REGULAR PAPER

Habitat associations of rainbow trout *Oncorhynchus mykiss* and brown trout *Salmo trutta* fry

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Abstract

Habitat restoration activities continue to increase in large rivers, but many of these projects focus on improving juvenile or adult habitats. Incorporating the habitat associations of fry into restoration designs will allow for broader successes from restoration for all life stages and may be useful for either multispecies or specific-species management. This study investigated the habitat associations of rainbow trout *Oncorhynchus mykiss* and brown trout *Salmo trutta* fry in the upper Colorado River, focusing on the mean substrate size (D_{50}), velocity (m s^{-1}), depth (m) and presence of wood in near-shore habitats. *S. trutta* and *O. mykiss* were found in higher numbers in fry sites with a D_{50} of 151 mm (ranging from 96 to 206 mm), velocities ranging from 0.20 to 0.23 m s^{-1} and depths ranging from 0.17 to 0.18 m. Although there was considerable overlap in habitat associations between the two species, there may be opportunities for single-species management, if this is a goal of such restoration activities, by adjusting design criteria based on differing habitat associations. In addition, the results suggest that including larger particle sizes in near-shore habitats and upstream of fry sites could decrease *Tubifex tubifex* habitat and thereby fry infection severity by reducing exposure to *Myxobolus cerebralis*. Stocking, interspecific competition and/or the presence of pathogens can affect fry habitat associations and cause deviations from demonstrated suitability indices. As such, evaluating system-specific differences in habitat associations may allow future habitat restoration activities to be more effective.

KEYWORDS
brown trout, Colorado River, habitat associations, *Oncorhynchus mykiss*, rainbow trout, *Salmo trutta*

1 | INTRODUCTION

Alteration of aquatic systems due to biotic factors, such as the implementation of dams, water and land use for agricultural development and physical manipulation of lotic systems (*e.g.*, whitewater parks), and abiotic factors, such as fires, floods and warming of stream temperatures (Fox *et al*., 2016; Gido *et al*., 2010; Kustu *et al*., 2010), has led to habitat degradation and resulted in changes to flow regimes, habitat connectivity, increased severity and spread of disease and, ultimately, fish population declines. For example, changing water

levels, shoreline development and loss of marshes in the Great Lakes have been related to the decline of northern pike *Esox lucius* L. populations (Casselman & Lewis, 1996). Salmon populations on the West Coast of the United States have been listed as threatened or endangered as a result of loss of habitat due to barriers to migration (Nehlsen *et al*., 1991; Northwest Power Planning Council, 1987; Sheer & Steel, 2006). Habitat degradation in the form of sediment accumulation in Windy Gap Reservoir, Colorado, has contributed to the establishment and perpetuation of *Myxobolus cerebralis,* the parasite that causes whirling disease, in the upper Colorado River,

resulting in rainbow trout *Oncorhynchus mykiss* (Walbaum 1792) population decline (Nehring, 2006). *Tubifex tubifex* worms, the secondary host for *M. cerebralis* (Markiw & Wolf, 1983; Wolf & Markiw, 1984), prefer sand/silt habitats with high organic matter (Granath Jr. & Gilbert, 2002), and accumulation of fine particles in near-shore salmonid fry habitats due to decreased or regulated flows contributes to *T. tubifex* proliferation (Thompson, 2011) and increased infection rates in susceptible individuals. Habitat is clearly a driving factor in fish population dynamics, and a broader understanding of how species interact with their habitat throughout their life cycle, and how habitat degradation affects those interactions, is needed for effective population management.

As an organism grows and matures, its use of habitat changes over time (Hayes *et al*., 1996; Shutter, 1990). Salmonids use a suite of habitats throughout their life cycle. Within streams, fry, as compared to older life stages, prefer the shallower and slower velocities typically found along the margins (Horner & Bjornn, 1976; Miller, 1957; Raleigh *et al*., 1984), with cover types that commonly consist of vegetation and interstitial spaces between rocks, allowing for easier escape from predators (Griffith, 1972; Raleigh *et al*., 1984). Overwinter fry habitat consists of shallow water with low velocity (Bustard & Narver, 1975; Huusko *et al*., 2007), with cobble-boulder substrate providing the main cover (Griffith & Smith, 1995). As fry grow, habitat preferences change (Cramer & Ackerman, 2009), and fish move into deeper and faster water that is shared with adults (Raleigh *et al*., 1984). The deeper and faster water provides larger prey (aquatic insects and fish) and cover consisting of larger substrate types (boulders), logs, debris, overhanging banks and riffles (Bustard & Narver, 1975). Juvenile and adult overwinter habitat tends to differ from summer habitat (Raleigh *et al*., 1984), where instream substrate, log jams, undercut banks and overhanging vegetation are often used if present (Wesche, 1980), as are deeper pools where depth is assumed to provide the requisite cover requirements (Cunjak, 1996).

Stocking is a key management strategy for reestablishing, maintaining or enhancing stream and river salmonid populations, and specific habitat variables likely play an important role in the retention, survival and growth of stocked fish. For example, stream temperature affects the survival of *O. mykiss* in their first winter (Meyer and Griffith, 1997), and temperature and water velocities have been shown to affect the growth of age-0 *O. mykiss* (Korman & Campana, 2009). Increasing the success of stocking events may require an understanding of habitat associations of both wild and stocked fish and stocking fish into the correct habitats to increase survival and recruitment. In addition, different strains of fish may be stocked for a myriad of reasons, *e.g*., varied angling opportunities or disease-resistance characteristics. Disease may be an especially important consideration in conjunction with habitat in systems where specific pathogens are established. Avila *et al*. (2018) showed that the stream characteristics in systems in which *M. cerebralis* was present or absent affected the survival of two *M. cerebralis*–resistant strains of *O. mykiss*, stocked as fry, 2 months after stocking. The presence of other species may also affect stocking success. Previous work has shown that brown trout *Salmo trutta* L. competition with *O. mykiss* results in the exclusion of

O. mykiss fry from desired habitats (Gatz *et al*., 1987), and fry stocking success may be affected by predation from larger *S. trutta* (Avila *et al*., 2018). Although mechanical removals may be an option for reducing competition and predation between stocked *O. mykiss* and *S. trutta*, removals can be both time intensive and expensive (Fetherman *et al*., 2015). Restoration activities could present an alternative to mechanical removals if habitat associations differed between the two species, especially in locations where these management actions are already planned or taking place.

