Increasing objectivity associated with anadromous fish redd identification using a discriminant function analysis

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Many fish species reproduce by creating nests (redds) in alluvial stream gravels, which can be used to track population trends. However, temporal and spatial overlap across multiple redd-building species can hinder redd species classification. This is further complicated when the corresponding adult is not present. Spawning surveys on the Lower American River (LAR) have been conducted since 2003 to document fall-run Chinook Salmon and California Central Valley (CCV) steelhead spawning. Other fish species on the LAR have overlapping reproduction timing, including Pacific Lamprey. Prior to 2016, a redd observed during field surveys that was not associated with a fish observation was assigned species identity based on seasonal timing and professional judgement. However, this method has potential to misidentify the species that built the redd due to overlap in spawning season and similarity in redd dimensions among LAR fish species. To decrease subjectivity associated with unoccupied redd identification, we used occupied redd data to build a discriminant function analysis (DFA), which predicts redd species identity based on field-measured parameters that vary across species including time of year, redd dimensions, and ambient conditions. We compared model accuracy across 6 years in which additional "fish on" observations were added annually to the discriminant function to test whether adding observational data improved model accuracy. We also applied the discriminant function to historical redd data in which species identification was made based on professional judgement to compare the two approaches. DFA accuracy improved with additional years of data, and in the iteration that included the most observational data it was highly accurate in identifying fall-run Chinook Salmon and CCV steelhead (96% and 97%, respectively). Accuracies for Pacific Lamprey were slightly lower (91%) than salmonids due to the relatively low number of "fish-on" redd observations for Pacific Lamprey. Comparisons between the DFA and historical identification based on professional opinion were generally similar, but with up to 19.6% disagreement in some years. Our study demonstrates that physical and temporal metrics can support more accurate species identification, and field data can be used to support more robust population estimates and inform future habitat restoration decisions.

KEYWORDS

Chinook Salmon, steelhead, Pacific Lamprey, spawning survey, redd identification, discriminant function analyses

Introduction

High spawning site fidelity is observed in many fish populations, allowing fish to place their offspring in the environmental conditions of parental or sibling generations, providing an important mechanism for metapopulation structure formation, as well as maintaining it through multiple generations (Wagner 1969; Stewart et al., 2004; Hayden et al., 2018). In many anadromous species, females construct nests or redds within specific alluvial stream reaches (Montgomery et al., 1996; McManamay et al., 2010; Zeug et al., 2013). Redds can be identified as substrate disturbances of various sizes and shapes, that can be quantified to track long-term population and habitat use trends (Burner 1951; Riebe et al., 2014; Mcmillan et al., 2015). Although there may be significant overlap in spawning habitat preferences among species, many select for specific environmental conditions including water depth, velocity and grain size, or segregate by river reach and timing to avoid density-dependent impacts (Mcmillan et al., 2015; Taylor et al., 2019). This habitat segregation maintains diversity by allowing for niche partitioning across populations or species, related to timing and physical capabilities of individuals within a particular population or species. Today, construction of large rim dams within the transition reaches of alluvial streams has been identified as a major contributor to population declines for many fish species, including salmonids, and many are now listed as endangered or threatened (Liermann et al., 2012; Desai et al., 2019). These structures are often complete barriers to migratory species, reducing available spawning habitat for many anadromous fishes and today many populations are relegated to marginal habitats further degraded by a myriad of cascading post dam processes (Barbarossa et al., 2020). To mitigate loss of spawning habitat quantity and quality below non-passable dams and rehabilitate listed populations, numerous restoration and enhancement activities have been implemented, including woody debris placement, floodplain rehabilitation, gravel augmentation and manipulation, and various flow prescriptions (Kondolf et al., 2006; Staentzel et al., 2020).

Population monitoring is essential to determine whether habitat restoration efforts or flow management actions are supporting fish species recovery in regulated rivers. Redd surveys are a primary means of tracking naturally spawning populations and utilization of restored spawning habitat. These surveys are relatively inexpensive and less invasive than capture-recapture monitoring studies (Zimmerman and Reeves 2000; Gallagher et al., 2010; Falke et al., 2013). In low-turbidity streams that are easily accessible, they have been shown to accurately reflect spawner numbers and provide a relatively robust estimate of the number of reproducing adults, or effective population size (Meffe 1986; Susac and Jacobs 2002; Merz et al., 2013). In-river spawning surveys are a key method used by resource managers to assess viable salmonid population (VSP) criteria (McElhany et al., 2000).

Although redd survey data may be used to track population recovery and response to management actions, redd survey accuracy may be impaired if species identification is incorrect (Gallagher and Gallagher 2005). This problem may be exacerbated when an identifiable fish is no longer associated with the redd, if the redd has been disturbed by subsequent spawners, or if multiple species co-occur that produce redds with similar architecture. The standard approach for most spawning surveys has been to assign a redd species identity primarily based upon professional judgement, which consisted of a surveyor determining the likely species identity based primarily on time of year (Adams et al., 2011; ODFW 2016). This method can be highly subjective if multiple species with similar redds are in the system, and ultimately may result in inaccurate abundance estimates, which is particularly problematic for salmonid populations with low or decreasing abundances, as it may hinder resource managers' ability to take corrective management actions until it is too late.

A discriminant function analysis (DFA) is a potentially powerful analytical tool to increase population estimate accuracy by reducing the subjectivity associated with unoccupied redd identification. A DFA identifies specific variables that differentiate two or more naturally occurring groups using a dataset with confirmed species identity (Brown and Wicker 2000), tests the strength of the model by predicting species identity for a subset of the "known" data, then applies the model to predict the identity of individuals within a dataset for which species identity is unknown. The technique has been applied to differentiate fish, bird, and insect populations or life stages based on morphometric measurements (Austin et al., 1999; White and Ruttenberg 2007; Herring et al., 2010; Barahoei et al., 2011). Similar analytical approaches such as logistical and stepwise regression have been used to identify salmon redds by species in a California coastal stream (Gallagher and Gallagher 2005) and an Alaskan river (Fukushima and Smoker 1998) and life history forms within a species for *Oncorhyncus mykiss* populations in the Deschutes River in Oregon (Zimmerman and Reeves 2000), with varying success.

