

Beaver dams, streamflow complexity, and the distribution of a rare minnow, *Lepidomeda copei*

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Abstract

Freshwater fishes are threatened globally, and often too little is known about threatened species to effectively guide their conservation. Habitat complexity is linked to fish species diversity and persistence, and degraded streams often lack habitat complexity. Beaver *Castor* spp., in turn, have been used to restore streams and increase habitat complexity. The northern leatherside chub *Lepidomeda copei* is a rare, small-bodied, drift-feeding minnow that has anecdotally been observed to use complex habitats associated with beaver dams in the western United States. To investigate this anecdote, we conducted fish and habitat surveys, the latter focusing on quantifying habitat complexity, in a sub-basin of the Upper Snake River Basin in the USA. Complementary generalised linear model and path analyses revealed that northern leatherside chub occurred more often at sites with complex streamflows, and streamflows were more complex when beaver dams were present and pools were deeper. Northern leatherside chubs were also more likely to occur when temperatures were warmer, aquatic macrophytes were abundant and stream channels were narrow and deep. The linkage between chubs, complex streamflows and beaver dams needs to be evaluated more broadly to completely understand its role in the rangewide status of the species. However, it does suggest that increased use of beaver reintroductions and dam analogues for stream restoration could be a boon for the northern leatherside chub, but such efforts should be monitored to determine their effectiveness to help adapt beaver-based restoration approaches to best benefit the species.

KEYWORDS

beaver dams, dam analogues, distribution, habitat diversity, northern leatherside chub, path analysis, restoration

1 | INTRODUCTION

Freshwater fishes are threatened globally. Nearly 70 of over 15,000 known freshwater fish species have gone extinct and 31% for which reasonable data exist are threatened with extinction (Darwall & Freyhof, 2016). The most common threats include pollution, human use of water resources, harvest, nonnatives species and habitat degradation among others (Helfman, 2007). While some species are well studied, the International Union for Conservation of Nature (IUCN)

Red List of Threatened Species—the only globally consistent threat assessment of species—shows there to be not enough information (i.e., data deficient) to even determine a status for over 1,500 freshwater fish species (Darwall & Freyhof, 2016). Even when the status is known, the biology of rare species may not be understood well enough to determine what is driving their status and what might be needed to improve it (Marcot & Flather, 2007).

Habitat complexity is linked to fish community diversity in stream systems. Several studies have shown this linkage, purporting that

higher diversity in habitat types results in more unique niches available to be occupied by more species (Gorman & Karr, 1978; Walrath, Dauwalter, & Reinke, 2016). Habitat complexity is also thought to be correlated with fish species persistence because complex habitats are more likely to have all habitats needed for a species to meet its life history requirements (Horan, Kershner, Hawkins, & Crowl, 2000). Degraded streams often have lower habitat diversity (Walrath et al., 2016), and increasing habitat complexity is often a goal of stream and river restoration (Palmer, Menninger, & Bernhardt, 2010). For example, Billman et al. (2013) determined that increasing habitat complexity through restoration of side channels facilitated coexistence of native fishes in the presence of a non-native predator in the Provo River, Utah, USA.

The Eurasian beaver *Castor fiber* and American beaver *Castor canadensis* are semiaquatic rodents that require water deep enough to support a winter food cache in cold climates, ensure that their burrow entrance remains submerged, provide predator refugia and aid in collection and transport of woody materials (Collen & Gibson, 2001; Novak, 1987). As a result, beaver often build dams on small streams to create impoundments of sufficient depth. Beaver dams, which often occur in multiples, can be built across a range of stream gradients (Beck, Dauwalter, Gerow, & Hayward, 2010; Macfarlane, Wheaton et al., 2017) and can drastically alter stream ecosystems, thus leading beaver to be considered a keystone species (Collen & Gibson, 2001). In brief, beaver dams and impoundments can alter stream hydraulics and channel morphology, stream hydrology, water temperatures and water quality (Hammerson, 1994). These changes, in turn, have been shown to alter macroinvertebrate and fish communities, with responses dependent on impoundment age and location within the stream network, among other factors (Collen & Gibson, 2001). One notable influence beaver have on stream ecosystems is that they increase stream channel and instream habitat complexity (Polvi & Wohl, 2012). For example, habitat complexity (heterogeneity) and fish diversity and abundance were shown to be greater around beaver dams in the Ipswich River, a low-gradient catchment in Massachusetts, USA (Smith & Mather, 2013).

The northern leatherside chub *Lepidomeda copei* is a rare small-bodied cyprinid residing in the Upper Snake River Basin and portions of the Bonneville Basin in the western United States (Johnson, Dowling, & Belk, 2004). Despite a broad geographic range where recent genetic studies suggest historical connectivity among populations, the species currently has a rare and patchy distribution within these basins (Blakney, Loxterman, & Keeley, 2014; Johnson et al., 2004; Schultz, Cavalli, Sexauer, & Zafft, 2016). The species is generally known to inhabit low-velocity areas (pools) of small streams with depth variability and to occasionally use intermittent streams (Schultz, 2014; Schultz et al., 2016; Wilson & Belk, 2001). Laboratory studies have shown the species to initiate spawning above 19°C and select spawning substrates 21 to 48 mm diameter in areas with higher water velocities (19 cm/s) (Billman, Wagner, & Arndt, 2008). Optimal growth of age-0 northern leatherside chub is achieved at 23°C, and the upper incipient lethal temperature (UILT) ranges from 26.6 to 30.2°C depending on acclimation temperature (Billman, Wagner, Arndt, &