The aim of this study was to first assess the physical habitat variables that affect fry abundance and distribution in the upper Colorado River, Colorado, and determine if fry habitat preferences differ between *S. trutta* and *O. mykiss* fry such that habitat restoration activities could target specific habitats to reduce competition between the two species during early life stages. Based on previous research (Fetherman *et al*., 2014) and observations from continued long-term monitoring, it was expected that mean substrate size, velocity and depth in near-shore habitats would differ between the two species and potentially between stocked and wild *O. mykiss* fry due to differences in their genetic background. In addition, the authors expected that habitat associations of both *S. trutta* and *O. mykiss* fry would differ from published suitability indices (SI) (Raleigh *et al*., 1984; Raleigh *et al*., 1986) due to interspecific competition, *O. mykiss* fry stocking or the presence of *M. cerebralis* (established). Second, the authors expected variations in habitat across sites to differentially affect exposure to *M. cerebralis* and thereby the presence and abundance of salmonid fry. Restoration activities could target favourable *T. tubifex* habitats that perpetuate *M. cerebralis* exposure, thereby increasing the survival and establishment success of *O. mykiss*.

2 | MATERIALS AND METHODS

2.1 | Site description

The fry habitat associations study was conducted in a 6.3 km section of the upper Colorado River (Grand County, Colorado; Figure 1). Flows through this section of the Colorado River are partially regulated by Windy Gap dam, with discharge over the course of the study (July through October 2018) averaging 3.8 m^3 s^{-1}, ranging from 1.8 to 7.7 m^3 s^{-1} (USGS, 2019). Temperatures in this section range from 3.4°C in the winter to 16.2°C in the summer, with a mean annual temperature of 10.7°C (Fetherman *et al*., 2014).

The whirling disease parasite *M. cerebralis* was established in the upper Colorado River in the early 1990s (Nehring, 2006). The result was the elimination of *O. mykiss* age-0 recruitment, leading to the collapse of the *O. mykiss* population, leaving *S. trutta* as the dominant salmonid in the system (Nehring & Walker, 1996). *S. trutta* are more resistant to *M. cerebralis* than *O. mykiss*, having evolved with *M. cerebralis* in their native, European home ranges (Hedrick *et al*., 1999; Hedrick *et al*., 2003; Hoffman, 1970), and reproduce naturally and are self-sustaining within the study section. *O. mykiss* populations in the river are primarily maintained through stocking of

FIGURE 1 Fry site locations used to obtain abundance estimates or single-pass counts for *Salmo trutta* and *Oncorhynchus mykiss* in the upper Colorado River study section in Grand County, Colorado, downstream of Windy Gap Reservoir. The 20 15.2 m sites, sampled five times from July through October 2018, included one abundance estimation and four single-pass sites at the Sheriff Ranch, four single-pass sites at Kinney Creek, two abundance estimation and five single-pass sites in the Red Barn area and one abundance estimation and three single-pass sites at Hitching Post
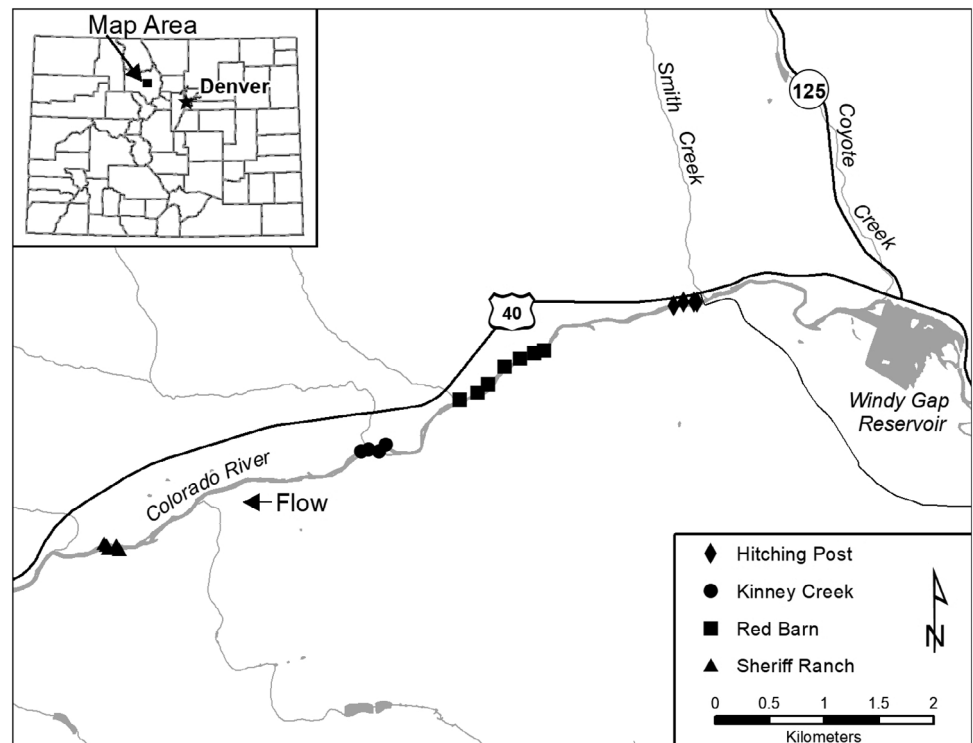
M. cerebralis–resistant *O. mykiss*, previously subcatchable fish [172–238 mm total length (TL); Fetherman *et al*., 2014] and more recently fry (<50 mm TL), although some natural reproduction does occur.

