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ORIGINAL ARTICLE

Rapid colonisation post-displacement contributes to native fish resilience

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Abstract

Native freshwater fish are experiencing global declines. Determining what drives native fish resilience to disturbance is crucial to understanding their persistence in the face of multiple stressors. Fish colonisation ability may be one factor affecting population resilience after disturbance. We conducted displacement experiments in headwater streams in Wyoming, USA, to evaluate mottled sculpin (*Cottus bairdii*) and mountain sucker (*Catostomus platyrhynchus*) colonisation ability. Specifically, we (1) determined whether fish could colonise sites rapidly after displacement, (2) evaluated site-level factors affecting colonisation, and (3) compared species-level differences in movement and colonisation capabilities. Mountain sucker recovered to pre-displacement abundances within 6–11 weeks, but mottled sculpin were still at slightly reduced abundances. For both species, the majority of colonists were unmarked new individuals and size–structure was similar to pre-displacement size–structure. Fish colonisation was best predicted by pre-displacement abundance and an interaction between per cent riparian cover and species identity. The slower colonisation rate of mottled sculpin may relate to movement ability as average daily movement rate and movement extent were significantly greater for mountain sucker. Our results demonstrate that colonisation is one mechanism allowing fish populations to be resilient in the face of disturbance and that species' traits provide insight into fish colonisation capabilities. Experimental approaches provide mechanistic insight into colonisation dynamics, enhancing our understanding of native fish resilience in degraded stream ecosystems and their response to restoration actions.

KEYWORDS
colonisation, defaunation, mottled sculpin, mountain sucker, movement, recovery

1 | INTRODUCTION

Streams organisms are well adapted to natural disturbance regimes (Lytle & Poff, 2004; Pickett & White, 1985). Disturbance events, such as floods or wildfires, can remove organisms from a section of stream, but many species exhibit high levels of resilience, or the ability to return to pre-disturbance abundances (Gido et al., 2019; Reice et al., 1990). Anthropogenic disturbances such as flow regulation, channelisation and bank stabilisation degrade stream habitat and reduce connectivity (Ward, 1998). In degraded streams, persistence relies on organisms tracking shifting spatial mosaics of suitable habitat patches (Thomas, 1994; Wiens, 1997). Native fish resilience in the presence of multiple stressors depends on the ability of a species to rapidly rebound from small abundances or colonise from nearby populations (Gido et al., 2019). Similarly, the success of stream restoration actions relies on fish colonising restored habitat (Stoll et al., 2014). Evaluating colonisation ability and the drivers of variation in colonisation is thus integral for predicting the consequences of disturbance events and restoration activities for fish populations.

Site- and species-level characteristics influence colonisation after disturbances. Site-level factors affecting the ability of fish to colonise areas after disturbance include local population abundance, the duration and spatial extent of the disturbance event, available refugia, habitat characteristics and stream connectivity (Albanese et al., 2009; Detenbeck et al., 1992; Falke et al., 2012). Mobility, flow preference and feeding group are key species-level traits that affect colonisation (Albanese et al., 2009; Stoll et al., 2014). Fish with greater movement rates are more likely to colonise sites after displacement (Albanese et al., 2009). Understanding the interaction between species-level and site-level characteristics in determining native fish colonisation is key to protecting local populations from extirpation.

Our goal was to examine short-term colonisation capabilities of two native fish species, mottled sculpin (*Cottus bairdii*) and mountain sucker (*Catostomus platyrhynchus*), and evaluate which site- and species-level factors most affected fish colonisation in headwater streams of the Wyoming Range. Our study system is characteristic of headwater streams subjected to frequent disturbance events from multiple land uses. Grazing and energy development are prevalent in our study streams, which has resulted in changes to the physical environment through increased sedimentation, channelisation and reduced woody vegetation (Girard & Walters, 2018). Native fish persist despite environmental alterations, providing an appropriate study system to examine mechanisms that allow for native fish resilience. We focussed on mottled sculpin and mountain sucker, as they are the most abundant species in the study system and contrast in their observed mobility (Aedo, 2008). Previous work examined year-to-year colonisation, persistence, and occupancy of mottled sculpin and mountain sucker in the Wyoming Range and found mottled sculpin had lower annual colonisation rates and occupancy rates than mountain sucker despite greater site-level persistence (Walker et al., 2019). Low site-level occupancy by mottled sculpin may be due to more limited movement and colonisation ability. We experimentally examined mountain sucker and mottled sculpin colonisation ability and compared species mobility to understand potential mechanisms underlying inter-annual occupancy dynamics.

We simulated a small-scale displacement event or restoration activity by removing fish and examined intra-seasonal colonisation. Our objectives were to (1) determine whether fish could colonise sites rapidly, within 6–11 weeks, after displacement, (2) evaluate site-level factors affecting colonisation for both species and (3) compare species-level differences in movement and colonisation capabilities. We predicted that fish would recover to pre-displacement abundance and size–structure because other studies found rapid recovery of stream fish density, richness, proportional composition and size–structure within a month (Hudy & Shiflet, 2009; Sheldon & Meffe, 1995). We predicted that colonisation would be positively correlated to initial fish abundances due to more potential colonisers and because higher fish numbers reflect higher quality habitat or a good habitat match (Albanese et al., 2009; Whitney et al., 2016). In addition, we predicted that mottled sculpin colonisation would be positively correlated to habitat complexity and per cent riparian cover because mottled sculpin exhibit greater sensitivity to degraded habitat (Girard & Walters, 2018). We predicted that mountain sucker would exhibit greater colonisation, movement rates and movement extent than mottled sculpin due to differences in life history and movement ability (Breen et al., 2009; Brown & Downhower, 1982; Deboer et al., 2015).

