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ARTICLE

Patterns and Potential Drivers of Steelhead Smolt Migration in Southern California

Michael T. Booth*
Department of Biological Sciences, University of Cincinnati, Rieveschl Hall 820D, Post Office Box 210006, Cincinnati, Ohio 45221-0006, USA

Abstract
Downstream migration of smolts is a critical aspect of the life history pathway for anadromous salmonids. Timing of downstream migration can vary along latitudinal and climatic gradients. Steelhead *Oncorhynchus mykiss* occur over a broad range of climate and hydrologic conditions, but relatively little is known about migration timing of smolts in the southern extent of the species' range. Using a 19-year data set (1994–2014) of smolt arrivals collected in a downstream migrant trap at the Vern Freeman Diversion facility on the Santa Clara River, one of the largest coastal watersheds in southern California, I report patterns of migration and potential environmental drivers determining migration timing. Large sections of the Santa Clara River and the confluences of its perennial tributaries are intermittent except during winter and spring stormflows, limiting migration opportunities. If tributaries were connected, smolts were regularly encountered in the downstream migrant trap between March and May, with rare observations of downstream migrants in January (0.1%) or February (0.3%). Although these migration data are limited by low smolt abundance and sampling efficiency during high-flow events, potential environmental drivers were identified as cues for smolt migration timing in this region. Day length was a consistent predictor of smolt migration, while hydrology was both a constraint and a cue, with migrants only arriving after tributaries had reconnected to the main stem and with many arrivals occurring weeks or months after storm events had passed. Smolt migration was not consistently synchronized with periods when intermittent sections of the main stem were wetted and passable to the ocean. Between 0% and 70% of smolts arrived at the Vern Freeman Diversion after natural flows were likely insufficient for passage to the ocean. Smolt migration is a critical piece of the management puzzle for southern California steelhead, and these data will serve to inform effective management strategies and research needs for the successful recovery of the species.

The substantial variation in steelhead *Oncorhynchus mykiss* (anadromous Rainbow Trout) life history (Thorpe 1998) is a likely driver of its ability to persist under a wide variety of environmental conditions—from the typically cool, wet, and perennial river systems of the northern latitudes to the hydrologically and thermally variable south. In addition to genetic factors (Pearse et al. 2014; Phillis et al. 2016; Kelson et al. 2020a), environmental conditions (e.g., temperature, day length, population density, food availability, etc.) play a role in determining the life history pathway that individual fish follow (Satterthwaite et al. 2009). The decision window for smoltification in the preparatory phase (physiological preparation for ocean conditions) appears to occur several months before actual migration (Mangel et al. 2010), while cues that drive the migratory phase (releasing factors that trigger downstream movement) occur during the actual period of migration (Spence and Dick 2013).

Although it is clear that a variety of environmental conditions influences migration timing, the cues driving the migratory phase exhibit substantial variation both among salmonid species and within populations of the

*E-mail: michael.booth@uc.edu
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same species. This variation is suggested to potentially synchronize juvenile migration with favorable conditions in the marine environment for some species (Hvidsten et al. 1995; Byrne et al. 2003; Davidsen et al. 2005; Spence and Hall 2010; Spence and Dick 2013). Along a latitudinal gradient, Coho Salmon *O. kisutch* show shorter, later, and more predictable migration patterns in northern versus southern populations (Spence and Hall 2010). Although increased flexibility in migration timing may promote persistence in the more variable southern region, obligate anadromy is likely one factor that restricts the southern distribution of Coho Salmon (central California; Moyle 2002) to systems with reliable yearly connections to the ocean. Due to their more plastic life history, steelhead have a much broader spatial distribution (Arismendi et al. 2014), but it is not clear whether (1) environmental drivers that cue migration vary, (2) environmental drivers provide synchronization to suitable ocean conditions similar to that observed for other salmonids, or (3) variable marine survival dictates migration timing. Instead, under more variable climatic and hydrologic conditions, migration may become opportunistic or have a wider temporal window that is not aligned with favorable marine conditions (Spence and Dick 2013). This would enable migrants to take advantage of storm-induced flows that provide connectivity from rearing habitats to the ocean and would ensure that some proportion of the migrants successfully migrate when conditions are suitable.

Early work suggested that after smoltification, reduced swimming performance leads to entrainment of out-migrants in high-velocity flows rather than active downstream swimming (Flagg and Smith 1981; Smith 1982), resulting in pulses of smolts essentially washing out of estuaries during storm events (Fukushima and Lesh 1998). More recent analyses indicate that reduced swimming performance is not consistently found in smolts; smolts can hold in place or use alternative habitats to avoid entrainment during high-flow events (Peake and McKinley 1998), and they actively migrate (head first; Davidsen et al. 2005). Migration during high-flow events may be energetically advantageous and may allow smolts to avoid visual predators (Aldvén et al. 2015). However, high-flow events may also result in exposure to poor water quality (e.g., turbidity) and high debris loads, causing salmonids to shelter or otherwise avoid the conditions (Bash et al. 2001) rather than migrate. If passable streamflows only occur adjacent to storms, asynchrony with flow pulses would result in missed opportunities for migration, failed migration and residualization, or stranding in unsuitable habitat, leading to mortality.

In the northern extent of the steelhead's range, anadromy is generally unlikely to be constrained by hydrology (as river channels are typically perennial and estuaries remain open to the ocean), while through the south-central portion of the range, smaller stream systems typically remain perennial, but their estuaries are only open after the initial storms of the winter season (Fukushima and Lesh 1998; Bond et al. 2008; Hayes et al. 2011; NMFS 2013). In coastal southern California, essentially all major river systems and many smaller streams have seasonally intermittent reaches and estuaries that are open to the ocean only after substantial rainfall (NMFS 2012). Along this gradient, the environmental cues that trigger downstream migration for smolts may vary, and selective pressure could lead to shifts in smolt migration timing to take advantage of any opportunities to reach the ocean. However, smolts are unlikely to have unlimited flexibility in migration timing due to the physiological constraints related to smoltification; thus, they may only be able to take advantage of opportunities within a particular seasonal window.

Southern California steelhead were listed as a federally endangered in 1997 (NMFS 1997). Throughout the Southern California Steelhead Distinct Population Segment (DPS), anadromous populations have declined substantially from their historic numbers and currently remain low (NMFS 2016). Multiple factors are considered responsible for the regional decline in steelhead, including the loss of habitat, periodically unsuitable ocean conditions, passage barriers, and water management (NMFS 2012, 2016).

Major challenges in developing management strategies and assessing recovery of the endangered Southern California Steelhead DPS include the lack of consistent monitoring of adults and juvenile migrants in the region and the significant unknowns regarding the drivers and relative frequency of different life history pathways (anadromy and resident pathways, as well as lagoon anadromy; NMFS 2012). Due to the limited data available for southern California, the best available data for regulatory purposes (NMFS 2012, 2013, 2016) are typically sourced from better-studied systems in central California (e.g., Waddell and Scott creeks; Shapovalov and Taft 1954; Bond et al. 2008; Hayes et al. 2011; Phillis et al. 2016), which have substantially different environmental conditions. In their summary of salmonid migration timing for coastal California streams containing steelhead, Fukushima and Lesh (1998) recognized that detailed information for most small coastal rivers was incomplete and thus did not report potential migration times for smolts in the Southern California DPS region. Unknowns regarding the timing and drivers of downstream smolt migration make it difficult to determine whether potential changes in water resource management (e.g., water diversion or reservoir releases) actually will result in improved opportunities for juvenile migration.

To begin to fill this data gap and its potential consequences for recovery of steelhead in the Southern

California DPS, I report patterns of smolt migration using a 19-year data set from the Santa Clara River—one of the largest river systems in the Southern California DPS—and I investigate environmental drivers that may trigger migration and assess whether recent patterns of smolt migration are synchronized with potentially successful freshwater migration windows. I hypothesized that tributary connection to the main-stem river would be required for smolts to migrate, that storms would serve to instigate migration, and that the majority of smolts should arrive in the main stem during periods when migration to the ocean is possible.

METHODS

Study site.— The Santa Clara River (186 km from headwaters to the estuary) is one of the largest coastal drainages in southern California (419,600 ha; Beller et al. 2011). The relatively high-elevation mountains of the northern San Gabriel Range and Transverse Ranges (1,000–2,000 m) compose the upper watershed; in typical years, portions of tributary streams (e.g., Sespe and Santa Paula creeks) provide year-round coolwater habitat that can support resident Coastal Rainbow Trout *O. mykiss irideus* and anadromous steelhead. Large portions of the main-stem Santa Clara River and portions of its tributaries are spatially and seasonally intermittent (Figure 1), while other reaches are typically perennial due to upwelling groundwater. The confluences of the major *O. mykiss*-bearing tributaries (Santa Paula, Sespe, and Piru creeks) are seasonally intermittent, and access to the main-stem Santa Clara River is typically restricted to periods after storm events. Although the predominant factor controlling the location of surface flows is the underlying geology, surface water diversion as well as groundwater extraction can substantially reduce the duration and magnitude of flow in the main-stem river (Beller et al. 2011).

The Vern Freeman Diversion (VFD) project was completed in 1991 by the United Water Conservation District (UWCD) to provide reliable surface water diversion from the Santa Clara River. The VFD is located downstream of all *O. mykiss*-bearing tributaries and is approximately 18 km upstream from the Santa Clara River estuary. Located between the VFD and the estuary is an intermittent, hydrologically losing reach (i.e., loses surface flows to groundwater due to high infiltration rates) that is typically about 6.5 km long, although its extent depends on local groundwater recharge. In all but the wettest years, this "critical reach" becomes intermittent between storm events but must be traversed by smolts as they migrate to the estuary and ocean.

