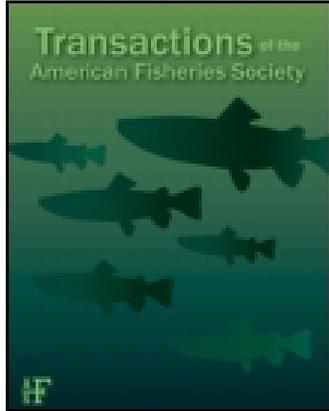


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Daniel C. Dauwalter^a, Seth J. Wenger^{ab} & Peter Gardner^a

^a Trout Unlimited, 910 West Main Street, Suite 342, Boise, Idaho 83702, USA

^b Present address: River Basin Center, University of Georgia, 203 D.W. Brooks Drive, Athens, Georgia 30602, USA.

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ARTICLE

The Role of Complexity in Habitat Use and Selection by Stream Fishes in a Snake River Basin Tributary

Daniel C. Dauwalter,* Seth J. Wenger,¹ and Peter Gardner

Trout Unlimited, 910 West Main Street, Suite 342, Boise, Idaho 83702, USA

Abstract

Impacts from grazing, agriculture, and other anthropogenic land uses can decrease stream habitat complexity that is important to stream biota and often is the goal of stream habitat restoration. We evaluated how microhabitat complexity structured a fish assemblage and influenced habitat selection by the Northern Leatherside Chub *Lepidomeda copei*, a recent candidate for listing under the U.S. Endangered Species Act, in Trapper Creek, a tributary to the Snake River in Idaho. Fishes were sampled using prepositioned areal electrofishing (about 1 m²), and microhabitat conditions were measured within a 1-m-diameter circle centered on the electrofishing anode. Constrained correspondence analysis showed complexity in water depths and velocity to structure the fish assemblage and partition habitat use by Northern Leatherside Chub, Rainbow Trout *Oncorhynchus mykiss*, and Redside Shiner *Richardsonius balteatus*. Habitat selection models showed that the chub used areas of heterogeneous depths and flows in addition to the low-velocity, deep habitats often considered to be the species' habitat. Additionally, chub were almost certain to occur in deep-water habitats when overhead cover—often from mature riparian shrubs—was present. The complex depths and flows structuring the fish assemblage, and selected by chub, were often directly tied to other structural stream features such as boulders, mature riparian vegetation, and beaver *Castor canadensis* dams, stream features that have direct ties to active and passive instream habitat restoration techniques. Our study suggests that habitat complexity should be routinely incorporated into studies evaluating fish habitat use, occupancy, and abundance. Doing so will result in models that are more informative to practitioners conducting stream restoration with a goal of improving habitat complexity.

Physical habitat provides a template for ecological strategies (Southwood 1977). Adequate quantities of usable habitat are needed to sustain viable populations, and when habitat features selected by a species are more abundant, that area is considered to have higher quality habitat (Manly et al. 2002). The importance of aquatic habitat to fish populations has been widely accepted in fisheries management, and much of recent fisheries research has focused on quantifying habitat quality, understanding causes of degradation and factors limiting to populations, and developing models useful for habitat restoration and enhancement (Fisher et al. 2012).

Complex habitat is often considered to be higher quality habitat for stream fishes (Kovalenko et al. 2012), but habitat

complexity has been defined differently across studies and the term has been used synonymously with habitat heterogeneity, diversity, and arrangement of habitat elements (Tokeshi and Arakaki 2012). Habitat complexity has been used to describe the number and diversity of habitat elements (cover types or substrate classes; Gorman and Karr 1978), increased variance in habitat variables such as water depths or channel widths (Grossman et al. 1998), and the unique combinations of different habitat elements (Fore et al. 2007). For example, complex stream reaches have more niche space meeting the life history needs of multiple species in a fish community (Gorman and Karr 1978; Schlosser 1991). In turn, stream habitat complexity has been shown to be positively correlated with abundance of

*Corresponding author: ddauwalter@tu.org

¹Present address: River Basin Center, University of Georgia, 203 D.W. Brooks Drive, Athens, Georgia 30602, USA.

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Cutthroat Trout *Oncorhynchus clarkii* (Fausch and Northcote 1992; Horan et al. 2000), and Horan et al. (2000) suggested that Colorado River Cutthroat Trout *O. clarkii pleuriticus* populations require more habitat complexity to persist in small patches of isolated stream habitat. Increased complexity has also been shown to be positively associated with the diversity of stream fishes (Gorman and Karr 1978; but see Grossman et al. 1998). Thus, complexity is often considered to be an important determinant of fish habitat use, species diversity, and even ecosystem stability, in streams (Kovalenko et al. 2012; Laub et al. 2012).

Land uses such as agriculture and grazing often impact riparian areas and degrade instream habitat quality (Rinne 1999; Allan 2004). Degraded streams often have low bank stability and wide, shallow stream channels with little or no wood; hence, instream physical habitat for fishes lacks complexity (Platts and Nelson 1985; Lau et al. 2006). Stream and watershed restoration can focus on reestablishing watershed-scale processes such as hydrology, sediment transport, and wood recruitment that influence channel morphology, physical habitat, and water quality in streams (Roni et al. 2002; Schwartz and Herricks 2007; Palmer et al. 2010). Alternatively, management may circumvent restoration of natural fluvial processes and, instead, create habitat complexity directly through manipulation and enhancement of stream habitat (Roni et al. 2008; Dauwalter et al. 2010). For example, creation of side channels increased habitat complexity in the Provo River, Utah, and facilitated habitat partitioning between the coexisting native and nonnative fish species (Billman et al. 2013). The addition of alcoves and wood in two Oregon streams improved winter habitat conditions and increased abundance and survival of anadromous salmonids (Solazzi et al. 2000). However, restoration does not always create habitat complexity (Laub et al. 2012). Even when it does, increased complexity may not always result in a detectable biological response because additional factors, such as proximity to source populations or upstream sediment inputs, may prohibit a fish population response (Platts and Nelson 1985; Lau et al. 2006; Roni et al. 2008).