2 | METHODS

2.1 | Study sites

Our study sites are along the eastern slope of the Wyoming Range in the Upper Green River Basin (42°24′N, 110°18′W). This includes two drainages: South Beaver Drainage to the north and Dry Piney Drainage to the south (Figure 1). South Beaver Drainage is a tributary to South Piney Creek that flows into the Green River at Big Piney, Wyoming and Dry Piney Drainage meets the Green River approximately 14 km south of Big Piney, Wyoming, but is often disconnected from the river due to intermittent stream segments. Elevation ranges from 2106 to 2503 m across the study area. The predominant land uses in the study area are oil and gas extraction and cattle grazing. Cattle grazing is similar across drainages but varies seasonally as ranchers move cattle up in elevation to track changes in forage availability. Oil and gas development is concentrated in the southern Dry Piney Drainage. Stream sites associated with less anthropogenic land use contain a higher proportion of shrub cover, greater stream depths, gravel substrate and riffle habitats, whereas sites associated with greater anthropogenic land uses contain more fine sediments and run habitats (Girard & Walters, 2018). In 2018–2019, we randomly selected 31 sites from 68 previously monitored sites (Walker et al., 2019) to conduct an experimental displacement and examine colonisation (Figure 1). In addition, we selected four sites to assess fish movement abilities in the absence of experimental displacement. Selected stream segments cover a gradient of habitat characteristics, oil and gas development, and fish abundances. Streams are relatively small; site stream discharge during June-August 2018 and 2019 ranged from 0.01 to 0.45 m^3/s with a median of 0.06 m^3/s.

2.2 | Study species

We focussed on two native species, mottled sculpin and mountain sucker, which comprise 93% of fish captures in our study area. Mottled sculpin are widely distributed across North America, consume primarily benthic macroinvertebrates, and are nest spawners (Bailey, 1952; Deboer et al., 2015). Mountain sucker are distributed across western North America and feed predominantly on algae,

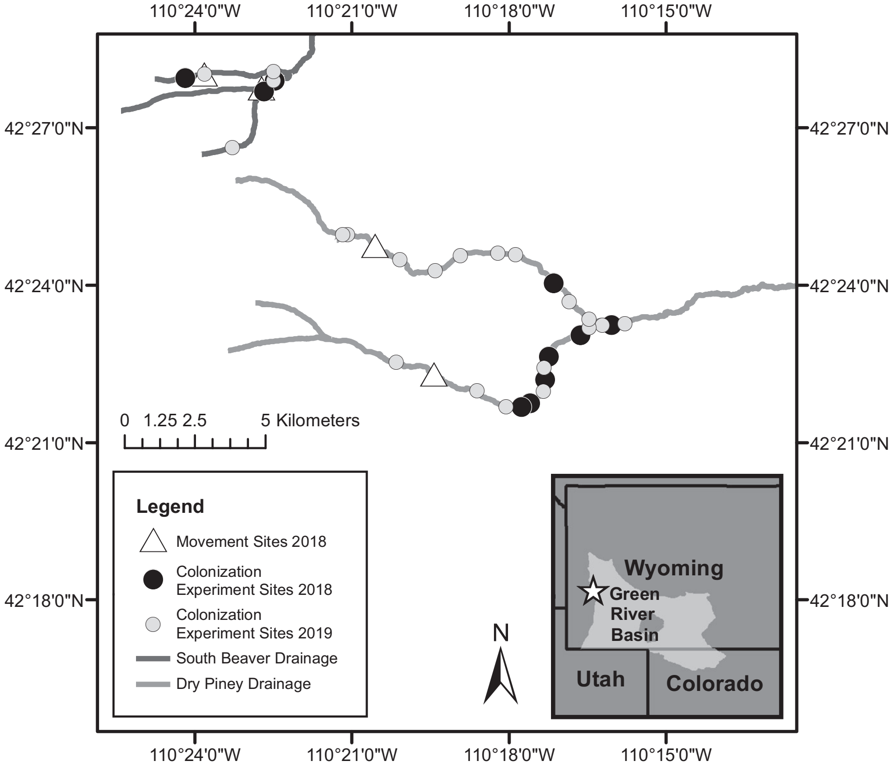

FIGURE 1 Map of study area in the Green River Basin, WY, where we conducted an experimental displacement at 31 sites (black and grey circles) to estimate native fish colonisation during 2018 and 2019. We also estimated fish movement at four sites (white triangles) during 2018

small invertebrates and organic matter (Belica & Nibbelink, 2006). Mottled sculpin prefer sites with less disturbed habitat and are fairly inactive being documented to move less than five m over a 45-day period (Girard & Walters, 2018; Petty & Grossman, 2004). In contrast, mountain sucker exhibit greater tolerance for degraded habitats and are more mobile, moving up to 1000 m prior to spawning in riffles (Belica & Nibbelink, 2006; Girard & Walters, 2018).

2.3 | Colonisation experiment

For the colonisation experiment, we removed fish from 31 experimental 100 m reaches to create an experimental displacement and examined short-term colonisation dynamics in relation to initial fish abundance and habitat characteristics. Fish were captured via multipass backpack electrofishing (Smith-Root LR-24) in 100 m closed reaches at experimental displacement sites from early June to early July during 2018 or 2019 (Figure 1). Reaches were closed during sampling to prevent emigration or immigration of fish into sites during fish removals. We completed up to five passes until no fish were seen during the last pass. We identified all fish to species and weighed, measured (standard length) and tagged individuals.