Fry stocking, which was considered to increase survival by reducing hatchery-related behavioural conditioning (Jackson & Brown, 2011; Olla *et al*., 1998), became the primary management option for this section of the Colorado River after low recruitment and survival rates were observed using subcatchable *O. mykiss* (Fetherman *et al*., 2014). Stocked *O. mykiss* fry have shown increased survival and recruitment compared to stocking larger fish in the Colorado and Gunnison rivers (Fetherman & Schisler, 2016). On 16 July 2018, *O. mykiss* fry (62,000; 37.7 ± 0.3 mm TL) were stocked from a raft in the margins on both sides of the river between Hitching Post and the lowermost Red Barn fry sampling site (Figure 1).

2.2 | Fry sampling

Fry were sampled at 20 15.2 m long sites, 4 in which abundance was estimated and 16 from which single-pass counts were obtained (Figure 1). Fry abundance was estimated at one site at the Sheriff Ranch, two sites in the Red Barn area and one site at Hitching Post. These four sites were historically sampled on an annual basis to monitor natural reproduction (Fetherman *et al*., 2014) and stocked fry survival. Fry estimates were accomplished using two Smith-Root LR-24 backpack electrofishing units running side-by-side to cover available fry habitat. Backpack settings for voltage were recorded from each site to determine their effect on fry detection probabilities, obtained

by running the quick set-up function on the LR-24 units. Three passes were completed through each site, and fry were removed on each pass. The number of *O. mykiss* and *S. trutta* fry captured was recorded, per pass, and all fry encountered were measured and returned to the site.

An additional 16 sites were included to increase sample size and inference regarding fry habitat associations: 4 sites at Sheriff Ranch, 4 sites at Kinney Creek, 5 sites in the Red Barn area and 3 sites at Hitching Post (Figure 1). Due to limited sampling time, only one removal pass was conducted through each of these 16 sites to obtain counts per site, by species, using the same electrofishing methods described earlier for fry abundance estimation. All 20 sites were sampled five times, twice in July, before and after *O. mykiss* fry stocking, and once a month near the end of August, September and October.

2.3 | Ethical statement

Sampling was approved by Colorado Parks and Wildlife (CPW), and care and use of experimental animals complied with the guidelines and policies of CPW, as approved by the CPW scientific collection permit DOW087.

2.4 | Habitat data collection

Habitat covariate data considered to explain fry habitat associations and distribution were collected from each of the 20 sites on all five sampling occasions. Covariates included mean substrate size (D_{50})

obtained through pebble counts, temperature (°C), dissolved oxygen concentration (percentage saturation and mg l^{-1}; August through October only), velocity (m s^{-1}), depth (m), fry site width (m) and presence of wood in the site (binomial; present or absent). Pebble counts were obtained, and D_{50} was calculated using the methods presented in Rosgen (1996). Because river discharge was low and relatively consistent across the 5 months of the study, pebble counts were collected once from each site in July and did not change between the July and October sampling occasions. Temperature and dissolved oxygen were obtained from the lower, middle and upper thirds of each fry site, using a YSI Pro 1020 dissolved oxygen and temperature meter. The sensor was placed at an average depth at half the fry site width, and values were recorded once consistency in the readings was achieved. Depth measurements and depth-average velocity, measured by setting a flow sensor to 0.6 of the measured depth from the water surface, were recorded at the same three locations using a Marsh-McBirney flowmeter attached to a wading rod that measured depth in 0.03 m increments (Avila, 2016; Richer et al., 2020). Fry site width was measured based on the farthest distance from shore a fry of either species was captured within the site and changed with each visit. Finally, wood, in the form of downed trees or woody growth from the bank, was recorded as present or absent in each site. Similar to pebble counts, the presence of wood in a site did not change between the July and October sampling occasions.

2.5 | *M. cerebralis* sample collection

Although stocking of *M. cerebralis*–resistant *O. mykiss* fry has resulted in increased survival and recruitment (Fetherman & Schisler, 2016), the pathogen continues to persist in the upper Colorado River and remains an obstacle for reestablishing *O. mykiss* in the system. In October, up to five *S. trutta* fry and five *O. mykiss* fry, dependent upon availability, were collected from each of the four abundance estimation sites at Sheriff Ranch, Red Barn and Hitching Post as part of a long-term monitoring study of *M. cerebralis* infection and prevalence in wild fish populations. In addition, one to two fry per species per site were collected from the 16 single-pass count sites in the Sheriff Ranch, Kinney Creek, Red Barn and Hitching Post areas. Collecting fry in October ensured full development of myxospores following previous natural exposure to the triactinomyxon, the infectious waterborne stage of the parasite (Hedrick & El-Matbouli, 2002) released by *T. tubifex*. Myxospores were enumerated (O'Grodnick, 1975) from whole fish using the pepsin–trypsin digest method (Markiw and Markiw & Wolf, 1974) by the CPW Aquatic Animal Health Laboratory (Brush, Colorado).

2.6 | Statistical analyses

Occupancy rates were estimated for each species using the occupancy estimation with detection <1 estimator in programme MARK (White & Burnham, 1999). Model sets were structured separately for *S. trutta* and *O. mykiss* fry using encounter histories constructed for each site

and including five encounter occasions, with each occasion containing a "1" if the species was detected and "0" if it was not detected. Encounter histories also included site-specific individual covariates for D_{50}, backpack voltage settings, velocity, depth, temperature and presence of wood, and the *O. mykiss* encounter histories included an additional individual covariate representing whether the site had been stocked in July. Model sets included intercept models for detection probability, P, and occupancy probability, ψ. Additional models were constructed in which P varied by the individual or additive combinations of D_{50}, backpack voltage and/or velocity, and ψ varied by D_{50}, velocity, depth, temperature, presence of wood and/or stocking status (*O. mykiss* only). Models were ranked using AIC corrected for small sample sizes (AIC$_c$), compared using AIC$_c$ differences (ΔAIC$_c$) and ranked using model weights (w_i; Burnham & Anderson, 2002). Model-averaged parameter estimates and associated unconditional standard errors were reported from each model set ($w_i > 0$; Anderson, 2008).