The goal of our study was to understand how stream habitat complexity influenced microhabitat use by the fish assemblage and habitat selection by the Northern Leatherside Chub *Lepidomeda copei* in Trapper Creek, Idaho. For our study we defined microhabitat complexity as the heterogeneity (i.e., variance) in water depths and velocities, as well as interactions among different habitat components (i.e., variables), and we examined how habitat complexity is created, in part, by secondary instream and riparian structural features (i.e., beaver *Castor canadensis* dams and mature riparian shrubs). Our intent was to expand insights into the current distribution of the Northern Leatherside Chub, a species of special concern (e.g., IDFG 2005) that is the focus of a multiagency, range-wide conservation agreement (UDNR 2009) and that is a recent candidate for listing under the U.S. Endangered Species

Act (Federal Register 76:63444–63478). We also discussed the role of habitat complexity, riparian vegetation, and beavers in restoration efforts targeting the broader fish assemblage in the current range of the Northern Leatherside Chub.

STUDY AREA

Trapper Creek is a tributary to Goose Creek, which lies in the Basin and Range Province, a broad physiographic region that extends north from Mexico to the Idaho, Nevada, and Utah borders. Goose Creek heads in the Sawtooth National Forest in southern Idaho (elevation, 2,200 m) and flows south into northeast Nevada and east into northwest Utah before flowing north into Lower Goose Creek Reservoir (elevation, 1,450 m) in Idaho near the Snake River plain, below which the creek is then diverted entirely for agricultural uses. Trapper Creek flows east from the Sawtooth National Forest and also flows directly into Lower Goose Creek Reservoir. The creek ranges from 2 to 5 m in width and has a riffle-run-pool morphology. The Goose Creek basin is a matrix of sagebrush *Artemisia tridentata* and pine *Pinus* spp., aspen *Populus tremuloides*, and juniper *Juniperus* spp. At higher elevations forests contain pine, fir *Pseudotsuga* spp, and aspen, whereas at lower elevations forests contain single-leaf pinyon *Pinus monophylla*, juniper, and curl-leaf mountain mahogany *Cercocarpus ledifolius*. Riparian areas are comprised of willows *Salix* spp., alders *Alnus* spp., cottonwoods *Populus* spp., and sedges (Family: Cyperaceae). Annual precipitation averages 18-cm, and streamflow patterns are dominated by snowmelt runoff.

Trapper Creek is a species rich tributary to Goose Creek, which is one of the most species-rich subbasins in the Upper Snake River basin above Shoshone Falls (near Twin Falls, Idaho). The following species have been collected from Trapper Creek in the recent past: Bluehead Sucker *Catostomus discobolus*, Mountain Sucker *Catostomus platyrhynchus*, Utah Sucker *Catostomus ardens*, Longnose Dace *Rhinichthys cataractae*, Specked Dace *Rhinichthys osculus*, Redside Shiner *Richardsonius balteatus*, Northern Leatherside Chub, Utah Chub *Gila atraria*, Mottled Sculpin *Cottus bairdii*, and Paiute Sculpin *Cottus beldingii* (Meyer et al. 2006; Blakney 2012; Meyer et al. 2013). Introduced Brook Trout *Salvelinus fontinalis* and Rainbow Trout *O. mykiss*, including Rainbow Trout × Cutthroat Trout hybrids have also been collected (Meyer et al. 2006). Yellowstone Cutthroat Trout *O. clarkii bouvieri* occur in other tributaries to Goose Creek, but no longer occur in Trapper Creek; however, Trapper Creek is one of only a few streams in Idaho where Northern Leatherside Chub are regularly collected (Blakney 2012). Long-term grazing has impacted fish populations in the Goose Creek drainage (IDFG 2007).

METHODS

Fish assemblage and Northern Leatherside Chub associations with microhabitat complexity were assessed using prepositioned

areal electrofishing (Fisher and Brown 1993) in Trapper Creek where Northern Leatherside Chub have recently been sampled (Blakney 2012). Fishes were collected using a Smith-Root, Inc. LR-24 backpack electrofisher positioned on the streambank and outfitted with an anode consisting of a nylon-coated 0.4-cm-diameter braided stainless steel wire (about 6 m long) with a 28-cm-diameter loop (uncoated). The anode for each sample was prepositioned in the stream 15 min prior to electrofishing to allow fishes to exhibit normal behavior and habitat use. Pulsed, direct current (40 Hz, 250–350 V) was applied for approximately 10 s, and one person netted all immobilized fishes; care was taken to not frighten additional fish into the electrical field. Fishes were identified to species, salmonids and Northern Leatherside Chub were measured for total length, and all fishes were released. We prepositioned 150 electrofishing samples among seven different areas (from 7 to 68 samples in each area) of Trapper Creek in August 2013.

Instream habitat was measured immediately after electrofishing in a 1-m-diameter circle centered on the prepositioned electrofishing anode. A 1-m diameter circle approximated the distance at which we observed fish to be immobilized and is near the immobilization range measured for other prepositioned electrofishing arrays (e.g., Schwartz and Herricks 2004). At each circle, water depth and velocity were measured at five locations, once at the array center and at four equidistant points along the circle perimeter. Water velocity was measured twice at each point; once at the stream substratum and at 0.6 m of water depth (10 total measurements). Dominant cover was noted as large wood (>4 m in length, >10 cm in diameter), small woody debris (<4 m in length, or <10 cm in diameter), boulder (>256 mm diameter), emergent vegetation, submerged vegetation, overhanging vegetation, undercut bank (>10 cm deep), or none. Dominant substratum was classified according to the modified Wentworth scale as bedrock, silt and clay (<0.064 mm diameter on *b*-axis), sand (0.064–2.0 mm), gravel (2–15 mm), pebble (15–64 mm), cobble (64–256 mm), and boulder (>256-mm; Cummins 1962). The density of overhead cover from riparian vegetation or instream wood above the water surface was ranked from 1 (none) to 5 (dense). Channel unit type was classified as riffle, run, or pool based on water depth and velocity (Hawkins et al. 1993). The presence of secondary habitat features influencing microhabitat conditions at electrofishing locations was also noted (e.g., beaver dams, beaver ponds, riparian shrubs). Water temperature and conductivity were measured with an Oakton PCSTestr 35 multi-parameter probe (Oakton Instruments, Vernon Hills, Illinois).