Fish were tagged so new colonisers could be distinguished from returning colonisers. During 2018 sampling, we inserted 12 x 2.1 mm PIT (passive integrated transponder) tags (0.08 g) into fish that weighed greater than 5 g (approximately 62 mm standard length) following protocol developed for mottled sculpin by Ruetz et al. (2006). We disinfected tags and tagging tools (12-gauge needles and syringes) in 70% isopropyl rubbing alcohol. We sedated fish with a 20 mg/L AQUI-S 20E (AQUI-S New Zealand Ltd.) solution (INAD Study # 11–741–18-147F) for approximately 2–4 min, inserted a 12 x 2.1 mm PIT tag into the body cavity of the fish using a 12-gauge hypodermic needle, and made a secondary mark on the fish by clipping a partial corner of the caudal fin. We held fish in net pens within experimental reaches for 12 h to estimate post-tagging survival. The following day, we evaluated mortality and tag loss. We recorded tag ID for fish that were deceased, and retagged and immediately released fish that survived but lost their tags. Lastly, we recorded tag ID, GPS location, time and date for every released fish.

In 2019, we switched from PIT tags to VIE (visual implant elastomer) tags, which allowed us to tag smaller individuals with minimum standard length of 30 mm (approximately 0.5 g). Due to this change in tagging protocol, we tagged 284 additional mottled sculpin with VIE tags. After collecting weights and lengths of individual fish, we sedated fish in AQUI-S 20 E solution as described above for the PIT-tagged fish. Prior to tagging, we prepared a sterile 0.3 cc injection syringe with visual implant elastomer following instructions from Northwest Marine Technology Inc. (2018). Each fish that was longer than 30 mm standard length was injected with a VIE tag ID which corresponded with the site at which the fish was captured. In 2019, fish were released the same day as sampling.

After tagging and environmental data collection (see below), we released fish 5–10 m upstream and downstream of the original site to imitate a small-scale displacement event or restoration activity. We determined this to be a reasonable distance to displace fish, as multiple studies have found mottled sculpin to be extremely sedentary, moving on average less than 5 m over an entire summer (Breen et al., 2009; Brown & Downhower, 1982; Deboer et al., 2015; Petty & Grossman, 2004). This displacement experiment left the 100-m site open and void of fish to allow for immediate colonisation.

We returned to each of the 31 colonisation sites, from late July to late August (6–11 weeks after displacement), to complete a final electrofishing survey to determine how many fish colonised the sites post-displacement. We completed three electrofishing passes to collect fish in 100-m closed reaches, placing netted fish into aerated buckets until processing. Between passes, we collected data on individuals including species, standard length, weight and tag ID for those with a PIT or VIE tag. After the three passes were complete and all fish were processed, we randomly distributed fish throughout the site, and re-opened the reach.

2.4 | Estimating pre-displacement abundance and colonists

Pre-displacement fish abundances per 100 m were estimated as the count of juvenile and adult fish that were captured during experimental fish removals (up to five passes). Colonist counts (per 100 m) were estimated as the count of juvenile and adult fish captured during the final electrofishing survey (three passes) including both tagged and untagged individuals. We considered using depletion estimates instead of fish counts; however, depletion estimates are less reliable for low fish counts and greater than 50% of sites had fewer than 10 mottled sculpin and/or mountain sucker during electrofishing surveys. Therefore, we retained fish counts for pre-displacement abundance and colonists counts. Due to low capture efficiency for small fish (Price & Peterson, 2010), we removed mottled sculpin and mountain sucker less than 30 mm standard length from analyses, which is the approximate minimum juvenile length for both species (Hauser, 1969; Petty, 1998; Wydoski & Wydoski, 2002).

To evaluate colonisation, we compared mean and standard error of fish abundances between the preliminary (pre-displacement) and final (post-displacement) electrofishing surveys using two paired *t* tests for each species. We also calculated the proportion of colonisers that were recaptures (PIT or VIE tagged fish). We examined the size–structure of captured fish, pre- and post-displacement, with length–frequency histograms and used a chi-square test with a 2000 iteration Monte Carlo simulation to compare distributions. We set $\alpha = 0.05$ as our significance level for all analyses.

2.5 | Environmental data

We collected environmental data at the 31 experimental displacement sites following fish capture and before fish release. At 10-m intervals along the colonisation sites, we created transects perpendicular to the stream flow and measured stream wetted width (m). At five equidistant points across each transect, we measured depth, substrate, water velocity and riparian cover (Yes/No). We categorised substrate as hardpan clay, silt, sand (0.06–2 mm), fine gravel (2–16 mm), coarse gravel (17–64 mm), cobble (64–250 mm) and boulder (250–1000 mm). We measured water velocity (m/s) using a Marsh McBirney Flo-MateTM velocity meter (Hach Company).

We estimated mean per cent riparian cover from transect data. This was included as a covariate in our global model as a metric of site-level disturbance. Sites with greater per cent riparian cover generally have lower anthropogenic land uses such as oil and gas development and cattle grazing. We estimated habitat complexity for each site using a matrix of our habitat measurements to calculate a three-dimensional Shannon diversity index following methods by Angermeier and Schlosser (1989) and Albanese et al. (2004). We categorised velocity, depth and substrate measurements into four categories for each point of measurement. Substrate sizes were categorised as S1 (hardpan clay), S2 (silt or sand), S3 (fine gravel or coarse gravel) or S4 (cobble or boulder). Depth measurements were labelled as D1 (2–17 cm), D2 (18–25 cm), D3 (26–35 cm) or D4 (greater than 35 cm). Velocity measurements were categorised as V1 (−0.13–0.18 m/s), V2 (0.19–0.36 m/s), V3 (0.37–0.57 m/s) or V4 (greater than 0.57 m/s). Then for each point of measurement taken at all sites, we combined the substrate, depth and velocity categories into unique string combinations (i.e. S1_D2_V4) and created a matrix with the frequency of occurrence for each unique categorical string at each site. From this matrix, we were able to calculate habitat complexity at each site using a three-dimensional Shannon–Wiener diversity index. We used this habitat complexity metric as a covariate in the global model evaluating site-level habitat characteristics affecting fish colonisation.

