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Multiple survey methods reveal greater abundance of endangered pupfish in restored habitats

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Abstract

1. Freshwater organisms inhabiting arid ecosystems are imperilled by human alterations to water-limited landscapes. This is especially true among desert-dwelling cyprinodontid fishes, 90% of which are imperilled by habitat destruction within limited or shrinking ranges. Constructing habitats that mimic natural habitat form and function may provide a tool for species conservation, especially within freshwater protected areas. However, pupfish population assessments within degraded compared with restored habitats are infrequent, and few comparisons among survey methods exist.
2. Density estimates were developed for Endangered Comanche Springs pupfish *Cyprinodon elegans* throughout altered and restored habitats in a freshwater protected area by using mark-recapture and *N*-mixture models fitted to data collected using minnow trap and visual count survey methods. This allowed comparison of habitats, survey methods, and statistical methods commonly used to generate population size estimates for imperilled pupfish.
3. Population estimates varied across major habitat types and were largest among habitats constructed to mimic naturally occurring ciénegas. Estimates using visual counts were higher than estimates from minnow traps where water was deeper and where macroalgae cover was highest. *N*-mixture models generally estimated higher abundances than mark-recapture and were not limited by recapture ability.
4. The results provide strong evidence that restored habitats house greater abundances of pupfish, but survey and statistical methods commonly used to detect these differences have trade-offs in performance according to the habitats surveyed. This work benefits the field of conservation biology by providing guidance for existing and emerging monitoring programmes assessing abundance-based fish responses to habitat improvements.

KEYWORDS

conservation evaluation, endangered species, fish, modelling, spring

1 | INTRODUCTION

Preserving aquatic biodiversity in the face of human domination of freshwater ecosystems is one of the greatest challenges facing conservation biology (Abbott et al., 2019). Freshwater ecosystems cover 2.3% of Earth's surface yet are inhabited by at least 9.5% of known biodiversity (Reid et al., 2019). Fishes are the dominant vertebrate group in fresh waters (Allan & Flecker, 1993), and freshwater fish conservation will play a critical role in addressing the conservation crisis facing freshwater biodiversity (Closs, Krkosek, & Olden, 2015). This is especially true of perennial waters in arid landscapes and their fish inhabitants (Davis, Kerezszy, & Nicol, 2017). Conflict between human water uses and fish habitat requirements in arid regions has put many fish species on the road to extinction (Minckley & Deacon, 1991), creating a need for conservation intervention (Meffe & Vrijenhoek, 1988). Among conservation approaches employed to conserve desert fishes (Pister, 1990), establishment of refuge habitats and populations within freshwater protected areas (FPAs) stands the best chance of conserving biodiversity in regions where human water demand has the potential to exceed availability for natural systems (Abell, Allan, & Lehner, 2007; Suski & Cooke, 2007). However, challenges facing FPAs include the need to develop scientifically defensible goals for endangered species abundances and evidence-based support for habitat improvement projects (Hermoso, Abell, Linke, & Boon, 2016; Nel et al., 2009). Addressing these issues will require additional research focused on endangered species abundances in degraded and restored habitats.

Fishes in the family Cyprinodontidae are representative of the plight facing fishes and their habitats the world over. Thirty-eight of the 43 (90%) species in this family are imperilled by habitat destruction, increasingly restricted ranges, and introgression with non-native species (Jelks et al., 2008). The majority of these pupfish (40 of 43; 93%) occur in arid landscapes of the American Southwest and isolated groundwater-dependent spring ecosystems that are shrinking because of human alterations to arid landscapes and riverscapes (Davis et al., 2017). For example, habitat destruction has relegated Shoshone pupfish (*Cyprinodon nevadensis shoshone*) to primarily artificial refuge areas, and Devils Hole pupfish (*Cyprinodon diabolis*) range naturally occurs in only one FPA (Hausner et al., 2016). Management of populations and habitats within FPAs is critical for maintaining the last remaining stocks of *Cyprinodon* spp. This includes habitat manipulations conducted to mimic natural conditions that also suppress non-native species (Scoppettone, Risler, Gourley, & Martinez, 2005). Monitoring and quantifying *Cyprinodon* spp. population responses to habitat improvements is critical for ensuring desired ecological outcomes from habitat restoration initiatives (Black et al., 2016). Unfortunately, there is considerable uncertainty regarding the most appropriate survey and statistical methods for monitoring pupfish abundances and responses to habitat improvements. Examples include survey methods, such as minnow traps (MTs) and visual counts (VCs), and statistical models based on mark-recapture protocols or quantification of unmarked individuals (Andersen & Deacon, 2001; Douglas,

Douglas, & Brunner, 2001; Jester & Suminski, 1982; Lewis et al., 2013; Williams & Sada, 1985; Winemiller & Anderson, 1997). No quantitative comparison of these survey methods or statistical methods exists despite the benefits such a comparison would provide for conservation and management. Specifically, determining trade-offs and limitations among these methods could provide critical decision-support tools for conservation practitioners faced with the challenges of monitoring, managing, and mitigating declining or last remaining pupfish populations.

The history of Comanche Springs pupfish (*Cyprinodon elegans*; CSP) is an example and common story for most Cyprinodontidae fishes. CSP was once distributed in two separate spring systems 90 km apart within the Pecos River catchment, including the type locality Comanche Springs in Fort Stockton, Texas, and a system of interconnected springs near Balmorhea, Texas (United States Fish and Wildlife Service (USFWS), 1980). The system of springs near Balmorhea, Texas, included artesian Phantom Lake, San Solomon, and Giffin springs, as well as gravity-fed Saragosa, East Sandia, and West Sandia springs. All of these springs formed ciénegas, or shallow, marshy wetlands, at their outflows that were historically inhabited by CSP (USFWS, 1980). However, groundwater pumping caused Comanche Springs to dry in 1955 and CSP was extirpated from that location (Hubbs, 1957). Near Balmorhea, Texas, flow reductions caused by groundwater pumping, water diversion through irrigation canals, and water retention in Lake Balmorhea caused extensive drying and near complete destruction of the ciénegas supported by the springs (Brune, 1981; Sharp, 2001), resulting in CSP being listed as Endangered by the USFWS (USFWS, 1980) and the International Union for the Conservation of Nature (NatureServe, 2013). Phantom Lake Spring has since failed, and a pump is required to maintain a small pool near the source of the spring that was recently inhabited by <150 CSP (Garrett, 2003; Lewis et al., 2013). Recent collections at Giffin Spring and East Sandia Spring yielded no specimens (Hargrave, Riskind, & Garrett, 2017), although a small population probably persists (R. Smith, The Nature Conservancy, personal communication). At present, the largest population of CSP exists in an interconnected series of habitats supported by San Solomon Springs on the grounds of Balmorhea State Park (BSP).