Fish assemblage associations with microhabitats and microhabitat complexity were evaluated using constrained correspondence analysis (CCA; canonical correspondence analysis), which is a direct gradient analysis that uses a unimodal species model to explain variation in assemblage structure (relative abundance) using environmental variables (ter Braak 1995). Exploratory detrended correspondence analysis showed

axis 1 gradient length (a measure of beta diversity) to be 3.45, suggesting that a unimodal distribution is probably more appropriate than a linear model (e.g., redundancy analysis; Lepš and Šmilauer 2003); CCA is also robust to the unimodal model assumptions (Palmer 1993). The species matrix used in the CCA was composed of only the 106 sites where at least one individual of one fish species was present; species abundances were untransformed. The habitat variables included in the CCA were mean water velocity (m/s), mean water depth (m), coefficient of variation (CV = 100·SD/mean) in water velocity, SD water depth (m), substrate rank, overhead cover rank, and wood cover and boulder cover categorical variables (presence = 1, absence = 0). Water velocity and depth variables were summarized using the 10 (velocity) or 5 (depth) measurements. Water complexity was estimated as the CV of water velocity and SD of water depth. We wanted to use unstandardized measures of variation in velocity and depth (i.e., SDs) as measures of complexity, but the SD of water velocity was highly correlated with mean velocity (Spearman's rank correlation, $r_s = 0.957$), so we used the CV instead ($r_s = -0.551$). Substrate size was an ordinal ranking of the modified Wentworth substratum classes from 1 (bedrock) to 7 (boulder; Fore et al. 2007). Cover type was grouped into wood (wood = 1, other = 0) and boulder (boulder = 1, other = 0) classes. Significance of CCA axes (comparing the full model to reduced model) and individual habitat variables were assessed using permutation tests with 9,999 permutations at $\alpha = 0.10$. A final model was refit using only significant variables. The CCAs were fit using the vegan package in Program R (R Core Development Team 2012).

Selection of microhabitats and microhabitat complexity by Northern Leatherside Chub was evaluated using a resource selection function (Manly et al. 2002). The selection function was based on the presence or absence (nondetection) of chubs at the 150 prepositioned electrofishing samples (i.e., sampling protocol A and Design I in Manly et al. 2002). Model selection and inference was used to identify the best model or a plausible set of models of microhabitat selection from a candidate set of models. Candidate models were composed of subsets of variables included in a global model containing predictor variables: mean velocity, mean depth, CV velocity, SD depth, overhead cover rank, substrate rank, wood cover, and boulder cover. A mean depth \times overhead cover interaction term was evaluated because of the potential synergistic effect of both variables on habitat selection and as another measure of habitat complexity; Northern Leatherside Chubs have been described to inhabit pool habitats and brushy areas near streambanks (Wallace and Zaroban 2013). Additional candidate models were constructed using all subsets of variables in the global model, except that mean velocity and mean depth were included in all candidate models to estimate effect size since the Northern Leatherside Chub does not use the highest water velocities or shallowest depths we sampled (Wilson and Belk 2001; Wesner and Belk 2012). Fit of the global model to

the data was evaluated using Hosmer–Lemeshow goodness-of-fit, and predictive performance of the most plausible model was assessed using the area under the curve (AUC) of a receiver operating characteristic (ROC) curve (Hosmer and Lemeshow 2000). Candidate models were compared using Akaike's Information Criterion for small sample size (AICc), with the model having the smallest AICc value being the best, most plausible model. Candidate models within 4 AICc units of the best model were also considered plausible (Burnham and Anderson 2002). If multiple candidate models were plausible, then parameter estimates (and variances) were averaged using Akaike weights and shrinkage (Burnham and Anderson 2002; Lukacs et al. 2010). In addition to unstandardized parameter estimates, we report standardized parameter estimates (from models fit with data that were standardized with mean = 0, and standard deviation = 1) for comparison of relative effect sizes for the microhabitat variables included in plausible models. Resource selection functions were fit using the glm function with a logit link in Program R (R Core Development Team 2012).

Associations among microhabitat variables, and between microhabitat variables and secondary habitat features, measured at the 150 electrofishing samples were assessed independent from the species data using a principal components analysis (PCA). Two secondary features associated with electrofishing sites, beaver dams and woody riparian shrubs, were included in the PCA because we observed them to directly influence microhabitat conditions. For example, beaver dams were the source of small woody debris at some sites. The branches of woody riparian vegetation directly provided overhead cover, and, in some cases, entered the water column to contribute small wood and create complex patterns in water velocity. The associations of these secondary habitat features with microhabitat variables were simultaneously assessed in the PCA by including them as binary variables; we omitted them as candidate variables in the CCA and resource selection analyses because they were directly associated (and presumably correlated) with microhabitat features used directly by fishes (e.g., small woody, overhead cover, variance in water velocity). A scree plot was used to determine the number of meaningful principal components for interpretation. The PCA was fit using scaled and centered data (mean = 0, SD = 1) and the correlation matrix in princomp in Program R (R Core Development Team 2012).