Fry abundance estimates, N, were obtained from three pass removal data using a Huggins closed capture–recapture estimator in programme MARK. As a removal estimate, only P was estimated from the likelihood, whereas the recapture probability, c, was set to zero since fish could not be recaptured on subsequent passes. Fry length was included as an individual covariate in the encounter histories. The model set included an intercept model for P, as well as models in which P differed individually or additively by pass, fish length, velocity, D_{50}, backpack voltage settings and stocking status, and N was estimated as a derived parameter (Huggins, 1989). *S. trutta* and *O. mykiss* abundances were estimated separately.

Fry abundance estimates and counts were used to explore habitat associations of *S. trutta* and *O. mykiss* fry. Initially, Proc Corr (SAS institute, 2019) was used to obtain Pearson correlation coefficients and determine if habitat variables were correlated. Width was highly correlated with fry TL, likely because fry move towards the centre of the river as they get larger (Chapman & Bjornn, 1969; Mitro & Zale, 2002; Northcote, 1992). Other habitat variables (*e.g.*, D_{50}) were collected based on site width and considered to be more explanatory, so width was removed from further analyses. Within the count data, presence of wood was correlated with velocity, D_{50}, and stocking status, and velocity, depth and temperature were correlated with each other. For the abundance data, presence of wood was correlated with velocity, temperature and depth. Although these habitat variables were later retained in the habitat association model sets, correlated variables were never included in the same model.

The authors used a general linear model (GLM) as implemented in SAS Proc GLM to evaluate fry habitat associations. Model sets were constructed separately using abundance or count data for *S. trutta* and *O. mykiss* and included an intercept model, and individual and additive combinations of D_{50}, presence of wood, temperature, depth, velocity and stocking status, within the confines of the previously described correlation analyses. In addition, a quadratic relationship was included for D_{50}, temperature, depth and velocity to determine if instead of a linear relationship a minimum or maximum value for these covariates existed within the range of measurements recorded. To balance parameter number and sample size, only one quadratic

relationship was included in any given model; nonetheless, other variables were considered additively with the quadratic relationship. Model weights and ΔAIC_c ranking were used to determine support for each of the models in the set, and parameter estimates were reported from the candidate model with the lowest AIC_c value (Burnham & Anderson, 2002).

Two AIC analyses were conducted using a GLM to determine how *M. cerebralis* exposure affected salmonid fry distribution across the sites and if certain habitat variables were associated with fry myxospore count. The first analysis included two models, an intercept model and a model in which the change in fry numbers between July and October was explained by myxospore count, as a measure of infection severity, obtained from fry collected in October. The second analysis included individual and additive combinations of the habitat variables measured in the fry sites as explanatory variables for fry myxospore counts obtained from the various sites. The results are presented as described earlier for the fry habitat association analyses.

3 | RESULTS

3.1 | Habitat characteristics of fry sites

D_{50} varied widely among fry sites, averaging 72 (S.E., 13) mm and ranging from 0 to 220 mm (Table 1). The average temperature range was fairly narrow across sites, ranging from 12.8 to 15.8°C, although temperatures in July reached 22.7°C and in October were as low as 3.3°C. Dissolved oxygen saturation was generally greater than 100%, and concentration was greater than 8 mg l^{-1}. As such, dissolved oxygen was not included as an explanatory variable for fry abundance or distribution because it never decreased below levels considered optimal for trout (Piper *et al.*, 1982). Average velocity ranged from 0.03 to 0.50 m s^{-1}, depth ranged from 0.09 to 0.22 m and width varied from 0.6 to 3.8 m. Depth and velocity were higher during periods of higher discharge in July, whereas fry site width was widest in October when fry started moving towards the centre of the river as they grew. Wood, either downed trees or woody growth from the shore, was present in 50% of the sites (Table 1).

3.2 | Fry occupancy

S. trutta fry were detected in all sites during all sampling occasions, with the exception of one site in the Kinney Creek area in October. Occupancy for *S. trutta* was estimated to be one, with depth and D_{50} being the best predictors of ψ, although regression coefficients for both overlapped zero. *S. trutta* P (±unconditional S.E.) within any given sampling occasion was ≥0.98 (±0.01). *O. mykiss* fry were not detected in all fry sites, with two sites in the Kinney Creek area in which *O. mykiss* fry were never observed. Despite less-frequent detection,

TABLE 1 Absolute (D_{50} and presence of wood) and average (±S.E.) values for temperature, dissolved oxygen (DO) concentration, velocity, depth and width for the 20 sites (Sheriff Ranch = SR, Kinney Creek = KC, Red Barn = RB and Hitching Post = HP) from which *Salmo trutta* and *Oncorhynchus mykiss* fry abundance estimates or single-pass counts were obtained in July through October 2018

