as the date at which 95% of the late-season migration detections occurred to limit the influence of outliers (Kastl et al. 2022). Outmigration end date per stream-year was used as the response variable in a linear mixed-effects model with latest date > 9.1 cm depth as an explanatory variable and stream as a random effect, using the *lmer* function of the *lme4* package in R (version 4.0.4, R Core Team 2018). We calculated conditional coefficients (including stream as a random effect) and marginal coefficients (excluding stream as a random effect) of determination (R^2) (Nakagawa and Schielzeth 2013), using the *r.squaredGLMM* function of the *MuMIn* package (version 1.47.1; Bartoń 2022).

Finally, to evaluate how variation in migration timing among streams is affected by dry years, when migration-limiting depths are more likely to occur, we also performed Kruskal-Wallis tests on outmigration timing among streams in each year. This analysis was restricted to four streams with six matching years of observations and no data gaps.

3 | Results

3.1 | Water Depths During Salmon Outmigration Period

Each study stream had a unique RCT depth-to-flow relationship (Figure 2), indicating that the streamflow required to reach a particular RCT depth varied among streams. The relationships were well described by power functions, although fitted lines among four streams included some scatter. Across all sites, the streamflow required to reach a depth of 9.1 cm (passage depth threshold; CDFW 2017) ranged from 0.02 to 0.11 m^3s^{-1} (0.71–3.89 cfs) among streams. Streams exhibited similar RCT depth-to-flow relationships in 2018 and 2019, before and after the 50-year flood event.

RCT depths during the outmigration period exhibited similar seasonal patterns among all streams. Water depths in the early spring frequently spiked during storms, then followed a consistent recession into the spring and early summer (Figure 3). Among the 17 stream-years for which depth data were available during peak outmigration, we detected 3519 juvenile Coho Salmon moving downstream across all stream-years combined. The average number of individual fish detections per stream-year was 207 (17–480, CV 0.6). Peak downstream movement of smolts occurred as water depths gradually receded throughout spring. During peak outmigration, the range (5–95 percentile) of water depths at the time of detections across all stream-years was 2.3–29.8 cm (mean 13.1 cm, CV 0.61). Over the same period, the range (5–95 percentile) of continuous depths reached shallower levels: 0.0–30.3 cm (mean 12.6 cm, CV 0.63). We found a significant difference between depths that occurred when fish were detected and depths continuously measured, with $p<0.01$ and an effect size of $eta^2=0.0002$ ("small magnitude"). Smolts were less frequently detected at the shallowest RCT depths that were measured continuously.

During the peak outmigration period, RCT depths during outmigration detections also varied among streams (Figure 4). Median outmigration detection depth at Mill Creek was 19.6 cm (11.1–28.7 cm, 5–95 percentile), Dutch Bill 11.5 cm (5.5–14.0 cm), Porter 7.9 cm (4.2–17.8 cm) and Willow 4.8 cm (2.6–13.7 cm). We found significant differences ($p<0.05$) between depths during outmigrant detections and continuous depth measurements in 8 of 17 stream-years, including 6 stream-years with $p<0.00001$. The greatest eta^2 effect size