VanDyke, 2008). A genetic study showed northern leatherside chub to have low allelic diversity and that populations are genetically unique even within sub-basins (~3,000 km²) owing to habitat fragmentation from land use, use of piscicides for fish management, and non-native predators (Blakney et al., 2014; Walser, Belk, & Shiozawa, 1999). In addition, some have purported that northern leatherside chub reside in areas with complex habitat and that the species' reduced distribution reflects a loss of habitat complexity rangewide due to declines in beaver, loss of riparian vegetation and impacts from over grazing (Blakney, 2012). In response to this assertion, Dauwalter, Wenger, and Gardner (2014) evaluated microhabitat use by northern leatherside chub with a focus on habitat complexity, riparian vegetation and beaver dams in Trapper Creek (Goose Creek sub-basin), a stream where northern leatherside chub are locally abundant. They determined that northern leatherside chub selected deep areas with heterogeneous depths and velocities, overhanging vegetation that was often branches from mature riparian shrubs, and wood associated with beaver dams. While the aforementioned study explained the small-scale distribution of the northern leatherside chub in Trapper Creek, a stream where the species is abundant, it still remained unclear whether habitat complexity, riparian vegetation and beaver dams influence the species' distribution within watersheds and rangewide as observed anecdotally by others (Blakney, 2012). Thus, our objective was to understand the role of habitat complexity and beaver dams in determining the reach-scale distribution of northern leatherside chub within the Goose Creek sub-basin in the Upper Snake River Basin at the western edge of the species' range. This additional understanding will help inform conservation strategies for the northern leatherside chub.

2 | STUDY AREA

The Goose Creek sub-basin straddles the borders of Idaho, Nevada and Utah in the western United States (Figure 1). Goose Creek heads in Idaho on the Sawtooth National Forest around 2,200 m elevation. It then flows south into Nevada, east into Utah and then north back into Idaho where it is impounded by Oakley Dam to form Lower Goose Creek Reservoir (1,400 m elevation). Below the dam all water is used for agriculture and, thus, Goose Creek no longer connects to the Snake River. Higher elevations are a matrix of sage steppe and mixed pine-aspen-juniper (*Pinus* spp.-*Populus* spp.-*Juniperus* spp.) forest; lower elevations are pine-juniper-mountain mahogany (*Cercocarpus* spp.). Riparian areas are primarily comprised of willows (*Salix* spp.), alders (*Alnus* spp.), cottonwoods (*Populus* spp.) and sedges (Cyperaceae). Goose Creek streamflow patterns are influenced by snowmelt runoff and summer thunderstorms. Portions of the sub-basin have been listed on state lists for impaired waters (IDEQ 2010; NDEP 2014). The major impairments of different Goose Creek tributaries result from faecal coliform and *Escherichia coli*, dissolved oxygen, phosphorous, sediment, suspended solids and temperature; these impairments result from roads, trails and livestock production (IDFG 2005, 2007). The Goose Creek mainstem is mainly surrounded by surface-irrigated hay and winter grazing pastures. The sub-basin has some

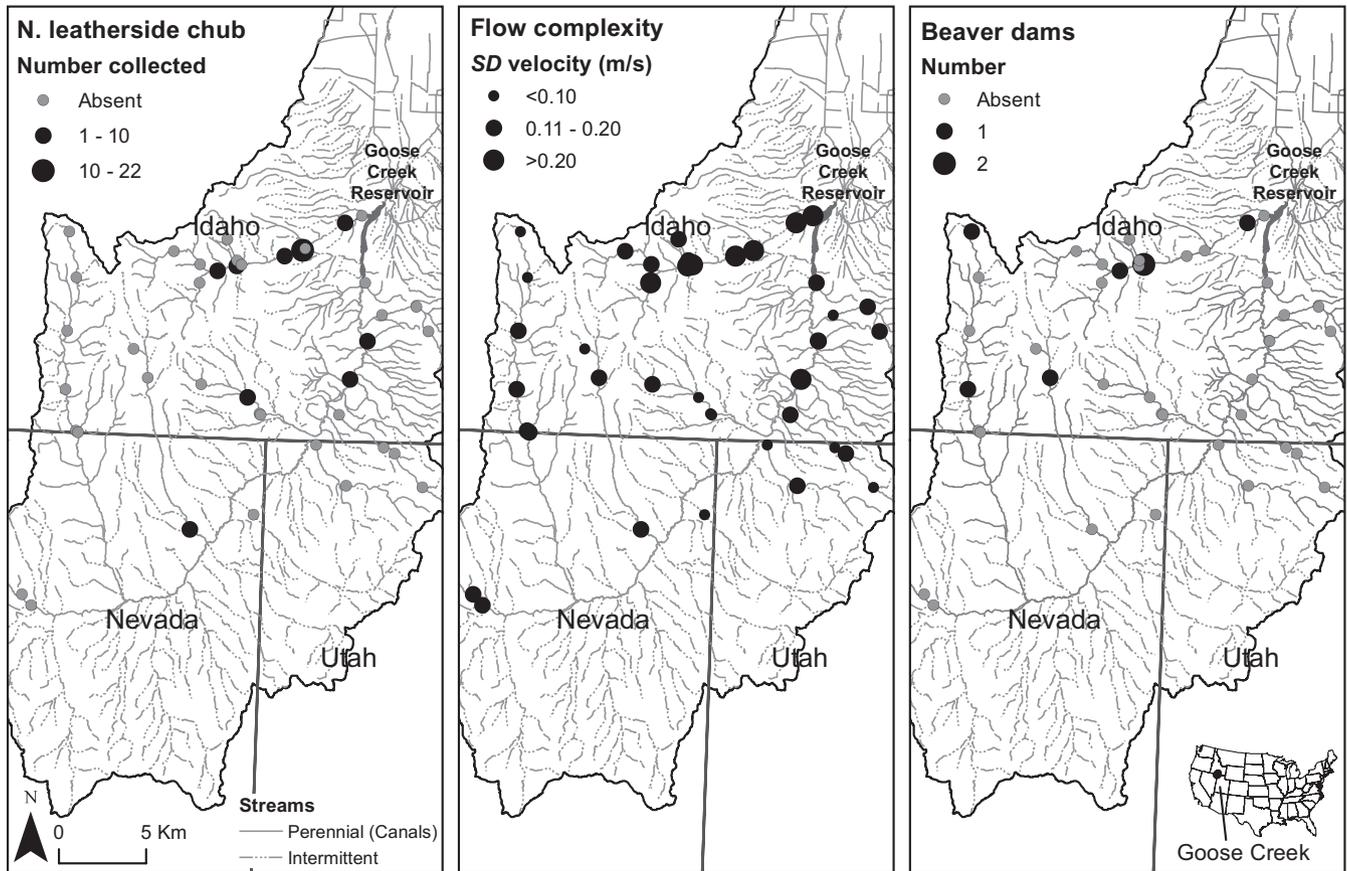


FIGURE 1 Distribution of sample sites and location of northern leatherside chub occurrences (left panel), streamflow complexity (middle panel) and the presence of beaver dams (right panel)