In this study, we developed a predictive DFA model to decrease subjectivity associated with unoccupied redd species identification during field surveys on a highly regulated California Central Valley (CCV) stream that supports several fish species of concern. We leveraged a long-term redd monitoring data set to build the model. Model variables included timing and measured redd dimensions taken from fall-run Chinook Salmon *Oncorhynchus tschawytscha*, CCV steelhead *O. mykiss* and Pacific Lamprey *Entosphenus tridentatus* redds between 2002 and 2020. We assessed whether model accuracy improved over time as additional occupied redd observations were incorporated into the model. Finally, we applied the model to historical redd data in which redds were identified using expert opinion to directly compare the two methods. The DFA modeling approach can enhance the
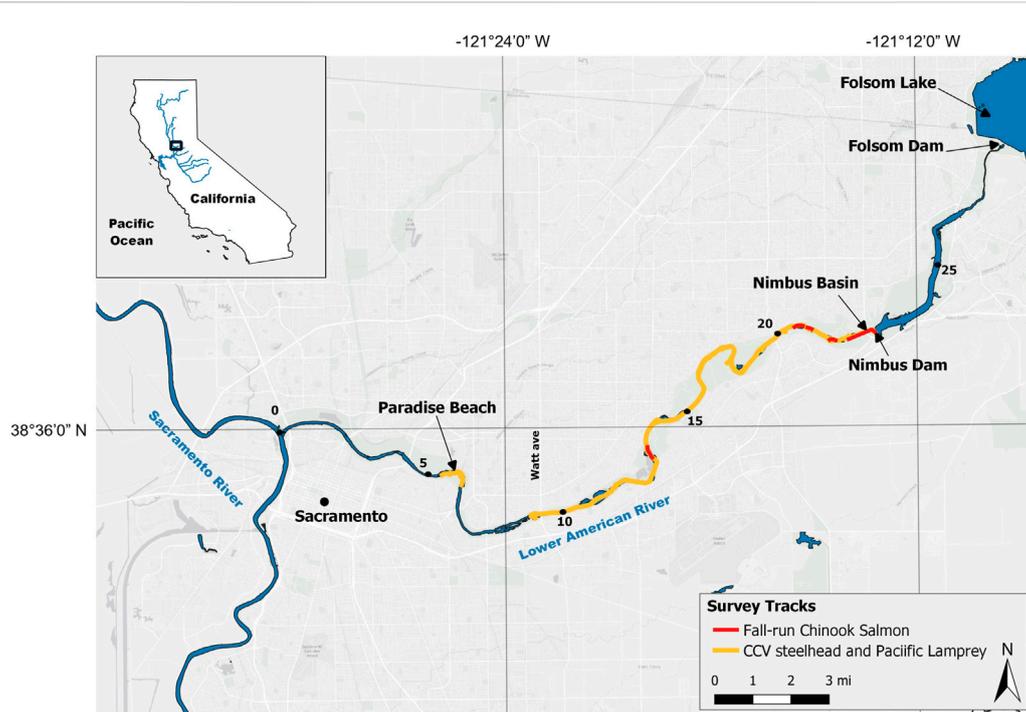
FIGURE 1
Map of the Lower American River in California. Yellow lines represent areas where CCV steelhead and Pacific Lamprey spawning surveys were conducted, and red lines represent areas where fall-run Chinook Salmon spawning surveys were conducted. River miles are represented by black dots with the confluence of the Lower American River and Sacramento River beginning at river mile 0.

integrity and accuracy of annual population estimates by providing a more objective species identification across years and monitoring crews, which ultimately will help resource managers assess population recovery and response to management actions. This study also demonstrates the utility of iteratively updating and refining models as additional data becomes available and provides a template that can be applied to similar datasets in other systems.

Methods

Watershed description

Redd surveys were performed on the American River, a mixed rain and snow-fed system (Yarnell et al., 2010; Lane et al., 2018) that drains roughly 1,900 square miles of the Western Sierra Nevada Mountains (Figure 1). The watershed starts at its headwater, 9,983 feet above mean sea level (AMSL) in El Dorado County, CA and enters the Sacramento River 119 miles downstream near the city of Sacramento. Similar to other CCV, the American River has been highly modified from flow regulation and diversion, water pollution, gold and gravel mining, hydropower and floodplain development, and the

introduction of numerous non-native aquatic species (Beakes et al., 2014). Just downstream of the American River north and south fork confluences, Folsom Dam was completed in 1955, blocking upstream habitat for migratory fishes such as anadromous salmonids. The United States Bureau of Reclamation (Reclamation) currently operates the dam for flood control, water storage, and hydropower generation. Upstream fish migration is blocked at river mile (RM) 23 by Nimbus Dam, a regulating facility for Folsom hydropower operations. Below Nimbus Dam, the lower American River (LAR) flows through a parkway surrounded by urban development and is a major recreational area for the Sacramento region (Williams 2001). The LAR is designated as a recreational river in the state and federal wild and scenic river systems and supports spawning and rearing habitat for anadromous fishes, including CCV steelhead (the anadromous form of Rainbow Trout), fall-run Chinook Salmon, Pacific Lamprey, and other native and non-native fishes (Yoshiyama et al., 2001; Hannon 2013 and references therein). On the LAR, flow regulation and the resulting combination of channel incision and coarsening of bed material have lowered streambed elevations, altered depths and velocities over once-productive spawning beds and reduced the magnitude and frequency of floodplain inundation important for juvenile rearing (James

1997; Sellheim et al., 2016). Channel degradation has, in turn, decreased overall habitat heterogeneity, hyporheic water quality, and macroinvertebrate production (Cramer Fish Sciences, unpublished data). Regulated flow and reservoir storage both influence habitat and water quality and, in turn, growth and health of rearing salmonids (Merz and Vanicek 1996).

Anadromous fish species

Habitat degradation due to the factors described above has adversely impacted several anadromous fish species that occur in the LAR. In California, the presence of impassable dams block an estimated 80% of historical habitat for CCV steelhead distinct population segment (DPS) and all historical spawning habitat for 38% of historical populations (Lindley et al., 2006). As a result, CCV steelhead populations are perilously low and federally listed as threatened (79 FR 20802) under the Endangered Species Act (ESA). CCV steelhead are not listed under the California Endangered Species Act (CESA) but hold a state rank of S2S3 (imperiled/vulnerable). In California, imperiled S2 rank states that a species is at high risk of extirpation due to restricted range, few populations or occurrences, steep declines, severe threats or other factors (California Natural Diversity Database, 2022). Both resident rainbow trout and anadromous steelhead occur in the LAR, and both life history strategies are included in the CCV steelhead DPS. Fall-run Chinook Salmon and Pacific Lamprey also occur on the LAR, are species of special concern for state and federal resource managers, and produce redds during similar time periods that are superficially similar in architecture to CCV steelhead (Gallagher et al., 2007). Therefore, there is potential for unoccupied redd species misidentification.

The three anadromous fish species present in the LAR all build redds in which they lay eggs, but they are differentiated to some extent in terms of spawning timing. In California's Mediterranean climate, fall-run Chinook Salmon tend to access spawning grounds at rainy season onset, which can vary inter-annually on the order of weeks or even months. However, spawning generally peaks during the months of November and December. Eggs incubate in the gravel and juveniles emerge and out-migrate the following spring. In contrast, CCV steelhead spawn in the winter and early spring, and juveniles may either out-migrate to the ocean or continue to rear in the river for one or more years. There is a less distinct environmental cue that initiates spawning for CCV steelhead and redds have been documented as early as late December (McEwan 2001; Hannon and Deason 2008; Chase 2010). Both salmonid species use hydraulic lift created by tail fanning to mobilize sediments from the redd site. However, redd size is known to vary across salmonids, primarily in relation to body size (Gallagher and Gallagher 2005; Riebe et al., 2014). Fall-run Chinook Salmon are larger, generally resulting in larger redds compared to later spawning CCV steelhead. In contrast, Pacific Lamprey spawning

peaks slightly later than CCV steelhead and lamprey may remain in the river for several years as ammocoetes prior to migrating to the ocean and then returning to the river to spawn. Adult Pacific Lamprey move substrate particles primarily by attaching their mouths to rocks and moving individual pieces. Pacific Lamprey also have smaller redds due to smaller body size.