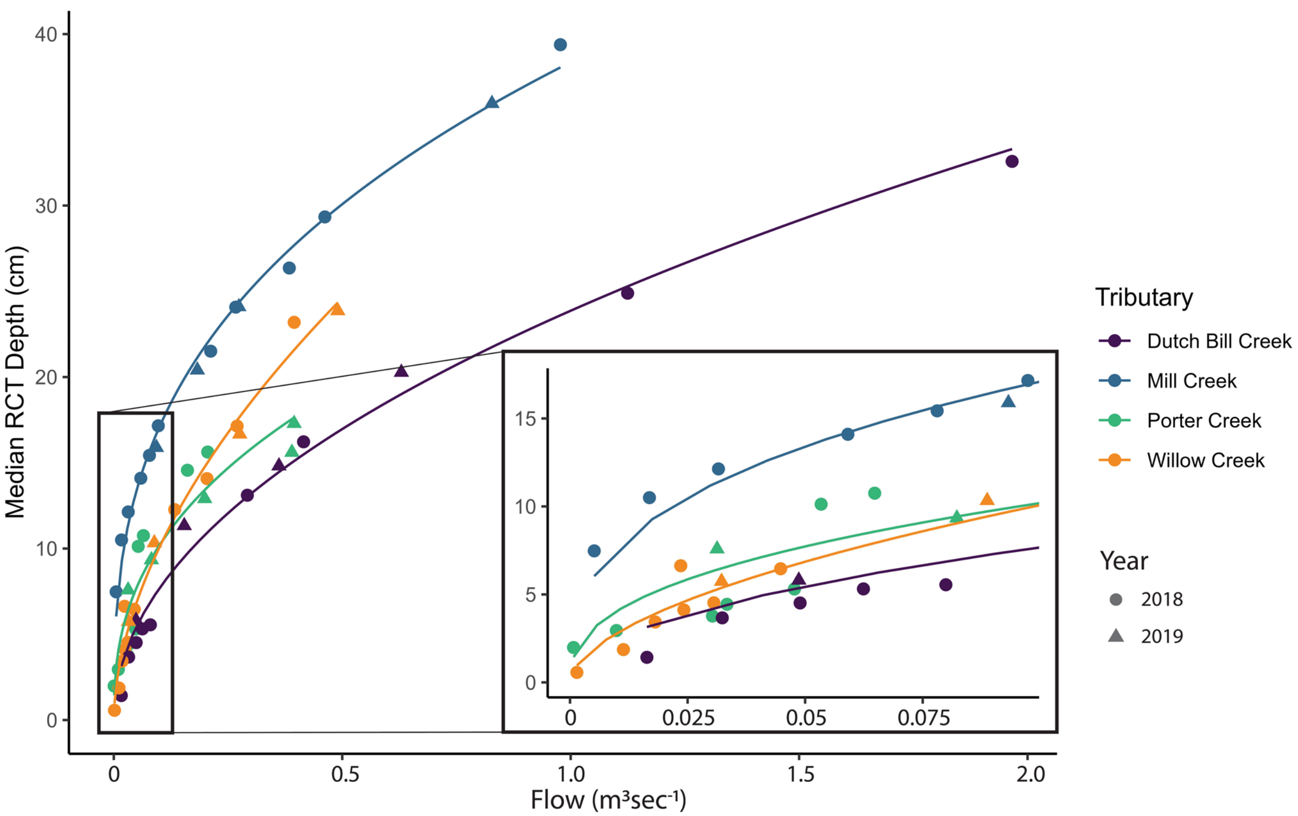

FIGURE 2 | Riffle crest thalweg (RCT) depth–discharge rating curves for the study streams over the full range of data collected and for shallow depths (inset figure). [Color figure can be viewed at wileyonlinelibrary.com]