of the highest fish diversity in the Upper Snake River Basin (Meyer, Lamansky, Schill, & Zaroban, 2013). In addition to the northern leatherside chub, the following species have been collected from Goose Creek in the recent past: Yellowstone cutthroat trout *Oncorhynchus clarkii bouvieri*, non-native brook trout *Salvelinus fontinalis*, non-native rainbow trout *Oncorhynchus mykiss*, bluehead sucker *Catostomus discobolus*, mountain sucker *C. platyrhynchus*, Utah sucker *C. ardens*, longnose dace *Rhinichthys cataractae*, specked dace *R. osculus*, redbelt shiner *Richardsonius balteatus*, Utah chub *Gila atraria*, mottled sculpin *Cottus bairdii* and Paiute sculpin *C. beldingii* (Blakney, 2012; Meyer et al., 2013). Goose Creek represents a genetically unique northern leatherside chub population (or populations) isolated from others (Blakney et al., 2014).

3 | METHODS

Forty-one sites were sampled from 2013 to 2015 in the Goose Creek watershed to determine the distribution of the northern leatherside chub and how it is associated with instream and riparian habitat with a focus on habitat complexity and beaver dams. Sites were selected based on a stratified (by stream order) random sampling frame used by Meyer, Schill, Lamansky, Campbell, and Kozfkay (2006) where first-order streams were undersampled but the remaining were sampled

in proportion to availability. The sampling frame was adjusted due to denied access to private land and, in some cases, to increase spatial coverage and the range of habitat conditions sampled. These sites also cover the general stream segments in the sub-basin sampled by Blakney (2012) to collect tissue samples for northern leatherside chub genetic analysis and are a subset of the streams where he anecdotally observed the association between northern leatherside chub, habitat complexity and beaver dams as described earlier. Sites were typically 100 m in length and isolated by 6.35 mm bar block nets, although site length was sometimes adjusted so that site boundaries coincided with habitat features to ensure secure block net sets. Sites were sampled using a single pass with one Smith-Root LR-24 backpack electrofisher and one or two netters at 37 sites, and two backpack electrofishers and four netters on mainstem Goose Creek where sites were greater than 5.4 m in wetted width. Up to three passes were conducted when salmonids were present. Electrofishing was conducted using direct current at 200-450 V and 40 Hz. All northern leatherside chub were counted.

Instream and riparian habitats were also measured at each site after electrofishing surveys. A transect was established every 10 m along each site perpendicular to the channel at bankfull height. Channel depth, water depth, water velocity, stream substrate and cover type were measured at 10 equally spaced points along each transect. Water velocity was measured at 0.6 of water depth using a Hach

FH950 velocity meter (HACH Company, Loveland, CO). Complexity in water velocity and depth were both calculated as a standard deviation. Stream substratum at each point was classified according to the modified Wentworth scale as follows: bedrock, silt/clay (<0.064 mm diameter on b-axis), sand (0.064–2 mm), gravel (2–15 mm), pebble (15–64 mm), cobble (64–256 mm) or boulder (>256 mm) (Cummins, 1962). Cover was classified as follows: boulder, large wood (>10 cm diameter, >4 m in length), small wood, aquatic vegetation (macrophytes), overhanging bank vegetation, undercut bank (>10 cm depth) or absent. Substrate and cover diversity were computed using the Shannon-Wiener index ($H' = -\sum_{i=1}^n p_i \cdot \log_e p_i$) where p_i represented the proportion of substrate or cover type i and n was the number of different types (Legendre & Legendre, 2012). Pools were identified as slow water habitat according to Hawkins et al. (1993), and residual pool depth was measured for all pools as maximum pool depth minus water depth at the downstream riffle crest. Woody riparian vegetation height was classified above each transect endpoint at bankfull as follows: 0.0–0.5 m, 0.5–1.0 m, 1.0–2.0 m, 2.0–4.0 m, 4.0–8.0 m and >8.0 m (Burton, Smith, & Cowley, 2011). We computed per cent woody riparian vegetation as the per cent of transect endpoints with woody vegetation greater than 1 m in height. Streambank stability was classified at each transect endpoint as follows: fracture, slump, slough, eroding or absent (Burton et al., 2011). Reach slope was measured as the difference in elevation between reach boundaries divided by reach length and multiplied by 100 (expressed as a percentage). Mean August stream temperature was measured using thermographs (TidbiT v2; Onset Computer Corporation, Bourne, MA, USA) that recorded temperatures once each hour at 34 locations in the Goose Creek watershed; temperatures at sites without a thermograph were determined using data from the nearest one (with an elevation correction) or two thermographs (distance interpolation). Beaver dams (both active and abandoned) within the sample reach were also counted.