2.6 | Colonisation model

We ran a global generalised additive mixed effects model (GAMM) with a negative binomial distribution and used backwards elimination to determine which covariates best predicted mottled sculpin and mountain sucker colonisation. The response variable in the global model was colonist counts per 100 m for each site, which included both tagged and untagged fish.

Prior to model selection, we examined the data for potential outliers, zero-inflation, collinearity and heterogeneity (Zuur et al., 2009). We removed two sites that were causing heteroscedasticity; the sites had exceptionally high fish abundances compared with the rest of the study system, likely due to high-quality habitat. The significant covariates predicting colonisation were the same for models with and without outliers. Removing outliers reduced our samples to 28 sites with mottled sculpin and 21 sites with mountain sucker which produced a total sample size of 49; species co-occurred at 20 of the sites. We did not find evidence that the response variable was zero-inflated, and there were no strong correlations between predictor variables (generalised variance inflation factor < 3). We used the “gamm4” package from Program R (version 3.3.3) to run a GAMM to examine effective degrees of freedom (edf) and found that the relationship between pre-displacement abundance and colonist counts per 100 m was non-linear (edf > 1). Therefore, we applied a smoother to pre-displacement abundance (allowing it to vary nonlinearly) and constrained the nonlinearity to a maximum of four knots, due to small sample size ($n = 49$). We examined heterogeneity of covariates with scatterplots and decided to account for temporal autocorrelation by including a fixed effect for year. Because the experiment was conducted over 2 years, 2018 and 2019, we used a fixed effect instead of a random effect to account for temporal autocorrelation. We considered including a random effect for stream name to account for spatial autocorrelation; however, stream name accounted for a negligible amount of variance during model exploration (variance = 1.78 e^{-5}). To examine site-level effects on colonisation, we included fixed effects for habitat complexity and per cent riparian cover in our global model. To examine species-level effects on colonisation due to differences in species traits, we included a fixed effect for species. We also included two interaction terms: the interaction between species and habitat complexity and the interaction between species and per cent riparian cover, because we predicted differing colonisation capabilities between species depending on site-level characteristics. We used backwards elimination to remove non-significant covariates from the global model until only significant covariates remained to find our best fitting model ($\alpha = 0.05$; Table 1). We also compared AICc scores and AICc weights of models throughout the backwards elimination selection process. Following model selection, we confirmed that the best model met model assumptions.

2.7 | Movement study

Species with greater mobility are more likely to colonise sites than species with limited mobility (Albanese et al., 2009). Therefore, we selected four additional sites (Figure 1) during 2018 to conduct a movement study and compare species mobility in the absence of experimental displacement. Fish were captured, measured, weighed and PIT tagged in early June following the same procedures as listed under the colonisation experiment; however, fish were released within 10 m of their capture location in open sites to reduce disruption of their natural movements.

During 2018, we conducted bi-weekly short-distance PIT-tag resurveys at movement sites with an Oregon RFID half-duplex mobile PIT-tag reader and antenna. We estimated movement for 200-m resurvey reaches centred on the original 100 m site. When a fish was located, we recorded the tag ID, GPS location, time and date. In total, we completed four short-distance (200 m) PIT-tag surveys at each movement site. In late July–early August, we conducted one long-range resurvey at each of the four movement sites, beginning the survey 600–1500 m downstream of the site and completing the survey 0–805 m upstream of the site, to find fish that moved further than 200 m. Long-range PIT-tag resurveys varied from 1640 to 2260 m in length. Discrepancies in long-range resurvey lengths were due to inaccuracies of National Hydrography Dataset (NHD) stream line data, which were used to select start and end GPS coordinates, and due to an impassible beaver dam fish barrier on the upstream portion of one movement site that we did not survey past.

2.8 | Movement analyses

We calculated movement rates for all fish relocations, which included short-distance movements within 200-m PIT-tag resurveys and recaptures from long-distance surveys at the four movement

TABLE 1 The best model included pre-displacement abundance per 100 m (*p*-value < .001) and a significant interaction between per cent riparian cover and species (*p*-value = .02)

Model	AICcWt	AICc	Δ_i	df
Pre-displacement Abundance, % Riparian Cover x Species, % Riparian Cover, Species	0.84	118.37	0.00	7
Pre-displacement Abundance, % Riparian Cover x Species, % Riparian Cover, Species, Complexity	0.12	122.36	3.98	8
Pre-displacement Abundance, % Riparian Cover x Species, % Riparian Cover, Species, Complexity, Year	0.03	124.95	6.58	9
Pre-displacement Abundance, % Riparian Cover x Species, Complexity x Species, % Riparian Cover, Species, Complexity, Year	0.01	127.55	9.18	10

Note:: Colonist counts (per 100 m) was measured for each species at each site from late July to August ($n = 49$). Pre-displacement abundance (per 100 m) was measured for each species at sites between June to early July.

Habitat complexity was measured for each site as a three-dimensional Shannon diversity index including water velocity, stream depth and substrate. Per cent riparian cover was calculated as a proportion of riparian cover present along transects.

Two sample years, 2018 and 2019, and two species, mottled sculpin and mountain sucker were included in the global model.

Backwards elimination model selection was used to drop non-significant covariates from the global model ($\alpha = 0.05$).

Abbreviations: AICcWt, Akaike's information criterion weight for each model; AICc, Akaike's information criterion corrected for small sample size; Δ_i, delta AICc for each model (i); df, degrees of freedom.

sites, as well as six incidental recaptures during fish monitoring efforts across the entire study system. To calculate distance moved, we hand-digitised stream lines using ArcGIS Basemap imagery (Esri) due to inaccuracy of NHD stream line data. We snapped GPS locations for individual fish to the stream line using the ArcGIS Analysis Near Tool and calculated the distance moved between consecutive points using Calculate Geometry in ArcGIS. We divided distance moved by the number of days between each location to determine a daily movement rate (m/day); and averaged all daily movement rates by PIT-tag ID. We compared mottled sculpin and mountain sucker movement rates based on the more frequent short-distance resurveys with a Mann–Whitney U test. We used long-distance resurveys and incidental recaptures to better determine maximum average movement rates for both species.