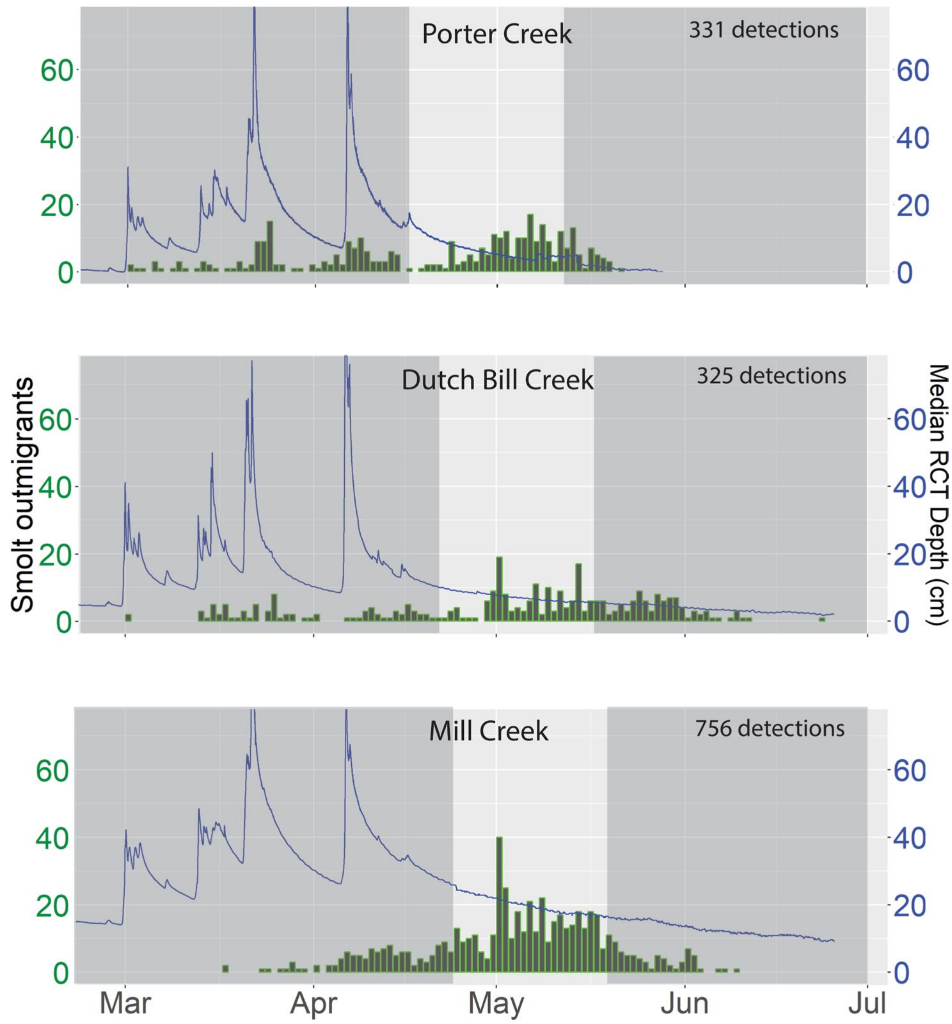

FIGURE 3 | Daily smolt detections (green bars) and median RCT (riffle crest thalweg) depths (blue lines) for three study streams during the 2018 outmigration season (a dry year). The highlighted background color shows the peak migration, which is centered on the median outmigration date for each stream-year. Three of four streams are shown because we did not have complete data for all streams for any single year. [Color figure can be viewed at wileyonlinelibrary.com]

of 0.11 ("moderate magnitude") was found at Porter Creek in 2020 ($p < 0.00001$), which was the stream-year with the shallowest 5–95 percentile continuous depth measurements of 0.0–6.5 cm. Among the shallowest 10th percentile of depths among stream-years during the peak outmigration period, we found an even greater statistical difference between depths encountered during outmigration detections and depths continuously measured. The greatest eta^2 effect sizes of 0.259 ("large magnitude") and 0.999 ("large magnitude") occurred in Willow Creek in 2016 and 2020 (each with $p < 0.0001$), which experienced 5–95 percentile depth ranges of 5.4–13.8 and 2.3–4.7 cm (second shallowest stream-year), respectively.

3.2 | Shallow Water Depths Affect Outmigration Timing

To evaluate how the timing of stream recession affected the end of the outmigration period, we considered when depths fell below 9.1 cm. We found that the latest date that RCT depths reached 9.1 cm within the migration period varied among sites and years (mean June 18, earliest May 17, latest July 3). The timing of 9.1 cm RCT depth occurrence explained a high degree of variation in outmigration end date (95% cumulative seasonal outmigration date, since 1 March; $p < 0.01$; marginal $R^2 = 0.32$; conditional $R^2 = 0.52$) and had stronger support than the null model, based on AIC values (delta 5.68). The significant positive relationship indicated that later dates of flows falling below 9.1 cm RCT depths are associated with longer periods of smolt outmigration (Figure 5). Over the range of conditions observed, an extension from 1 May to 3 July in the latest date >9.1 cm depth can extend the outmigration end date 16 days: from 20 May (13–27 May 95% CI) to 5 June (28 May—13 June 95% CI). All streams show similar positive relationships between the maximum date that RCT depths reached 9.1 cm and outmigration end date, although streams vary in their outmigration end date and the water depth at which outmigration ends (Figure 3).