Conservation actions in locations like BSP are critical to fulfilling the need for FPAs to mitigate biodiversity declines (Watson et al., 2016). Intentional isolation paired with habitat augmentations that boost imperilled species abundance are two conservation tools currently applied at BSP (Garrett, 2003; Rahel, 2013). However, the efficacy of these actions requires quantification to inform and improve CSP management and provide tools to assess other isolated cyprinodontid populations throughout the Desert Southwest. The purpose of this study was to assess CSP abundance responses to habitat restoration. To accomplish this goal, two objectives were developed. The first objective was to estimate population size using both mark-recapture and unmarked techniques in four habitats of contrasting architecture, including two ciénega mimics. The second objective was to assess how population size estimates varied for trap-based versus visual-based recapture methods. This comparison is necessary

because traps are commonly used to assess pupfish abundance despite concern over fish behaviour (Peterson, Scheerer, & Clements, 2015; Seber, 1970) and the use of VCs of unmarked individuals that reduce fish handling is becoming more common (Mollenhauer & Brewer, 2018; Zubik & Fraley, 1988). Results from these comparisons will be useful for informing surveys of other imperilled organisms inhabiting other FPAs, to improve abundance estimates, and ultimately provide an assessment of ecological responses to habitat restoration.

2 | METHODS

2.1 | Study area

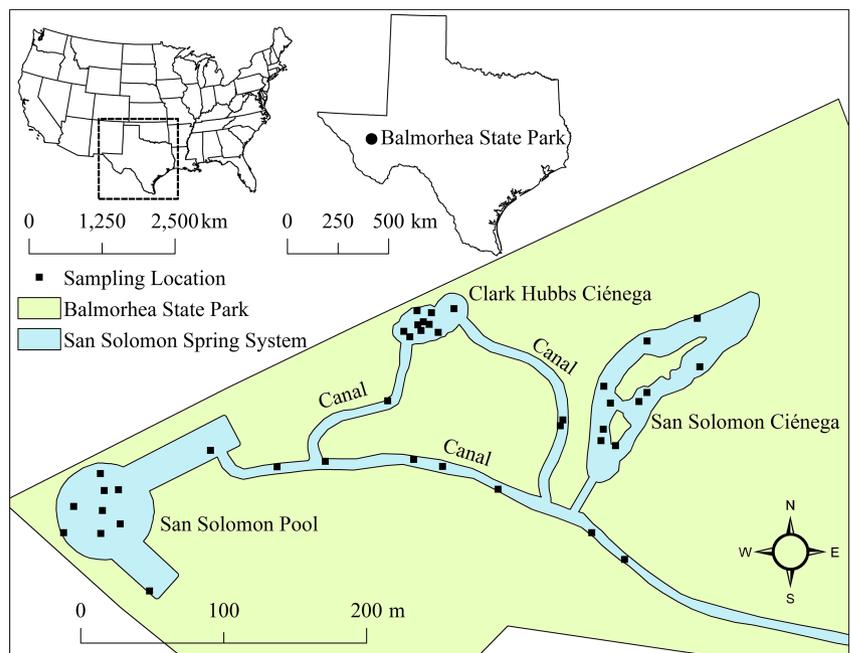
BSP was established and opened to the public in 1968 and is operated by the Texas Parks and Wildlife Department under Texas Administrative Code Title 31, Part 2, Chapter 59, Subchapter F. This legislation prevents unsanctioned development of land or water resources within the park and regulates the take from, or introduction of, wildlife on the park premises. Construction of a spring-fed swimming pool at the spring source destroyed the naturally occurring *ciénega* that supported CSP (USFWS, 1980). Beginning in 1995, construction began to create habitat that mimicked the natural *ciénega* prior to the swimming pool (Garrett & Edwards, 2001). Two *ciénegas* were created, San Solomon *Ciénega* (constructed in 1996) and Clark Hubbs *Ciénega* (constructed in 2010), and both were designed to simulate the geomorphology (i.e. shallow water, dense vegetation) and hydrology (greater water residency time) of naturally occurring *ciénegas*. The park contains four principal aquatic habitats (USFWS, 2013): the artificial pool (surface area 5,427 m²), a canal system (surface area 2,698 m²), and two mimic *ciénegas*, San Solomon *Ciénega* (3,747 m²)

and Clark Hubbs *Ciénega* (922 m²). The current spatial structure of BSP was mapped and a digital polygon was created of the aquatic habitats with ArcGIS v 10.6.1 (Esri Inc., Redlands, CA) using National Aerial Imagery Program (NAIP) 1 m resolution aerial imagery (US Department of Agriculture, 2014). A grid was overlaid to create a network of 1 × 1 m² cells throughout BSP. Ten cells were randomly selected within each major habitat for a total of 40 locations to be surveyed during March and October 2019 (Figure 1).

2.2 | Habitat characteristics and abundance covariates

Variables useful for describing differences across the principal habitats in BSP were collected. The percentage cover of fine sediments was visually estimated within each of the 40 1 × 1 m² grid cells selected for surveys. Sediment sizes were identified as silt (0.004–0.62 mm diameter), sand (>0.62–2 mm), gravel (>2–32 mm), or cobble (>32–256 mm) based on a modification of the scale developed by Wentworth (1922). The percentage cover of silt and sand was summed to estimate fine sediment, substrate that was most likely present in natural *ciénega* habitats (Garrett, 2003). The percentage cover of macroalgae (*Chara* spp.) at each location was visually estimated, a reel was used to measure water depth (cm), and a YSI ProDSS multi-parameter water quality meter (YSI, Yellow Springs, OH) was used to measure afternoon water temperature (°C). The spatial position of each sampling location relative to all other locations was calculated using the principal coordinates of neighbour matrices (PCNM) method developed by Borcard and Legendre (2002) using the 'pcnm' function from the 'vegan' package in R version 3.5.3 (Oksanen et al., 2019). For the PCNM analysis, Euclidean distances constrained to the wetted area polygon (i.e. hydrographical distance)

FIGURE 1 Study area map illustrating Balmorhea State Park in West Texas and the San Solomon Spring System. Points ($n = 40$) represent survey locations spread across the four principal habitats: San Solomon Pool, the canal network, Clark Hubbs *Ciénega*, and San Solomon *Ciénega*



were used for analysis, and the first three axes were retained for interpretation.