Hydrology.— To account for the seasonality of rainfall in southern California and its influence on stream hydrology and the potential migration season, I used water year (WY) as the reference timescale. The designated WY begins on October 1 of the previous calendar year and ends on September 30 (e.g., WY 1994 began on October 1, 1993 [WY day 1], and ended on September 30, 1994 [WY day 365]).

The UWCD provided average daily diversion rates at the VFD and operational records as well as model-estimated average daily discharge for the Santa Clara River at the VFD and discharge in the downstream losing reach under hypothetical conditions of natural flows (i.e., no water diversion/anthropogenic groundwater recharge). Flows for the Santa Clara River at the VFD were modeled by UWCD due to frequent relocation of gauging sites resulting from practical limitations of gauging a sand-bed, highly fluctuating river channel. The model and details for the hydrologic model construction are available upon request from UWCD (Freeman Operations Model version 2.3 documentation).

Based on personal and UWCD observations of the intermittent reaches downstream of the U.S. Geological Survey (USGS) gauges between 2008 and 2017, I estimated the date of tributary connection as the first date during the WY on which average daily flow at either the Sespe Creek gauge (USGS 11113000) or the Santa Paula Creek gauge (USGS 11113500) was at least 0.71 m^3/s. Although it is possible that a tributary connection potentially occurred at flows lower than the 0.71-m^3/s threshold, in all but 1 year (1994) there was less than a 2-d change in the number of days between estimated connection and first smolt observation with a 20% reduction in this threshold.

Migrant sampling.— The VFD is a large, roller-compacted, cement grade control diversion structure, with the weir crest located at the historical (and current) streambed elevation. The weir crest encompasses the full width of the river channel (0.3 km) and is approximately 8.5 m tall relative to the river channel downstream of the facility (Figure 2).

Diverted water entered a screened fish bay (4.7-mm wedge wire), which was typically operated at a depth of 1.0–2.4 m. A downstream migrant trap was located in a small bay at the downstream end of the screened fish bay and operated at a depth of 0.6–1.0 m. Water and fish entered the downstream migrant trap over a small weir that poured into an enclosed screened box (3-mm punchplate mesh; length × width × height = 1.25 × 1.25 × 1.86 m). Each morning (in 2010 and 2011, morning and evening), the weir was closed and the screened box was lifted out of the trap bay by an electric winch. Captured fish were identified, enumerated, and sorted by life history stage (*O. mykiss* life stages: young of the year, resident, hatchery, smolt, and kelt). Smolts were identified by the following characteristics: increased skin reflectance, larger heads, slimmer bodies, longer caudal peduncle, loss of parr marks, and darker margin of the dorsal fin (UWCD

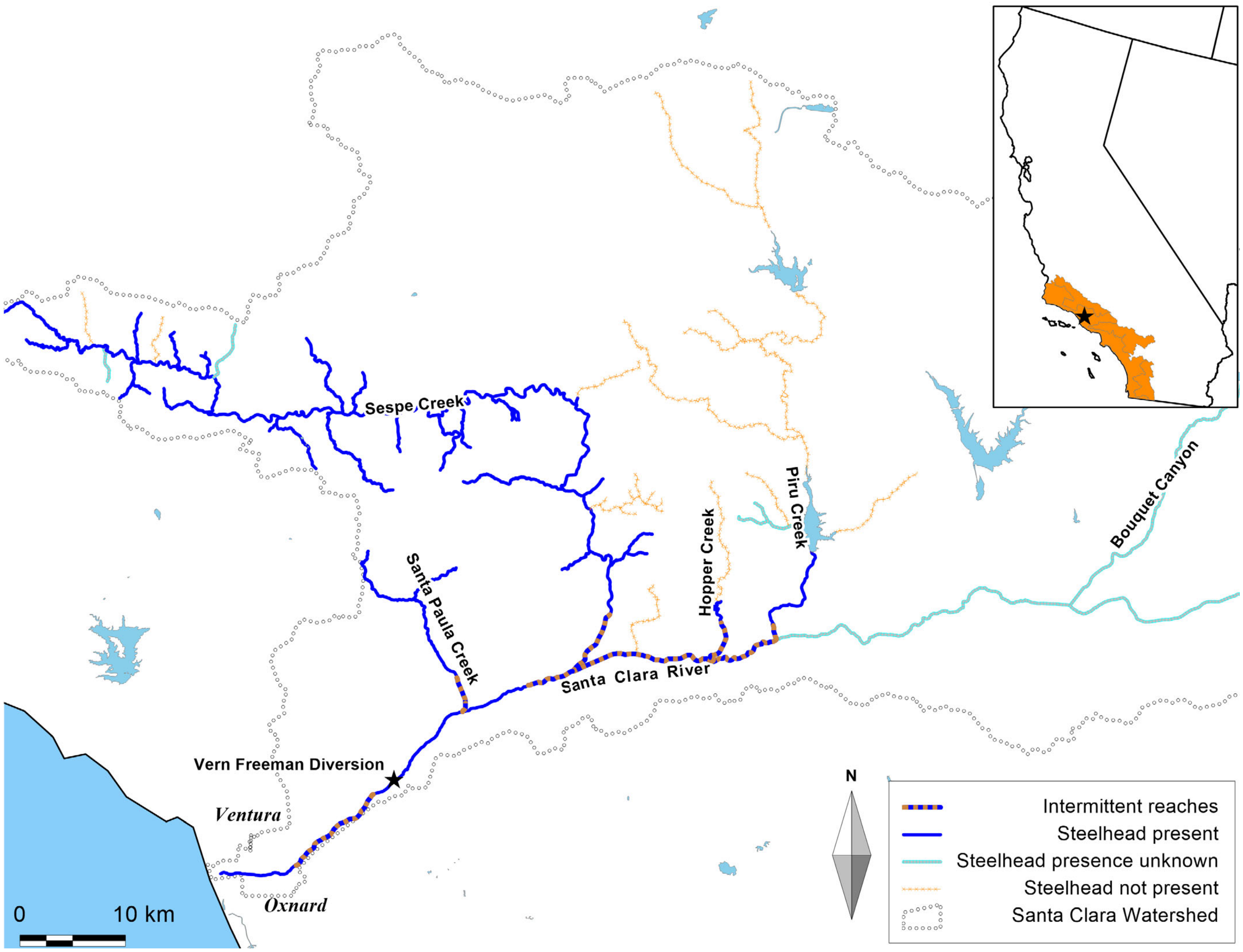

FIGURE 1. Map of the Santa Clara River watershed and tributaries, showing the location of the Vern Freeman Diversion (VFD) and steelhead presence (data courtesy of the National Marine Fisheries Service, West Coast Region). Intermittent reaches are shown only for reaches where steelhead were considered present; the upper Santa Clara River toward Bouquet Canyon and additional reaches of Sespe Creek may be intermittent during drought periods. Inset shows the location of the VFD within the Southern California Steelhead Distinct Population Segment.

2010). In 1995 and 1996, scale samples were analyzed to determine fish age. Captured smolts were released downstream of the VFD or transported in aerated buckets via truck to the Santa Clara River estuary, directly to the ocean, or to the Ventura River estuary (~7 km north of the Santa Clara River estuary).

From 1994 to 1998, the downstream migrant trap was generally operated between January and June during periods in which UWCD diverted water (1997 monitoring began in November 1996; 1998 monitoring began in April due to permitting delays but continued through July; Figure 3). During this initial monitoring period, inconsistencies in diversion operations likely impacted trapping operations (1994–1998). From 1999 to 2014, the downstream migrant trap was operated from January to June during periods when flows in the Santa Clara River were sufficient to maintain consistent water levels in the fish screen bay. No monitoring data were collected in 2005 due to frequent flood conditions, facility damage, sedimentation, and extended shutdown of the VFD facility.

Additional observations of juvenile *O. mykiss* occurred during occasional stranding surveys within the facility (fish screen bay, fish ladder, and canal); the fish screen bay was sampled most frequently, typically any time water diversion ceased (e.g., at the beginning of storms) as well as at cessation of the trapping season. Because arrival time could not be unambiguously defined for smolts in the fish bay (i.e., individuals might hold for an unknown duration prior to a survey in the fish bay), they were not used to determine the “last observed smolt” for the WY in