RESULTS

We collected seven fish species from the 150 prepositioned electrofishing stations in Trapper Creek (Table 1). Water conductivities (corrected for water temperature) ranged from 250 to 280 $\mu\text{S}/\text{cm}$, and water temperatures ranged from 15°C to 23°C. At least one fish was collected at 106 of the samples. Speckled dace were the most numerically abundant species and occurred at most electrofishing sites; Rainbow Trout were

TABLE 1. Fishes collected, in order of relative abundance, during 150 prepositioned areal electrofishing samples in Trapper Creek, Idaho, August 2013.

Common name	Percent occurrence	Relative abundance
Speckled Dace	48.0	40.1
Redside Shiner	16.0	18.0
Bluehead Sucker	22.6	16.7
Longnose Dace	22.7	10.5
Northern Leatherside Chub	16.0	8.6
Paiute Sculpin	15.3	5.1
Rainbow Trout	3.3	0.9

collected least often and had the lowest relative abundance across species. Northern Leatherside Chub were collected at 16% of sites; their relative abundance was 8.6% among all fishes collected. The 47 chubs collected ranged in total length from 40 to 125 mm.

Fish assemblage structure was influenced by water depths and velocities, including complexity in both, as well as overhead cover and instream wood. The first four axes of the CCA were significant ($P \leq 0.079$); mean velocity, mean depth, SD depth, CV velocity, overhead cover, and wood were significantly related to assemblage structure, whereas substrate and boulder cover were not (Table 2). Variance inflation factor scores were 2.02 or less for each variable, indicating a lack of correlation among constraining variables. The CCA refit using only significant ($P < 0.10$) habitat variables showed Longnose Dace and Paiute Sculpin to occur in shallow, high velocity habitats, and Northern Leatherside Chub, Rainbow Trout, and Redside Shiner used deeper habitats (Figure 1). However, Northern Leatherside Chub, and to a lesser extent, Rainbow Trout, used deeper habitats with more complex water depths and velocities than did the Redside Shiner. Northern Leatherside Chub and Bluehead Sucker were two species most

TABLE 2. Significance (P -value) and variance inflation factor (VIF) for microhabitat variables (permutation test with 9,999 permutations) included in a constrained correspondence analysis to evaluate their potential effects on fish assemblage structure. Wood and boulder metrics were noted as present (1) or absent (0).

Variable	P -value	VIF
Mean velocity (m/s)	0.030	2.02
CV velocity (%)	0.023	1.78
Mean depth (m)	0.064	1.19
SD depth (m)	0.027	1.37
Substrate (rank: 1–7)	0.433	1.44
Overhead cover (rank: 1–5)	0.015	1.15
Wood	0.051	1.36
Boulder	0.980	1.26

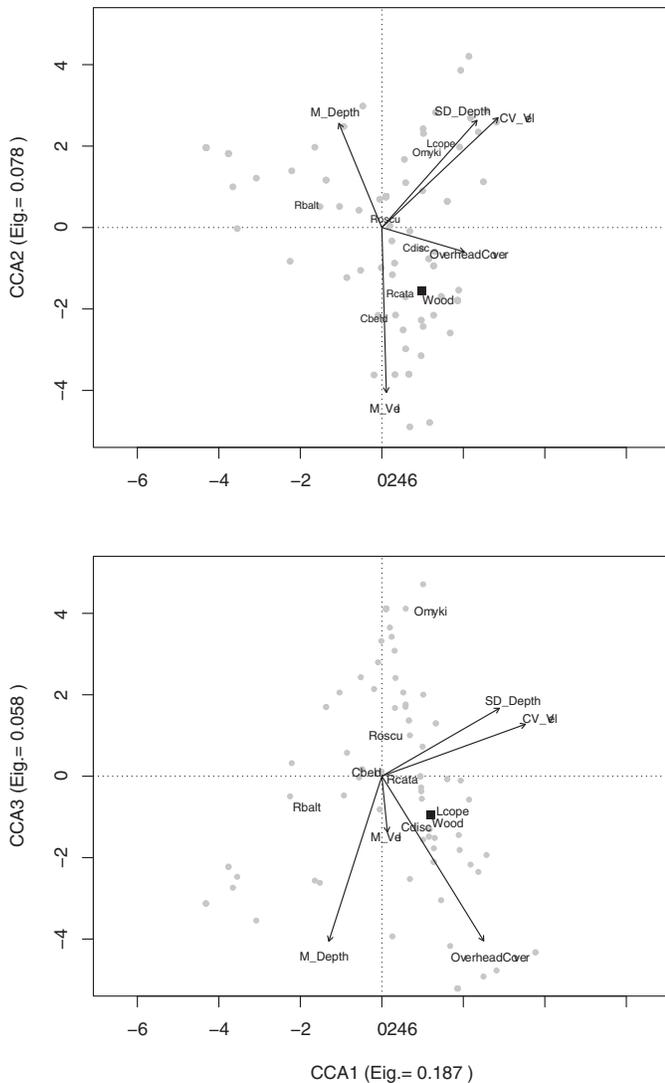


FIGURE 1. Biplots of constrained correspondence analysis (CCA) axes (1 versus 2 [top panel] and 1 versus 3 [bottom panel]), showing associations between fish species, continuous (arrows) and categorical (squares) microhabitat variables, and prepositioned areal electrofishing sites (gray points). Species are abbreviated as first letter of genus, and first four letters of the species epithet: Cbeld = Paiute Sculpin; Cdisc = Bluehead Sucker; Lcope = Northern Leatherside Chub; Omyki = Rainbow Trout; Rbalt = Redside Shiner; Rcata = Longnose Dace; Roscu = Speckled Dace.

associated with overhead cover, and Speckled Dace was not strongly associated with any microhabitat feature that was measured.