We evaluated the influence of instream and riparian habitat, including habitat complexity and diversity, on northern leatherside chub occurrence using two complementary analyses as follows: multiple logistic regression and path analysis. The multiple logistic regression analysis was performed under a model selection framework. The response variable for occurrence was binary (presence = 1, absence = 0). We evaluated several riparian and instream habitat variables as predictor variables in the multiple logistic regression that are proximal to northern leatherside chub life history needs (as currently understood) or that otherwise influence those proximal habitats. Proximal variables were as follows: SD of velocity as a measure of flow complexity important to drift feeding (Grossman, Rincon, Farr, & Ratajczak, 2002), residual pool depth as a measure pool quality (Wallace & Zaroban, 2013), per cent overhanging vegetation as a measure of cover and refuge from predation (Wallace & Zaroban, 2013), per cent aquatic vegetation (macrophytes) as it can provide cover for small fishes, per cent pebble substrate that is important for spawning (Billman, Wagner, & Arndt, 2008) and mean August temperature because of temperatures known influence on growth and thermal tolerance (Billman, Wagner, Arndt, & VanDyke, 2008). Other covariates were based on factors that influence those proximal habitat variables. A Spearman rank correlation of

$r_s > 0.7$ was used to identify correlated variables potentially causing variance inflation and, if necessary, one of the correlated pair was removed from consideration. Candidate models were constructed using all combinations of variables with a limit of four predictor variables per model to keep variable to sample size ratios near 10:1. Candidate models were fit, and model plausibility was determined using Akaike's Information Criterion for small sample size (Burnham & Anderson, 2002). Any candidate models within 4 AIC_c units of the best model (minimum AIC_c) were considered plausible. Fit of the most plausible occurrence model was evaluated using a Hosmer–Lemeshow test with five bins, and predictive ability was evaluated using a fivefold cross-validated area under the curve (AUC) of a receiver operating characteristic plot (Hosmer & Lemeshow, 2000).

Because we hypothesised that beaver dams influence streamflow complexity and that streamflow complexity influences northern leatherside chub distribution, we did not evaluate beaver dams as a covariate in the logistic regression models because of the potential for variance inflation that would then lead to imprecise parameter estimates perceived to be unimportant. Instead, we explored the influence of beaver dams on streamflow complexity in two ways. First, differences in SD of velocity were compared between sites with and without beaver dams present using a t test ($\alpha = 0.10$). A Bartlett's test was used to assess homogeneity of variances, an assumption for parametric t tests, in SD of velocity between sites with and without beaver dams. Second, we used multiple regression and model selection to evaluate other habitat variables that might influence streamflow complexity. SD of velocity was the response variable, and candidate models were constructed using all combinations of the following predictor variables: number of beaver dams, residual pool depth, per cent woody riparian vegetation, per cent streambank with sloughing or slumping, channel width: depth ratio, reach slope, per cent aquatic vegetation and per cent large wood. As in the logistic regression analysis above, the maximum number of variables allowed in a model was four, and candidate models within 4 AIC_c units of the best model (minimum AIC_c) were considered plausible. Model fit of the best model was evaluated using the adjusted R^2 . The sum of Akaike weights (w_i) was computed for each model i having each predictor variable as a measure of relative variable importance.

In addition to the more traditional generalised linear modelling and model selection approach(es), we used path analysis to evaluate the association of northern leatherside chub occurrence with proximal habitat variables (as above), as well as test for explicit linkages among other instream and riparian habitat features potentially influencing those proximal habitats, including the connection between beaver dams and streamflow complexity. Path analysis is a multivariate modelling approach that is an extension of multiple regression with the intention of estimating the magnitude and significance of direct and indirect relationships between sets of variables while accounting for their covariance (Shipley, 2000). It has an advantage of producing a directed graph (path diagram or model) that shows the direction and magnitude of these interrelationships (Shipley, 2000). Therefore, it is a powerful approach for the analysis of complex multivariate relationships and is often thought of as more confirmatory

of causal relationships than other statistical modelling approaches (Grace & Pugesek, 1998). We developed an initial path diagram that represented a conceptual model of the aforementioned relationships and informed our initial path analysis. It included the hypothesised link between beaver dams and flow complexity and the link between flow complexity and northern leatherside chub occurrence, while incorporating other linkages between stream morphology, riparian habitat, instream habitat and northern leatherside chubs and restraining the number of variables due to our sample size ($n = 41$). We used the presence of northern leatherside chub as the response variable (i.e., presence = 1, absence = 0). The initial path model was fit using the lavaan package in R (R Core Team 2015; Rosseel, 2012); the semPaths function was used to display the directed graph (Epskamp, 2015). The directed graph was considered the full model and its fit was evaluated using maximum likelihood. We used standardised coefficients to examine the significance of each pathway using $p < .15$. We then fit a reduced model with only significant terms. We compared the full and reduced model using AIC.

4 | RESULTS

The northern leatherside chub was collected at 22% of sites (9 of 41) surveyed by electrofishing in the Goose Creek drainage, where from one to 22 individuals were collected in streams from 0.7 to 5.8 m wetted width. When multiple electrofishing passes were conducted, chubs were never collected during a later pass when absent from the first pass. Across all sites, SD of velocity ranged from 0.016 to 0.313 m/s, and leatherside chubs only occurred when SD of velocity was 0.09 m/s or greater. Beaver dams were observed at six sites (14.6%), and only one site had more than one dam (two dams total). Northern leatherside chub were collected at two of six sites (33%) with beaver dams present; they were observed at seven of 35 sites (20%) without a beaver dam.

Streamflow complexity was important in explaining the distribution of northern leatherside chub in the Goose Creek watershed. The SD of velocity and SD of depth were the only highly correlated habitat variables ($r_s = 0.77$) and so we restricted candidate multiple logistic regression models to only have one of the two variables but not both. Only one candidate model was plausible given the data (i.e., $\Delta AIC_c < 4$; Table 1). In addition to containing SD of velocity as a covariate, this top

model also contained mean August temperature, channel width: depth ratio and per cent aquatic vegetation as covariates. The Hosmer-Lemeshow test showed the model fit the data ($\chi^2 = 5.06$, $p = .751$), and the model showed good fivefold cross-validated predictive ability (AUC = 0.896). Standardised parameter estimates showed all four habitat variables to have similar influence on northern leatherside chub occurrence, and they showed that chubs were more likely to occur at sites with higher flow complexity (SD of velocity), warmer temperatures, narrower and deeper channels (lower width: depth ratio) and more aquatic vegetation (Table 2; Figure 2). Standardised parameter estimates suggested that an increase in the SD of velocity of 0.07 (i.e., 1 SD) would increase the odds of northern leatherside chub being present at a site by approximately an order of magnitude ($e^{2.347} = 10.5$).