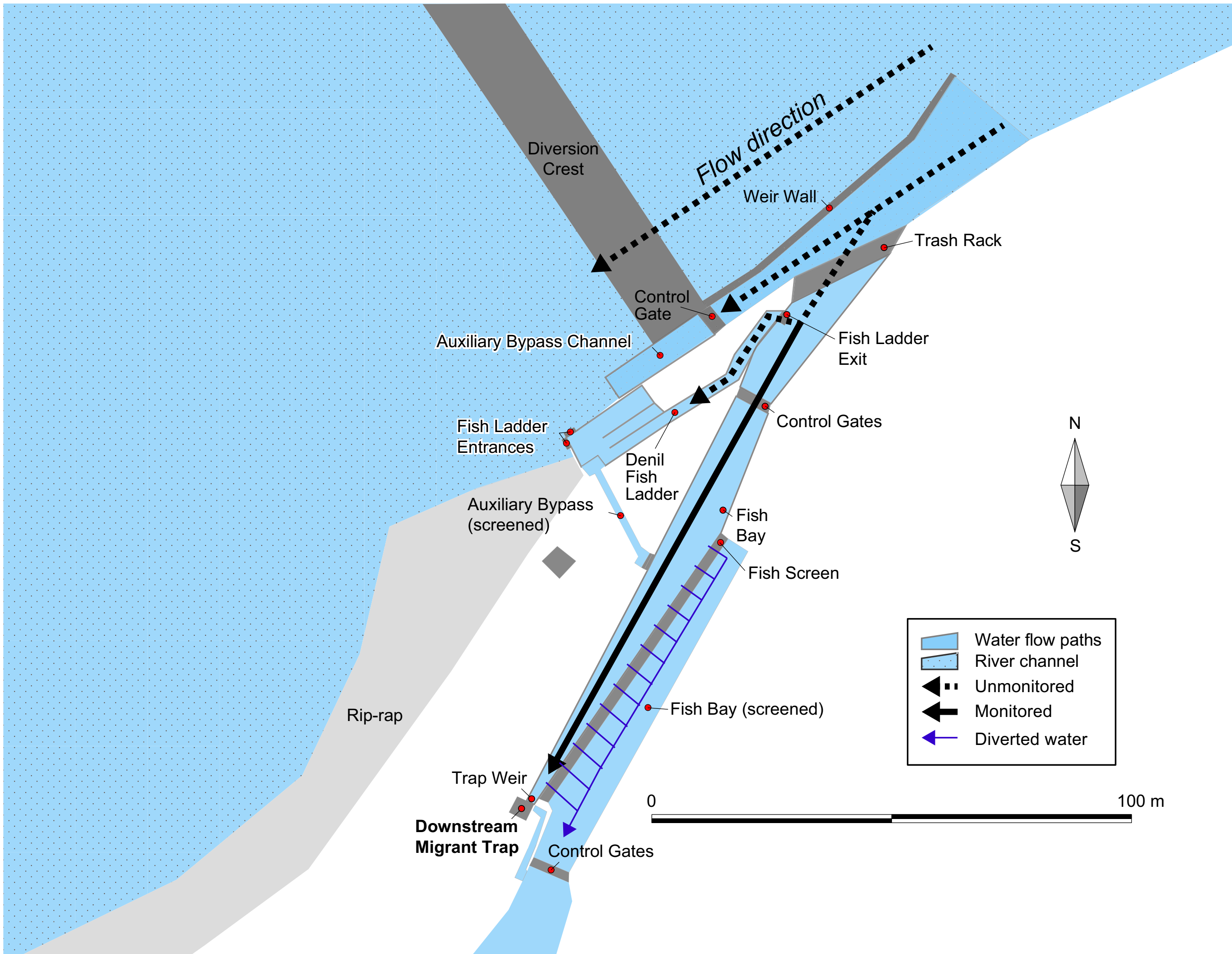

FIGURE 2. Flow schematic of the Vern Freeman Diversion, showing unmonitored and monitored potential flow paths for downstream migrant steelhead smolts. Migrating smolts were collected in the downstream migrant trap at the downstream-most end of the fish bay. Occasional surveys of the fish bay were performed when the facility was dewatered. A fish screen (4.7-mm wedge wire) prevented fish from entering the diverted water.

Supplement A (available in the online version of this article) but are shown in Figure 3.

River flow sampled.— Downstream migrants had four potential routes through the VFD (Figure 2): (1) over the crest of the diversion, (2) through the bypass channel, (3) through the fish ladder, and (4) into the downstream migrant trap. Only the downstream migrant trap was consistently monitored.

During both the initial and later monitoring years, effectivity of the downstream migrant trap likely varied depending on diversion and bypass flow operations. Trap efficiency was not directly estimated via traditional methods (Sandstrom et al. 2013), but to provide a relative measure I estimated the proportion of river flow sampled as the diversion rate (i.e., flow entering the screened fish bay) divided by the total river flow for any day that the downstream migrant trap was operated. During all periods in which the total river flows exceeded 10.6 m^3/s (the maximum diversion capacity) as well as when alternative flow paths were operated (e.g., fish ladder, dam cresting), a reduced proportion of the total river was sampled. However, due to the rapid recession of the river the proportion sampled was generally high: 100% for 63% of sampling days and over 70% for more than 75% of sampling days. Due to operational limitations and high sediment loads, sampling rarely occurred during the peaks of storms (Figure 3) but was usually initiated within 1–2 d of the storm peak and at flows less than 57 m^3/s. Adjacent to these storm events, the proportion of flow sampled was lower and it

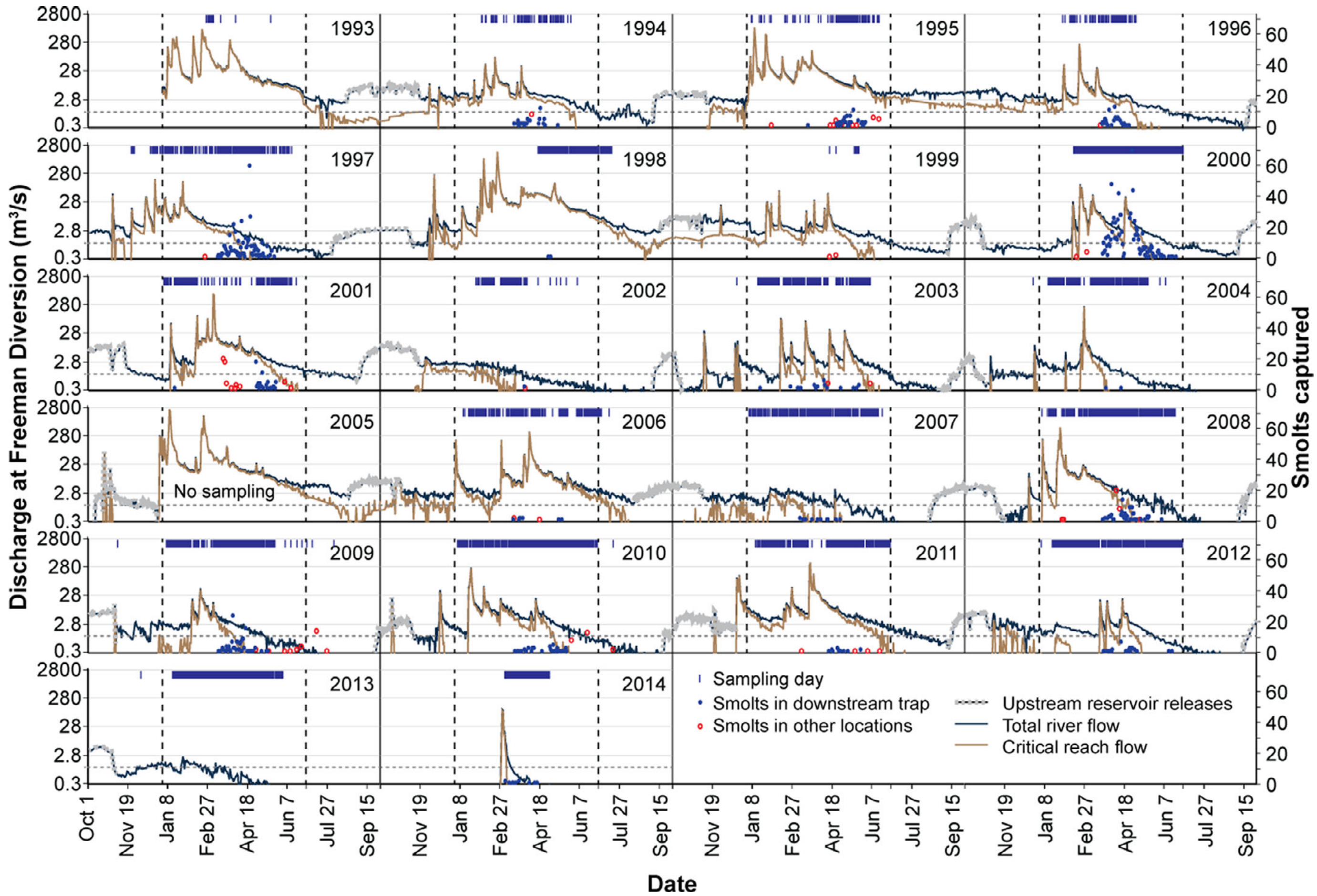

FIGURE 3. Hydrology of the Santa Clara River at the Vern Freeman Diversion and model-estimated downstream flows within the strongly losing "critical reach," assuming no water diversion. Fall reservoir releases from Lake Piru (used to recharge upstream groundwater basins) artificially increase total river flows, typically from September to November. Sampling days include operation of the downstream migrant trap, surveys of the fish bay, or stranding surveys adjacent to the diversion facility. Smolt arrivals are daily totals separated by collection location. The dashed vertical lines indicate January 1 (water year [WY] day 93) to June 30 (WY day 274); the horizontal dashed line indicates the estimated potential downstream passage limit for migration through the critical reach.

is likely that fish passed the diversion without being sampled—on 8% of sampling days, trap effectiveness was less than 25%. Fish were not captured at flows higher than 54 m^3/s, which occurred on 3% of all days and 1% of sampling days between November 1 and June 30 in WYs 1994–2014.

Because high flows regularly occurred during the early part of the season (lower proportion of flow sampled) and low flows (higher proportion of flow sampled) predominantly occurred later in the season, it was not possible to directly distinguish whether the lack of smolt observations (i.e., absence) in the early season was a result of time of year or the availability of alternative migration pathways (i.e., decreased detection probability). To indirectly investigate this contrast, I examined the catch rates of numerically more abundant nontarget fish species to assess whether detection patterns showed similar trajectories (Supplement B available in the online version of this article). No other taxa showed temporal patterns of detection similar to those of steelhead smolts (although some taxa displayed seasonal movements with different timing), and catch of particular nontarget taxa (cyprinids) remained relatively consistent throughout the sampling season, indicating that the lack of smolt presence in the early season was likely not attributable to impaired trap effectiveness.

Environmental drivers.— Based on the approach of Sykes et al. (2009), I developed logistic regression models to explain the presence (1) or absence (0) of migrating steelhead smolts in the downstream migrant trap. Due to low smolt counts and missing data for some drivers (e.g., water temperature) in some years, initial model selection was restricted to a subset of WYs (Supplement A). All statistics were completed in JMP Pro version 12.2 (SAS

Institute, Cary, North Carolina) and in the programming language R (R Core Team, Vienna).