Site	D_{50} (mm)	Temperature (°C)	DO (% sat.)	DO (mg l^{-1})	Velocity (m s^{-1})	Depth (m)	Width (m)	Wood
SR1	96	14.1 ± 3.3	105 ± 6	9.2 ± 0.4	0.19 ± 0.04	0.20 ± 0.01	2.7 ± 0.5	−
SR2	53	12.8 ± 2.8	103 ± 5	9.2 ± 0.5	0.32 ± 0.05	0.31 ± 0.02	1.8 ± 0.4	−
SR3	31	13.7 ± 3.0	107 ± 5	9.3 ± 0.5	0.13 ± 0.04	0.15 ± 0.01	2.4 ± 0.3	+
SR4	177	13.8 ± 3.0	107 ± 5	9.3 ± 0.4	0.28 ± 0.07	0.17 ± 0.01	2.6 ± 0.3	−
SR5	6	14.2 ± 3.0	105 ± 6	9.1 ± 0.5	0.11 ± 0.05	0.15 ± 0.03	0.7 ± 0.1	−
KC1	115	14.0 ± 2.6	106 ± 2	8.7 ± 0.5	0.08 ± 0.03	0.14 ± 0.01	2.2 ± 0.3	+
KC2	26	14.6 ± 2.5	103 ± 3	8.5 ± 0.6	0.03 ± 0.02	0.17 ± 0.02	1.5 ± 0.3	+
KC3	0	14.5 ± 2.4	116 ± 3	9.6 ± 0.6	0.26 ± 0.07	0.15 ± 0.01	0.6 ± 0.1	−
KC4	81	15.3 ± 2.2	113 ± 3	9.0 ± 0.5	0.07 ± 0.04	0.18 ± 0.02	1.5 ± 0.2	−
RB1	82	15.4 ± 1.8	118 ± 1	9.4 ± 0.5	0.22 ± 0.04	0.16 ± 0.01	3.4 ± 0.7	−
RB2	112	15.8 ± 1.8	115 ± 3	9.1 ± 0.5	0.35 ± 0.06	0.15 ± 0.02	1.9 ± 0.4	+
RB3	30	15.6 ± 1.6	118 ± 3	9.2 ± 0.5	0.17 ± 0.04	0.09 ± 0.01	1.8 ± 0.2	−
RB4	19	15.5 ± 1.6	119 ± 3	9.3 ± 0.5	0.50 ± 0.08	0.22 ± 0.01	1.4 ± 0.3	+
RB5	44	15.0 ± 1.7	110 ± 3	8.8 ± 0.5	0.25 ± 0.08	0.14 ± 0.01	1.8 ± 0.2	+
RB6	10	14.7 ± 1.7	102 ± 4	8.2 ± 0.6	0.07 ± 0.03	0.22 ± 0.01	1.2 ± 0.3	+
RB7	220	14.5 ± 1.7	100 ± 3	8.1 ± 0.6	0.04 ± 0.01	0.14 ± 0.02	3.0 ± 0.4	+
HP1	120	14.4 ± 2.1	105 ± 4	8.7 ± 0.2	0.18 ± 0.04	0.19 ± 0.01	3.5 ± 0.7	−
HP2	39	13.7 ± 1.8	109 ± 2	9.0 ± 0.4	0.11 ± 0.05	0.14 ± 0.01	1.7 ± 0.2	+
HP3	66	14.3 ± 1.8	111 ± 5	9.0 ± 0.3	0.15 ± 0.04	0.19 ± 0.01	2.7 ± 0.5	+
HP4	121	14.4 ± 2.1	103 ± 5	8.4 ± 0.3	0.12 ± 0.03	0.13 ± 0.01	3.8 ± 0.7	−

O. mykiss fry ψ was estimated to be 0.99 (±0.01), with D_{50} being the best predictor of ψ, although the regression coefficient overlapped zero. Nonetheless, *P* was lower than that for *S. trutta* fry at 0.65 (±0.06). D_{50} had a positive effect on *P*, suggesting that *O. mykiss* were more likely to be detected in sites with a larger D_{50}.

3.3 | *S. trutta* fry habitat associations

A quadratic relationship for D_{50} appeared in the top four models of the *S. trutta* single pass count analysis and had the highest cumulative weight of any variable in the model set (cumulative AIC_c weight = 0.81). The number of *S. trutta* fry per site was maximized at a D_{50} of 151 mm and was ≥10 per site (658 fry per km) between a D_{50} of 96 and 206 mm (Figure 2). Temperature (cumulative AIC_c weight = 0.35) appeared in the top model, but the next highest model in which it was included had a ΔAIC_c of 4.85. Depth and velocity (cumulative AIC_c weights of 0.11), linear relationships of which were included in models with ΔAIC_c of 2.29 and 2.39, respectively, appeared to have lesser effects on *S. trutta* fry counts (Figure 2). Upon further examination of fry sites with a D_{50} between 96 and 206 mm containing ≥10 *S. trutta* fry per site (*n* = 13), counts were highest when depth averaged 0.18 (±0.03) m and velocity averaged 0.20 (±0.09) m s^{-1}. Sites meeting these average depth and velocity criteria contained 2.2 and 1.5 times more *S. trutta* fry than stocked *O. mykiss* fry, respectively.
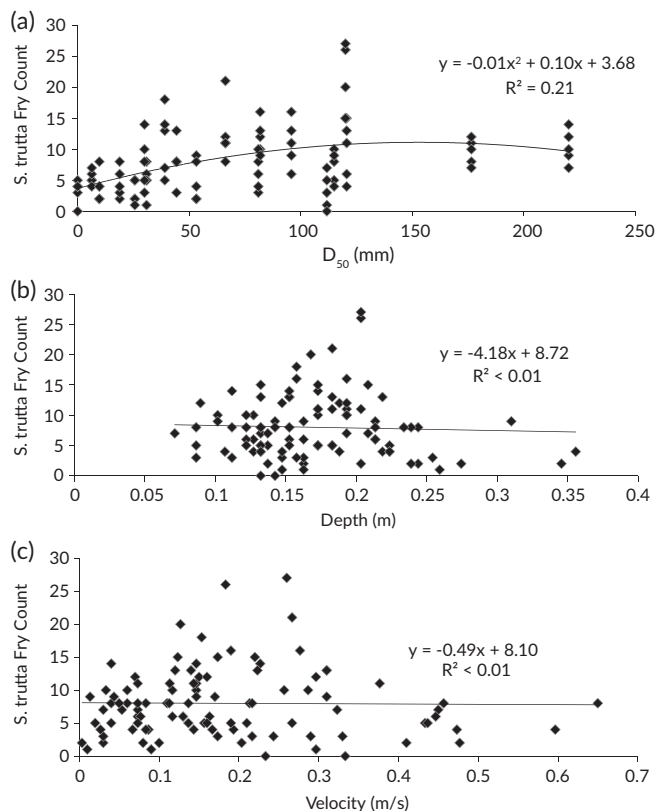

FIGURE 2 *Salmo trutta* fry single-pass counts and associations with (a) D_{50}, (b) depth and (c) velocity

S. trutta abundance was similarly predicted by a quadratic relationship for D_{50}, which appeared in all but the second model of the set, and had a cumulative AIC_c weight of 0.90. Abundance was highest in the site with a D_{50} of 120 mm, within the optimum range obtained from the *S. trutta* fry count data. Presence of wood (cumulative AIC_c weight = 0.99) was the only other variable to have an effect, appearing in the first two models. *S. trutta* abundance was lowest in one of the four sites that contained wood (Figure 3).