Field methods

Fall-run Chinook Salmon spawning surveys were conducted from 2011 to 2015 and generally occurred every other week from late October to late December, which is when fall-run Chinook Salmon typically spawn in the Central Valley (Williams 2001). These surveys were targeted to assess habitat use following habitat enhancement and were conducted only in gravel augmentation sites at Nimbus Basin, Sailor Bar, Upper Sunrise Side Channel, and Riverbend Park (Figure 1; total coverage varied between 5–8 total rkm, depending on survey year). CCV steelhead spawning surveys were conducted from 2003–2021, with the exception of 2006 and 2008 when surveys were not successful due to high turbidity. Surveys occurred between early January and mid-April and encompassed the entire spawning reach, from Nimbus Basin downstream to Paradise Beach (29 rkm). Pacific Lamprey redds were not explicitly targeted by surveys but were instead observed and measured opportunistically during CCV steelhead spawning surveys. Occasionally, fall-run Chinook Salmon were recorded during CCV steelhead surveys and *vice versa*.

Spawning surveys were conducted either on foot or *via* rafts/motorized boat by teams of two to four surveying the river from bank to bank, including side channels, visually searching for redds. Surveyors wore polarized sunglasses to improve their ability to see below the water surface. When a redd was observed, a global positioning system (GPS) location and physical measurements were recorded on a Trimble Geoexplorer GPS unit. Redd measurements were based on those used in California coastal spawning surveys (Gallagher 2002). Physical measurements were only taken on redds whose dimensions were not obscured during digging activity by other spawners. Egg pocket length and width were measured along the longest and widest axes (Figure 2). Tailspill length was measured from the back of the pocket to the end of the tailspill. Tailspill width was measured twice, at one-third and two-thirds of total tailspill length, and average width was calculated from these two values. Pocket depth was measured at the redd nose and directly over the egg pocket, and ambient depth was measured upstream from the egg pocket. Depth was recorded from a top-setting velocity rod and depth-averaged velocity was approximated by assuming a logarithmic velocity profile and taking a measurement at 60% of the depth with an

FIGURE 2
Diagram showing measurements taken within a redd.
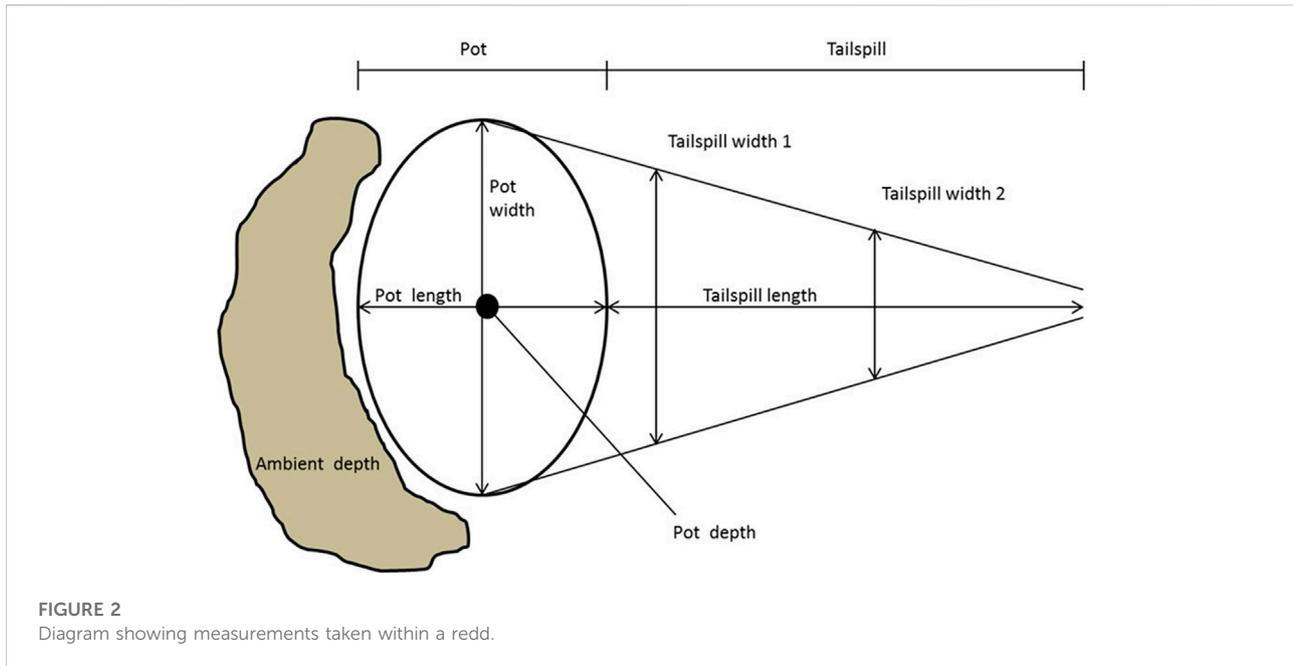
electromagnetic Hach FH 950 Flow Meter (Hach manufacturing, Loveland, CO). For depths greater than 0.6 meter (m), two velocity measurements were recorded at 20% and 80% of total depth, and these values were averaged (Hynes 1970). Velocity measurements were taken over a 20-s average and recorded to the nearest 0.01 meter per second (m/s). When a fish was observed associated with a redd, it was identified to species and sex if possible and its length estimated. If visible, surveyors also recorded the presence or absence of an adipose fin. The Nimbus Hatchery has been in operation since 1958 and produces both Chinook Salmon and CCV steelhead. All CCV steelhead produced at the hatchery have their adipose fin clipped to compare hatchery-versus wild-spawned returning adults. Since 2007, 25% of Chinook Salmon from the Nimbus Hatchery have also been clipped as juveniles prior to release.

Spatial data were differentially corrected to increase GPS point accuracy using Trimble Pathfinder Office software (Trimble Navigation, Ltd., Sunnyvale, CA). When redds from two successive surveys were recorded by GPS unit within 5 m of each other, the data were examined in ArcGIS to determine whether these were likely to be the same redd. If both redds were identified as "new, still clear," it was assumed these dimensions represented a single redd completed over the two survey periods. Therefore, only the second redd and its associated measurements were used in the composite shapefile for the year. For the 2020 and 2021 surveys, this post-processing step resulted in removal of one redd from the raw dataset.

Discriminant function analysis

A DFA model predicts a categorical variable (X) based on known responses (Y). We used a DFA to predict redds to species based on observed values of several continuous variables. Data used to build the predictive model consisted of a sample of observations with known group membership (i.e., fish associated with a redd was identified to species) and several continuous variables that define the physical characteristics or timing of a redd. Model variables were transformed to meet the DFA requirements (i.e., normally distributed data with equal variance). Continuous variables and transformations used in this model included redd depth (no transformation), pot length [natural log(ln)], pot width (ln), pot depth (no transformation), tailspill length (no transformation), river velocity (no transformation), and observation day (no transformation). Observation day was assigned based on the seasonal timing of redd observations, starting at the earliest date on which a redd was recorded and ending on the last recorded date (i.e., October 23–May 2 = 1–190). This is similar to the concept of Julian Day, but reflects the fact that observations recorded at the end of the year (i.e., late December) are more similar to those occurring early in the beginning of the year (i.e., early January), which is not possible if Julian days are used.