3.3 | Variability in Outmigration Timing in Dry Years

Among the four streams with matching 6 years of observation (2014, 2016–2020), we found that variation in outmigration

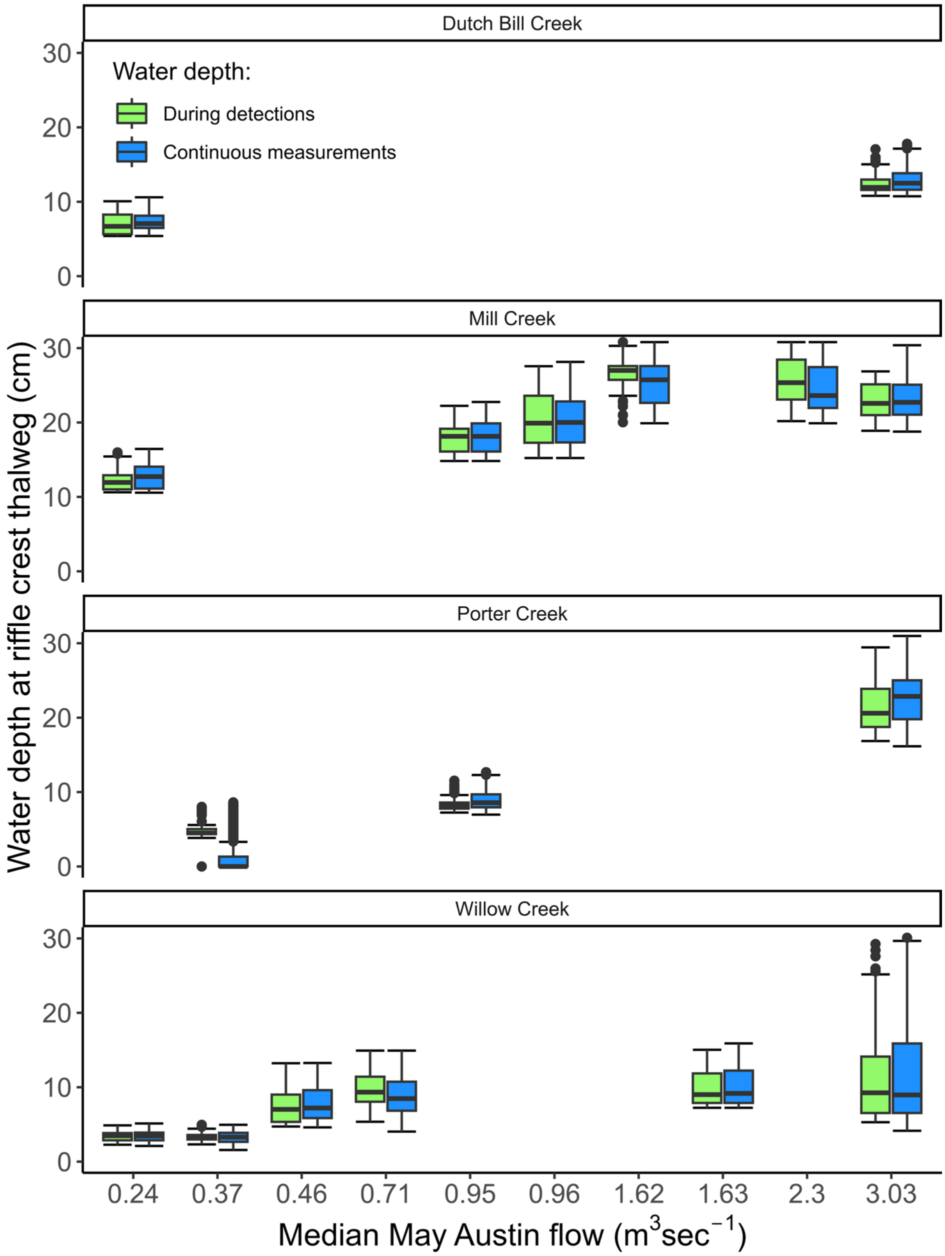

FIGURE 4 | Box plots of riffle crest thalweg (RCT) water depths measured during outmigration detections (green) and continuously (blue), over the peak outmigration period (25.2 days centered around the median outmigration date of each stream-year). Thick horizontal lines represent the median, box top and bottom show upper and lower quartiles, ends of whiskers show 1.5 times the interquartile range, and dots are outliers. Values above each box plot represent smolt detections per stream-year. Each stream-year included 2394 continuous depth measurements, made every 15 min. Median annual May flow reported for USGS gage 11,467,200 (Austin C Nr Cazadero CA), which is the closest long-term flow monitoring station, is used to illustrate the inter-annual variation in flow conditions. [Color figure can be viewed at wileyonlinelibrary.com]