Candidate models were developed using potential drivers of downstream migration and smolt arrival: day length, log-transformed total river flow at the VFD (m^3/s), days since flow peak, water temperature, and moon phase. Photoperiod/day length was calculated using the National Oceanic and Atmospheric Administration's solar calculator (https://www.esrl.noaa.gov/gmd/grad/solcalc/calcdetails.html). The onset of increasing day length was expected to trigger smoltification, and day length should be a reliable temporal cue indicating the time of year for migration (Wagner 1974). Water temperature (nearest 0.5°C) was measured in the fish trap bay during each trap check (typically between 0800 and 1100 hours) in most years subsequent to WY 2000 (Supplement A). Water temperature data for WY 1997 were not available, so 1997 was not included in initial model selection. For WYs 2001–2003, some missing temperature values were estimated from the regression of WY day versus temperature for that year to allow modeling of all sample dates. Flow peaks were assigned a value of zero days and were defined as any day on which the total river flow at the VFD exceeded 14 m^3/s and flow in the subsequent day was 10% lower. Moon phase was retrieved from the U.S. Naval Observatory (https://aa.usno.navy.mil/data/docs/MoonFraction.php). To account for temporal autocorrelation in the data, I included a first-order autoregressive error structure, with WY day grouped within WY.

Prior to defining potential models, I assessed the model parameters for evidence of collinearity by using linear regression. For each pairwise regression, I calculated the variance inflation factor (VIF), equivalent to $1/(1 - R^2)$. Values of VIF greater than 3 indicate strong collinearity (Zuur et al. 2010). Of the model parameters, only day length and water temperature showed a significant linear relationship; however, no parameters exhibited strong collinearity based on the VIF. I developed 16 candidate models to test biologically reasonable potential drivers for smolt migration (Table 1) and used an information theoretic model comparison procedure to identify the best-performing models (Burnham and Anderson 2004). I used Akaike's information criterion adjusted for small sample size (AIC_c) and the AIC_c difference (ΔAIC_c) to rank models. In cases where ΔAIC_c was less than 2, I ranked models with fewer parameters higher. For the best model, I computed parameter estimates (β) for each parameter. I used the Z-statistic to determine statistical significance of parameters within each model at an α of 0.05. Models were fitted using the package glmmTMB (Magnusson et al. 2020), and model comparison was performed using the "dredge" function in the MuMIn package (Barton 2020).

Using the best candidate model identified during model selection, I validated model performance by fitting models on an iteratively constructed training data set (7 of 8 WYs) and predicting presence/absence for the remaining WY. I used the area under the receiver operating characteristic curve (AUC; Pearce and Ferrier 2000) to estimate the relative proportions of correctly and incorrectly classified predictions from the binary model using the package pROC (Robin et al. 2020). I compared AUC between the training data set and the validation data set, and I considered fits with an AUC greater than 0.7 to provide reasonable discrimination (Pearce and Ferrier 2000).

Size and age at migration.— Smolt size is considered to be a potential factor in triggering migration, and larger size is associated with a greater likelihood of ocean survival (Mangel et al. 2010; Hayes et al. 2011; Arriaza et al. 2017). I used ANOVA to test for a relationship between smolt size and migration timing, both on the full data set and for each individual WY. To assess whether smolts holding in habitats adjacent to the VFD were larger than those migrating, I used a one-way ANOVA to test for differences in size between smolts collected in the fish bay or downstream stranding surveys versus those captured in the downstream migrant trap.

Passage synchronization.— To determine whether smolt migration was synchronized with periods in which successful passage to the estuary and ocean was likely to be possible, I estimated a lower flow limit for passage through the critical reach (methods available in Supplement C available in the online version of this article) and determined the latest date of flows for each WY above the low-flow limit. At flows in the critical reach ranging from 1.1 to 1.7 m^3/s, the thalweg depth is typically less than 0.15 m and there is not a contiguous channel with a maximum depth that exceeds the recommended passage depth for juvenile steelhead (0.12 m; California Department of Fish and Wildlife 2017). I applied this range of flows as a passage threshold on the model-estimated hypothetical natural flow conditions in the critical reach. I calculated the potential proportion of smolts during each WY that arrived at the VFD but would be unlikely to successfully migrate to the ocean due to the natural hydrology of the river. The intention for this calculation was not to prescribe a minimum flow threshold for fish passage but to determine the overall synchronization of smolt migration with flow conditions that are likely to provide successful passage to the ocean. To provide an estimate of uncertainty around the flow threshold, I also used a 25% lower flow threshold (0.85 m^3/s) to calculate a lower bound for the proportion of individuals that were unlikely to encounter passable conditions. To determine whether a migration timing mismatch in the observed data set was representative of conditions encountered over longer-term climate oscillations (e.g., El Niño), I used a 71-year (WY 1944–2014) modeled flow data set for the critical reach (provided by UWCD) to calculate the proportion of days per

TABLE 1. Model selection statistics for the potential binary models describing drivers of steelhead smolt downstream migration in the Santa Clara River, California (AIC_c = Akaike's information criterion corrected for small sample size; ΔAIC_c = difference in AIC_c between the given model and the best-performing model; $w_i = AIC_c$ model weight). Variables include day length, natural log-transformed total river flow at the Vern Freeman Diversion ($\log_e$[TotalRiver]), days since flow peak (DaysFlowpeak), water temperature (WaterTemp), and moon phase.

Model	Rank	AIC_c	ΔAIC_c	w_i
DayLength + DaysFlowpeak + $\log_e$(TotalRiver)	1	762.66	0.00	0.34
DayLength + DaysFlowpeak + $\log_e$(TotalRiver) + MoonPhase	2	764.49	1.82	0.14
DayLength + DaysFlowpeak + $\log_e$(TotalRiver) + WaterTemp	3	764.62	1.96	0.13
DayLength	4	765.90	3.24	0.07
DayLength + DaysFlowpeak	5	766.12	3.46	0.06
DayLength + DaysFlowpeak + $\log_e$(TotalRiver) + MoonPhase + WaterTemp	6	766.43	3.77	0.05
DayLength + $\log_e$(TotalRiver)	7	766.70	4.04	0.05
DayLength + MoonPhase	8	767.57	4.91	0.03
DayLength + DaysFlowpeak + MoonPhase	9	767.89	5.23	0.02
DayLength + WaterTemp	10	767.92	5.25	0.02
DayLength + DaysFlowpeak + WaterTemp	11	768.14	5.48	0.02
DayLength + $\log_e$(TotalRiver) + MoonPhase	12	768.34	5.67	0.02
DayLength + $\log_e$(TotalRiver) + WaterTemp	13	768.67	6.00	0.02
DayLength + MoonPhase + WaterTemp	14	769.58	6.91	0.01
DayLength + DaysFlowpeak + MoonPhase + WaterTemp	15	769.92	7.26	0.01
DayLength + $\log_e$(TotalRiver) + MoonPhase + WaterTemp	16	770.29	7.62	0.01

year when the logistic model predicted downstream migrants to be present (WY days 104–268) and conditions would be passable to the estuary.

RESULTS

Hydrology

The period of record included both exceptionally wet years (WYs 1998 and 2005) and dry years (WYs 2002, 2007, 2013, and 2014). Water year annual rainfall at Santa Paula Creek (Ventura County rainfall gauge 173A) varied between 179 and 1,548 mm (mean ± SD = 581 ± 365 mm). Typically, tributary connection (Figure 1) began after the first appreciable rainfall of the year and ceased by late summer except after very wet years (e.g., WY 1998) and generally reconnected after the first measurable rainfall of the WY (Supplement A). Large storm events (Sespe Creek flow > 100 m^3/s) exclusively occurred between December and mid-April. Early season storms (October and November) were short (1–2 d) and resulted in much smaller flows in Sespe Creek (<57 m^3/s). The bulk of total flow (>60%) in the Santa Clara River is the product of discharge from Sespe and Santa Paula creeks and is strongly dependent on rainfall events. An extended duration of elevated base flows occurred in years with substantial snowfall. Typical storms elevate the main stem for 3–7 d before returning to base flow, which is dependent on the magnitude and frequency of prior storms (i.e., elevated groundwater levels during a wet year result in longer and higher-magnitude flows). Flows downstream of the VFD cross the critical reach with variable percolation rates up to 1.7–4.5 m^3/s, and during the receding limb of most storm events this critical reach becomes too shallow for fish passage and eventually loses a surface hydrologic connection (Figure 3).

Migration Timing

Smolt arrival timing varied among years. The earliest observed smolts arrived in mid-January (WY days 109–110), but only three individuals out of the total of 2,128 were observed in January and only nine individuals were observed prior to March. During the study period, the majority (95%) of smolts arrived between mid-March (WY day 171) and late May (WY day 235). The overall median migration date was mid-April (WY day 198) but ranged from mid-March (WY day 170) to mid-May (WY day 223; Figure 4; Supplement A). Smolts only were captured in the downstream fish trap until late June (WY day 265 in WY 2000) despite the trap operating into July during several years (WYs 1998 and 2006). Smolts were encountered in the fish bay as late as mid-July (WY day 292 in WY 2010) and in stranding surveys downstream of the facility until the end of July (WY day 300 in WY 2009; Figure 3).