Streamflow complexity was 1.5 times higher on average when beaver dams were present within the stream reach (Figure 3). The SD of velocity was significantly higher when one or more beaver dams were present (mean = 0.20 m/s; 1 $SD = 0.09$ m/s) than when they were absent (mean = 0.13 m/s; 1 $SD = 0.06$ m/s). A t test showed this difference to be significant ($t = 2.09$, $df = 39$, $p = .043$); a Bartlett's test showed variances in SD of velocity to be homogenous (i.e., not significantly different), thus meeting the equal variance assumption of the t test ($K^2 = 1.31$, $df = 1$, $p = .253$). Multiple regression models also showed beaver dams to influence SD of velocity. There were 43 plausible candidate models with $\Delta AIC_c < 4$ suggesting much uncertainty in identifying a correct model. However, beaver dam presence was a predictor in 36 of the 43 plausible models (84%), and it was the most important variable explaining SD of velocity as evidenced by the magnitude of standardised parameter estimates and sum of Akaike weights as a measure of relative variable importance ($\sum w_i = 0.88$; Table 2). Other habitat variables influencing SD of velocity most were residual pool depth ($\sum w_i = 0.68$) and per cent streambank sloughing and slumping ($\sum w_i = 0.63$). Interestingly, there was little evidence that instream features such as boulders and large wood influenced flow complexity; large wood was only found at two of the 44 sites. Model-averaged parameter estimates of all variables had 90% confidence intervals that included zero, with beaver dams just barely so (Table 2). The most plausible model containing beaver dams, per cent streambank sloughing and slumping, and residual pool depth had an adjusted $R^2 = 0.24$.

Path analysis showed a linkage between northern leatherside chub occurrence, flow complexity and beaver dams more directly

| Candidate model | K | Log-Likelihood | AIC _c | ΔAIC_c | w_i |
|---|---|----------------|------------------|----------------|-------|
| SD Velocity + Temperature + WD Ratio + Aq. Vegetation | 5 | -9.20 | 30.12 | 0.00 | 0.759 |
| Temperature + WD Ratio + Aq. Veg + Overhanging Veg. | 5 | -11.32 | 34.35 | 4.23 | 0.092 |
| SD Velocity + Temperature + Aquatic Vegetation | 4 | -12.90 | 34.91 | 4.78 | 0.069 |
| SD Depth + Temperature + WD Ratio + Overhanging Veg. | 5 | -12.13 | 35.98 | 5.86 | 0.041 |
| SD Velocity + Temperature | 3 | -14.70 | 36.04 | 5.92 | 0.039 |

TABLE 1 Number of parameters (K), Log-likelihood, AIC_c, ΔAIC_c and Akaike weights (w_i) of the top multiple logistic regression models predicting occurrence of northern leatherside chub at stream sites in the Goose Creek watershed. Only candidate models with $\Delta AIC_c < 6$ are shown

TABLE 2 Standardised parameter estimates, standard errors and 90% confidence limits for best multiple logistic regression model predicting occurrence of northern leatherside chub (presence = 1, absence = 0) or multiple regression predicting SD of velocity (m/s) at streams sites in the Goose Creek watershed. Parameter estimates from the multiple regression model are averaged across plausible models with shrinkage (43 candidate models $\Delta AIC_c < 4$)

| Parameter | b_i | SE(b_i) | Lower 90% CL | Upper 90% CL | Σw_i |
|-------------------------------------|--------|-------------|--------------|--------------|--------------|
| Response: N. leatherside chub (P/A) | | | | | |
| Intercept | -4.085 | 1.616 | -7.585 | -2.050 | 1.00 |
| % Aquatic Vegetation | 2.295 | 1.016 | 0.908 | 4.404 | 1.00 |
| Mean August Temperature (C) | 2.899 | 1.301 | 1.190 | 5.627 | 1.00 |
| Width: Depth Ratio | -2.552 | 1.257 | -5.085 | -0.790 | 1.00 |
| SD Velocity (m/s) | 2.347 | 1.004 | 1.007 | 4.408 | 1.00 |
| Response: SD of velocity (m/s) | | | | | |
| Intercept | 0.000 | 0.139 | -0.234 | 0.234 | 1.00 |
| Beaver dams (#) | 0.288 | 0.175 | -0.005 | 0.581 | 0.88 |
| % Streambank Slough/Slump | -0.178 | 0.179 | -0.476 | 0.120 | 0.63 |
| Residual Pool Depth (m) | 0.201 | 0.184 | -0.106 | 0.508 | 0.68 |
| % Aquatic Vegetation | -0.087 | 0.153 | -0.341 | 0.167 | 0.35 |
| Width: Depth Ratio | 0.055 | 0.122 | -0.148 | 0.258 | 0.26 |
| % Woody Riparian Vegetation | -0.032 | 0.104 | -0.205 | 0.140 | 0.16 |
| % Boulder | 0.019 | 0.073 | -0.102 | 0.140 | 0.13 |
| % Large Wood (>4-m length) | 0.014 | 0.062 | -0.090 | 0.118 | 0.10 |
| % Slope | -0.005 | 0.053 | -0.095 | 0.084 | 0.07 |