2.3 | Abundance surveys

For each sampling period (March and October), CSP was surveyed at all 40 locations using MT and VC techniques. MTs were set during nocturnal hours once per night for three consecutive nights (four nights during October), and VCs were conducted during diurnal hours the day after traps were set. Before the first sampling occasion, all locations were georeferenced using a Garmin Oregon 700 (Garmin Ltd, Olathe, KS) and marked with a numbered plastic stake. These markers allowed for repeated counts at exact locations across the study period. Unbaited MTs (40 cm length, 22 mm diameter entrance, 3 mm mesh) were deployed nightly and had a mean (\pm SD) soak time of 1,019 min (\pm 112 min) per night. All CSP captured in MTs were marked on their dorsal surface with a 3 mm long visible implant elastomer (VIE) injection (Northwest Marine Technology, Shaw Island, WA) before being released back to the habitat from which they were captured. After traps were removed and fish were marked and released, VCs were conducted within 1×1 m² polyvinyl conduit quadrats placed on the substrate at each sample location. Observers wearing a snorkel and dive mask swam to a marker and allowed at least 2 min to pass before the count survey was initiated. Following the wait period, the observer counted CSP that entered the quadrat during a 2 min interval and recorded the number of fish, including VIE-marked fish. Observers were careful not to count the same individuals more than once if they remained within the quadrat, or moved back and forth over the edge of the quadrat while staying in view; it was not possible to determine whether individuals that swam out of view returned to be double counted. Two locations in Clark Hubbs Ciénega (quadrats 4 and 6) were too shallow for floating visual counts and were therefore observed with the surveyor out of the water but <1.5 m from an edge of the quadrat.

2.4 | Mark-recapture

Population size was estimated in each habitat using mark-recapture techniques. The VIE-tagged fish captured in MTs and recaptures from MTs or VCs were used to calculate a Schnabel estimate (Schnabel, 1938). Mark-recapture sampling occurred over a short time interval (3 days), while allowing 24 h to pass between trap sets. Estimations and 95% confidence intervals were calculated using the 'schnabel' function from the 'fishmethods' package in R (Nelson, 2018). A Schnabel population estimation could not be calculated for San Solomon Ciénega during March because none of the marked individuals were recaptured through MT or VC methods. To ensure this limitation was not repeated, sampling was extended in the October sample from three to four trap nights. October population estimates are presented with three and four sampling nights to illustrate improvement with an additional data point. A Schnabel estimator

was fitted to data from fish recaptured in traps separately from tagged fish that were sighted during snorkel surveys. Population estimates and 95% confidence intervals from mark-recapture are presented and then transformed to density estimates for comparison with *N*-mixture estimates. Density was calculated for each habitat by dividing the population estimate from the surface area of each respective habitat.

2.5 | *N*-mixture modelling

The open population *N*-mixture model developed by Dail and Madsen (2011) was fitted to the data. Dail and Madsen (2011) extended the work of Royle (2004) by relaxing the closed population assumption and including terms estimating arrival (through birth or immigration; γ) and survival (through death or emigration; ω). An advantage to *N*-mixture models is that parameters for abundance, detection, arrival, and survival can be modelled as constant (null model) or variables based on location-specific and occasion-specific covariates. Candidate models included all possible combinations of predictor variables, ranging from a null model with no covariates and a global model with all covariates. *N*-mixture models using the 'pcountOpen' function from the 'unmarked' package in R were fitted using a Poisson error distribution (Fiske & Chandler, 2011). The 'dredge' function from the 'MuMIn' package in R (Barton, 2019) was used to build candidate models and evaluate the top-ranked models for each season independently (Priol et al., 2014). The top five best-fit models are presented for sampling method across the two seasons based on Akaike information criterion adjusted for small sample size (AIC_c). The 'model.avg' function was then used to average parameter estimates for competing models with Δ AIC_c < 2. Finally, predicted abundance was estimated from the averaged models for VCs and MTs using the mean abundance covariate values within each of the four principal habitats in the San Solomon Spring System. This allowed for comparison between mark-recapture estimates and *N*-mixture model estimates across the entire system as well as within the four principal habitats.

2.6 | Model assessment and mapping

Model accuracy was assessed visually from mapped predicted abundances across the springscape. Predictions from best-fit models from the *N*-mixture analysis were regressed against mean observed abundances during the three days of sampling in each season to assess agreement between predicted and observed values. The top model from VC and MT samples was used for each season to calculate the best unbiased predictors and their uncertainty using the 'ranef', 'bup', and 'confint' functions from the 'unmarked' package. The mean and 95% confidence intervals were plotted for posterior distributions as a function of observed abundances across the three sampling occasions conducted during March and the three occasions conducted during October. The predicted values from the fitted models and 95% confidence intervals were plotted as a function of observed abundances across the two sampling seasons (March and October) for both

sampling methods (VC and MT). Points falling along the 1:1 line represent agreement between observed and predicted abundances. Abundance covariates measured at each sampling location ($n = 40$) were interpolated across BSP using the Spline with Barriers tool in ArcGIS. Interpolation was restricted to the water boundary using a polygon created around the San Solomon Spring System within the BSP boundary. This process was repeated for predicted density values for each location from the averaged N -mixture models and then the raster calculator tool was used to subtract MT spline estimates from the VC spline estimates to produce a map showing the difference in predictions between the two alternative sampling methods. Spline analysis was also used to plot continuous maps of the habitat and spatial covariates.

3 | RESULTS

3.1 | Abundance covariates

Habitat parameters measured as abundance covariates differed among the principal habitats within the San Solomon Spring System. Habitats were shallowest in Clark Hubbs Ciénega, followed by the canal network, San Solomon Ciénega, and the pool (Figure 2a). Afternoon water temperature was homogeneous across the spring system during March, but Clark Hubbs Ciénega and San Solomon Ciénega were warmer than other habitats by October (Figure 2b). March *Chara* cover was greatest in Clark Hubbs Ciénega, the nearby canal, and deep portions of the pool, but San Solomon Ciénega had nearly 100% cover by October (Figure 2c). Fine substrates varied little between sampling periods and dominated San Solomon Ciénega as well as Clark Hubbs Ciénega and the nearby canal (Figure 2d). Spatial covariates showed strong signals for Clark Hubbs Ciénega and the pool along PCNM 1 (Supporting Information Figure S1a), San Solomon Ciénega and the pool along PCNM 2 (Figure S1b), and the canal system along PCNM 3 (Figure S1c).