Environmental Drivers

The three top-ranked models had ΔAIC_c values less than 2 (Table 1); therefore, I ranked the model with fewest parameters the highest. All top-ranked models included

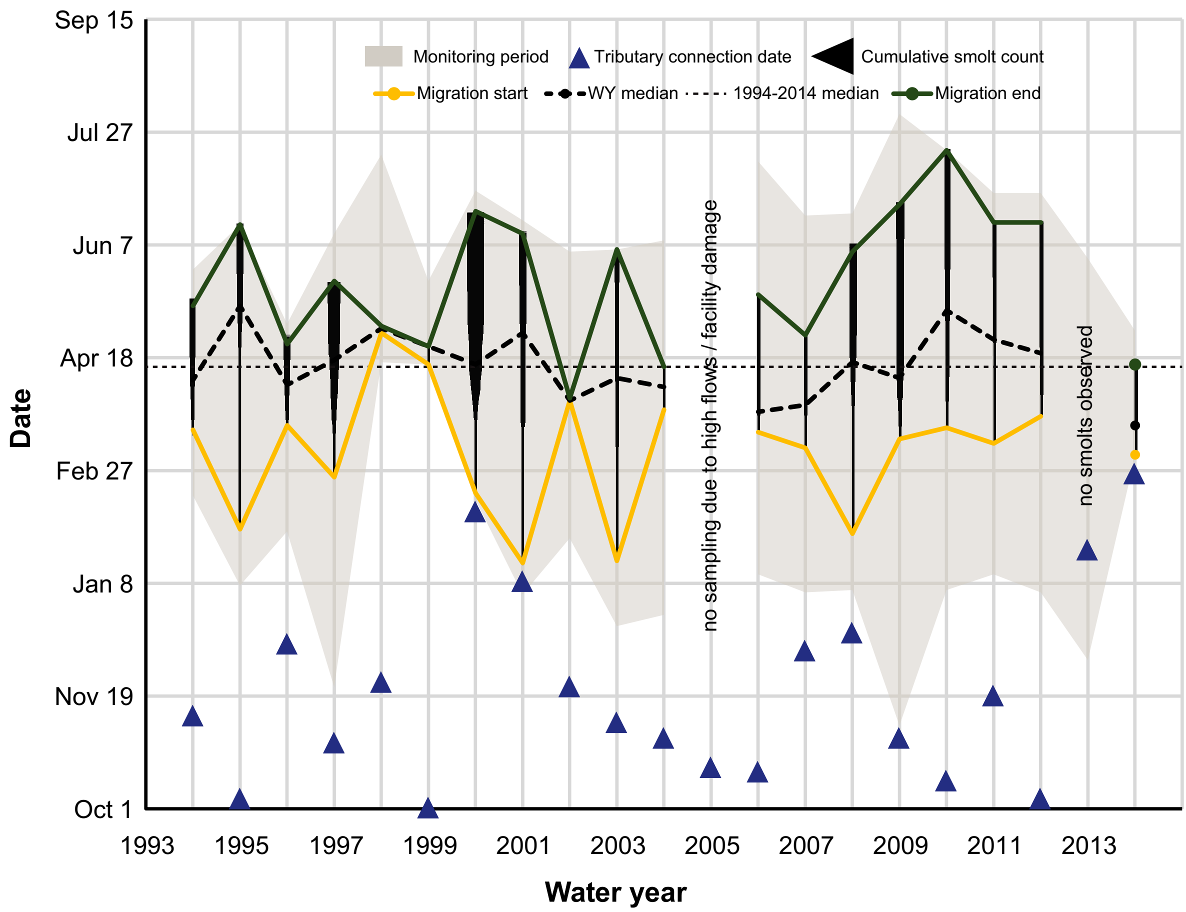

FIGURE 4. Cumulative steelhead smolt arrivals (first, median, last) in the downstream migrant trap at the Vern Freeman Diversion, with the date of first tributary connection (WY = water year). The monitoring period shown includes the entire season during which monitoring potentially occurred within each WY; however, monitoring did not occur continuously throughout (details shown in Figure 3). Smolts were never observed prior to tributary connection. Smolts typically arrived well after monitoring began.

day length, days since flow peak, and total river flow (DayLength + DaysFlowpeak + $\log_e$[Total River]) as significant predictors (Table 2). Increasing day length had a positive influence on migration, while days since flow peak and total river flow had a negative influence on the probability of migration. The AUC was 0.94, indicating a good fit to the binary model (Figure 5). Validation on withheld data (Table 3) indicated that the model structure provided reasonable prediction for 5 of the 8 WYs (AUC > 0.7) but that the effect of the first-order autoregressive error term was heterogeneous among years, resulting in lower model performance for the withheld data.

Excluding the nine smolts that were observed in January and February, migrants began arriving when day length exceeded 12.25 h (WY day 153) and the rate of day length increase was fastest. Day length at median migration ranged from 13.0 to 14.3 h (WY days 170–221). Smolts were never observed at the VFD prior to a tributary connection with the main stem (Figure 4). In several WYs with dry preceding autumns (2000, 2001, and 2014), the first smolts were observed at the VFD within 1 week of the first storm that connected tributaries to the main stem. However, in 13 of 19 years smolts were not observed at the VFD for over 95 d after tributary connection (Supplement A). There was a significant negative relationship between days since flow peak and smolt presence, indicating some degree of time lag between storm events and smolt arrivals (Figure 6). In some years, smolt migration occurred in the midst of storm events (e.g., WYs 1994, 2000, and 2003), while in other years most or all smolt arrivals occurred well after storm events (>20 d; e.g., WYs 1997, 2008, and 2009). High-flow events (>28 m^3/s) predominantly occurred between February and April (WY days 124–212), while smolt arrivals generally occurred during the receding limb of the seasonal hydrograph.

Water temperatures during the monitoring season ranged between 6°C and 24°C. The top-ranked models did not include water temperature as a predictor for smolt

TABLE 2. Regression parameter values for the highest-ranked models (see Table 1) describing drivers of steelhead smolt downstream migration in the Santa Clara River.

Variable	β	SE	Z	P	95% confidence limits Lower	Upper
DayLength	0.0263	0.0060	4.3	<0.0001	0.0144	0.0381
$\log_e$(TotalRiver)	−0.7745	0.3452	−2.2	0.0249	−1.4511	−0.0979
DaysFlowpeak	−0.0307	0.0119	−2.6	0.0003	−0.0539	−0.0074
Constant	−18.507	5.1497	−3.6	<0.0001	−28.600	−8.413

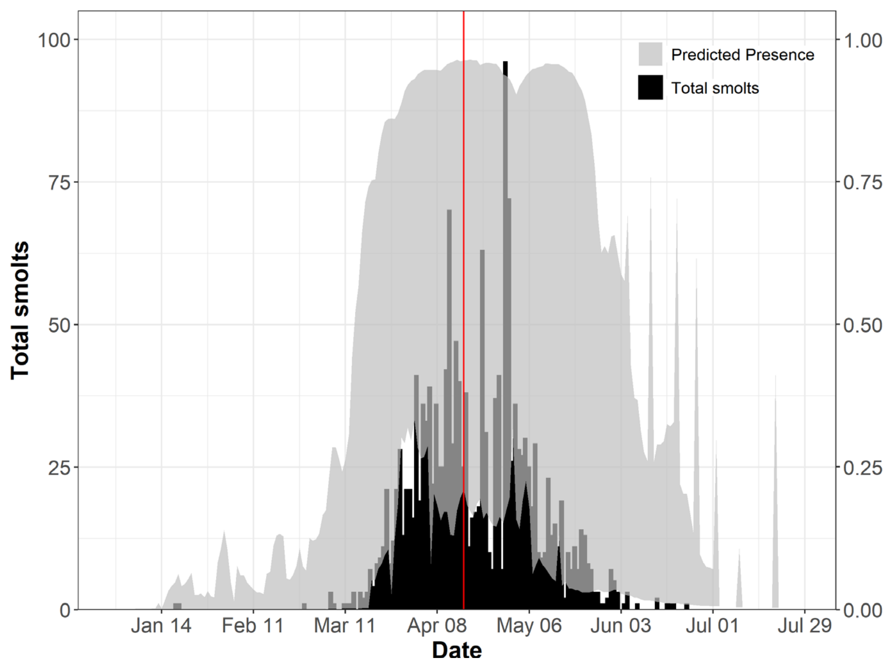

FIGURE 5. Observed smolt counts and modeled probability of steelhead smolts in the Santa Clara River at the Vern Freeman Diversion (VFD). Smolts were collected in the downstream migrant trap at the VFD. The model predicted the probability of smolt presence/absence using logistic regression, with day length, days since flow peak, and total river flow as factors grouped within water year. Predicted presence is shown as the maximum and minimum predicted presence for all model years. The vertical red line indicates the median arrival date of smolts.

presence/absence, but the majority (95%) of smolts were observed when water temperatures ranged between 12°C and 18.5°C (Supplement D available in the online version of this article). Smolt arrivals began within 1–3 weeks of average water temperatures at the VFD reaching 12°C, excepting lone fish in WYs 2001, 2003, and 2008 that arrived 1–2 months earlier than the rest of the migrants.

Size and Age at Migration

Downstream migrant smolts ranged in size from 80 to 360 mm FL (mean ± SD = 177.8 ± 30.2 mm FL; Supplement E available in the online version of this article). There was no relationship between size and migration timing for fish collected in the downstream migrant trap (R^2 = 0.001) with all years combined or analyzed individually. However, overall, fish collected in the downstream migrant trap (173.5 ± 0.9 mm FL) were significantly smaller than those collected in the fish bay (188.9 ± 2.2 mm FL) and downstream stranding surveys (257.9 ± 5.5 mm FL; ANOVA: df = 2, 1,086; F = 130.8; P < 0.0001), which typically occurred later in the season (June and July).

Of the 167 fish that were aged in 1995 and 1996, 106 were age 1 (77–229 mm FL), 51 were age 2 (152–386 mm FL), and 1 was age 3 (326 mm FL); age could not be determined for 9 of the 167 fish. Fish ages were not determined via scale analysis after 1996 due to the listing of southern California steelhead as endangered in 1997. However, given these size ranges and the overall size distribution of captured smolts, the majority of smolts were likely 1 or 2 years old (Supplement E).

TABLE 3. Model validation of the top-ranked binary model (see Table 1), using a "leave 1 year out" approach in which model parameters were fitted on 7 of the 8 water years (WYs) and smolt presence/absence was predicted for the withheld year. Area under the receiver operating characteristic curve (AUC) is shown; AUC values greater than 0.7 were considered to provide a reasonable fit (CL = confidence limit).