Northern Leatherside Chub selected deeper, slower, and more complex habitats (Table 3), which was shown by the resource selection models. The global model fit the data (Hosmer-Lemeshow test: $\chi^2 = 1.66$, $df = 8$, $P = 0.990$). In all, 16 candidate models were plausible (i.e., $\Delta AICc \leq 4$; Table 4). The most plausible model showed acceptable discrimination between used and unused sites (10-fold cross-validated AUC = 0.76, sensitivity = 0.67, specificity = 0.76;

Hosmer and Lemeshow 2000). Because model-averaging cannot be done across models with and without interaction terms, we averaged parameter estimates over 13 of the 16 plausible models that contained a depth \times overhead cover interaction term. A model with averaged parameter estimates showed very good in-sample predictive performance (in-sample AUC = 0.82, sensitivity = 0.67, specificity = 0.76; Hosmer and Lemeshow 2000). Importantly, model-averaged parameter estimates showed a complex interaction between depth and overhead cover. Selection probability increased slightly with depth when overhead cover was absent, but Northern Leatherside Chub were almost certain to be present in deep water when overhead cover is dense, and they selected areas with slower but more complex water velocities (Figure 2). There was some evidence of a positive effect of water depth complexity on habitat selection, as well as a positive effect of boulders and a negative effect of wood. However, unconditional standard errors on those parameters suggested that the magnitude, and even direction, of effect was highly uncertain (Table 5).

The PCA showed most of the variation in microhabitats surveyed was associated with a riffle-run-pool gradient, as indicated by axis 1 (Figure 3). Mean water depth, SD of water depth, and CV of water velocity were negatively related to axis 1, which explained 24.4% of the variation in habitat variables; mean water velocity and substrate size were positively related to axis 1. The second PCA axis (18.7% of variation) represented a gradient of instream (wood and boulder) and overhead cover and showed that overhead cover was tightly coupled with riparian shrubs. Shrubs and beaver dams were highly correlated with PCA axis 3 (12.1%) and showed that these features often, but not always, were associated with wood cover and complex water velocities and depths. When Northern Leatherside Chub abundance was plotted for each site in the PCA plots, it showed chubs occurred more frequently and were more abundant in deeper habitats with variable depths and more overhead cover, conditions that were often created by mature riparian shrubs and beaver dams. The scree plot suggested axes 1 through 3 explained the most variation among the variables included; therefore, we did not interpret PCA axes 4 or higher.

DISCUSSION

Our study showed fish assemblage structure and habitat selection by the Northern Leatherside Chub to be influenced, in part, by habitat complexity at the microhabitat scale in our study system. Our multivariate analysis showed complex water velocities and depths to structure fish assemblages in deep-water habitats, with Northern Leatherside Chub and Rainbow Trout being more common where water velocities and depths were heterogeneous. In contrast, Redside Shiner occurred in deep, homogenous habitats (e.g., beaver ponds). Our habitat selection models also showed the Northern

TABLE 3. Summary statistics for microhabitat variables measured at prepositioned electrofishing samples, where Northern Leatherside Chub were present ($n = 24$) versus absent ($n = 126$). The wood metrics was noted as present (1) or absent (0).

Variable	Presence	Mean	SD	Minimum	Maximum
Mean velocity (m/s)	Present	0.22	0.12	0.04	0.42
	Absent	0.29	0.17	0.01	0.74
CV velocity	Present	131.4	26.4	99.0	195.7
	Absent	120.3	21.7	94.9	190.0
Mean depth (m)	Present	0.43	0.13	0.21	0.73
	Absent	0.32	0.13	0.06	0.76
SD depth (m)	Present	0.07	0.03	0.02	0.14
	Absent	0.06	0.04	0.01	0.21
Substrate (rank: 1–9)	Present	4.0	1.5	2.0	6.0
	Absent	4.0	1.5	1.0	7.0
Overhead cover (rank: 1–5)	Present	2.2	1.0	1.0	4.0
	Absent	1.6	0.9	1.0	4.0
Wood cover	Present	0.5	0.5	0	1
	Absent	0.4	0.5	0	1

Leatherside Chub to select deep areas more often, and the species was almost certain to use deep areas when overhead cover was dense. The selection models also showed, to a lesser extent, that chub occurred more frequently in habitats with complex water velocities and depths. As shown by the PCA, overhead cover is tightly coupled with woody riparian shrubs, and complex water depths and velocities are commonly

created by both mature riparian vegetation at the water surface and beaver dams.

The selection of microhabitats by Northern Leatherside Chub in our study confirmed the general habitat use patterns shown by other studies, but our study also highlights the role of complexity in microhabitat selection. Wilson and Belk (2001) found that Northern Leatherside Chub in Trapper

TABLE 4. Number of parameters (K), log-likelihood, Akaike's Information Criterion for small samples (AICc), Δ AIC, and Akaike weights (w_i) for candidate resource selection probability function models describing habitat selection by Northern Leatherside Chub in Trapper Creek, Idaho. Models with interaction terms also include main effect terms.