DFA analysis was run iteratively from 2016–2021; during each year, any additional "fish on" observations were added each year to improve the model. Analyses were completed using linear DFA in R (R Program Core Team, 2020) using the lda() function in the MASS package (Venables and Ripley 2002). Eigenvalues

TABLE 1 Summary of redds observed by year and species, and unoccupied redds. The data range when each year of surveys was conducted and the average and range of flows during that timeframe is also provided. Insufficient data were available for 2006 and no surveys were conducted in 2008.

Survey season year	Date range(s)	Fall-run Chinook Salmon	Pacific Lamprey	CCV steelhead	Unoccupied redds	Total redds	Flow range (cms)	Average flow (cms)
2003	1 January–4 April	0	14	43	145	202	44.5–156.9	82.4
2004	17 December–17 June	0	0	40	101	141	46.4–224.6	83.7
2005	20 December–3 May	0	3	23	85	111	39.4–430.4	111.2
2007	12 December–2 April	0	0	12	15	27	48.4–71.1	52.5
2009	11 February–17 March	0	0	6	1	7	21.0–44.5	26.3
2010	15 December–20 April	0	0	21	31	52	31.4–54.7	42.0
2011	28 December–15 April	0	0	13	30	43	69.4–744.7	225.7
2012	25 October–14 April	50	0	26	93	169	27.4–95.4	45.2
2013	23 October–3 April	63	0	13	135	211	47.6–281.2	91.5
2014	28 October–3 April	5	0	9	130	144	14.0–38.8	24.8
2015	30 October–3 April	20	2	7	67	96	15.7–30.3	25.0
2016	3 November–14 April	31	1	7	59	98	13.6–572.0	87.1
2017	4 January–19 April	0	0	0	14	14	102.2–2,333.3	549.9
2018	10 January–14 May	0	11	11	50	72	42.2–699.4	125.2
2019	8 January–29 April	2	10	17	51	80	49.0–682.4	227.2
2020	8 January–28 April	2	5	13	42	62	34.0–68.8	51.1
2021	1 January–6 April	6	0	7	55	68	27.3–103.6	38.1
Total redds		179	46	268	1,104	1,597	—	—

(trace), which describes the proportion of between class variance explained by linear discriminants (LD1 and LD2), was also estimated using lda (). Cohen's Kappa, which measures percent agreement of species identity, was estimated using the Cohen. kappa() function in the psych package (Revelle 2016). A scatter plot was generated to visualize inter-species differences and variation in the linear discriminants (LD1 and LD2).

Comparisons of redd metrics across species were made using an Analysis of Variance (ANOVA) and pairwise comparisons between species were made using a Tukey *post-hoc* test, using a significance threshold of $p = 0.01$. All analyses were run using the R package *car* (Fox and Weisberg 2019).

Historical survey species identification comparisons

The 2021 iteration of the DFA model was applied to historical data collected between 2003–2015 in which no fish were observed but redd measurements were recorded and species identification was assigned based on professional opinion. To determine the similarity in outcome between the two approaches, professional opinion identification was compared to the model's predicted species identification and proportion agreement in identification between the methods was calculated for each survey season (Oct–May) by summing the number of disagreements for a given year and dividing that number by the total redds observed that year.

Results

A total of 1,597 redds were documented in the LAR between 2003 and 2021 (Table 1). Of the redds observed, 1,104 were unoccupied, 179 were occupied by fall-run Chinook Salmon, 46 by Pacific Lamprey, and 268 by CCV steelhead. Fall-run Chinook Salmon spawning surveys (2011–2016) were conducted from late October through late December; CCV steelhead spawning surveys (2003–2021) were conducted from early January through April. During the period when the surveys were conducted, flows ranged from a low of 13.6 cubic meters per second (cms) in 2015–2016 to a high of 2,333.3 cms in 2017 (Table 1).

Discriminant function analysis

The DFA model included the following predictors: Seasonal Timing, Redd Depth, Velocity, Pot Length, Pot Width, Pot Depth, and Tailspill Length. Pot Length and Pot Width were
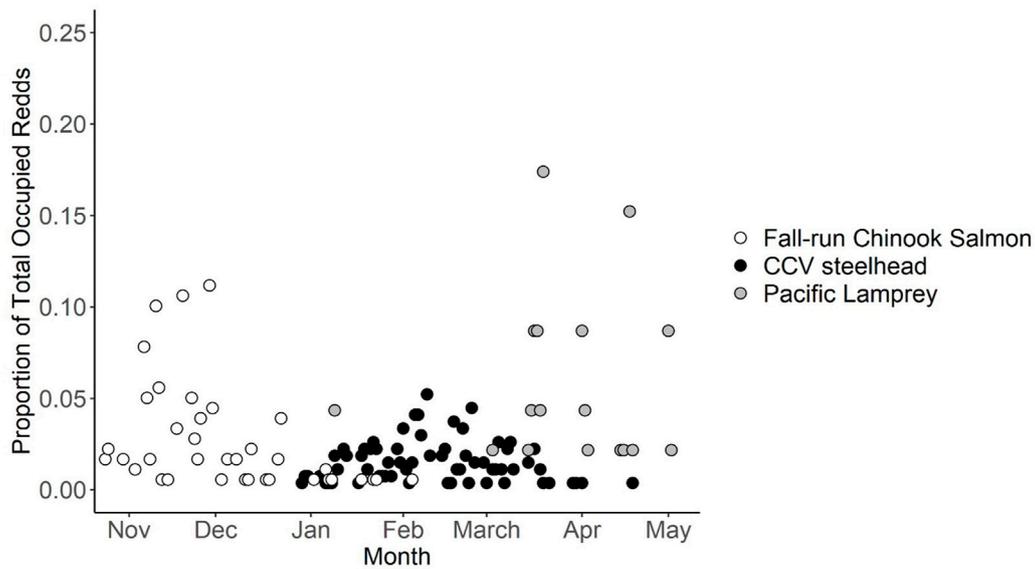
FIGURE 3
Temporal distribution of proportion of redds observed occupied by either Fall-run Chinook Salmon, CCV steelhead and Pacific Lamprey between 2003 and 2021.

natural log transformed to meet model assumptions. In 2016 and 2017, the model only included data from CCV steelhead and fall-run Chinook Salmon; in 2018, Pacific Lamprey data were added to the model after it was recognized that their spawning time overlapped substantially with CCV steelhead. Redds were excluded from analysis if they lacked key variables that were necessary to build the model. The final (2021) iteration of the discriminant function was built using 183 fall-run Chinook Salmon redds, 268 CCV steelhead redds, and 46 Pacific Lamprey redds with positively identified fish observations, collected between 2003 and 2021. Redds observed occupied by fall-run Chinook Salmon were recorded between 23 October and 4 February, with the peak number of redds recorded on 23 November (SD = 18 days). Redds observed by occupied by CCV steelhead were observed between 29 December and 19 April, with a peak number of redds observed on 10 February (SD = 20 days). Redds observed occupied by Pacific Lamprey were recorded between 9 January and 18 May, with a peak number of redds observed on 28 March (SD = 24 days) (Figure 3). Differences in seasonal spawning timing were significantly different across all species (all Tukey $p <$ 0.001).