		Validation AUC		
WY withheld	Training AUC	Mean	Lower 95% CL	Upper 95% CL
1997	0.94	0.90	0.87	0.93
2000	0.95	0.75	0.67	0.83
2003	0.97	0.62	0.50	0.75
2008	0.96	0.67	0.58	0.76
2009	0.96	0.75	0.67	0.84
2010	0.96	0.77	0.69	0.85
2011	0.97	0.74	0.65	0.84
2012	0.96	0.57	0.49	0.66

Passage Synchronization

In most years, a subset of the migrating smolts (9–83%) arrived at the VFD after it was unlikely that sufficient flows were available to permit swimming through the critical reach to the estuary and ocean (Figure 7B). Estimates of successful passage may be conservative if fish require more than 1 d to traverse the river from the VFD to the estuary, since the criteria for passage was the last day within the migration season with flows exceeding 1.1 m^3/s in the critical reach. In years characterized by early season or low-magnitude storms (e.g., WYs 1997, 2009, and 2010), the majority of downstream migrants arrived when passage to the estuary and ocean was unlikely. Years with a combination of sustained high base flow or later-season storms showed higher relative passage success (e.g., WYs 1995, 1996, 2000, and 2012). Several WYs (e.g., 1998 and 2005) with regular storms and high base flow had limited or no sampling, but any smolts migrating during these years would have experienced passable conditions through July. The passage availability observed during the study period was consistent with the longer 71-year historical record (Figure 7A, C), with substantial variation in availability of passage among years and several extended droughts during which passage opportunities were limited. In 51 of the 71 years, the date of the last potential migration opportunity was earlier than the observed median arrival dates for this data set; as a result, a majority of the smolt migration for the year likely did not successfully reach the estuary and ocean (Figure 7D).

DISCUSSION

One of the major challenges for managing steelhead in southern California is the overall lack of data regarding their natural history in this region, necessitating regulatory reliance on observations from better-studied systems in central California (e.g., Waddell and Scott creeks; Shapovalov and Taft 1954; Bond et al. 2008; Hayes et al. 2011; Phillis et al. 2016) with substantially different environmental conditions. Given the geomorphic, hydrological, and climatic differences between streams in the northern and southern portions of the range, drivers for important life history transitions like out-migration may differ. Understanding these patterns and drivers is critically important, as mismatches between management actions and the species' needs may result in a failure to recover the endangered Southern California DPS. Given the historical and ongoing reliance of human communities on extracting water from regional surface and groundwater sources, achieving a better understanding of the timing and drivers of smolt migration in southern California will ensure that human use of water resources does not preclude the recovery of endangered steelhead or further exacerbate their decline.

Patterns of Smolt Migration

Although it was not possible to estimate total smolt out-migration with this data set, observed counts were consistently low for a river system of this size. Assuming that the observed counts are within an order of magnitude and given optimistic smolt–adult return rates from the Snake–Columbia River system (3–5%; Scheuerell et al. 2009), adult returns to the Santa Clara River would likely be much less than 100 individuals/year, well short of the annual migrant returns targeted for the DPS (NMFS 2012). However, observed adult returns at the VFD during the monitoring period were typically less than 2 individuals/year (16 total during the study period; Dagit et al. 2020), suggesting that smolt–adult return rates in this system and the region are low.

Smolt migration in the Santa Clara River typically occurred between mid-March and late May, although median timing varied by up to 50 d within the monitoring period. Some of this variation in median timing was potentially an artifact of low smolt numbers—6 of the 9 years with "high" smolt numbers (>50 fish) had median arrival times within 19 d of one another (early to late April; WY days 187–206). Three years (WYs 1995, 2001, and 2010) had similarly "high" smolt counts, but due to the shape of the arrival distributions there is potentially greater uncertainty in median estimates of arrival time. Very few smolts (0.4% of the total) were observed prior to March, although in most years migration would have been possible because the first winter storms and tributary hydrological connections occurred well before February (Figure 4). Smolts were not captured in the downstream migrant trap after June despite their presence in stranding surveys within or downstream of the VFD through July,

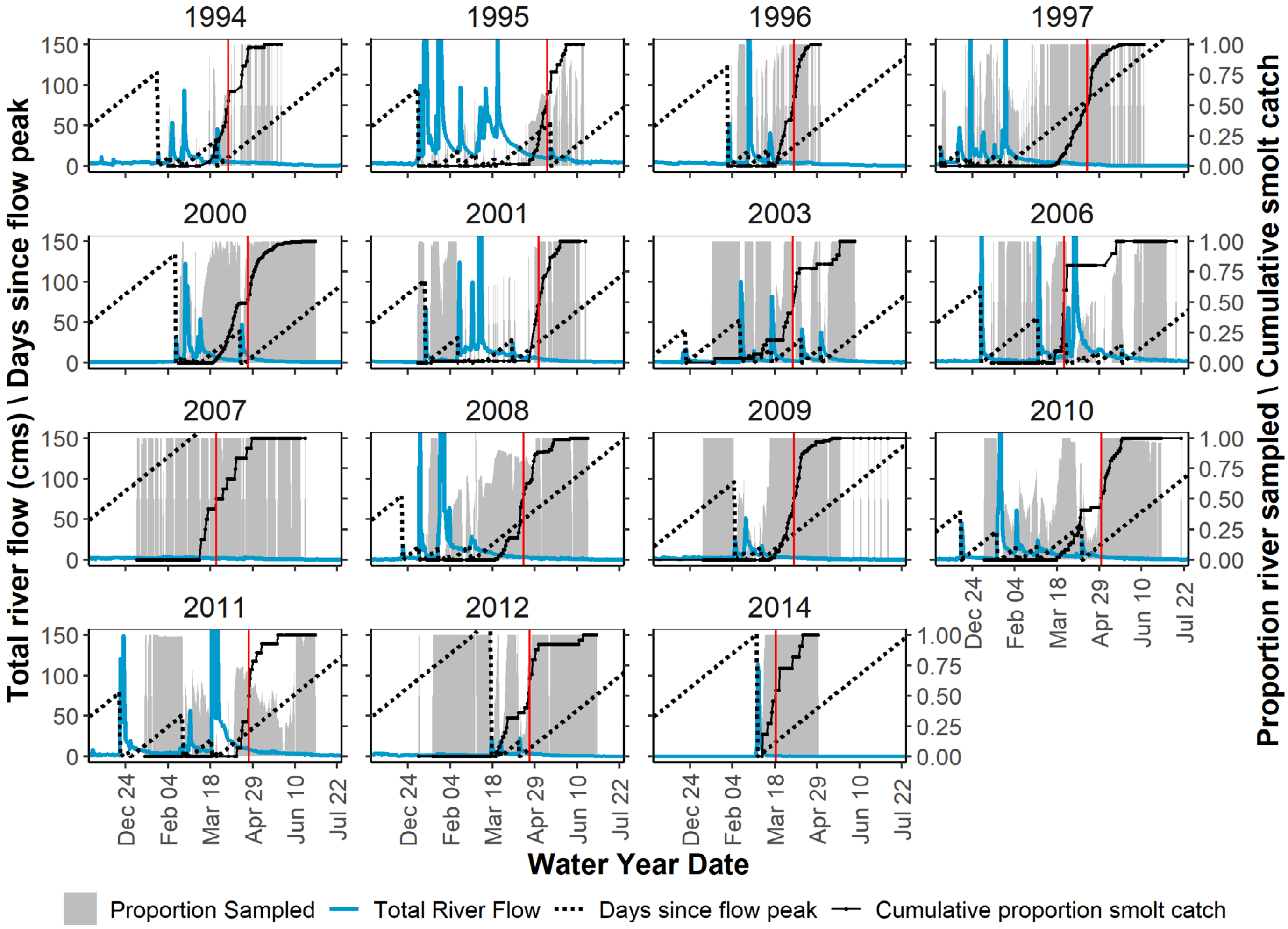

FIGURE 6. Cumulative steelhead smolt arrivals in relation to the proportion of river sampled (an estimate of potential variation in trap effectiveness) and hydrology in the Santa Clara River at the Vern Freeman Diversion (VFD) for water years with smolt counts of at least 10. Cumulative smolt arrivals were calculated as the proportion for each year. The proportion of river sampled was calculated based on flow entering the diversion. Total river flow (m^3/s [cms = cubic meters per second]) was estimated at the VFD; although flow peaks exceeded 150 m^3/s in several years, the full range is not shown to allow display of smaller storm events. Days since flow peak was calculated as the number of days since the total river flow exceeded 14 m^3/s and flow in the subsequent day was 10% lower. Vertical red lines indicate the median arrival date for smolts in each water year.

potentially indicating that fish had ceased migrating and were instead holding and rearing in the main-stem Santa Clara River.

Consistent with the findings reported here, median migration dates appear relatively similar within the South-Central California Coast DPS region despite the fact that river channels often become spatially intermittent due to the natural hydrology of the region and migration or dispersal may only be possible during elevated flows (Spina et al. 2005). In San Luis Obispo Creek, smolts were observed migrating from March through early June, with median migration occurring in April. Similar to the occasional early arrivals observed at the VFD, a few presmolts were captured in late fall and early winter in San Luis Obispo Creek; Spina et al. (2005) attributed this to the addition of treated wastewater, which kept a naturally intermittent stream perennial. In small tributary headwaters of the Santa Ynez River (Hilton and Salsipuedes creeks), smolts were observed migrating coincident with elevated flow as early as January, but the majority were observed between February and May. Smolts were captured downstream in the main-stem Santa Ynez River predominantly from March to May, when flows connected intermittent sections of the channel (COMB Fisheries Division 2016).