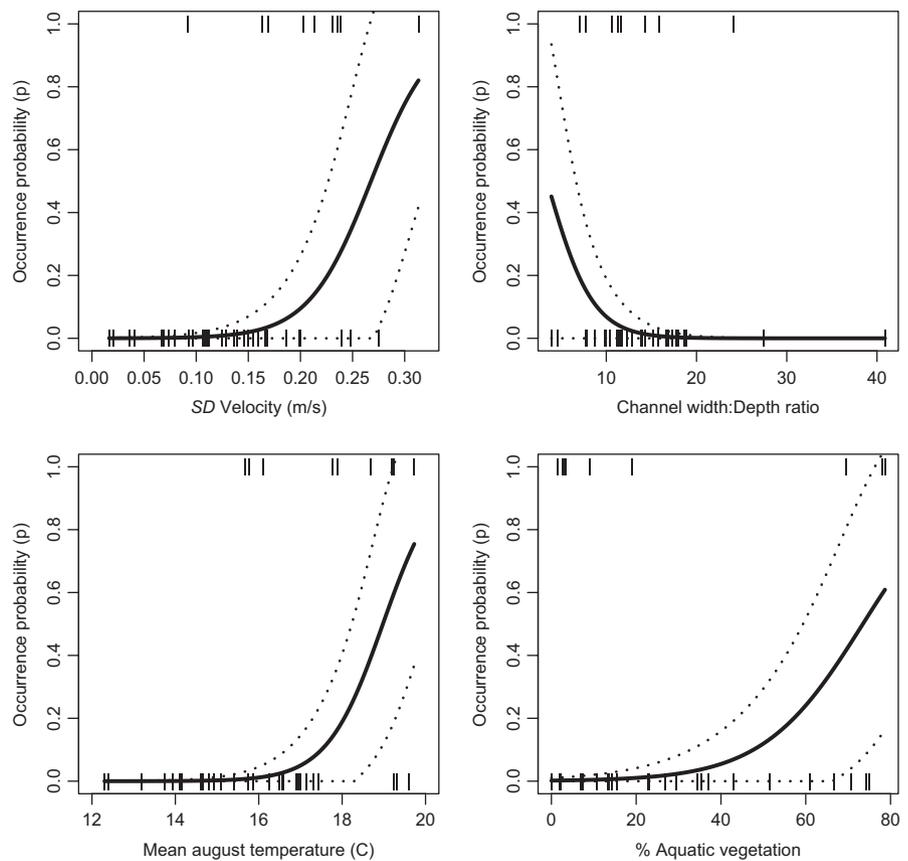


FIGURE 2 Northern leatherside chub occurrence probability as function of SD of velocity, channel width: depth ratio, mean August temperature and % aquatic vegetation from the only plausible multiple logistic regression model

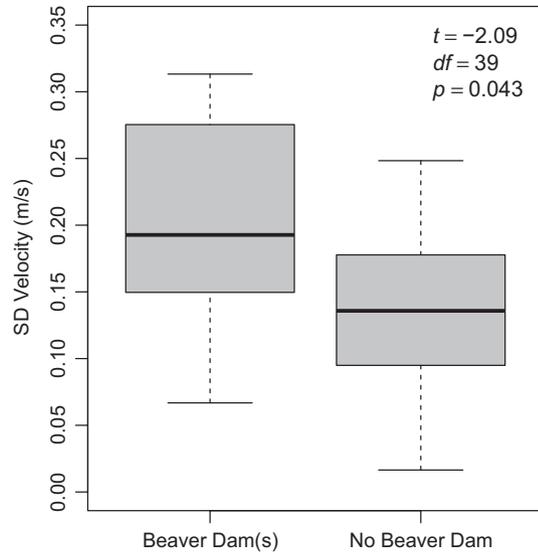


FIGURE 3 Box plots showing significant differences in streamflow complexity—measured as the SD of velocity—at sample sites with and without active or abandoned beaver dams present

than the generalised linear modelling analyses, in addition to revealing other important relationships (Figure 4). After fitting the full conceptual model, nonsignificant variables ($p > .15$) were removed and a reduced model was fit; the only variable connection retained at $p > .05$

was the beaver dam effect on residual pool depth, which also had a low standardised coefficient suggesting a weak association (Table 3). The reduced model was a more parsimonious model than the initial model ($\Delta AIC = 1,674$) and it showed acceptable fit (comparative fit index = 0.853; root mean squared error approximation = 0.158). The final reduced model showed northern leatherside chub to occur more frequently when flow complexity was higher (Figure 4). In turn, flow complexity was higher when active or abandoned beaver dams were present, but it was also higher when pools were deeper. The reduced model also showed chubs to occur more frequently with higher mean August stream temperatures, with the strength of this association similar to that of flow complexity as revealed by the standardised path coefficients (Table 3). Pools were deeper and temperatures were warmer in lower gradient reaches typical of the lower Goose Creek mainstem—the largest stream we studied (5.4 to 6.2 m wetted width).

5 | DISCUSSION

We found that northern leatherside chub occurred more often at sites with complex streamflows, and complex streamflows were more prevalent when active or abandoned beaver dams were present. Thus, despite small samples sizes (only nine chub occurrences) our data and complimentary analyses support the general field observations made by others and on which our study was founded (Blakney, 2012). The