The other factors included in the DFA model are summarized across the three species in Figure 4. There was variation across species in most of the factors, except for Pot Depth which did not differ significantly in any pairwise comparisons (Tukey *post-hoc* test, all $p >$ 0.01). Fall-run Chinook Salmon spawned in shallower depths compared to the other two species, Pacific Lamprey differed from the

salmonid species in velocity and pot dimensions, and all three species had distinct average tailspill lengths.

The eigenvalue (trace) for the final (2021) iteration of the model was 0.95 for LD1 and 0.05 for LD2. This indicates that 95% of the between-group variance exists along the first discriminant axis, which is heavily weighted by velocity (Table 2). Overall, model accuracy was 95.7% and the Cohen's Kappa was predicted as 0.94, indicating high model agreement for species categorization.

Velocity was the dominant model covariate and was weighted heavily in both LD1 and LD2 (0.456 and −1.167, respectively). Seasonal timing was the second highest coefficient in LD1 (0.049) but was low in LD2 (0.005). Pot length was the highest coefficient (1.744) in LD2 but was relatively low in LD1 (−0.264). These three factors strongly differentiated Pacific Lamprey from the two salmonid species (Table 2). The other variable coefficients were small for both LD1 and LD2, indicating that they had a relatively small impact on species prediction (Table 2). A scatter plot visualizing LD1 and LD2 variation across species of redd metrics is provided in Figure 5.

Accuracy of the DFA model in predicting redd species using historical data from known redd identity between 2016–2021 is provided. Overall, the model had over 96% accuracy for both salmonid species for all 6 years in which it was applied. Fall-run Chinook Salmon accuracy decreased slightly from 99% accuracy in 2016 through 2019 to 97% accuracy in 2020 and 96% accuracy in 2021 when additional later spawning fall-run Chinook Salmon observations were
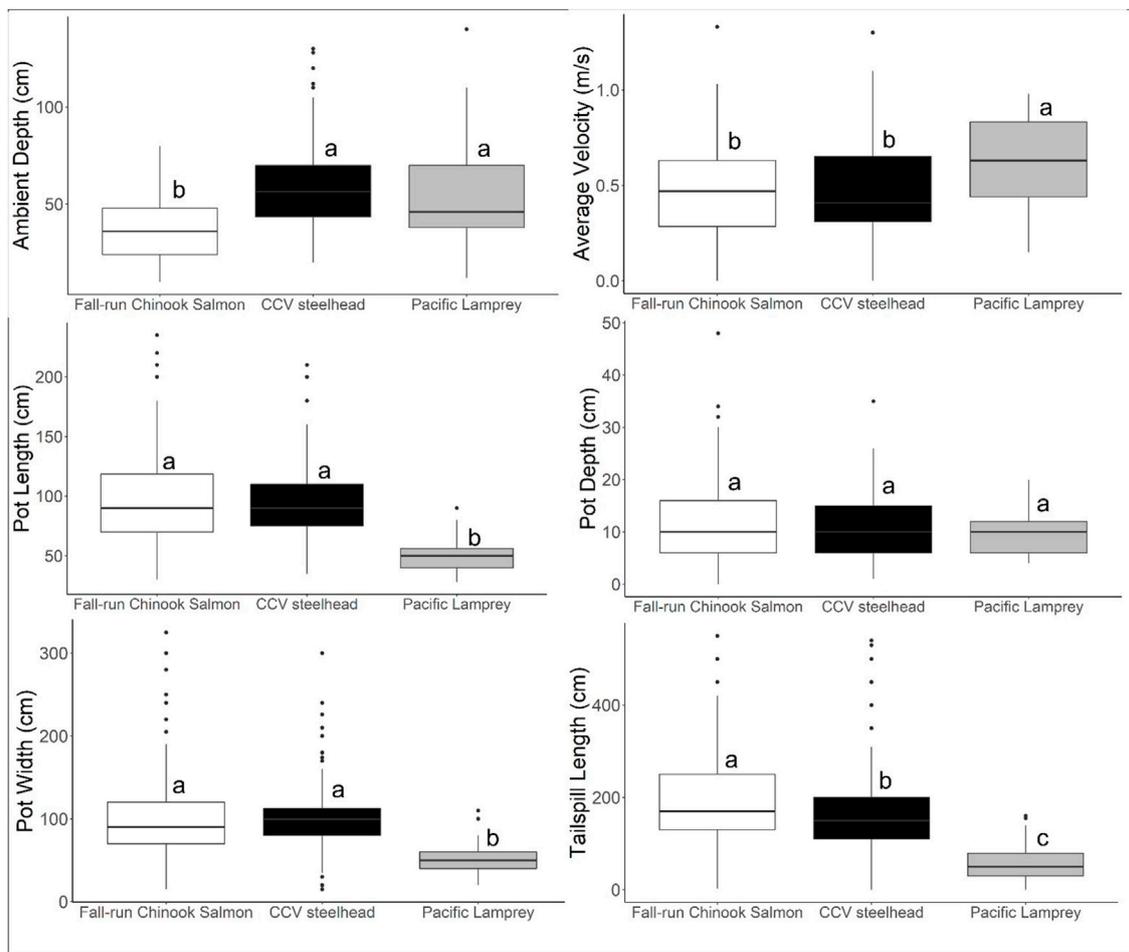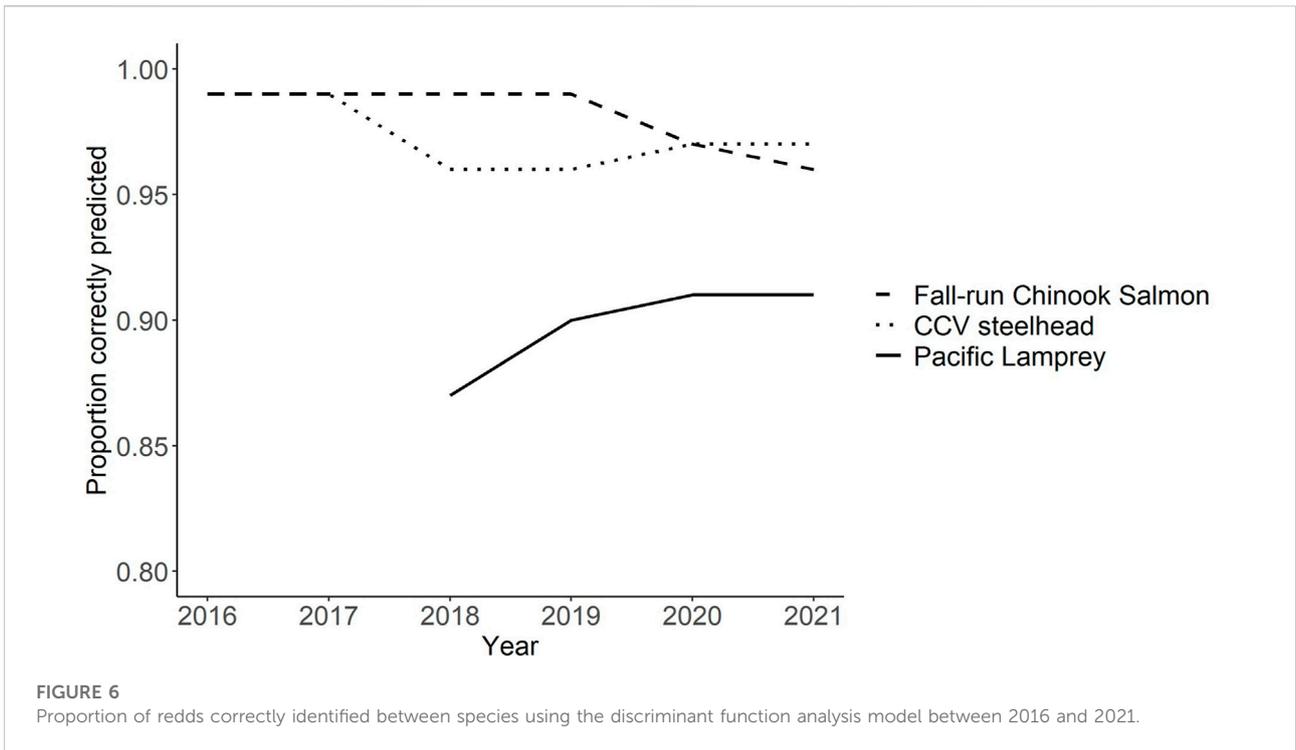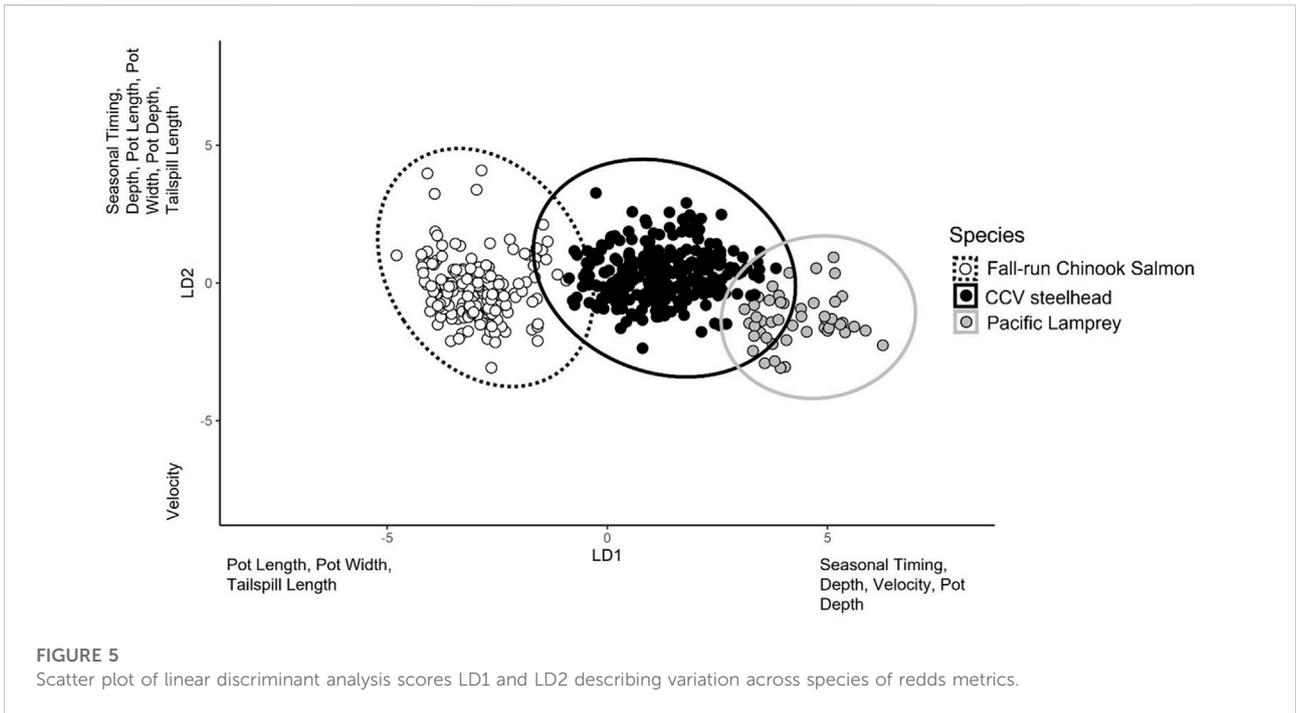
FIGURE 4
Comparison across species of redd metrics used for developing DFA. Within each redd metric, box plots with different letters indicate significant pairwise differences using a Tukey *post-hoc* test, using a significance threshold of *p* = 0.01.