timing among streams was greater in dry years than in wet years (Figure 6), consistent with our hypothesis. Dry years show greater variation in outmigration timing among streams, ranging in *eta*^{2} effect sizes (inter-stream variation) from 0.14 during a low streamflow year in May (frequently when migration-limiting water depths are experienced) to 0.03 during a higher May streamflow year (among all years: $p < 0.00001$). Among the 6 years analyzed, 3 years with lower May streamflow each had "moderate magnitude" effect sizes, and 3 years with the higher May streamflow each had "small magnitude" effect sizes.

4 | Discussion

Findings from this study describe the influence of stream water depths on outmigration, across a variety of streams and water year types, and on the navigable season of outmigration. Coho Salmon smolts outmigrate over a range of depths, which vary by stream, due to differences in RCT depth-to-discharge relationships among streams and interannual differences in streamflow. Smolts consistently outmigrate throughout the peak migration period, but they appear to avoid moving

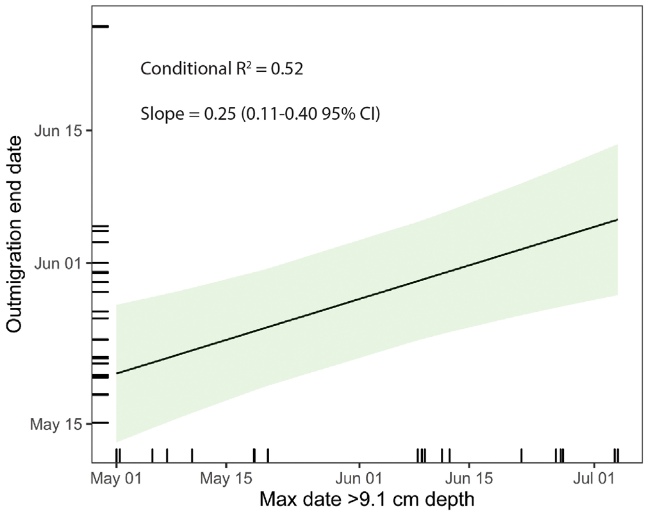

FIGURE 5 | Partial dependence plot including model estimate (solid line) and 95% confidence interval (shading) for latest date that RCT depth was greater than 9.1 cm vs. outmigration end date (95% cumulative seasonal outmigration since 1 March) from linear mixed-effects model. Tick marks on *x*- and *y*-axes indicate observations. Conditional R^2 values include the study stream as a random effect. [Color figure can be viewed at wileyonlinelibrary.com]

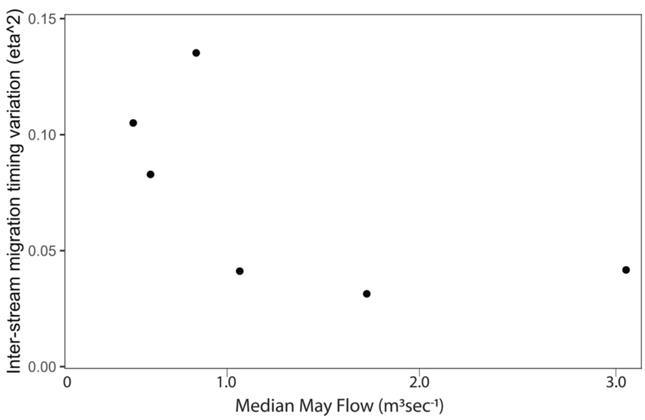

FIGURE 6 | Median annual May flow vs. outmigration timing variation (Kruskal-Wallis eta^2 effect size) among four study streams. Flow was continuously measured at USGS gage 11,467,200 (Austin C Nr Cazadero CA), which is the closest long-term flow monitoring station.

through the shallowest depths that occur, consistent with our hypothesis (H2). The timing at which water depths fall below the standard body depths of fish is strongly correlated with the end of the outmigration season, supporting our hypothesis (H2) that shallow water depths in the late season restrict outmigration. Finally, as expected (H3), migration timing of fish among streams is more variable during dry years, which is explained by greater variation in the timing of movement-limiting depths among streams.