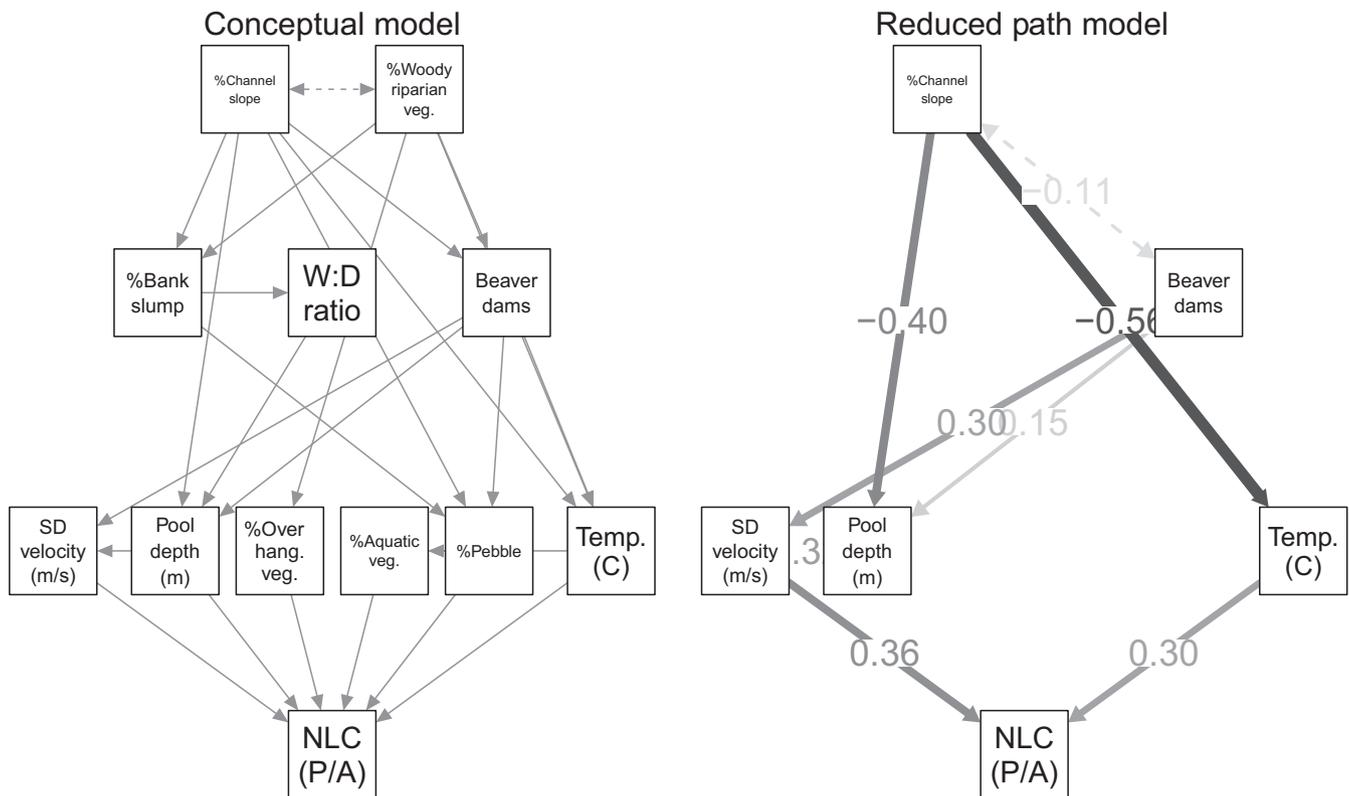


FIGURE 4 Left panel shows a conceptual model with hypothesised linkages between measured riparian and instream habitat variables, including beaver dams, and the occurrence of northern leatherside chub, and a reduced path diagram showing only significant ($p < .15$) linkages between habitat variables, including beaver dams, and occurrence of northern leatherside chub

TABLE 3 *p*-values for predictors of full path model and standardised parameter estimates (1 SE) from a reduced model refit with parameters *p* < 0.15 from the full model

| Response | Predictor | <i>p</i> -value | <i>b_i</i> | 1 SE(<i>b_i</i>) |
|-------------------------|-------------------------|-----------------|----------------------|------------------------------|
| Leatherside Chub (P/A) | Residual Pool Depth (m) | .752 | | |
| | % Pebble | .910 | | |
| | SD Velocity (m/s) | .015 | 2.097 | 0.828 |
| | % Aquatic Vegetation | .192 | | |
| | % Overhang. Vegetation | .712 | | |
| SD Velocity (m/s) | Temperature (C) | .029 | 0.062 | 0.030 |
| | Beaver Dams (#) | .035 | 0.048 | 0.034 |
| Residual Pool Depth (m) | Residual Pool Depth (m) | .024 | 0.126 | 0.057 |
| | Width: Depth Ratio | .934 | | |
| | % Slope | .005 | -0.029 | 0.011 |
| % Overhanging Veg. | Beaver Dams | .147 | 0.059 | 0.062 |
| | % Woody Riparian | .177 | | |
| % Aquatic Veg. | Temperature (C) | .154 | | |
| | % Pebble | .392 | | |
| % Pebble | % Slough/Slump | .271 | | |
| | % Slope | .692 | | |
| | Beaver Dams (#) | .003 | | |
| Temperature (C) | % Slope | .019 | -0.444 | 0.166 |
| | % Woody Riparian | .371 | | |
| | Beaver Dams (#) | .238 | | |
| % Slough/Slump | % Woody Riparian | .565 | | |
| | % Slope | .190 | | |
| Width: Depth Ratio | % Slough/Slump | .496 | | |
| Beaver Dams (#) | % Slope | .263 | | |
| | % Woody Riparian | .438 | | |

working hypothesis for this association is that higher flow complexity increases the chance that flowing and standing water are juxtaposed (aka, current seams) in a way that can be used by drift feeding to maximise consumption of prey with minimum energy expenditure (Grossman et al., 2002). However, additional research is needed to document the behavioural feeding ecology of northern leatherside chub (Hughes & Dill, 1990; Rincón, Bastir, & Grossman, 2007). Furthermore, manipulation of streamflow complexity and current seams used for drift feeding (sensu Fausch, 1993) and quantification of drifting prey could lead to a more mechanistic explanation of why the distribution of northern leatherside chub is linked to streamflow complexity.

Beaver dams influenced flow complexity directly, but reaches with dams also had deeper pools where flows were also more complex; no other habitat variables influenced flow complexity more in our dataset. While northern leatherside chubs are not likely obligate users of beaver dams themselves, those dams appear to create conditions favourable to chubs when they exist and other stream conditions, such as temperature, are suitable. Other streams where leatherside chubs are abundant also have large beaver dam complexes

(L. Mabey, Caribou-Targhee National Forest, personal communication) and Blakney (2012) observed this pattern while collecting northern leatherside chubs from streams across the species' range, both suggesting the pattern we observed extends beyond just the Goose Creek sub-basin. More research is needed to determine whether the connection between northern leatherside chub and streamflow complexity extends across the species' range and what role beaver dams play in creating streamflow complexity when it would otherwise have not existed.