3.2 | Abundance surveys and mark-recapture

Across the 40 sampling locations, March counts yielded 1,328 CSP (VC = 600; MT = 728) and October counts yielded 2,209 CSP (VC = 1,209; MT = 1,000). March VC abundances were highest in the swimming pool and lowest in San Solomon Ciénega, whereas MT abundances were highest in Clark Hubbs Ciénega and lowest in San Solomon Ciénega (Table 1). October VC abundances were highest in San Solomon Ciénega and lowest in the pool, whereas abundances based on MT were highest in San Solomon Ciénega and lowest in the canal. March recapture rates based on VC were highest in the canal and absent from San Solomon Ciénega, whereas MT recaptures were highest in Clark Hubbs Ciénega and the canal and absent from San Solomon Ciénega. October recapture rates based on VC were highest in the pool and lowest in San Solomon Ciénega, whereas MT recaptures were highest in the pool and San Solomon Ciénega. Estimated

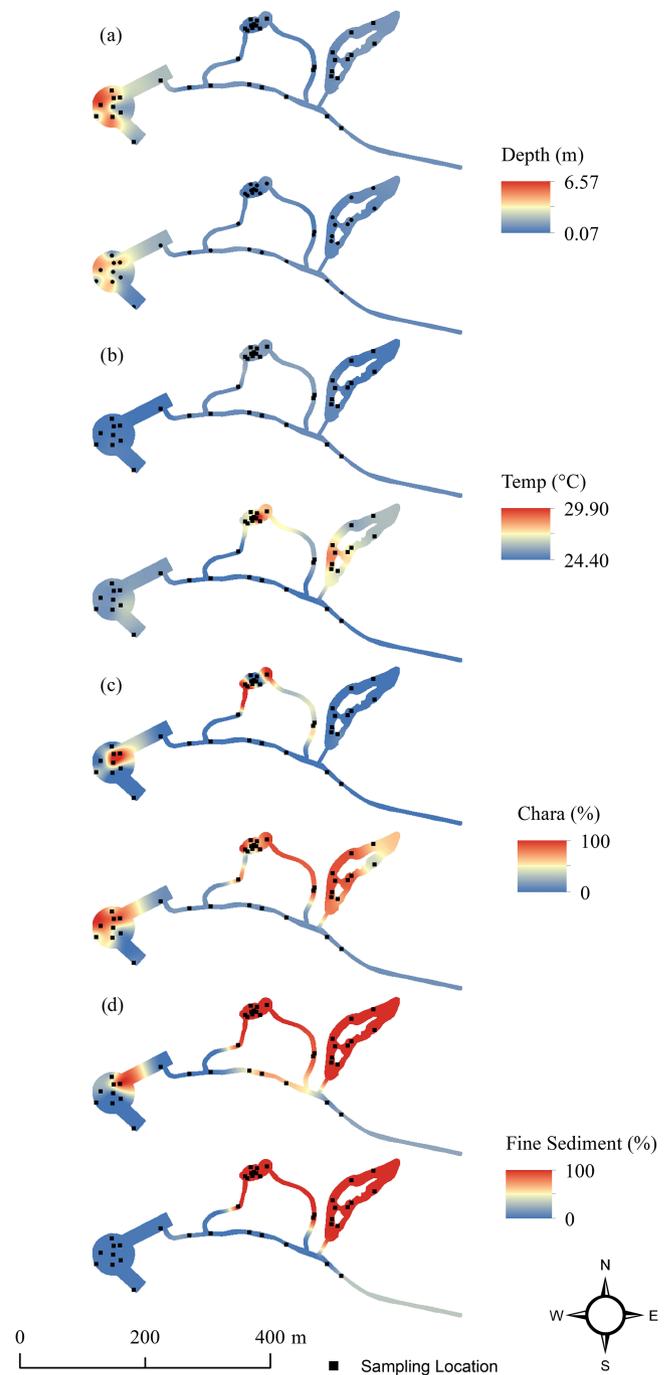


FIGURE 2 Spline interpolation of habitat covariates collected at Balmorhea State Park, Texas, within the San Solomon Springs System in March (upper plot in (a)–(d)) and October (lower plot in (a)–(d)) 2019. Habitat covariates collected: (a) depth (m); (b) *Chara* spp. cover (%); (c) fine substrates (%); (d) water temperature (°C)

abundances were consistently highest in the Clark Hubbs Ciénega across seasons, although the estimate for San Solomon Ciénega increased substantially from March (unestimated) to October. Density estimates generated by dividing total population size by habitat surface area based on VC versus MT were consistent within principal habitats (Figure 3a), although neither VC nor MT yielded estimates for San Solomon Ciénega during March, and MT did not result in any recaptures in the canal during October.

TABLE 1 Comanche Springs pupfish survey results for habitats at Balmorhea State Park conducted in March and October 2019 using visual count (VC) and minnow trap (MT) survey methods

Season and method	Canal	Clark Hubbs	Pool	San Solomon	Total
Site detections					
March, VC	4	8	10	4	26
March, MT	3	10	9	10	32
October, VC	9	10	10	10	39
October, MT	7	10	10	10	36
Observed					
March, VC	132	156	294	18	600
March, MT	111	448	90	79	728
October, VC	111	370	190	538	1,209
October, MT	94	356	130	420	1,000
Recaptures					
March, VC	10	5	5	0	20
March, MT	9	13	2	0	24
October, VC	4	5	11	2	22
October, MT (3)	0	5	8	4	17
October, MT (4)	3	9	14	14	40
Mark-recapture population estimates					
March, VC	311 (183–779)	5,145 (2,572–25,724)	1,930 (965–9,650)	–	7,966 (5,494–13,277)
March, MT	439 (263–987)	4,435 (2,745–9,608)	1,281 (514–∞)	–	6,724 (4,747–10,759)
October, VC	935 (468–3,741)	15,591 (7,796–77,956)	1,145 (700–2,520)	44,724 (17,890–∞)	25,588 (17,592–43,302)
October, MT (3)	–	5,901 (2,950–29,507)	443 (253–1,182)	4,701 (2,351–18,805)	9,631 (6,298–18,193)
October, MT (4)	1,021 (438–∞)	5,114 (3,069–11,507)	427 (272–853)	4,327 (2,754–8,654)	9,125 (6,887–13,037)
Density estimates					
March, VC	0.11 (0.06–0.28)	5.58 (2.78–27.90)	0.35 (0.17–1.77)	–	0.62 (0.42–1.03)
March, MT	0.16 (0.09–0.36)	4.81 (2.97–10.42)	0.23 (0.09–∞)	–	0.52 (0.37–0.84)
October, VC	0.34 (0.17–1.38)	16.9 (8.45–84.55)	0.21 (0.12–0.46)	11.93 (4.77–∞)	2.00 (1.37–3.38)
October, MT (3)	–	6.40 (3.19–32.00)	0.08 (0.04–0.21)	1.25 (0.62–5.01)	0.75 (0.49–1.42)
October, MT (4)	0.37 (0.16–∞)	5.54 (3.32–12.48)	0.07 (0.05–0.15)	1.15 (0.73–2.30)	0.71 (0.53–1.01)