We also calculated movement extent for all fish, which we defined as the greatest distance between relocation points along the stream line for each individual fish over the 77-day study period, using ArcGIS Calculate Geometry tool (m). Movement extent was calculated using the same fish resurvey points and stream lines that were prepared for the movement rate analysis, which included fish recaptured during short-distance resurveys, long-distance resurveys and six incidental recaptures. We used a Mann–Whitney U test to compare species movement extent.

3 | RESULTS

3.1 | Colonisation results

Fish were able to colonise sites 6–11 weeks after displacement. Mountain sucker abundances did not differ between pre- and post-displacement (*p*-value = .17, df = 21), but mottled sculpin abundances were reduced in post-displacement surveys (*p*-value = .04, df = 29; Figure 2). Average mottled sculpin abundance per 100 m site was 27 ± 9 (mean ± standard error) pre-displacement and 22 ± 8 post-displacement. Average mountain sucker abundance per 100 m site was 7 ± 2 pre-displacement and 9 ± 2 post-displacement. During 2018 post-displacement electrofishing surveys, we recaptured 10% of PIT-tagged mottled sculpin and 2% of PIT-tagged mountain sucker. During 2019 post-displacement electrofishing surveys, we recaptured 14% of VIE tagged mottled sculpin and 6% of VIE tagged mountain sucker.

Mottled sculpin and mountain sucker size-structure did not significantly differ between pre- and post-displacement populations (mottled sculpin *p*-value = .09, mountain sucker *p*-value = .06; Figure 3). Median mottled sculpin standard length was 52 mm pre-displacement and 57 mm post-displacement, and median mountain sucker standard length was 90 mm pre-displacement and 90 mm post-displacement.

Our top multivariate model (AICc weight = 0.84) predicting mottled sculpin and mountain sucker colonist counts (per 100 m) included an interaction term between per cent riparian cover and species and three fixed effects: pre-displacement fish abundance (per 100 m), per cent riparian cover and species (adjusted $r^2 = 0.75$, $n = 49$; Table 1). Habitat complexity was not in the top model. There was a strong positive relationship between pre-displacement fish abundances and colonisation (*p*-value < .001, edf = 2.57; Figure 4). There was a weaker interaction with per cent riparian cover being positively related to mottled sculpin colonisation (*p*-value = .02, beta = 0.01; Figure 4) and negatively related to mountain sucker colonisation (*p*-value = .02, beta = −0.01; Figure 4).

3.2 | Movement results

We tagged a total of 88 mottled sculpin and 104 mountain sucker during the 2018 movement study. Overnight PIT-tag retention was 99% for mottled sculpin and 100% for mountain sucker. Overnight survival for PIT-tagged fish was 97% for mottled sculpin and 99% for mountain sucker. We recaptured 81% of mottled sculpin and 80% of mountain sucker during bi-weekly PIT-tag resurveys at the four movement sites.

Mottled sculpin individual movement rate was less than mountain sucker individual movement rate for bi-weekly short resurveys (200 m; *p*-value = .04, $n = 96$). Median mottled sculpin movement rate was 0.75 m/day ($n = 61$), and median mountain sucker movement

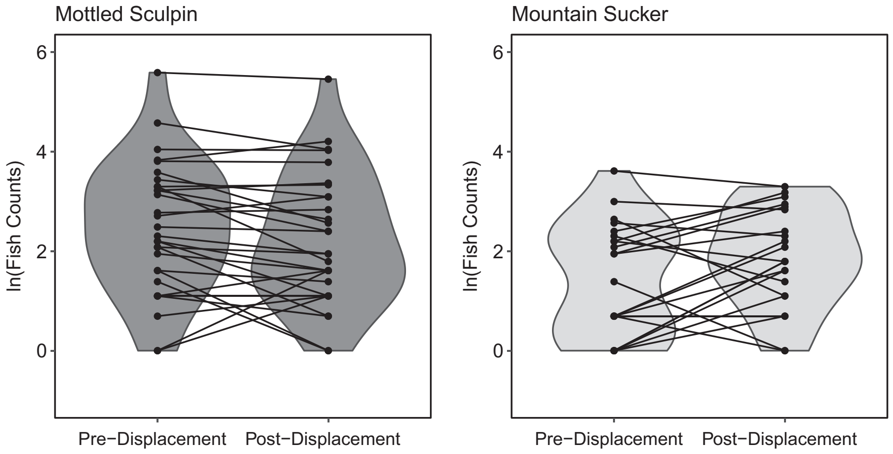

FIGURE 2 Violin plots of paired ln (fish count +1) per 100 m of mottled sculpin (left) and mountain sucker (right) at sites before and 6–11 weeks after experimental displacement in the Wyoming Range. Mottled sculpin abundance differed between pre- and post-displacement populations (*p*-value = .04, df = 29), whereas mountain sucker did not (*p*-value = .17, df = 21)