Candidate models	K	Log-likelihood	AICc	Δ AICc	w_i
Mean Depth \times OverheadCover + Mean Velocity + CV Velocity	6	-50.846	114.28	0.00	0.213
Mean Depth \times OverheadCover + Mean Velocity + CV Velocity + Substrate	7	-50.428	115.64	1.37	0.108
Mean Depth \times OverheadCover + Mean Velocity + CV Velocity + Boulder	7	-50.568	115.92	1.65	0.094
Mean Depth \times OverheadCover + Mean Velocity + CV Velocity + SD Depth	7	-50.715	116.22	1.94	0.081
Mean Depth \times OverheadCover + Mean Velocity + CV Velocity + Wood	7	-50.822	116.43	2.15	0.073
Mean Depth + OverheadCover + Mean Velocity + CV Velocity	5	-53.092	116.60	2.32	0.067
Mean Depth \times OverheadCover + Mean Velocity + CV Velocity + Substrate	8	-50.089	117.20	2.92	0.050
Mean Depth \times OverheadCover + Mean Velocity + CV Velocity + Substrate + Boulder	8	-50.244	117.51	3.23	0.042
Mean Depth \times OverheadCover + Mean Velocity	5	-53.603	117.62	3.34	0.040
Mean Depth + OverheadCover + Mean Velocity + CV Velocity + Substrate	6	-52.528	117.64	3.37	0.040
Mean Depth \times OverheadCover + Mean Velocity + CV Velocity	8	-50.428	117.88	3.60	0.035
Mean Depth + OverheadCover + Mean Velocity + CV Velocity + Boulder	6	-52.658	117.90	3.62	0.035
Mean Depth \times OverheadCover + Mean Velocity + CV Velocity + SD Depth + Boulder	8	-50.442	117.91	3.63	0.035
Mean Depth \times OverheadCover + Mean Velocity + CV Velocity + Wood + Boulder	8	-50.568	118.16	3.88	0.031
Mean Depth \times OverheadCover + Mean Velocity + SD Depth	6	-52.837	118.26	3.98	0.029
Mean Depth \times OverheadCover + Mean Velocity + SD Depth + Substrate	7	-51.742	118.27	3.99	0.029

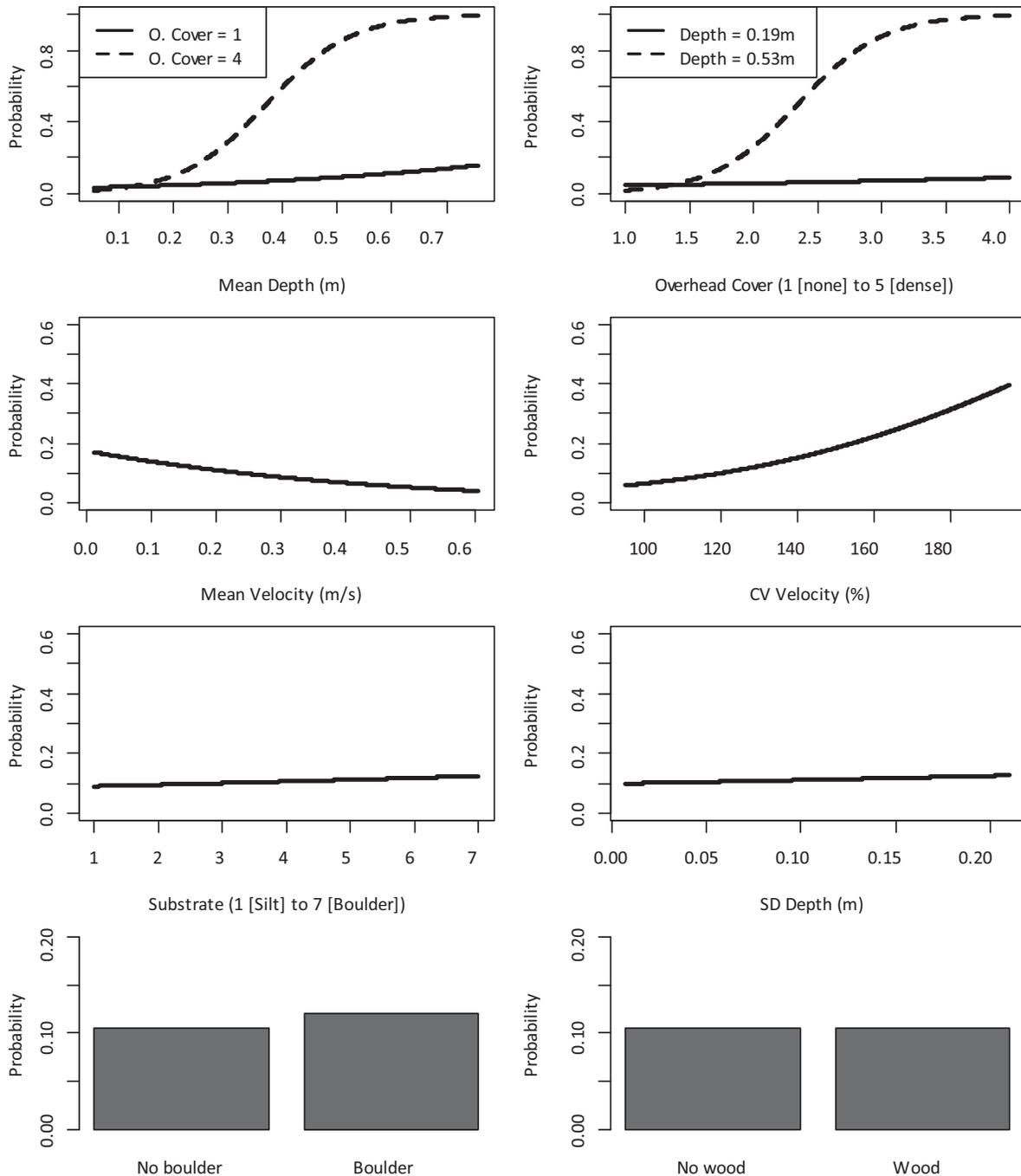


FIGURE 2. Habitat selection probabilities of Northern Leatherside Chub for different microhabitat variables in Trapper Creek, Idaho. All values of habitat variables were held at their mean value for prediction unless specifically varied for a panel.