Note: For each habitat and the entire spatial extent (Total) the number of traps or quadrats in which fish were detected (Site detections), number of pupfish observed (Observed), number of marked fish that were recaptured (Recaptures), estimated population size (upper and lower 95% confidence interval), and fish density estimates (m^{-2}) are shown. The results of extending MT from three to four nights in October are shown.

3.3 | N-mixture models

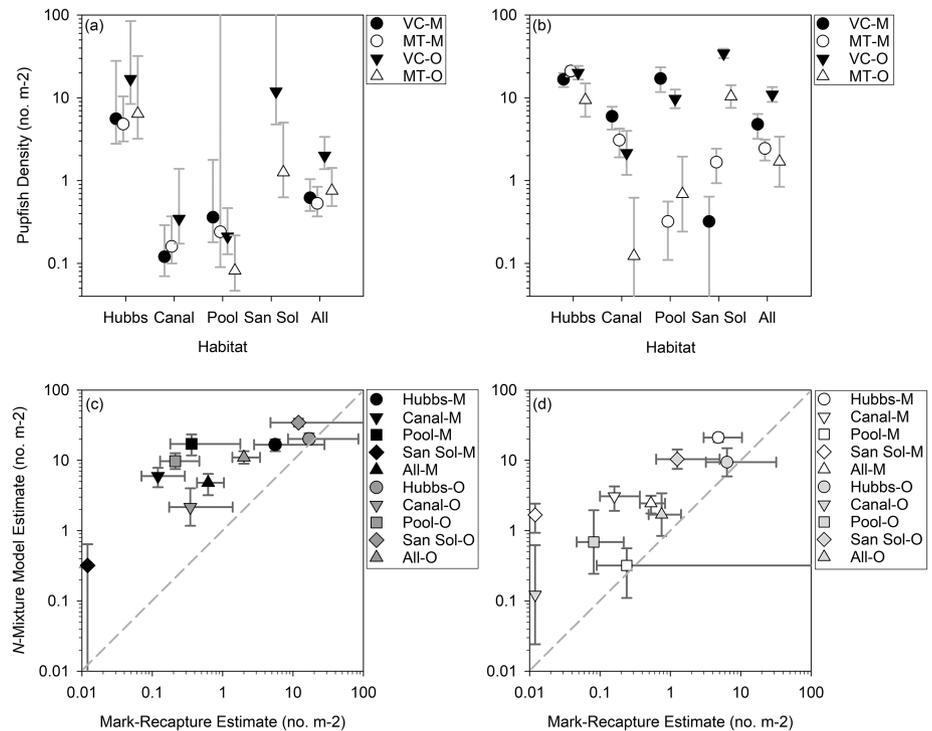
Top-ranked candidate *N*-mixture models for March differed between VC and MT survey methods. Model selection for March VC data produced two competing models ($\Delta AIC_c < 2$) that included *Chara* spp., depth, temperature, fine sediments, and the second PCNM as abundance covariates (Table 2). Arrival (1.6) and survival (0.61) rates' intercepts were both significant; however, the intercept for detection probability (0.57) was non-significant. Model selection for March MT data produced two competing models ($\Delta AIC_c < 2$) that included *Chara* spp., depth, fine sediments, and all three PCNM axes as abundance covariates. Arrival (2.17) and survival (0.33) rates' intercepts were both significant, as was the intercept for detection probability (0.98).

Top-ranked candidate *N*-mixture models for October differed between VC and MT survey methods. Model selection for October VC data produced a single top model that included *Chara* spp., fine

sediments, and all three PCNM axes (Table 2). Arrival (3.7) and survival (0.83) rates' intercepts were positive and significant; however, the intercept for detection (0.53) was not significant. Model selection for October MT data produced a single model that included *Chara* spp., depth, fine sediments, temperature, and all three PCNM axes. The arrival rate (3.21) intercept was significant, but survival rate (0.63) and detection probability (0.71) intercepts were not significant. Model-averaged parameter estimates for all sampling occasions can be found in Table 3.

Density estimates based on *N*-mixture models fitted to VC and MT data were not always consistent among habitats or with mark-recapture estimates (Figure 3b). *N*-mixture models showed generally lower densities for MT data compared with VC collected in October, especially in Clark Hubbs Ciénega and the canal. Comparative scatter plots illustrated four instances of overlap between mark-recapture and *N*-mixture models fitted to VC data, including low CSP density in

FIGURE 3 Density estimates and 95% confidence intervals for Comanche Springs pupfish for principal habitats in the San Solomon Spring System based on (a) mark-recapture methods and (b) *N*-mixture modelling. VC: visual count; MT: minnow trap. (c, d) Comparison of density estimates generated from mark-recapture methods versus *N*-mixture modelling based on (c) visual counts and (d) minnow trap counts. Habitats are Clark Hubbs Ciénega (Hubbs), the Canal Network (Canal), San Solomon Pool (Pool), San Solomon Ciénega (San Sol), and all habitats combined (All). See Figure 1 for locations of habitats. The dashed lines in (c) and (d) represent a 1:1 line (intercept: 0; slope: 1). All estimates with '-M' appended are from March 2019 and those with '-O' are from October 2019



San Solomon Ciénega during March, high CSP density in Clark Hubbs Ciénega during March and October, and high CSP density in San Solomon Ciénega during October (Figure 3c). Otherwise, fish density estimates derived from the VC *N*-mixture model were 1–11 m^{-2} higher compared with estimates derived from the VC mark-recapture model. Scatter plots illustrated three instances of overlap between mark-recapture and *N*-mixture models fitted to MT data, including low CSP density in the pool in March, intermediate CPS density in all habitats in October, and high CSP density in Clark Hubbs Ciénega during October (Figure 3d).