TABLE 2 Coefficients from the 2021 DFA model, which show the loading of each covariate on the discriminants.

	LD1	LD2
Seasonal Timing	0.049	0.0047
Depth	0.012	0.017
Velocity	0.456	−1.167
Pot Length	−0.264	1.74
Pot Width	−0.26	0.596
Pot Depth	0.009	0.003
Tailspill Length	−0.002	0.003

added to the model. The model had relatively high CCV steelhead accuracy throughout the 5 years, ranging from 96%–99% (Figure 6).

In 2021, the model correctly predicted 171 of the 179 (95.5%) total fall-run Chinook Salmon redds; eight incorrect assignments were predicted to be CCV steelhead (Table 3). Forty-two of the 46 Pacific Lamprey were correctly predicted (91.3%), and the remaining four were predicted to be CCV steelhead. A total of 259 of the 268 CCV steelhead redds were correctly assigned (96.6%). Of the nine CCV steelhead redds that were incorrectly assigned, two of these were predicted to be fall-run Chinook Salmon and seven were predicted to be Pacific Lamprey redds. Most incorrect assignments across species were caused by fish in the population with atypical spawning timing or redd dimensions. For example, fall-run Chinook Salmon that were predicted to be CCV steelhead had an average spawning date of 13 January, when the overall population had a peak number of redds observed on 23 November. Pacific Lamprey redds that were predicted to be CCV steelhead had a spawning date of 9 January

FIGURE 5
Scatter plot of linear discriminant analysis scores LD1 and LD2 describing variation across species of redds metrics.

FIGURE 6
Proportion of redds correctly identified between species using the discriminant function analysis model between 2016 and 2021.

(population peak number redds observed on 28 March) or had a tailspill lengsh and/or pot widths greater than 100 cm (mean = 56.8 cm and 52.7 cm, respectively). Several CCV steelhead that were incorrectly predicted to be Pacific Lamprey had pot lengths between 50 cm and 60 cm (mean = 95 cm).

TABLE 3 Predicted (column) and actual (row) species designations in discriminant function analysis. "Total" column indicates predicted number of redds, and "Total" row indicates actual number of redds for each species.

	Predicted fall-run Chinook Salmon	Predicted Pacific Lamprey	Predicted CCV steelhead	Predicted total
Actual fall-run Chinook Salmon	171	0	8	179
Actual Pacific lamprey	0	42	4	46
Actual CCV steelhead	2	7	259	268
Actual total	173	49	271	493

TABLE 4 Comparison between redd identification based on professional opinion versus the discriminant function analysis.