Other factors also influenced northern leatherside chub occurrence. Chubs occurred where stream temperatures were warmer. Goose Creek flows into Lower Goose Creek Reservoir before temperatures reach the upper thermal tolerance for northern leatherside chub (UILT = 27 to 30°C; Billman, Wagner, Arndt, & VanDyke, 2008); however, little is known about whether temperatures in small headwater streams can be too cold for northern leatherside chub populations to be viable. Optimal growth by juvenile northern leatherside chub is achieved at 23°C, but they still grow, albeit slowly, at temperatures as low as 13°C (Billman, Wagner, Arndt, & VanDyke, 2008). What is unknown is whether slow growth in cold headwater streams prohibits

northern leatherside chubs from becoming large enough, or obtaining enough energy reserves, to ensure overwinter survival; larger individuals with more energy reserves commonly have higher overwinter survival in other fish species (Biro, Morton, Post, & Parkinson, 2004; Oliver, Holeton, & Chua, 1979). In addition, headwater streams may also not be deep enough nor have the streamflow complexity to be suitable for chubs, as suggested by our path model showing flow complexity was higher in reaches with deeper pools (a weak effect independent from beaver dams). Chubs were also less likely to occur in streams with wide, shallow channels that can be symptomatic of impaired streams. Removal of woody riparian vegetation to minimise water loss from evapotranspiration and overgrazing in riparian areas can result in wide, shallow channels with shallow pools (Kauffman & Krueger, 1984). This suggests that land management could also be influential in improving habitat complexity for the northern leatherside chub (Swanson, Wyman, & Evans, 2015).

The positive association between chubs and aquatic vegetation is less clear; the association was revealed by the logistic regression analysis only. Aquatic macrophyte biomass in small streams of the Upper Snake River Basin has been shown to be higher in unshaded streams with stable streamflows (and less streambed substrate mobility) and higher nutrient concentrations (Mebane, Simon, & Maret, 2014). Aquatic macrophytes (mostly *Elodea* spp.) in Goose Creek, when abundant, were in large patches where velocities were negligible within patches but high between them. This condition could create current seams used for drift feeding (Sand-Jensen & Mebus, 1996), but lack of correlation between SD of velocity and per cent aquatic vegetation ($r_s = -0.16$) and weak negative effects in the multiple regression models (Table 2) suggests our data did not capture this phenomenon if present. The association with aquatic vegetation could also reflect an indirect effect of stable streamflow regimes (spring-fed or groundwater dominated) on northern leatherside chub habitat that we did not anticipate or evaluate. Finally, it could also reflect differences in prey densities, as macrophytes stands have been shown to have higher invertebrate taxa richness and abundance than adjacent benthos (Gregg & Rose, 1985), although as previously mentioned the feeding ecology of the northern leatherside chub is not well understood.

The distribution of northern leatherside chub is patchy throughout its range (Blakney et al., 2014). Individuals also have a clustered distribution in the streams where they occur (Dauwalter et al., 2014). This patchiness at both the landscape and stream scales makes it difficult to detect northern leatherside chub occurrence and precisely define the species' distribution at a stream scale during large-scale, spatially distributed fishery surveys using standard stream surveying techniques such as electrofishing in 100 to 200-m stream reaches (e.g., Meyer et al., 2013). As beaver dams increase streamflow complexity, beaver dams and complexes could be targeted to identify new populations because they are an easily identifiable element of the landscape. Beaver ponds and complexes can be located across large areas using aerial flights (Beck et al., 2010), aerial imagery (Pearl, Adams, Haggerty, & Urban, 2015) or habitat suitability modelling (Macfarlane, Wheaton et al., 2017). Employing stratified or adaptive sampling at beaver dams or complexes may potentially

improve the efficiency of large-scale surveys targeted at identifying new populations or precisely defining distributions in some streams (Thompson, 2004). Beaver complexes can, however, be difficult to sample efficiently using electrofishing or passive gears (Hubert, Pope, & Dettmers, 2012; Thompson & Rahel, 1996), potentially making it difficult to document the presence of northern leatherside chubs when they occur in low abundances. eDNA is a new sampling technique that if coupled with an efficient sampling design shows promise as a technique for documenting new populations of leatherside chub in difficult to sample beaver complexes (Baldigo, Sporn, George, & Ball, 2017).

Interest in using beaver as a stream restoration tool could be a boon for northern leatherside chub. Habitat restoration is one conservation action described in a multiagency conservation strategy developed for the species (UDWR 2011), and beaver reintroduction and the use of beaver dam analogues are increasingly being used in stream restoration, especially in incised stream channels in the interior western USA that typically have low habitat complexity (Bouwes et al., 2016; Cluer & Thorne, 2014; Marston, 1994; Pollock et al., 2014). In fact, new tools are available to identify the capacity for streams to support beaver (Macfarlane, Wheaton et al., 2017), and these tools have been combined with information on native fisheries to prioritise stream restoration using beaver dam analogues to optimally benefit rare native species (Macfarlane, McGinty, Laub, & Gifford, 2017). Such an approach could help prioritise streams near extant northern leatherside chub populations for beaver-based restoration with a goal of improving habitat complexity to expand populations or improve their population dynamics.

Although use of beaver for restoration could benefit northern leatherside chub by increasing streamflow complexity in streams where little exists, any such practices should be evaluated in an adaptive management context. Beaver-based restoration projects should be closely monitored so that new data can help refine conceptual models of the northern leatherside chub habitat needs, understand project effectiveness on populations and inform restoration approaches so they can be adapted to maximise effectiveness, as has been useful for other rare fishes (Roberts, Anderson, & Angermeier, 2016). This is especially important as stream restoration is often focused on increasing habitat complexity and heterogeneity under the premise that it will benefit aquatic organisms, including freshwater fishes in peril (Palmer et al., 2010), but most of what is known about how beaver dams and complexes influence fishes is from North American studies on salmonids (Family: Salmonidae) and what little that is known about their influence on nonsalmonids is often anecdotal or speculative (Kemp, Worthington, Langford, Tree, & Gaywood, 2012). What is learned through an adaptive management approach, then, may help in the recovery of other species with similar traits that are imperilled globally in areas where beaver are native.

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