In contrast, observations in central California streams have shown juvenile movement throughout the year

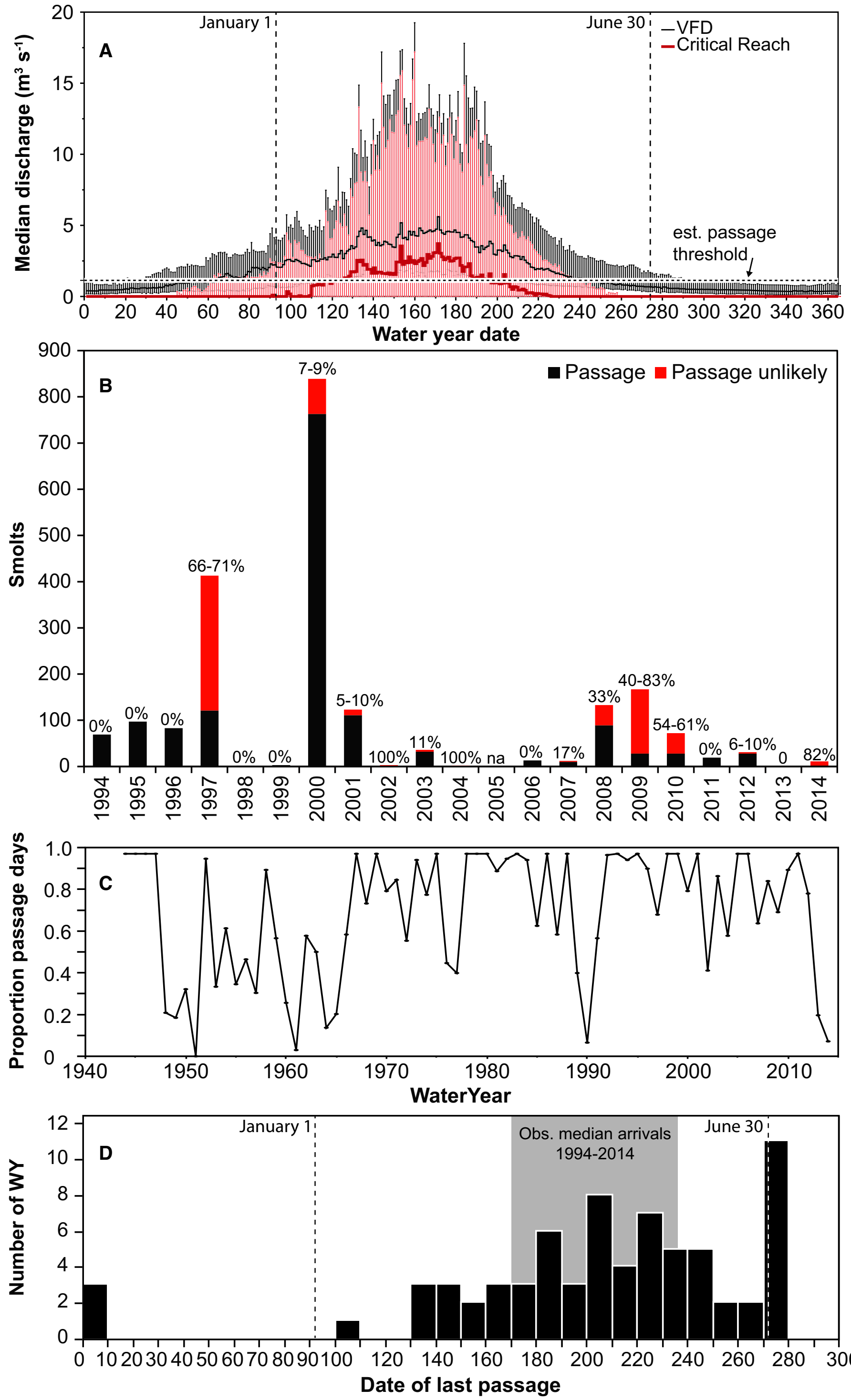

FIGURE 7. Synchronization of downstream-migrating steelhead smolts with passable migration conditions on the Santa Clara River: **(A)** model-estimated median flows (±25% and 75% quartiles) for each water year (WY) date at the Vern Freeman Diversion (VFD) and at the downstream end of the critical reach for WYs 1994–2014 (the horizontal dotted line indicates the estimated [est.] passage threshold used to calculate whether passage was unlikely); **(B)** observed data set for WYs 1994–2014 at the VFD, with percentage ranges representing the proportion of smolts in that WY that were unlikely to encounter passable conditions downstream of the VFD based on their arrival time and a minimum flow threshold (0.85–1.1 m^3/s; WY 2005 was not sampled, and no smolts were observed in WY 2013); **(C)** proportion of days during the migration season on which passage was likely to be possible in WYs 1944–2014; and **(D)** histogram of the WY date of last passage for WYs 1944–2014, showing the range of median arrival dates for smolts from the observed data set (WYs 1994–2014), which suggests that many smolts would have arrived at the VFD after the date of last passage.

(Waddell Creek: >21% between August and February; Shapovalov and Taft 1954) as well as multiple smolting migrations for individual fish (Scott Creek: >15% of out-migrants typically arrived in January and February; Hayes et al. 2011). These small coastal streams are short (total migration distance to ocean < 20 km) and perennial, such that within-stream movement may be possible year-round but out-migration is not because the estuary remains closed to the ocean until the first rainfall of the year (typically late autumn or early winter) due to barrier sandbars that form across the mouth. This hydrology also permits some smolts to adopt a lagoon anadromous life history strategy wherein juveniles migrate to the estuary during spring, use the high-resource lagoon to grow during summer, return upstream in the autumn when lagoon water quality is poor, and then "re-smoltify" and out-migrate again as early as December in the subsequent winter (Hayes et al. 2011).

Sampling Efficiency

I had two main concerns regarding sampling efficiency: (1) the inability to sample during high flows that are potentially an important transport mechanism for out-migrants (Flagg and Smith 1981; D. Boughton, National Oceanic and Atmospheric Administration, Southwest Fisheries Science Center, personal communication) and (2) the regular occurrence of high flows early in the migration season that might reduce the chance of observing smolts. These are typical problems for downstream migrant trapping (Roper and Scarnecchia 1999; Hedgecock et al. 2001; Spina et al. 2005; Spence and Hall 2010; Hayes et al. 2011) but may be exacerbated in a river like the Santa Clara River because streamflow regularly encompasses multiple orders of magnitude between base flow and storm peaks.

Storms occurred more regularly early in the season, but the duration of low relative trap effectiveness was typically short and few or no smolts were observed in the early season, even when the proportion of the river sampled was high (e.g., WYs 1997 and 2012; Figure 6). In addition, high-flow events only occasionally coincided with periods when smolts were encountered at the VFD. Smolt arrivals at the VFD did not begin until several weeks after storm events in most years, despite a high proportion of total flow sampled in the period prior to smolt arrival. Thus, it does not seem likely that occasional periods with a low proportion of flow sampled could explain the lack of smolt observations in the downstream migrant trap during the early season. However, if large numbers of smolts migrate downstream during storms within their typical migration season, low trap effectiveness during and adjacent to storms is likely to underestimate out-migrant run size due to low capture rates and also may result in estimates of median arrival shifting later in the season.

Environmental Drivers

In other systems, various environmental drivers have been shown to cue smolt migration: day length/photoperiod (Wagner 1974; Byrne et al. 2003; Spence and Dick 2013; Budnik and Miner 2017), hydrology (Sykes et al. 2009; Spence and Dick 2013; Aldvén et al. 2015), water temperature (Wagner 1974; Hvidsten et al. 1995; Roper and Scarnecchia 1999; Sykes et al. 2009; Chapman et al. 2013; Spence and Dick 2013; Aldvén et al. 2015), and moon phase (Grau et al. 1981; Hvidsten et al. 1995; Spence and Dick 2013). Since migration data for the Santa Clara River are limited by generally low smolt abundance and limited sampling efficiency during high-flow events, specific parameter estimates for environmental drivers (particularly hydrology) should be interpreted with caution. However, these models provide a framework for future investigations of smolt timing and can inform development of predictive models.

Similar to other systems, day length in the Santa Clara River appeared to be a general cue for the initiation of smolt migration. Despite within- and among-season variation in most other variables (e.g., hydrology and temperature), in most years median arrival times were quite similar. Wagner (1974) suggested that day length was the dominant driver of smolting in *O. mykiss*, with other variables serving to intensify the response. Artificial changes in day length can initiate smoltification out of season (Björnsson and Bradley 2007), but in natural systems day length may also serve as potential constraint to large shifts in run timing (Satterthwaite et al. 2009), thereby limiting the ability of smolts to take advantage of early season storms.

Contrary to expectations, hydrology appeared to have a variable role in smolt migration. I had initially expected that storm events, even early in the year, would trigger migration because high flows should be a reliable cue for whether smolts can actually traverse the river and enter the ocean. However, high-flow events in the main-stem Santa Clara River also are characterized by extreme turbidity (>3,000 NTU), which is likely to be damaging to salmonids (Lloyd 1987), so avoiding movement during the peaks of storms may be advantageous. Smolts (as well as other *O. mykiss* life stages) were never observed at the VFD prior to tributary connection or the first storm-related flow of the year, so downstream migrants clearly required storm events with flows that were sufficient to reconnect tributaries and permit movements within the watershed. However, smolt arrivals lagged behind storm pulses. If smolts were triggered to move or were pushed downstream during storm events (Flagg and Smith 1981; Smith 1982), smolt abundance should have increased at the peak (assuming sufficient detectability in the downstream migrant trap) or soon after on the receding limb of the storm hydrograph. I saw no evidence for this pattern in the data set—smolt arrival at the VFD did not appear to be instigated by storm events, similar to findings by Kelson and Carlson (2019), but often occurred several weeks after storms (e.g., in WY 1997, the early storms did not result in any migrants—all arrived well after the last storms of the year). However, in WY 2014 the first (and only) storm of the season occurred within the typical smolt season and smolts began to arrive 7 d after the storm—similar to the findings of Byrne et al. (2003)—indicating that smolts can make use of storm pulses that coincide with their typical migration window. At migration rates observed in other systems (0.25–0.83 km/h; Manning et al. 2005), travel time from headwater tributaries to the VFD may be at least 4–15 d or substantially longer if fish do not continuously migrate (e.g., nocturnal migration; Chapman et al. 2013). Given the VFD's location low in the watershed, it remains possible that smolts in the upper watershed begin migration during storms and that travel time (or pauses in migration) from rearing habitats to the VFD explain the time lag between storms and smolt arrivals.