		Fall-run Chinook Salmon		Pacific Lamprey		CCV steelhead	
Survey Season Year	Total # Redds	Professional opinion	DFA	Professional opinion	DFA	Professional opinion	DFA
2003	145	0	0	2	13	143	132
2004	101	0	0	4	21	97	80
2005	85	1	0	2	3	82	82
2007	15	0	0	0	0	15	15
2009	1	0	0	0	0	1	1
2010	31	0	1	0	4	31	27
2011	30	0	0	0	1	30	29
2012	93	83	83	0	3	11	7
2013	135	73	73	0	0	62	62
2014	130	37	35	0	2	93	93
2015	67	67	67	0	0	0	0
Totals	833	261	259	8	47	565	528

Historical surveys species identification comparisons

Prior to the development of the DFA model in 2016 to predict redd species identity, 833 unoccupied redds were observed and identified using professional opinion between 2003 and 2015. To compare the species identifications using professional opinion with that predicted by the DFA model, we applied the 2021 iteration of the model to this dataset (Table 4).

During the first few years in which redd surveys were conducted, a relatively large proportion of redds visually identified as CCV steelhead were categorized by the DFA as Pacific Lamprey redds (7.7% in 2003, 17.5% in 2004; Figure 7). Disagreements between identifications based on professional opinion and the DFA prediction were lower in future years, but there were at least a few disagreements between the two methods in 2005, 2010, 2011, 2012, and 2014, primarily with redds identified visually as CCV steelhead being identified as either fall-run Chinook Salmon or Pacific Lamprey by the model.
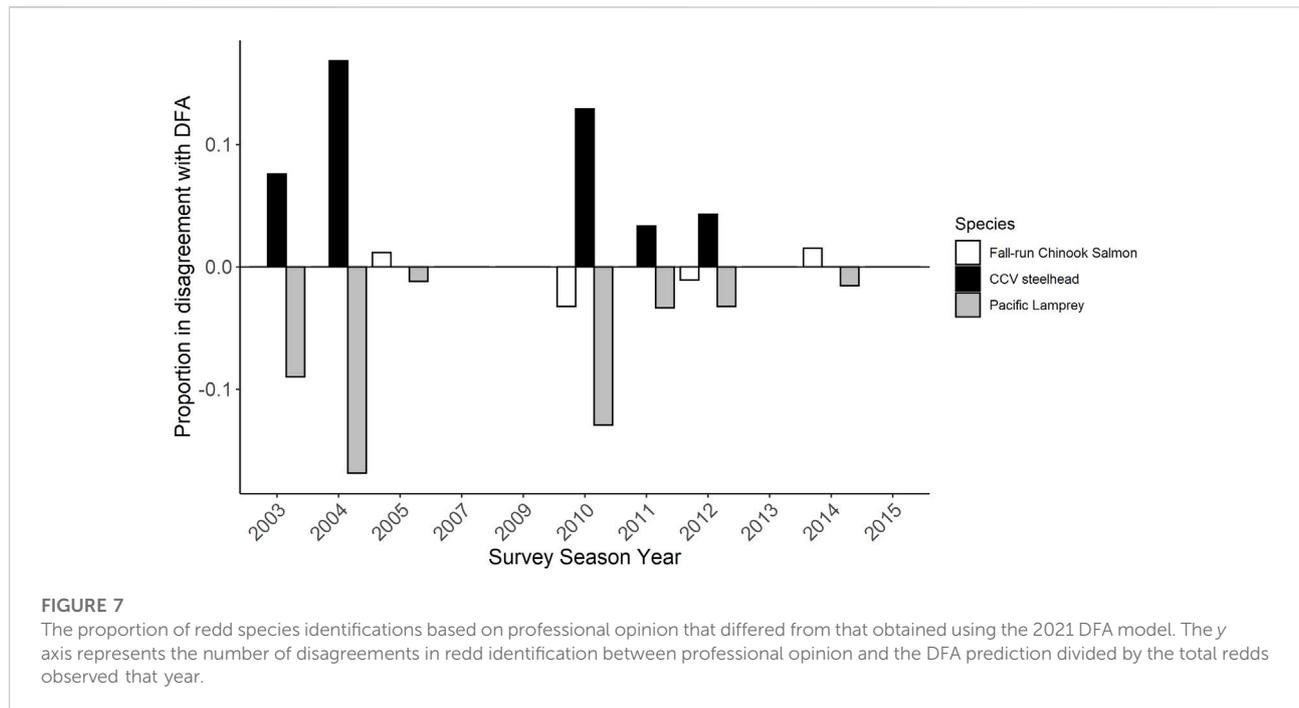
Another application of the DFA is retro-actively identifying historically unidentified redds. In the LAR dataset, this approach allowed a predictive identification of a total of five Pacific Lamprey redds in 2004, one Pacific Lamprey and two CCV steelhead redds in 2005, and seven CCV steelhead redds in 2015 that were previously excluded from total redd counts and any subsequent annual population estimates derived from the data.

Discussion

Resource partitioning in degraded systems

Habitat is a major dimension of resource partitioning in stream fishes and may arise from each species' genetically determined tendency to select different microhabitats independent of other species (Schoener 1974). Quantifying differential habitat selection (also known as niche partitioning) is a common approach used by ecologists to understand ecological segregation between closely-related but spatially overlapping species (e.g., Morris 2003; Nicholls and

FIGURE 7
The proportion of redd species identifications based on professional opinion that differed from that obtained using the 2021 DFA model. The *y* axis represents the number of disagreements in redd identification between professional opinion and the DFA prediction divided by the total redds observed that year.

Racey 2006; Pita et al., 2011), and there is growing evidence that habitat selection is a scale-dependent process (Mayor et al., 2009). However, in a dynamic or highly degraded environment a high degree of habitat specialization may not be a successful ecological trait for species persistence, and individuals within a population may demonstrate plastic and opportunistic habitat use (Schwemmer et al., 2008; Moss et al., 2016). This flexibility can make it difficult to quantify habitat preference by guild, especially when individuals are not physically present within an observed territory. However, our results demonstrate that if relevant habitat metrics are incorporated, a predictive model can be a powerful tool to improve the objectivity and accuracy of redd identification of three co-occurring anadromous fish species. This has implications for optimizing restoration practices and water management decisions in a highly impacted system with multiple species of concern.

Niche differentiation across species in the LAR

While all three LAR native anadromous fish species tend to spawn in gravel rich habitats predominantly associated with pool tail-outs and low gradient riffles, we found strong evidence for niche differentiation within these habitat patches which may result from species-specific distinctions in spawning timing, body size, and how each species perceives and uses preferred habitats

including redd construction mechanisms. Fall-run Chinook Salmon timing coincided with the onset of the rainy season (November–December, while CCV steelhead spawned peak spawning occurred in February-March and Pacific Lamprey spawned primarily in March and April. Redd size varied across species, associated with body size and method of redd construction, with Chinook Salmon producing the largest redds and Pacific Lamprey producing the smallest redds. These inter-species distinctions resulted in the DFA model being driven by three variables: water velocity, seasonal timing, and redd (pot) size.