3.4 | Model assessment and mapping

Scatter plots of posterior distributions against observed abundances showed a trend of agreement between methods characterized by higher estimation of abundances based on *N*-mixture models compared with mark-recapture. Agreement between *N*-mixture models and mark-recapture was generally higher for MT than with VC survey methods for March (Figure S2) and October (Figure S3). When plotted spatially, the highest estimates of CSP density based on VC were for deep areas of the pool in March and the upper section of San Solomon Ciénega during October (Figure 4a). The highest estimates of CSP density based on MT were for the upstream extent of Clark Hubbs Ciénega and the canal downstream of Clark Hubbs Ciénega in March, and the upper extents of both ciénegas during October (Figure 4b). Discrepancies in density estimates between VC and MT showed higher estimates from VC in deep water and higher estimates from MT in shallow water, although VC densities in San Solomon Ciénega emerged as higher during October (Figure 4c).

4 | DISCUSSION

Reliable and repeatable baseline population estimates are vital to preservation of aquatic biodiversity, especially for managed populations occupying FPAs (Adams, Setterfield, Douglas, Kennard, & Ferdinands, 2015). Desert pupfishes, such as CSP, commonly occupy FPAs where habitat improvements often occur, but abundance-based assessments of the benefits of habitat improvement are hampered by uncertainty surrounding methods (Andersen & Deacon, 2001; Jester & Suminski, 1982; Lewis et al., 2013; Williams & Sada, 1985). This work provides a comprehensive comparison of two commonly used sampling methods (VC and MT) and two widely applied modelling frameworks (Schnabel estimator and *N*-mixture models) to show that habitat restoration resulted in greater abundance of the target species than in non-restored habitats. General agreement in inference gained among sampling methods was found when the Schnabel estimator was fitted to VC and MT data, including an emergent pattern of greater CSP abundance in habitats that were constructed to mimic ciénegas. Greater differences emerged when *N*-mixture models were applied to these same sampling methods, although a consistent pattern of greater CSP abundance in restored ciénegas was apparent. This essentially means that, in circumstances where pupfish cannot be captured or marked, *N*-mixture models fitted to VC data represent an alternative for developing abundance indices that could benefit conservation actions. From this perspective, this research provides insight into the trade-offs between traditional handling and marking of individuals and less invasive census protocols (Ficetola et al., 2018; Griffiths, Fister, Wilkinson, & Sewell, 2015; Kidwai, Jimenez, Louw, Nel, & Marshal, 2019) aimed at addressing the challenge of establishing quantitative measures of response to habitat improvement (Hermoso et al., 2016; Nel et al., 2009).

TABLE 2 Candidate *N*-mixture models developed to estimate abundance for Comanche Springs pupfish in the San Solomon Springs System in March and October 2019

Model	<i>K</i>	LL	AIC _c	ΔAIC _c	AIC _c Wt	CumWt
Visual counts, March						
λ (chara + depth + temp + PCNM2), $p(\cdot)$, $\gamma(\cdot)$, $\omega(\cdot)$	8	-479.26	979.17	0	0.43	0.43
λ (chara + depth + temp + fine + PCNM2), $p(\cdot)$, $\gamma(\cdot)$, $\omega(\cdot)$	9	-478.15	980.3	1.13	0.24	0.67
λ (chara + depth + temp + PCNM1 + PCNM2), $p(\cdot)$, $\gamma(\cdot)$, $\omega(\cdot)$	9	-478.93	981.87	2.7	0.11	0.78
λ (chara + depth + temp + PCNM2 + PCNM3), $p(\cdot)$, $\gamma(\cdot)$, $\omega(\cdot)$	9	-479.24	982.48	3.31	0.08	0.86
λ (chara + depth + temp + fine + PCNM2 + PCNM3), $p(\cdot)$, $\gamma(\cdot)$, $\omega(\cdot)$	10	-478.07	983.72	4.56	0.04	0.9
Minnow traps, March						
λ (depth + fines + PCNM1 + PCNM2 + PCNM3), $p(\cdot)$, $\gamma(\cdot)$, $\omega(\cdot)$	9	-797.49	1,619.0	0	0.43	0.43
λ (chara + depth + fines + PCNM1 + PCNM2 + PCNM3), $p(\cdot)$, $\gamma(\cdot)$, $\omega(\cdot)$	10	-795.76	1,619.1	0.13	0.4	0.83
λ (depth + temp + fines + PCNM1 + PCNM2 + PCNM3), $p(\cdot)$, $\gamma(\cdot)$, $\omega(\cdot)$	10	-797.17	1,621.9	2.96	0.1	0.93
λ (chara + depth + temp + fines + PCNM1 + PCNM2 + PCNM3), $p(\cdot)$, $\gamma(\cdot)$, $\omega(\cdot)$	11	-795.68	1,622.8	3.81	0.06	0.99
λ (depth + fines + PCNM1 + PCNM2), $p(\cdot)$, $\gamma(\cdot)$, $\omega(\cdot)$	8	-813.79	1,648.2	29.24	<0.01	0.99
Visual counts, October						
λ (chara + fine + PCNM1 + PCNM2 + PCNM3), $p(\cdot)$, $\gamma(\cdot)$, $\omega(\cdot)$	9	-790.477	1,605.0	0	0.713	0.71
λ (chara + depth + fine + PCNM1 + PCNM2 + PCNM3), $p(\cdot)$, $\gamma(\cdot)$, $\omega(\cdot)$	10	-790.456	1,608.5	3.54	0.121	0.83
λ (chara + fine + temp + PCNM1 + PCNM2 + PCNM3), $p(\cdot)$, $\gamma(\cdot)$, $\omega(\cdot)$	10	-790.499	1,608.6	3.63	0.116	0.95
λ (chara + depth + fine + temp + PCNM1 + PCNM2 + PCNM3), $p(\cdot)$, $\gamma(\cdot)$, $\omega(\cdot)$	11	-790.447	1,612.3	7.37	0.018	0.97
λ (fine + PCNM1 + PCNM2 + PCNM3), $p(\cdot)$, $\gamma(\cdot)$, $\omega(\cdot)$	8	-796.093	1,612.8	7.88	0.014	0.98
Minnow traps, October						
λ (chara + depth + fine + temp + PCNM1 + PCNM2 + PCNM3), $p(\cdot)$, $\gamma(\cdot)$, $\omega(\cdot)$	11	-504.879	1,041.2	0.00	0.843	0.843
λ (chara + fine + temp + PCNM1 + PCNM3), $p(\cdot)$, $\gamma(\cdot)$, $\omega(\cdot)$	9	-511.192	1,046.4	5.2	0.065	0.91
λ (chara + fine + temp + PCNM1 + PCNM2 + PCNM3), $p(\cdot)$, $\gamma(\cdot)$, $\omega(\cdot)$	10	-510.117	1,047.8	6.63	0.032	0.94
λ (chara + depth + fine + temp + PCNM1 + PCNM3), $p(\cdot)$, $\gamma(\cdot)$, $\omega(\cdot)$	10	-510.173	1,047.9	6.75	0.03	0.97
λ (chara + depth + fine + PCNM1 + PCNM2 + PCNM3), $p(\cdot)$, $\gamma(\cdot)$, $\omega(\cdot)$	10	-513.971	1,055.5	14.34	<0.01	0.97