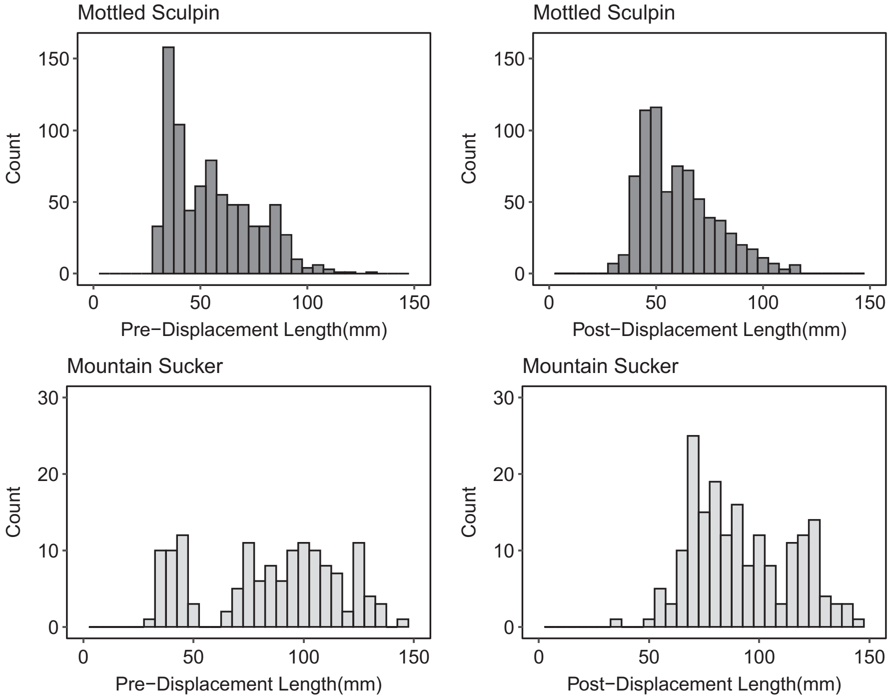

FIGURE 3 Mottled sculpin (top, p-value = 0.09) and mountain sucker (bottom, p-value = .06) population size–structure did not significantly differ between pre-displacement and post-displacement populations

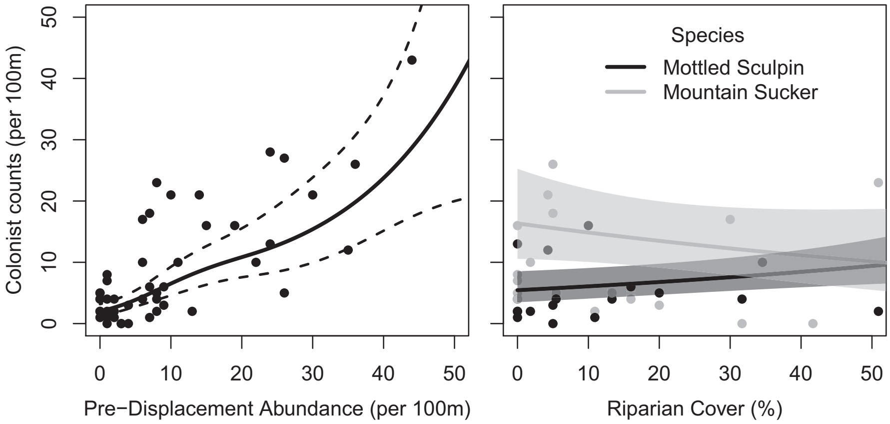

FIGURE 4 Colonist counts (per 100 m) at sites post-displacement are positively correlated to pre-displacement fish abundance (per 100 m) for both species (left, p-value < .001, $n = 49$, adjusted $r^2 = 0.75$). Mottled sculpin colonist counts are positively correlated to per cent riparian cover and mountain sucker colonist counts are negatively correlated to per cent riparian cover (right, p-value = .02, $n = 49$, adjusted $r^2 = 0.75$)

rate was 1.21 m/day (n = 35; Table 2). Individual maximum movement rates detected during long resurveys (>1600 m) were 70.47 m/day ($n = 14$) for mottled sculpin and 372 m/day ($n = 69$) for mountain sucker (Table 2). Movement extent was greater for mountain sucker than mottled sculpin (p-value < .001, n = 178). Median movement extent for mottled sculpin was 42 m ($n = 74$) and for mountain sucker was 108 m (n = 104). Maximum detected movement extent for mottled sculpin was 4064 m and for mountain sucker was 4092 m (Figure 5).

4 | DISCUSSION

High colonisation abilities among fishes can confer resilience in the face of natural and anthropogenic disturbance. We conducted repeated small-scale displacement experiments across a gradient of anthropogenic land use and habitat characteristics to examine colonisation ability of two native fish species. Native fish in the Wyoming Range were able to colonise suitable habitats and recover to pre-displacement size–structure within 6–11 weeks following small-scale displacement events. Other defaunation experiments also report rapid colonisation after disturbance (Hudy & Shiflet, 2009; Peterson and Bayley, 1993; Sheldon & Meffe, 1995). Pre-displacement fish abundance was the main driver of the count of fish colonising sites, emphasising the value of nearby species pools contributing to local recovery (Stoll et al., 2014). The species had differing colonisation capabilities with mountain sucker recovering to pre-displacement abundances and exhibiting greater mobility than mottled sculpin. As a result, mountain sucker appear more resilient than mottled sculpin to a displacement disturbance, but both species demonstrated the ability to colonise local sites and move substantial distances.

We found that new individuals predominantly drove colonisation; only 16% of mottled sculpin and 3% of mountain sucker colonists were recaptures. Average capture probability estimates were 0.38 for mottled sculpin and 0.35 for mountain sucker, so this is unlikely to be just due to low capture probability. We expected a higher

TABLE 2 Summary statistics of average movement rates (m/day) per individual PIT-tagged fish during 2018 movement study at four sites in the Wyoming Range

Species	Survey type	Range (min–max)	Median	Mean	SD	n	SE
Mottled Sculpin	Short (200 m)	0.03–5.67	0.75	1.03	1.10	61	0.14
Mountain Sucker	Short (200 m)	0.00–6.00	1.21	1.53	1.34	35	0.23
Mottled Sculpin	Long (>1600 m)	1.85–70.47	3.33	12.62	22.05	14	5.89
Mountain Sucker	Long (>1600 m)	1.09–372.00	2.50	10.81	46.40	69	5.59

Note:: Survey type denotes the length of mobile PIT-tag antenna surveys; four short (200 m) and one long (>1600 m) surveys were completed at each of the four movement sites.