Although water temperature was not a significant predictor of smolt migration, some patterns were generally apparent. More than 99% of smolts arrived after average water temperature reached 12°C at the VFD and migration was typically complete prior to temperatures exceeding preferred water temperatures (9.8–22.2°C; Spina 2007). By June, water temperatures occasionally exceeded 22°C and fish were no longer found in the downstream migrant trap, although they were sometimes observed in the fish bay or surrounding areas. Typical summer temperatures in the main-stem Santa Clara River near the VFD range from 25°C to 32°C, exceeding stressful temperatures (Spina 2007) and thermal maxima for *O. mykiss* (Sloat and Osterback 2013), so it is likely that unsuccessful migrants in the main stem eventually may die if they do not attempt to return to the Santa Clara River tributaries, which are typically much cooler and within the preferred temperature ranges for the species (Boughton et al. 2007).

The model used in this study had good specificity and sensitivity (AUC > 0.9), and identified day length and two measures of hydrology as significant factors explaining smolt presence at the VFD. However, model validation demonstrated that random year-specific variation limited the performance of the model as predictive of future conditions, suggesting that other factors not included in the model may play a role in migration timing. The predictive ability of the logistic approach also was likely limited by the inconsistent presence of smolts during the migration season (frequent "0" absence observations, potentially driven by low overall smolt abundance). Despite these limitations, the model provides a reasonable probability distribution of smolts' arrival timing at the VFD.

Synchronization with Successful Migration Windows

The relatively consistent smolt timing (March–May) observed here indicates that as long as a hydrologic connection provides access from tributaries to the main stem of the Santa Clara River, smolts will attempt to migrate regardless of storm events. The likely success of that migration, however, will be dependent on whether elevated flows from storms coincide with the migration window. For example, in WY 1997, one of the largest outmigrations observed in the monitoring period, the vast majority of fish were unlikely to have encountered passable conditions downstream of the VFD under natural flow conditions. Conversely, in 2000 the median arrival date was a week later, but due to consistent storms throughout the period the bulk of out-migrants were likely to have successfully migrated. In very dry years (e.g., WYs 2002, 2013, and 2014), passable conditions to the estuary were rare or non-existent and the estuary did not naturally open to the ocean. In essence, it appears that regardless of which cues are being used to initiate migration, the timing of downstream smolt migration in the Santa Clara River often may occur too late in the season to be synchronized with likely opportunities for downstream migration to the estuary and ocean. The bulk of years in the 71-year flow record (WYs 1944–2014) had a date of last passage opportunity that was earlier than the observed median dates of arrival; this suggests that if the observed migration timing is representative of historical conditions, then it is a relatively common occurrence for smolts in the Santa Clara River to be unable to successfully migrate to the ocean. It is important to note that these calculations are based on modeled "natural" hydrology for the critical reach (i.e., no water extraction or diversion upstream). In dry or normal flow conditions, diversion of water and groundwater extraction from upstream areas are likely to further limit the availability of downstream passage except during exceptionally wet periods, when artificial groundwater recharge from diversions at the VFD can result in elevated groundwater levels near the river and increased flow in the critical reach.

This lack of synchronization appears evolutionarily counterintuitive, particularly given evidence of rapid shifts away from a migratory life history for *O. mykiss* (Phillis et al. 2016) and other salmonids (Palkovacs et al. 2012; Abadía-Cardoso et al. 2013). However, recent work has demonstrated the potential for shifts in migration-linked genotypes to be bidirectional, depending on variation in landscape permeability over time (Kelson et al. 2020a, 2020b). In contrast to hydrological data, there is no information on the timing of migrants in the Santa Clara River prior to construction of the VFD. Although the migration timing observed in this study is not well matched to the current or historical hydrology, it is impossible to know whether this (1) represents the historical pattern of migration; (2) is evidence of selection toward a different migration regime due to anthropogenic habitat modification, consistent with the idea of ecological and evolutionary traps (Schlaepfer et al. 2002); or (3) is simply dispersal to seasonal foraging habitat with abundant prey (Sogard et al. 2012). Further work is necessary to determine whether the migration patterns observed in the Santa Clara River are consistent with the rest of this region or are the result of within-watershed selective pressures or alternative life history strategies.

Implications for Management

It has been hypothesized that juvenile *O. mykiss* may rear in the main stem during wet years (NMFS 2012) or in estuaries (Hayes et al. 2011), where food resources are more abundant, thus allowing them to achieve a greater size at migration. Compared to fish in Scott Creek, smolts in the Santa Clara River were large, with more than 75% of individuals exceeding the 150-mm FL marine survival size threshold, similar to individuals following the lagoon anadromous strategy (Hayes et al. 2011). Although the warmer temperatures found in southern California likely lead to higher growth rates, juveniles may be rearing in high-resource habitats during part or all of the year or may be predisposed to higher growth, similar to Central Valley lineages (Beakes et al. 2010). Large size at smolting generally leads to higher ocean survival (Bond et al. 2008; Satterthwaite et al. 2009) and suggests that juvenile steelhead in the Santa Clara River have a higher probability of survival—assuming that they can complete their migration to the ocean.

The assessment of synchronization between migrants and passable conditions for this study assumed that a single day with flows exceeding 1.1 m^3/s in the critical reach would be sufficient for successful migration. Although this likely overestimates the passage windows (i.e., more flow is likely necessary to achieve consistent passage), direct observations of smolt migration behavior, particularly while traversing the shallow, braided critical reach, are crucial to inform water management. Water resource managers need clear guidelines for the necessary pattern, magnitude, and duration of flows that will consistently provide successful migration opportunities, but these are difficult to determine without data on downstream migrant behavior.

The apparent lack of synchronization between smolt migration timing and passable conditions in the river is particularly troubling for management because there is not a clear mechanism to re-align migration timing with passable conditions. Regardless of water extraction, many smolts are likely to arrive at the VFD after downstream conditions become impassable for the season under a natural flow regime. However, at low flows water extraction from the river during the migration season has potential to further truncate passage opportunities even when natural flows would otherwise be adequate to permit passage through the critical reach. Unlike many northern watersheds, where water stored in reservoirs can substantially contribute to downstream flow, total river flow in the lower Santa Clara River is predominantly dictated by tributary hydrology and groundwater upwelling. There is not a local source of additional water to augment or extend flows in the river during the migration season and promote late-season passage opportunities. Migration opportunities only result from storm events of sufficient magnitude and duration to generate extended surface flows. In addition, migration opportunities may be further limited under climate change, which is predicted to further shift regional hydrology toward greater extremes—higher-magnitude but less-frequent storm events (Pagán et al. 2016).

To minimize impacts to smolts, water extraction should be reduced to ensure that sufficient flows remain in the river during the typical migration period (March–May) when conditions are passable for smolts. Conversely, extraction outside of the migration season or during periods in which total river flows are insufficient to ensure passage through the critical reach is unlikely to impact smolt migration. However, water management plans should ensure that unsuccessful late migrants can return upstream or otherwise find adequate rearing habitat to mature in freshwater or attempt migration in the future. Future work (e.g., PIT tagging and tracking of within-watershed movements for late-season arrivals) could identify the degree to which main-stem rearing (and subsequent upstream or downstream migration or residualization) is a typical life history strategy in this region. Given the important contribution that resident fish are likely to make in these *O. mykiss* populations (Bell et al. 2011), unsuccessful late-season migrants returning upstream may play a critical role in the persistence of the Southern California DPS.

Historically, under low- or no-flow conditions in the critical reach, smolts captured at the VFD were "trap-and-haul" transported to the estuary regardless of its open or closed status. Such transport was perceived to ensure ocean entry under marginal flow conditions in the critical reach when the estuary is open. If the estuary is closed, however, it is unclear whether it serves as an effective rearing habitat for juvenile steelhead. Given the large extent of the critical reach and the low probability of passable conditions to the upper watershed during the late season, the lagoon anadromous life history strategy (i.e., downstream migration to estuary, hold and rear, move upstream in fall, and "re-smoltify" and migrate during the following season) seems unlikely to be historically important in the Santa Clara River. Poor water quality conditions in the estuary are likely to occur in fall, but unlike the juveniles in Scott Creek (Hayes et al. 2011), juvenile steelhead in the Santa Clara River will not be able to access better conditions in upstream habitats due to the impassable, dry critical reach. Even if juveniles survive in the estuary through fall and winter, they may not be sufficiently prepared to survive ocean entry at the first estuary breach: Hayes et al. (2011) observed that many "re-smolting" individuals delayed ocean entry for 2–3 months after the onset of winter storms. Understanding the potential role of the estuary in migration and rearing is critical to developing appropriate management practices, particularly with respect to facilitated migration via trap and haul, which may not improve smolt–adult returns.

Although this data set provides valuable information on timing and potential migration cues, there remain significant unknowns regarding the natural history of steelhead in the region—namely, the migration speed and flow conditions necessary for passage. These parameters will dictate how quickly smolts can traverse the watershed as well as the duration and magnitude of flow that are necessary for successful downstream passage. Understanding movement patterns and potential travel times can clarify how much earlier migration initiates in tributary streams and whether particular flow or environmental conditions may modify downstream migration.

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ORCID

Michael T. Booth https://orcid.org/0000-0002-9842-085X

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SUPPORTING INFORMATION

Additional supplemental material may be found online in the Supporting Information section at the end of the article.