3.4 | *O. mykiss* fry habitat associations

Stocking had the largest effect on *O. mykiss* fry single-pass counts (cumulative AIC_c weight = 0.95), appearing in all models with ΔAIC_c ≤ 5.58. The top model also contained the effects of D_{50} (cumulative AIC_c weight = 0.5) and temperature (cumulative AIC_c weight = 0.33), although the effect of temperature was expected given a similar effect in *S. trutta* fry counts. Velocity (cumulative AIC_c weight = 0.20) appeared in the third model of the set (ΔAIC_c = 0.94). Because stocking had a large effect on fry count, D_{50} and velocity were compared between sites where stocking did or did not (*i.e.*, natural reproduction) occur. There was no observable relationship between counts and D_{50} or velocity in sites in which only natural reproduction occurred, likely due to the lower counts obtained from those sites. *O. mykiss* fry numbers in stocked sites increased with an increase in D_{50} (Figure 4), although *S. trutta* and *O. mykiss* fry counts were similar at the maximum measured D_{50} of 220 mm. Similarly, increased velocities resulted in increased counts of *O. mykiss* fry in stocked sites (Figure 4). In sites containing more than five *O. mykiss* fry (328 fry per km), D_{50} averaged 118 (±71) mm, 22% lower than the average D_{50} for *S. trutta* fry, and velocity averaged 0.23 (±0.13) m s^{-1}, 13% higher than the average velocity for *S. trutta* fry.

Stocking also had the largest effect on *O. mykiss* trout fry abundance (cumulative AIC_c weight = 0.62), appearing in the top three models of the set. A quadratic effect for velocity appeared in the top
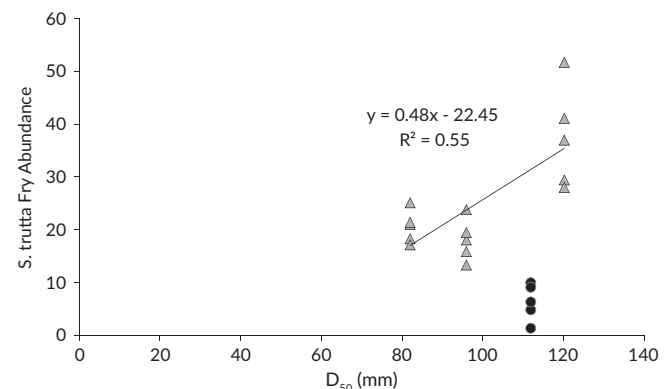

FIGURE 3 *Salmo trutta* fry abundances from the four sites in which three pass removals were conducted in July through October 2018 and associations with D_{50} and presence of wood. The trendline shows the relationship between *S. trutta* fry abundance and D_{50} in the three sites in which wood was absent (●) Wood (△) No Wood
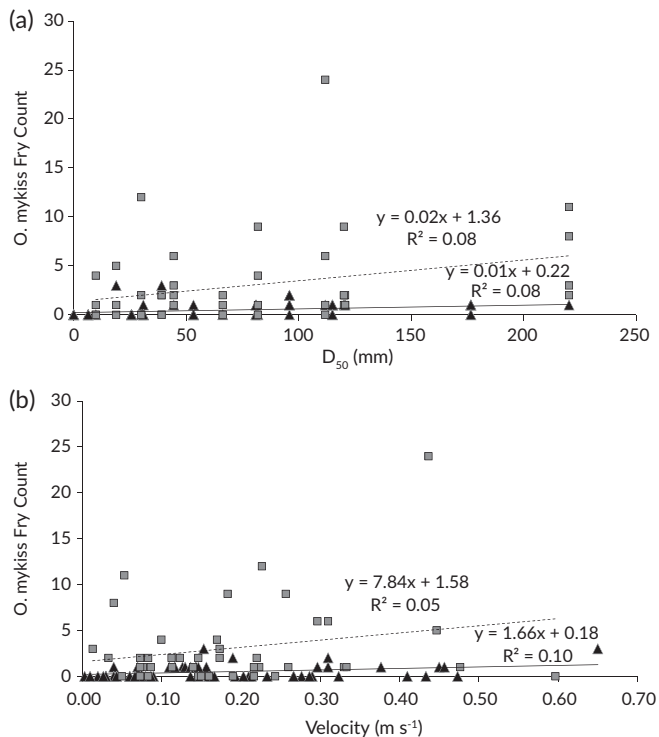
FIGURE 4 *Oncorhynchus mykiss* fry counts from sites in which *O. mykiss* were or were not (*i.e.*, natural reproduction) stocked and associations with (a) D_{50} and (b) velocity. A trendline shows the relationship between each habitat variable and the fry count data for both the sites that were stocked (dotted line) and not stocked (solid line) (▲) Not Stocked (■) Stocked

model, and when compared across sites that were or were not stocked, a similar positive relationship was observed between velocity and abundance as for the count data (Figure 5). The average velocity in the stocked sites was 0.24 (±0.09) m s^{-1}, but the highest abundance was obtained from sites with a velocity of 0.45 m s^{-1}. Despite lower *O. mykiss* fry abundance overall, 1.5 times more stocked *O. mykiss* fry were present than *S. trutta* fry in sites with a velocity of 0.45 m s^{-1}. Depth had the second-highest cumulative AIC$_c$ weight (0.35) relative to stocking. The average depth in stocked fry sites was 0.17 (±0.03) m, and overall, depth had a negative effect on *O. mykiss* fry abundance in stocked sites (Figure 5). The highest abundances were obtained in sites with a depth of 0.13 m, which contained 1.7 times more stocked *O. mykiss* fry than *S. trutta* fry. Unlike *O. mykiss* fry counts, no effect of D_{50} on *O. mykiss* fry abundance was observed.