Abbreviations: *n*, sample size; SD, standard deviation; SE, standard error.

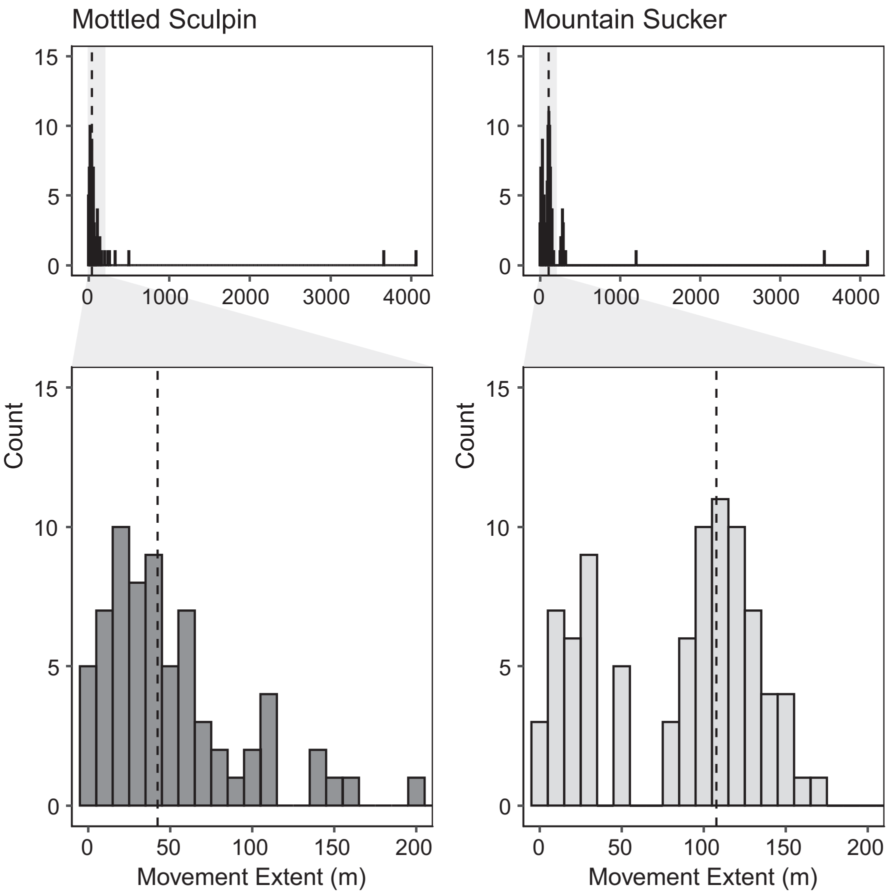

FIGURE 5 Movement extent (m) per individual PIT-tagged fish during 2018 movement study at four sites in the Wyoming Range differed between species (p-value < .001, $n = 178$). Median movement extent is denoted by the dashed line. The top panels include seven outliers with large movement extents that were removed from the bottom panels

recapture rate because mottled sculpin usually show high site fidelity due to small home range sizes (Petty & Grossman, 2004). Mountain sucker site fidelity has not been thoroughly documented but other catostomids demonstrated strong spawning tributary fidelity (Fraser et al., 2017; Hooley-Underwood et al., 2019). Tagging and the experimental displacement may have affected fish movement behaviour. We had a higher proportion of recaptures at movement sites where fish displacement was minimised. There are contradictory results on post-tagging flight responses of suckers; Fraser et al. (2017) found that the majority of suckers emigrated from their study stream within 48 h post-tagging whereas Hooley-Underwood et al. (2019) found no such response.

Few studies have examined recovery of stream fish size–structure following a disturbance event (Detenbeck et al., 1992), but this is important for maintaining stable populations with strong reproductive potential. We found that pre- and post-displacement size–structure were similar for both species as predicted. We did not account for growth over the study period; for ten recaptured PIT-tagged fish (one mountain sucker and nine mottled sculpin), growth was between 6 and 16 mm over the course of 8–11 weeks. This growth could explain the increase in median size for mottled sculpin and the lack of small mountain sucker (<50 mm) post-displacement (Figure 3). Growth did likely contribute to some differences in size distributions, but our conclusion of no substantial shifts in size–structure appears valid.

Intra-annual fish colonisation was strongly related to pre-displacement fish abundances, as predicted, and seen in other studies (Albanese et al., 2009; Erős et al., 2015; Sheldon & Meffe, 1995;

Taylor & Warren, 2001; Whitney et al., 2016). Sites with greater fish abundances have more potential nearby colonisers, and high fish abundance could generally be a sign of higher quality habitat with high carrying capacity for colonisers. We predicted habitat complexity and riparian cover would be positively associated with colonisation as these characteristics are associated with higher quality, less disturbed habitat. We especially thought this would be the case for mottled sculpin, the less disturbance-tolerant species at our sites (Girard & Walters, 2018). We saw some support for this hypothesis with % riparian cover positively correlated to colonisation for mottled sculpin, but negatively correlated to colonisation for mountain sucker. Habitat complexity was not a significant covariate in our model. The lack of an association could be because our fish species respond more to specific habitat characteristics than complex habitats per se. In addition, high habitat complexity might reduce fish movement ability (Albanese et al., 2009).