Note: λ is population size; p is detection probability; γ is arrival rate; ω is survival rate; chara is the percentage cover of *Chara* spp.; depth is water depth (m); temp is afternoon water temperature (°C); fine is percentage cover of fine substrates (<2 mm diameter); PCNM1–3 are principal coordinates of neighbourhood matrices axes 1–3; *K* is the number of model parameters; LL is log-likelihood; AIC_c is Akaike information criterion; ΔAIC_c is the difference between each model and the top-ranked model; AIC_cWt is the conditional probability that each model is the top-ranked model; and CumWt is the cumulative conditional probability for each model plus all higher-ranked models.

The FPA at BSP hosts a diversity of spatially and temporally heterogeneous habitats that influence local abundances of pupfish. In general, mimic ciénega habitats hosted the greatest abundances of CSP among the four principal habitats. Population size estimates generated using VC and MT data were remarkably similar within habitats in March, and to a lesser extent in October. This is likely to be attributable to the dynamic nature of *Chara* spp. and temperature in the two constructed ciénegas. *Chara* spp. were sparse and temperatures

mild in San Solomon Ciénega during March, but by October the afternoon temperatures were higher and *Chara* spp. cover much greater. Consistent with these changes in habitat was increased abundance of CSP in San Solomon Ciénega. Dynamic habitats characterized by periods of shallow water, high temperatures, and wide cover of *Chara* spp. best approximate descriptions of the natural ciénega that existed before large-scale destruction of habitats (USFWS, 1980, 2013). Most desert pupfish species express opportunistic life-history strategies

TABLE 3 Parameter estimates and significance tests for averaged top-ranked N -mixture models fitted to Comanche Springs pupfish abundances observed during visual counts and minnow traps in the San Solomon Spring System in March and October 2019

Parameter	Visual counts						Trap counts					
	March			October			March			October		
	Estimate	Z value	P value	Estimate	Z value	P value	Estimate	Z value	P value	Estimate	Z value	P value
λ (intercept)	-32.22	4.538	<0.01	0.008	0.018	0.9	0.59	1.711	0.09	-10.734	-5.100	<0.01
λ (chara)	0.006	4.083	<0.01	0.006	3.255	<0.01	-0.001	0.733	0.46	-0.026	-6.800	<0.01
λ (depth)	0.2	3.546	<0.01	-	-	-	-2.057	9.605	<0.01	-0.757	-2.430	0.02
λ (PCNM1)	-	-	-	-6.108	-4.861	<0.01	-9.144	5.449	<0.01	-18.920	-5.640	<0.01
λ (PCNM2)	-8.654	6.129	<0.01	-3.397	-3.294	<0.01	-12.788	9.94	<0.01	-13.034	-5.100	<0.01
λ (PCNM3)	-	-	-	3.134	5.497	<0.01	2.544	5.411	<0.01	5.150	4.250	<0.01
λ (temp)	1.339	4.751	<0.01	-	-	-	-	-	-	0.305	4.860	<0.01
λ (fine)	0.001	0.574	0.57	0.034	5.634	<0.01	0.043	7.142	<0.01	0.100	6.290	<0.01
γ (intercept)	0.484	2.084	0.04	1.3	6.12	<0.01	0.777	9.03	<0.01	1.170	9.970	<0.01
ω (intercept)	0.444	2.113	0.03	1.6	4.84	<0.01	-0.723	6.433	<0.01	0.526	1.460	0.14
p (intercept)	0.301	1.389	0.16	0.147	0.0951	0.12	4.133	3.214	<0.01	0.914	1.830	0.07

Note: λ is population size; p is detection probability; γ is arrival rate; ω is survival rate; chara is the percentage cover of *Chara* spp.; depth is water depth (m); temp is water temperature ($^{\circ}$ C); fine is percentage cover of fine substrates (<2 mm diameter), and PCNM1–3 are principal coordinates of neighbourhood matrices axes 1–3.