Seasonal timing was historically the primary factor used for professional opinion identification between fall-run Chinook Salmon, CCV steelhead and Pacific Lamprey. However, there is temporal overlap during the spawning period for the two salmonid species and lamprey, particularly in heavily managed systems where flow is not necessarily correlated with precipitation or during years with delayed rainy season initiation. A trend towards later fall-run Chinook Salmon spawning timing in particular has been observed in recent years on the LAR, possibly due to a combination of prolonged drought, stressful water temperatures in the early fall, and flow and hatchery management practices (CDFW unpublished data; Quinn et al., 2002; Austin et al., 2021). Flow management practices on the LAR include operating Folsom and Nimbus facilities to avoid high flows during fall run Chinook Salmon spawning. This operational decision is meant to prevent spawners from building redds at higher flows which could

cause future redd dewatering if low winter precipitation results in flow reductions to conserve reservoir storage. This may also explain the shallower spawning depths observed in the LAR for fall-run Chinook Salmon compared to CCV steelhead and Pacific Lamprey. Despite the temporal overlap, because the three species differed in hydraulic preferences and redd architecture, model results enabled identification of historically unidentified or potentially mis-identified redds, enhancing data quality and subsequent population estimates.

Despite the overall tendency for habitat segregation, fall-run Chinook Salmon, CCV steelhead and Pacific Lamprey showed considerable overlap in habitat preferences within the highly managed and marginalized habitat of the LAR. For example, pot depth was similar across all three species, ambient depth was similar for CCV steelhead and Pacific Lamprey, and pot width and length were similar for fall-run Chinook Salmon and CCV steelhead. There are certain essential habitat characteristics for substrate spawners, including material that can be mobilized but not scour and cool, oxygenated water carried to and metabolic wastes removed from incubating embryos (Merz et al., 2019; Bilski et al., 2022). While spawning habitat restoration practices such as gravel augmentation can provide core habitat for a range of species provided that water quality is suitable, inter-specific differences must also be taken into account when selecting augmentation features and locations. These differences are also important for developing species-specific habitat suitability predictions for restoration designs that integrate depth and velocity conditions under varying flows (Wheaton et al., 2004). The DFA model presented here and the data used to generate the model can help restoration practitioners identify key habitat requirements that may support multiple target species. However, future work is needed and additional metrics such as substrate size and distance from impassable dam could be incorporated into future model iterations.

The ability to incorporate physical and temporal variables to predict species spawning sites from a guild of three species with a range of management implications offers a powerful management tool and highlights the value of data collection quality, even on perceived, less valuable species. Fall-run Chinook Salmon have the highest commercial economic value, CCV steelhead is a highly-prized sport fish and focus of federal protection and are often competitive for limited LAR water resources (McEwan, 2001; Williams 2001). In contrast, Pacific Lamprey are harvested primarily for bait (sturgeon fishing), receiving relatively little management attention, even though they are an important ecological component within the CCV (Close et al., 2002). Given the temporal and spatial overlap in spawning with these other species. Limiting data collection to salmonid species reduces accuracy of CCV steelhead redd identification and, subsequently, population estimates.

Iterative model refinement

Our results also demonstrate the utility of iteratively updating and refining models as additional data become available. Comparison with data from occupied redds demonstrated that the model had a high degree of accuracy and model robustness increased across several iterative incorporations of new data, with >96% accuracy for the two salmonids and >91% for Pacific Lamprey. This DFA modeling approach has the potential to enhance survey integrity and accuracy of where species identification for redd surveys or other surveys that involve challenging species identification is based on biometrics or physical habitat metrics for which a reference dataset is available. With subsequent years of data collection, particularly on Pacific Lamprey redds, the model accuracy in predicting species identity is expected to further increase. Increased objectivity in species identification across survey years and geographical regions will ultimately support more informed management decisions.

Limitations and future research

Substrate size is also known to be an important factor in female spawning site selection and tends to scale with females body size, with female salmonids typically spawning in gravel substrates with a median diameter up to about 10% of their body length (1.3–2.6 cm) (Bjornn and Reiser 1991; Kondolf and Wolman 1993). Zeug et al. (2013) found that grain size had a strong influence on both fall-run Chinook Salmon and CCV steelhead site selection as well as the size and shape of completed redds. While average substrate size was often recorded in field measurements, ultimately these data could not be incorporated into our model because we identified dataset irregularities indicating this metric was not standardized across surveys. No clear protocol was available for collecting substrate size information during redd surveys as it was for the other redd metrics, limiting the data's utility. Because of its clear relationship with female site selection and body size, incorporating additional field metrics to record substrate size information, such as standardized photographs, would allow substrate to be incorporated into future iterations of this model. Obtaining high quality data for this habitat metric, in particular, has strong implications for habitat restoration in a sediment-starved river, where the stream bed tends to armor over time and the use of overly coarse sediment for gravel augmentation may exclude smaller-bodied species such as CCV steelhead and Pacific Lamprey (Zeug et al., 2013). Standardized sediment data could inform design of gravel

augmentation actions intended to target CCV steelhead populations by providing a distribution of substrate size preferences for this species.

Management implications

Inaccurate species identification can impact subsequent population estimates, management decisions, and restoration approaches. CCV Steelhead survey data has been used to develop population estimates for this federally threatened species on the LAR for the past two decades. During this time, annual redd counts have ranged from 12–314, with subsequent population estimates between 45–504 reproducing adults. With such a low number of individuals in the system, even a few misidentified redds could significantly reduce the accuracy of the resulting population estimate. In addition to informing resource managers about annual salmon population size, physical redd measurements from both CCV steelhead and fall-run Chinook Salmon on the LAR has been used to inform restoration designs and determine site utilization on recent gravel augmentation projects (Zeug et al., 2013; Merz et al., 2019; cbec, personal communication). If redd species identification is incorrect, this could lead to a misrepresentation of species' spatial distribution or preferred physical parameters (e.g., substrate size, depth, and velocity) for target species, subsequently reducing restoration effectiveness. The modeling approach described here can increase data accuracy and objectivity, providing higher quality information to support decision making.

On the American River, as in all other major CCV rivers, most historic salmonid and presumably Pacific Lamprey spawning habitat is impounded behind impassible dams, greatly reducing channel types and gradients available to these three species (Yoshiyama et al., 1998). In addition, the region has experienced prolonged periods of drought in recent years that have resulted in low streamflow and stressful temperature conditions, particularly during the early fall. As mentioned above, this has resulted in a trend towards later spawning by fall-run Chinook Salmon and subsequently greater temporal niche overlap between this species and CCV steelhead. Gabor et al. (2001) have reported that mammals have documented higher inter-specific overlap during harsh environmental conditions, such as droughts. The degraded condition of the LAR and other rivers throughout the CCV may force fish species to utilize habitats outside their optimal range, which could obscure our ability to detect niche differentiation across species (Gaines et al., 2000; Kozlowski et al., 2012; Huber and Carlson 2020). However, even in the highly impacted LAR and with a relatively limited dataset, it was possible to successfully classify redds to species using relevant habitat metrics.

Conclusion

By detecting niche segregation between species, modeling like that described here can improve understanding of the functional scales of habitat fragmentation, thereby providing information on critical thresholds regarding the spatial extent and distribution of resources for target species (Thompson and McGarigal, 2002). This approach can allow resource managers to target habitat restoration design for particular species, or generate designs that provide habitat for all three species, and track species management success where multiple species have overlapping but distinct habitat requirements.

Data availability statement

The raw data supporting the conclusion of this article will be made available by the authors, without undue reservation.

Ethics statement

Ethical review and approval was not required for the animal study because the data was collected using observation and measurement of anadromous fish redds in the wild. No fish were physically handled or harassed during sampling.

Author contributions

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Numerous Bureau of Reclamation and Cramer Fish Sciences field staff collected the data used in the analysis.

Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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