Other potentially important factors that we did not assess were water temperature and interspecific interactions. Fish may move upstream to seek refuge from warming water temperatures as summer progresses (Hansbarger et al., 2010). However, maximum lethal thermal tolerance for mountain sucker is 34.0°C and mottled sculpin is 33.8°C when fishes are acclimated to 25°C (Schultz & Bertrand, 2011 and Walsh et al., 1997) and maximum recorded stream temperature for 2018–2019 was 26°C. Given comparable thermal tolerances, temperature was unlikely to affect species variation in colonisation. A PIT-tag array study would allow a better understanding of how daily variation in flow or temperature may affect movement. While mottled sculpin and mountain sucker co-occurred at 20 sites, we did not specifically examine interspecific competition. We believe interspecific competition is unlikely due to different diet requirements; mountain sucker primarily consume algae and mottled sculpin consume benthic macroinvertebrates (Belica & Nibbelink, 2006 and Dineen, 1951). The other fish species present at some sites was Colorado cutthroat trout (*Oncorhynchus clarkii pleuriticus*). Juvenile mountain sucker have been documented to shift habitat use in the presence of brown trout (*Salmo trutta*) and may behave similarly in presence of cutthroat trout (Olsen & Belk, 2005). Similarly, mottled sculpin and brown trout consume macroinvertebrates, although trout feed throughout the water column with mottled sculpin being benthic feeders (Dineen, 1951). Cutthroat trout were only present at seven sites and were generally at low abundances, so any effect on results would likely have been minimal.

Species-level variation in colonisation is often associated with differences in mobility (Aedo, 2008; Albanese et al., 2009). Mottled sculpin exhibited less mobility than mountain sucker and did not recover to pre-displacement abundances during the study time frame. Mountain sucker exhibited greater movement extents and rates; similarly, a laboratory study found that mountain sucker swimming speed, relative to body size, was greater than mottled sculpin (Aedo, 2008). We felt we were effectively able to compare species-level differences in movement due to high recapture rates (80%–81%) at our four movement sites. In contrast, other movement studies have recaptured 24%–39% of individuals (Bailey, 1952; Brown & Downhower, 1982; Hill & Grossman, 1987; McCleave, 1964). Our greater proportion of recaptures is likely because most recaptured fish were located at one site that had beaver dams upstream and downstream of the site potentially constraining movement, and the short time period of our study. We still likely missed many long-distance movement events. Sample sizes for our short movement surveys were greater for mottled sculpin ($n = 61$) than mountain sucker ($n = 35$) and the opposite was the case for the long surveys: mottled sculpin ($n = 14$) and mountain sucker ($n = 69$). This provides further support that mottled sculpin generally move less. Interestingly, maximum movement extent was similar between species with one mottled sculpin moving 4064 m upstream over 71 days and one mountain sucker moving 4092 m upstream over 11 days. To date, this may be the greatest recorded movement for a mottled sculpin. The longest fish movements were upstream in Dry Piney Drainage which has lower elevation, lower slope and less riparian cover than South Beaver Drainage so it may be both species were moving to cooler habitat.

Our experiment was representative of a small-scale restoration action or a displacement event where environmental variables rapidly return to their prior state. Fish may require years to recover following large-scale disturbances (e.g. mining, logging, debris flows or channelisation) that induce long-term changes to physical habitat (Detenbeck et al., 1992; Foster et al., 2020; Niemi et al., 1990). For example, in 2012 a pipeline spill occurred in Dry Piney Drainage and mottled sculpin were absent at affected sites for 4 years following the spill event. Similarly, after a stream relocation project in Indiana, pool size and quantity decreased, fine sediment increased, large woody debris decomposed, and mottled sculpin took 6 years to recover to pre-restoration abundances in one of the restored reaches (Shirey et al., 2016). Wydoski and Wydoski (2002) reported one case where it took mountain sucker 4 years to colonise a restored watershed. Overall, mountain sucker and mottled sculpin exhibit the ability to colonise new habitat, but colonisation rates will likely be longer than found in this study following large-scale habitat degradation.

Headwater streams are increasingly susceptible to anthropogenic disturbance events, which also affect the Wyoming Range study streams, with frequent small-scale disturbance events associated with ongoing oil and natural gas developments (e.g. pipeline and road construction), cattle grazing and intermittency. Our experimental approach provided mechanistic insight into factors that maintain persistence of native fish in this disturbed landscape. Longer-term occupancy models found high site-level persistence of mottled sculpin, likely due to high site-level abundance where present, but lower occupancy across the landscape than mountain sucker (Walker et al., 2019). Greater mobility and colonisation rates for mountain sucker likely make them more resilient to disturbance events, compared with mottled sculpin, and explain the higher occupancy rates in areas with higher anthropogenic land use. Combining long-term data sets and mechanistic experiments increased our understanding of stream fish population dynamics.

Movement and colonisation behaviours are central factors contributing to persistence of native fishes in degraded streams and successful restoration activities rely on fish colonising the restored reaches. While both site-level and species-level characteristics affect colonisation, our research highlights the importance of species abundance and traits, especially mobility, in driving colonisation dynamics (Albanese et al., 2009; Stoll et al., 2014). This demonstrates the conservation challenges faced by rare, low mobility fish species that may both have lower persistence in the face of disturbance and be less likely to benefit from restoration activities. An understanding of fish colonisation after disturbance and drivers of regional occupancy dynamics is important for managing fish populations in increasingly disturbed landscapes (Bergerot et al., 2013).

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AUTHOR CONTRIBUTION

S.A. and A.W. designed the study, S.A. collected the data and conducted the analyses, S.A. and A.W. wrote the manuscript.

CONFLICT OF INTERESTS

The authors of this manuscript have no conflict of interest to declare.

DATA AVAILABILITY STATEMENT

Data generated in this study are available in Alford and Walters (2021) at https://doi.org/10.5066/P9Z0W4IK.

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