3.5 | *M. cerebralis* habitat correlations

Myxospore counts (±S.E.) for *O. mykiss* averaged 12,268 (±9333) myxospores per fish, ranging from 0 to 109,233 myxospores per fish across the sites, whereas *S. trutta* averaged 11,123 (±4744) myxospores per fish, ranging from 0 to 134,678 myxospores per fish. Myxospore count did not appear to have an effect on the change in salmonid fry numbers within a site between July and October, with
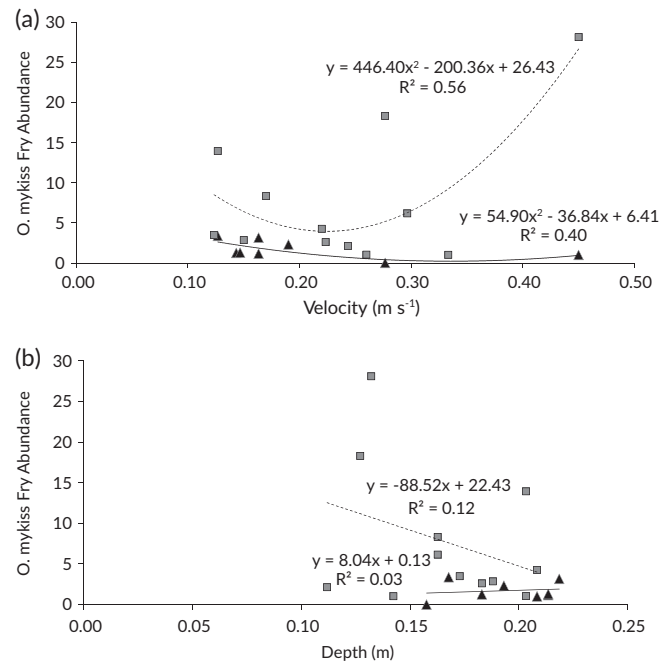

FIGURE 5 *Oncorhynchus mykiss* fry abundances from the four sites in which three pass removals were conducted in July through October 2018 and associations with (a) velocity and (b) depth. A trendline shows the relationship between each habitat variable and the fry abundance data for both the sites that were stocked (dotted line) and not stocked (solid line) (▲) Not Stocked (■) Stocked

the intercept model as the top model ($w_{intercept} = 0.72$, $w_{change} = 0.28$). In addition, the measured habitat variables appeared to have little effect on myxospore count, with the intercept model being the top model of the set. Nonetheless, models containing individual habitat covariates appeared in models with a $\Delta AIC_c \leq 2.24$. D_{50} (cumulative AICc weight = 0.40) had a negative effect on myxospore count, suggesting that myxospore counts decreased with an increase in D_{50}. Although depth, velocity and temperature appeared in weighted models within the set (cumulative AIC$_c$ weights = 0.26, 0.24 and 0.24, respectively), no effect on myxospore count was observed for these three variables.

4 | DISCUSSION

The results show that *S. trutta* and *O. mykiss* fry exhibit varying but overlapping habitat associations in the upper Colorado River, especially with respect to mean substrate size, velocity and depth. Occupancy results suggest that there were no fry sites that contained only *S. trutta* or *O. mykiss* fry, which resulted in weak statistical relationships between occupancy and measured habitat variables, such as D_{50}, because all sites contained both species. Had there been more sites in which one or the other species was absent, the relationship between occupancy and D_{50} would likely have been more apparent. Nonetheless, detection probability results suggest that *O. mykiss* were more likely to occupy sites with a higher D_{50}, and this was supported

by the fry count results showing that *O. mykiss* numbers in stocked sites increased with an increase in D_{50}. Given the overlap in site occupancy and average habitat associations of *S. trutta* and *O. mykiss* fry, differences in expected (Raleigh *et al*., 1984) and observed suitabilities for *O. mykiss* may be a result of competitive exclusion from more suitable habitat by *S. trutta* fry (Gatz *et al*., 1987), which are more abundant. *S. trutta* densities increased in many of Colorado's rivers after the loss of *O. mykiss* populations to whirling disease (Nehring & Thompson, 2001), with similar declines observed in several drainages in Montana (Baldwin *et al*., 1998; Granath Jr. *et al*., 2007). Mechanical removal of *S. trutta* populations has been studied as a management option for reintroducing or increasing *O. mykiss* populations in Colorado waters, with some locations showing greater success than others (Fetherman *et al*., 2015; Fetherman *et al*., 2018). *S. trutta* population manipulation has not been attempted in the upper Colorado River, and current management, *O. mykiss* fry stocking, has resulted in increased fry survival and recruitment (Fetherman & Schisler, 2017). Despite overlapping associations, the results suggest that there may be an opportunity to further increase *O. mykiss* fry survival through exclusion of *S. trutta* fry, which could be accomplished by incorporating higher velocities (>0.23 m s^{-1}) and shallower depths (<0.17 m) into near-shore habitats during restoration. This is supported by the higher *O. mykiss* vs. *S. trutta* abundances observed in shallower and higher-velocity sites even though *O. mykiss* fry were less abundant overall throughout the study section.

Habitat associations for both *S. trutta* and *O. mykiss* fry were similar to published SI for some habitat variables but differed for others. Habitat SI for *S. trutta* fry are highest (SI = 1.0) in gravel (particle size 2–64 mm) and lower (SI = 0.35) in cobble/rubble (particle size 64–250 mm) substrate types (Raleigh *et al*., 1986). Nonetheless, the results suggest that *S. trutta* fry are more often associated with cobble/rubble in the Colorado River and less so with gravel, although high counts were obtained from some gravel-dominated sites. The depth at which *S. trutta* numbers were highest is well shallower than that considered optimal for *S. trutta* fry (0.40 m; Raleigh *et al*., 1986), although all of the sites were shallower than 0.40 m (SI < 0.19 for depth across all sites). Velocity was within the optimal range (SI = 1) previously reported for *S. trutta* fry (Raleigh *et al*., 1986). Cover is also an important component in *S. trutta* fry habitat suitability (Raleigh *et al*., 1986), with a maximum suitability when cover is greater than 10%. The presence of wood did not increase fry counts or abundances for either species, although the percentage of the site occupied by wood was not quantified and could have been lower than 10%, or wood may not have functioned as cover. *S. trutta* abundances were lowest in one of the four sites that contained wood, but this site was also shallower with higher velocities that likely made the site less suitable for *S. trutta* fry. Temperature was within the optimal range for both *S. trutta* and *O. mykiss* fry (Raleigh *et al*., 1984; Raleigh *et al*., 1986); nonetheless, an effect of temperature was observed for both species. Overall, fry numbers were reduced in later sampling months when temperatures were cooler, which has been observed previously (Fetherman *et al*., 2014) and is likely a result of life history (Chapman & Bjornn, 1969; Mitro & Zale, 2002; Northcote, 1992).