Creek selected slower water velocities, but they found no effect of water depth, substrate, instream cover (aquatic vegetation, wood, undercut banks), overhead cover, or surface turbulence on selection. In experimental tanks, the Northern Leatherside Chub selected small cobbles for reproduction (Billman et al. 2008). While no other studies of microhabitat selection for Northern Leatherside Chub have been conducted, the closely related Southern Leatherside Chub *L. aliciae*

(Johnson et al. 2004) has been found to select slow water velocities and coarse substrates (Wilson and Belk 2001), and in areas without Brown Trout *Salmo trutta* it occupies deep, silty habitats (Walser et al. 1999). At the reach scale, the presence of Northern Leatherside Chub in a stream reach in the Bear River basin was positively correlated with more pool, backwater, and side-channel habitats and more understory woody and nonwoody vegetation, and abundance was

TABLE 5. Unstandardized and standardized unconditional parameter estimates (model averaged using shrinkage) and standard errors for a resource selection probability function for Northern Leatherside Chub in Trapper Creek, Idaho. Parameter averages were done excluding three candidate models without a depth \times overhead cover interaction term. Akaike weights (w_i) were summed across all models as a measure of variable importance. Wood and boulder metrics were noted as present (1) or absent (0).

Variable	Unstandardized		Standardized		Sum(w_i)
	$\tilde{\beta}_t$	$SE_{\tilde{\beta}_t}$	$\tilde{\beta}_t$	$SE_{\tilde{\beta}_t}$	
Intercept	-5.677	1.868	-2.119	0.222	1.00
Mean depth (m)	-1.072	3.290	0.665	0.211	1.00
Overhead cover (rank: 1-5)	-0.424	0.626	0.710	0.193	1.00
Mean depth \times Overhead cover	3.496	1.592	0.434	0.197	0.86
Mean velocity (m/s)	-2.654	2.226	-0.354	0.297	1.00
SD depth (m)	1.331	2.375	0.048	0.086	0.17
CV velocity	0.023	0.008	0.531	0.193	0.24
Substrate (rank: 1-7)	0.060	0.084	0.089	0.124	0.27
Wood	-0.009	0.006	-0.004	0.003	0.10
Boulder	0.146	0.298	0.049	0.100	0.22

positively associated with pool density and amount of coarse substrate (Wesner and Belk 2012). However, these studies did not evaluate the influence of habitat complexity, either measured as the variation in a habitat variable or the interaction between two or more variables, on microhabitat selection, occurrence, or abundance of Northern or Southern Leatherside chubs at the reach scale. The fish assemblage in our study system showed clear associations with complex water velocities and depths, and the Northern Leatherside Chub showed a synergistic response to overhead cover and water depth. Habitat complexity has been a major theme in stream ecology and restoration for over a decade and has been shown to influence microhabitat selection of stream fishes (Dauwalter and Fisher 2007; Ayllón et al. 2009), as well as fish occurrence, abundance, and diversity at the reach scale (Gorman and Karr 1978). However, complexity is still not routinely evaluated in studies of fish habitat selection, occupancy, and abundance.

The extent to which our results can be generalized to other streams and seasons requires further evaluation because we only conducted our study in one stream during one summer. However, Trapper Creek is one of a few remaining streams in the Upper Snake River basin where the Northern Leatherside Chub is consistently collected, and where the general patterns of habitat use we observed match other qualitative descriptions (Wallace and Zaroban 2013; J. Wesner, University of South Dakota, personal communication). Ayllón et al. (2010) showed that Brown Trout routinely selected deep, slow habitats across several stream systems but that selection of a specific cover type varied by stream. The authors suggested that selection of specific habitats can vary based on habitat availability driven by environmental conditions set at larger spatial scales (e.g., watershed). Kanno et al. (2012) also found that microhabitat selection by the Spotfin Chub *Erimonax monachus* varied spatially as habitat availability changed with

stream size and seasonal variation in water temperature. Future studies of the Northern Leatherside Chub and co-occurring species should focus on understanding the influence of microhabitat and macrohabitats, including the role of complexity, across space and time to assess the generality of our results as they relate to the species' life history requirements and those of other sympatric species. If our findings do apply beyond Trapper Creek, they suggest that degraded riparian conditions from livestock grazing and beaver-trapping and eradication activities may have reduced the availability of complex habitats and negatively influenced the distribution of the Northern Leatherside Chub rangewide, as purported in other studies (Zafft et al. 2009; Blakney 2012).

The complex microhabitats in our study system were also associated with other components of stream systems—mature riparian vegetation and beaver dams—that are often a focus of stream restoration. Riparian vegetation is often negatively impacted by cattle grazing and can lead to wide, shallow, and simple stream channels with high sedimentation levels, little recruitment of wood, and low terrestrial invertebrate inputs that are consumed by fishes (Platts and Nelson 1985; Saunders and Fausch 2009). Many restoration projects focus on excluding cattle from riparian areas through fencing or limit their impact by use of rotational, short-term, or seasonal grazing regimes (Roni et al. 2008), which can increase instream physical habitat complexity, terrestrial food subsidies, and fish population biomass (Saunders and Fausch 2009). The Goose Creek watershed, one of the few remaining watersheds where the Northern Leatherside Chub occurs in Idaho (Meyer et al. 2013; Wallace and Zaroban 2013), has extensive grazing impacts to riparian areas (IDFG 2007), and our study suggests that restoration of mature riparian vegetation in the watershed may provide important habitat for the Northern Leatherside Chub in tributaries other than Trapper Creek.