During the peak outmigration period in California's Russian River watershed, Coho Salmon smolts were detected migrating over a wide range of depths in all streams and years, but consistently ceased to migrate when depths were shallowest. Avoidance of shallow depths might have occurred due to low-flow channel obstructions or adaptations related to heightened predation risk (Power 1984) that deter smolt movement during outmigration. Because the juvenile Coho Salmon we monitored originated from the same local genetic stock, we conclude that variation in depth navigated during outmigration is related to environmental factors and not local adaptation. Smolts in some streams move over greater depths than in others, possibly due to inter-stream differences in available depths. For example, fish moved at consistently greater depths in Mill Creek, which has larger substrate grain sizes and lower width–depth ratios than the other study streams (Table 1; Figure 4).

Water depths at or below the standard body depth of juvenile salmon were observed in most of our stream-years during the migration period. Our results identifying the positive relationship between the last date of water depths > 9.1 cm and outmigration end date support our hypothesis that shallow depths in the late migration season likely inhibit outmigration. Low flow in Russian River tributaries has been shown to hasten the Coho Salmon outmigration end date (Kastl et al. 2022) and the present study suggests that shallow water depth is a mechanism by which smolt movement is limited during low flow. If water depths are not sufficiently deep before the full potential outmigration season concludes, smolts likely become trapped upstream, where over-summer survival of smolts is uncommon due to expansive stream network drying (Moidu et al. 2021). In-person observations of trapped Coho Salmon smolts are made regularly after stream disconnection during drought years (e.g., Sonoma Resource Conservation District 2022). Furthermore, there is little evidence that Russian River Coho Salmon express a two-year freshwater life history strategy (e.g., of 4795 PIT-tagged smolts captured in traps during the study period, only 17 were age-2 (0.35%)), suggesting that smolts that are unable to outmigrate likely perish. Thus, we conclude shallow water depths are a significant limiting factor to smolt outmigration in our study system.

High inter-stream variability in outmigration timing is associated with dry years (lower median May flow). This finding is explained by the fact that, in dry years, there was pronounced variation in the timing in which migration-limiting stream depths occurred (Figure 3). As the frequency and magnitude of droughts increase in California (Swain et al. 2018), the severity and frequency of migration-limiting water depths are also expected to increase. Considering that low flows generally shorten the duration of the outmigration season (Kastl et al. 2022), the increasing variability in outmigration timing among streams suggests that some streams will disproportionately experience a truncation of the outmigration season, limiting the contribution of juvenile smolts from some Russian River tributaries to the population.

We acknowledge that flow conditions only partially explain outmigration patterns and that other environmental and endogenous controls influence smolt movement. For example, previous work shows that higher temperatures at the time of migration are associated with a greater probability of Coho Salmon outmigration along the North American west coast (Spence and Dick 2014), and greater cumulative temperature experience extends the outmigration end date in the Russian

River (Kastl et al. 2022). There is also evidence that the outmigration of Coho Salmon is naturally dispersed to hedge against the highly variable ocean upwelling period in California (Spence and Hall 2010), which increases the chance that at least a portion of smolts will arrive to the ocean when food resources are plentiful. Thus, late migrants that navigate shallow flows, despite the risk of stranding and predation, may experience greater growth rates (and greater subsequent marine survival and reproductive success) than earlier migrants, if their arrival to the ocean coincides with favorable upwelling conditions (Satterthwaite et al. 2014).