O. mykiss fry counts exhibited a linear increase with D_{50} up to 220 mm, which is consistent with habitat SI, suggesting highest suitability (SI = 1) in cobble/rubble and boulder (particle size 250–4000 mm) substrates and SI ≤ 0.13 in substrates classified as gravel or smaller (Raleigh *et al*., 1984). A similar effect was not observed with *O. mykiss* abundance, likely due to the smaller number of abundance estimation sites which contained a wide range of D_{50} values, depths and velocities that may have affected their suitability for *O. mykiss* fry. Suitability for *O. mykiss* fry typically decreases in both sites that are shallower and have higher velocities (Raleigh *et al*., 1984), but the authors found the opposite associations with depth and velocity in their study. Nonetheless, it is important to note that values for velocity and depth were obtained independently (*i.e.*, no interaction), so it is unknown whether a combination of higher velocities and shallower depths would be beneficial for *O. mykiss* fry. Interactions were not included in the model sets to prevent over-parameterization. Statistical relationships and habitat association inferences may have been stronger if the data set had been large enough to include interactions, and the authors suggest incorporating interactions between habitat variables into future studies, if possible.

O. mykiss fry habitat associations were especially apparent in sites in which *O. mykiss* had been stocked, primarily because natural reproduction in the upper Colorado River remains low (Fetherman *et al*., 2014) and wild fry were more difficult to detect. It is probable, given their genetics and history of domestication (Hedrick *et al*., 2003; Schisler *et al*., 2006), that stocked *M. cerebralis*–resistant fry act differently from more wild-type fish and may exhibit different habitat associations than those previously described (Raleigh *et al*., 1984). *O. mykiss* fry stocking shows promise for restoring *O. mykiss* populations reduced by whirling disease (Avila *et al*., 2018; Fetherman *et al*., 2018) and will likely continue to be the primary management option for reestablishing or enhancing *O. mykiss* populations in systems where *M. cerebralis* is established. As such, understanding the habitat associations of stocked *O. mykiss* fry increases the knowledge of how these fish will interact with a novel lotic environment. The lack of clear habitat associations for wild *O. mykiss* fry may also suggest that habitat restoration activities initially designed to increase the survival of stocked *O. mykiss* fry will not have detrimental effects on wild fry survival when these systems eventually become wild fry dominated and rely on stocking declines, especially because wild populations established using *M. cerebralis*–resistant *O. mykiss* will have similar genetic backgrounds.

Overall, infection severity, as measured by myxospore count, did not have an effect on the change in fry number between July and October. Nonetheless, only those individuals more resistant to *M. cerebralis* are expected to be present in October (Fetherman *et al*., 2014), which may have resulted in the lack of an effect. Myxospore count decreased with an increase in D_{50}. *T. tubifex* worms prefer sand/silt habitats with high organic matter (Granath Jr. & Gilbert, 2002), and releases of the waterborne infectious stage of the parasite, triactinomyxons, from the worms likely drive salmonid infection severity (Hedrick & El-Matbouli, 2002; Kerans & Zale, 2002). As such, the results suggest that including larger particle sizes in near-shore habitats could decrease *T. tubifex* habitat and thereby infection severity,

especially in *O. mykiss* fry. It is important to note, however, that habitat variables were collected within the fry sites only. Triactinomyxons are buoyant and distributed throughout the water column (Kerans & Zale, 2002). Therefore, additional upstream habitat manipulations, specifically increased particle sizes to reduce *T. tubifex* habitat and increased velocities to prevent sediment deposition, may be required to reduce the production of and contact with triactinomyxons in near-shore fry habitats.

Habitat restoration activities continue to increase in large rivers (Roni *et al*., 2008; Vigmostad *et al*., 2005), including the upper Colorado River. Although many of these projects focus on improving juvenile and adult fish habitat (Roni, 2019; Roni *et al*., 2008), it is important to consider fry habitat and other ecosystem disturbances that may affect early life-stage survival during these activities as part of a broader biomic restoration approach (Johnson *et al*., 2020). In addition, restoration activities could be useful for either specific species or multispecies management, depending on the goals of the project. Current management in the Colorado River is focused on reestablishing *O. mykiss*, and the results suggest that there are opportunities for exclusion of *S. trutta* fry by adjusting design criteria based on differing habitat associations. Nonetheless, once *O. mykiss* are established, the goal will be to manage for both *S. trutta* and *O. mykiss* fry to provide diverse angling opportunities for Colorado anglers. The results suggest that a D_{50} of 151 mm (96–206 mm) will maximize fry number and abundance for both species, as will velocities ranging from 0.20 to 0.23 m s^{-1} and depths ranging from 0.17 to 0.18 m. Management strategies being used to (re)establish, maintain or enhance populations, *e.g*., stocking, should be considered as they may affect how salmonid fry associate with, distribute across and, ultimately, survive in near-shore habitats. In systems where pathogens, *e.g*., *M. cerebralis*, are established, the effects of habitat on the persistence of the pathogen life cycle should be considered for all primary-host susceptible life stages and species and incorporated into habitat restoration designs. Finally, the results show that factors such as interspecific competition, stocking and presence of pathogens can cause deviations in habitat associations from demonstrated SI and that evaluating system-specific differences may allow future habitat restoration activities to be more effective.

AUTHOR CONTRIBUTIONS

E.R.F. assisted with data generation, data analysis and manuscript preparation. B.W.A. helped with concepts, data generation and manuscript preparation.

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