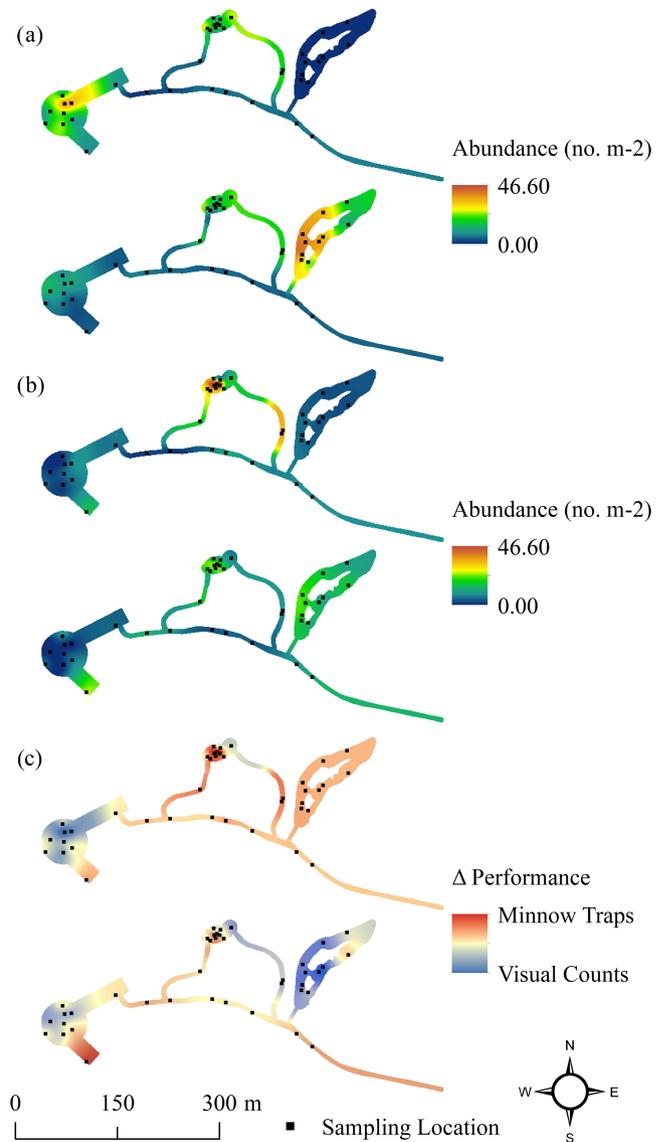


FIGURE 4 Spline analysis of the San Solomon Springs network within Balmorhea State Park, Texas, for March (upper plot in (a)–(c)) and October (lower plot in (a)–(c)). (a) Visual count and (b) minnow trap abundance interpolation results; (c) difference in abundance estimates given sampling methodology. White values indicate no difference in pupfish abundance estimates between methods, red colours indicate that minnow traps detected more pupfish, and blue colours indicate that visual counts detected more pupfish

(Winemiller & Rose, 1992) that allow rapid population expansion when habitat conditions are optimal and population contraction when habitats move to become suboptimal (Miller, 1943). The mark-recapture and N -mixture abundance estimates provided evidence for population expansion between March and October, especially within ciénega mimic habitats. These results provide empirical evidence for the benefits that constructed ciénegas can provide for CSP by mimicking the natural habitat structure and function. More broadly, this work provides empirical evidence for the often cited, but rarely tested, benefits of restoring habitat to boost densities of imperilled species (Black et al., 2016; Török & Helm, 2017).

This research has implications for conservation of imperilled fauna in other systems. Most of the *Cyprinodon* spp. in the American Southwest are in need of conservation through habitat preservation and restoration, including species in Mexico (Varela-Romero et al., 2002). The majority of *Cyprinodon* spp. engage in social breeding systems, including territoriality by males and strong mate choice by females. The extent to which these behaviours influence population density estimates has not been intensively studied, although territorial behaviour can be used as a metric for gauging progress towards conservation goals (Al-Shaer, Bloch, Little, & Itzkowitz, 2018). The open population models fitted in this study are derivatives of hierarchical models developed to model abundance of breeding birds; thus, the methods presented here are robust to the effects of territoriality and apply to a variety of species (Royle, 2004). Although these methods are robust to such behaviour, it should be noted that no males were observed defending a territory within the quadrats during this study. Development of FPAs, conservation goals, and fish monitoring protocols in regions such as India (Sarkar, Pathak, & Lakra, 2008), Australia (Chessman, 2013), and elsewhere in the USA (Thieme, Rudolph, Higgins, & Takats, 2012), among others, could benefit from application of the quantitative monitoring framework presented here. Development of this study was, in part, to address research needs required for improving the conservation status of CSP, and conservation practitioners plan to implement monitoring based on the findings from this study (M. Bean, Texas Parks and Wildlife Department, professional communication). The application of structured and replicable survey methods will benefit tracking long-term changes in abundance of CSP, and therefore overcomes previous challenges in comparing multiple methods (Garrett, 2003).

The results from this study provide evidence that census of only unmarked individuals is dependent upon the survey method used to conduct counts. *N*-mixture models fitted to unmarked individuals that entered traps as well as unmarked individuals that swam within 1 m of trap locations after traps were removed were completed in this study. A major difference between these approaches is that MTs are dependent on individuals entering the trap, whereas visual observations are not. In addition, MTs are known to underestimate population size because individuals become familiar with the trap and are subsequently captured more frequently (Peterson et al., 2015). The results presented here suggest that the most appropriate method for counting unmarked individuals is dependent on habitat. For deep water, VC surveys detected a greater number of fish than MT surveys do, yet the opposite was true in shallow water. These discrepancies highlight two observational challenges: seeing fish but not being able to trap them, and trapping fish but not being able to see them. Both challenges are likely to be related to pupfish behaviours and interactions with habitat features, particularly *Chara* spp. In the pool, the highest densities of fish visually observed were in deep water where *Chara* spp. had the greatest cover, the same locations where traps captured very few fish. This pattern points to fish in deep water expressing a tendency to avoid traps when other cover is present. In San Solomon Ciénega during March, when the ciénega was nearly devoid of *Chara* spp., very few CSP were visually observed, but many were still

captured in nocturnal MTs. However, in October, this habitat was almost entirely engulfed in *Chara* spp., and VCs performed well in this habitat whereas MTs captured few CSP in the same areas. These findings provide some guidance for monitoring strategies for other species within other FPAs that are ultimately constrained by available conservation resources (e.g. personnel, time, or funding), permitted fish handling (e.g. mark-recapture versus only visual observations), and local habitat templates (e.g. deep versus shallow habitats).

A major reason for the uncertainty regarding the status of the CSP population within BSP is the inconsistent sampling methods used during monitoring (Garrett, 2003). This is due, in part, to uncertainties surrounding efficacy and accuracy of contrasting methods – an issue that affects many *Cyprinodon* spp. in other FPAs and in the wild (Chaudoin, Feuerbacher, Bonar, & Barrett, 2015; Dzul, 2011). The results from this study suggest that visual counts can produce density estimates that, when monitored through time, provide an index of population status. If repeated biannually or annually, this technique would meet the recommendations of USFWS (2013) for routine population assessment for recovery of the species. Given that abundance goals are inherent to most conservation plans for imperilled species, the quantitative comparison of survey methods and modelling tools provides guidance for monitoring plans currently under development or revision for a variety of species. The models fitted to marked and unmarked individuals could be repeated with emerging technologies, such as underwater video cameras, to monitor populations. The use of cameras would eliminate fish behavioural changes resulting from human presence, and underwater video cameras are known to provide accurate estimates of known population sizes in closed systems (Wilson, Allen, Ahrens, & Netherland, 2015). As with other *Cyprinodon* spp. in other desert springs, the CSP population in BSP is the last stronghold for the species, and consistent abundance monitoring is required for managers to track unexpected fluxes in abundance and develop response plans. Outside of FPAs, monitoring pupfish in the wild with the quantitative techniques used here will address research needs related to understanding current population sizes and their trajectories (Moyle, Katz, & Quiñones, 2011). As human water-demand in arid landscapes increases, the number of conflicts between human needs and ecosystem needs will increase (Davis et al., 2017). This study provides evidence that restoration of habitat to mimic natural habitat, such as the constructed BSP ciénegas, can support conservation efforts through increased abundance of target species.

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SUPPORTING INFORMATION

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

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