Our findings provide evidence that shallow depths limit the outmigration period and likely impair the movement of smolts, especially in drought years. However, we were unable to estimate the number of Coho Salmon smolts that failed to migrate as a result of depth-limiting conditions. As streamflows recede, some fish may be able to avoid stranding by migrating earlier in the season. Yet, the consistent cessation of movement at shallow depths and regular observations of smolts being trapped (particularly during dry years) in reaches that have become disconnected from downstream receiving waters suggest that flow depths are indeed limiting. Streamflow enhancement projects and water diversion curtailments that improve streamflow would likely support downstream movement and allow for an extended duration of seasonal outmigration. Additionally, Coho Salmon may adapt to changing hydrologic conditions, including a shift to an earlier outmigration season during years with warmer water temperatures (Kastl et al. 2022). Still, a need remains for monitoring to detect these changes and understand their population-level consequences.

Our study demonstrates the application of new methods to monitor smolt movement in streams to assess stream-specific fish passage depth requirements. RCT rating curves may be useful indicators in predicting which streams are predisposed to migration-limiting shallow depths. Rating curves describe the flow required to reach depths that support outmigration and capture important differences among streams. Although channel geomorphology can evolve over time, rating curves from 2018 and 2019 were similar (Figure 2), indicating that the median RCT-Q relationships within stream reaches are stable. We did not systematically evaluate the influence of geomorphic characteristics on RCT-flow relationships and discharge thresholds for passage. Still, we found that stream reaches with narrower active channels (i.e., low width-to-depth ratios) and coarser bed material (e.g., Mill Creek) (Table 1) were associated with lower flow requirements to meet RCT depth thresholds than other streams (e.g., Dutch Bill Creek), which has a wide channel and smaller sediment size (Table 1). Steep, narrow channels are also more likely to have higher water velocity, which may be more likely to support outmigration. This suggests that management interventions that modify channels to sustain passable depths at lower flows (e.g., stabilizing stream banks with native riparian vegetation to maintain bank steepness, reduce fine sediment input, and maintain channel depths) may benefit outmigrating smolts. However, we also acknowledge that many streams in our study system are incised because of anthropogenic activities. There is a general need to broaden and raise the elevation of stream channels in order to improve hydrologic connectivity with the adjacent riparian zone. Therefore, the design of restoration projects should consider the need to increase the overall W/D ratio of the channel while maintaining lower W/D ratios within the portion of the channel that is active during outmigration.

By deploying stage loggers in pools and establishing the corresponding depth of downstream RCTs, it is possible to obtain continuous estimates of shallow-passage depths for a channel reach. Monitoring of downstream smolt movement via PIT tags/antennas can then be coupled with depth measurements to assess the depths that fish navigate (or avoid). These methods represent an important advancement over traditional approaches that estimate passage depths based on generic body size dimensions of salmon (CDFW 2017). While our approach to estimate movement depths at RCTs differs from the “critical riffle method” used by the California Department of Fish and Wildlife (CDFW) to estimate passage flow requirements (CDFW 2017), our approach is less time intensive. Our observations of fish movement indicate that 9.1 cm is a conservative depth threshold likely protective of smolt passage, but that stream-specific minimum passage requirements may be more effective than universal requirements. Developing RCT depth to flow relationships at streams throughout the region could be helpful in identifying those most likely to experience depth-limiting flows and setting instream flow recommendations. We suggest that additional studies such as ours that directly monitor fish movement over natural and artificial barriers are needed to develop flow requirements protective of fish passage at different life stages, including adults, rearing juveniles, and out-migrating smolts.

5 | Conclusions

As the effects of climate change become more pronounced, low streamflows in the spring and summer season are expected to further decline in coastal California streams (Grantham et al. 2018). Moreover, human water use pressures are likely to grow, particularly during periods of drought, increasing the risk of streamflow depletion. Here we showed that shallow water depths associated with low streamflow may be a significant limiting factor to the outmigration of juvenile Coho Salmon in Russian River tributaries. This work suggests that efforts to protect and enhance streamflow in coastal streams during the spring flow recession—such as water conservation, environmental flow protection, water collection during winter for use during spring, flow augmentation from off-channel storage (Rossi et al. 2023), and watershed restoration activities—are warranted and may help to recover endangered salmon populations in the region.

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Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

Data and code (Kastl et al. 2025) are available from Dryad: https://doi.org/10.6078/D1599B.

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Supporting Information

Additional supporting information can be found online in the Supporting Information section.