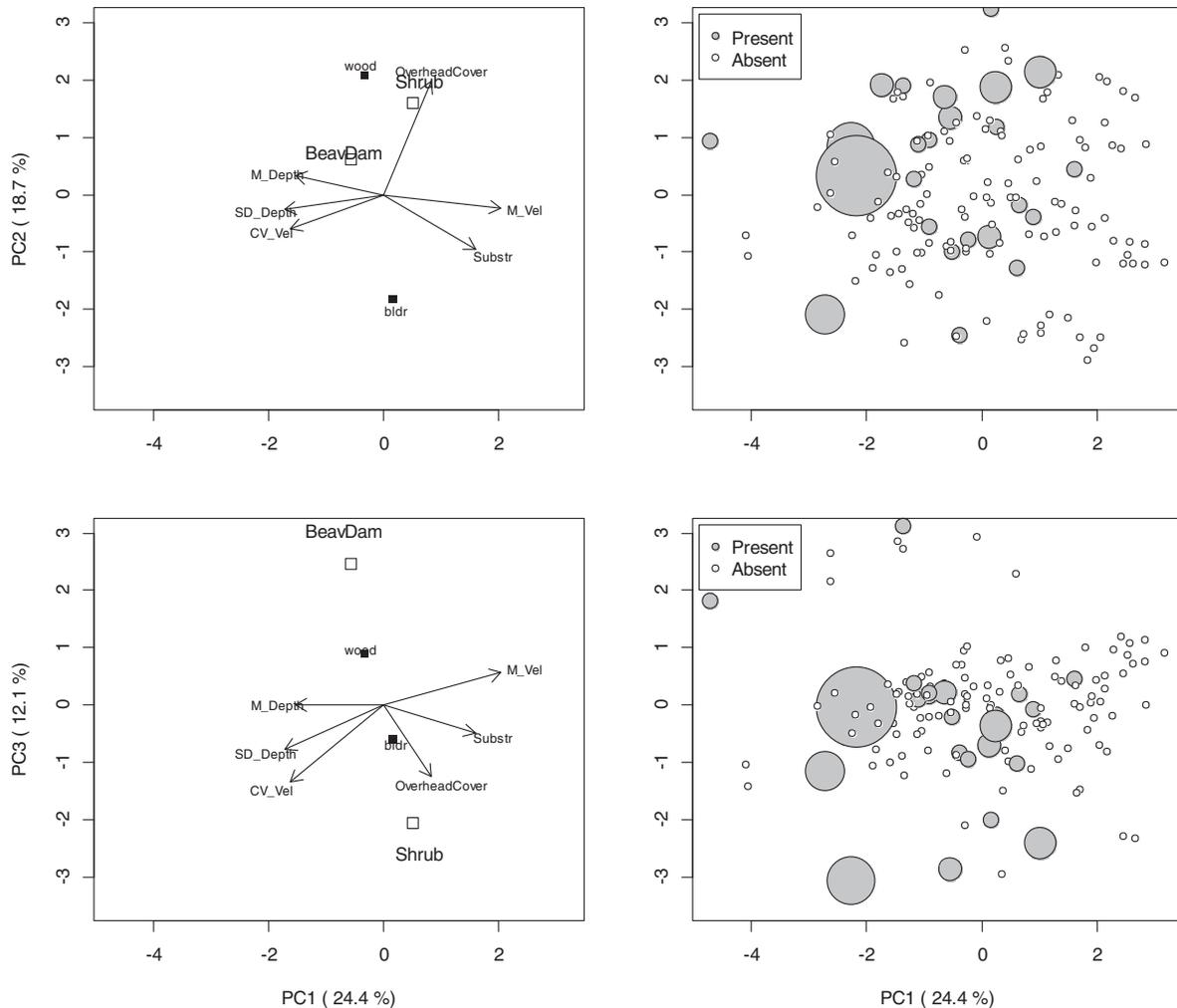


FIGURE 3. Biplots of principal components analysis (PCA) axes: 1 versus 2 (top panels) and 1 versus 3 (bottom panels). Left panels show arrows for continuous habitat variables (scores times 4), centroids for wood and boulder cover (black), and beaver dams and woody shrubs (white). Right panels show site scores with symbol size scaled by number of Northern Leatherside Chub collected (gray = 1–9 individuals; white = absent).

Active and abandoned beaver dams sometimes, but not always, provided the microhabitat complexity used by fishes in our study system. Beaver dams can create discontinuities in riverine systems that alter physical habitat and biogeochemical processes over decadal time scales (Burchsted et al. 2010). Beaver dams can impede riverine connectivity important to the viability of fish populations (Collen and Gibson 2001). However, beaver-influenced stream systems can act as refuge areas during extreme drought conditions because of their ability to retain water (White and Rahel 2008), and beaver have been used to restore incised stream channels (Pollock et al. 2014). Beaver dams are common in Trapper Creek where the Northern Leatherside Chub is most abundant in Idaho, and we collected individuals at some dams during our study. The species has also been collected at beaver dams, including abandoned dams, in tributaries to the Salt River near the Idaho–Wyoming boarder (J. Blakney, Idaho State University,

personal communication). Reduced abundance of beavers and beaver dams, and subsequent loss of habitat complexity associated with beaver dams, throughout the range of Northern Leatherside Chub has been cited as a potential reason for the chub's decline (Blakney 2012). This suggests that beaver reintroduction may be a simple and cost effective restoration strategy for Northern Leatherside Chub, as long as suitable food resources for beaver are available at reintroduction sites (Beck et al. 2010).

Habitat complexity has been documented as an important determinant of habitat use, abundance, and diversity in stream biota for over 30 years (e.g., Gorman and Karr 1978), but it is still not routinely evaluated in studies of fish habitat quality. We argue that habitat complexity should routinely be assessed in studies evaluating fish-habitat relationships and developing models useful to practitioners managing and restoring streams and watersheds. For example, transect-based stream habitat

survey methods have been used for over three decades, and the data collected in that way are amenable to quantifying habitat complexity (Arend and Bain 1999; Fisher et al. 2012). Instead, data are routinely summarized using measures of central tendency (means and median). We argue that additional measures of complexity (e.g., variance, diversity) should also be quantified using those same data. This would allow formal evaluation of hypotheses regarding the effects of stream habitat complexity on stream fishes (including re-analysis of data from past studies) and would provide more informative models for use by managers in an era of unprecedented habitat alteration and expenditures toward stream restoration (Kovalenko et al. 2012; Bernhardt et al. 2005).

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