Physical habitat complexity partially offsets the negative effect of Brook Trout on Yellowstone Cutthroat Trout in the peripheral Goose Creek subbasin

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ABSTRACT.—Nonnative Brook Trout *Salvelinus fontinalis* often reduce the long-term persistence of native Cutthroat Trout *Oncorhynchus clarkii* populations in the western United States. However, there are some instances where the 2 species have co-occurred for decades, and healthy and diverse stream habitat conditions have been suggested to facilitate sympatry. Our goal was to evaluate how habitat diversity may interplay in the negative interactions between Brook Trout and Yellowstone Cutthroat Trout *O. c. bouvieri* in the Goose Creek subbasin in the western United States. We determined that neither species was abundant when they occurred in sympatry. Yellowstone Cutthroat Trout were present at 8 of the 41 sites sampled, and they were sympatric with Brook Trout at 4 sites. Quantile regression revealed that Brook Trout represented a limiting factor for age-1 and older Cutthroat Trout density (fish/100 m²). Lower variation in water depth reflecting poor physical habitat conditions also appeared to be a limiting factor. Age-0 Cutthroat Trout were also in poorer body condition in the presence of Brook Trout. Multiple linear regression showed Brook Trout of all sizes to have a negative effect, and diversity of cover elements a positive but lesser effect, on age-0 Cutthroat Trout body condition. Brook Trout appear to negatively influence the early life stages of Yellowstone Cutthroat Trout in the Goose Creek subbasin, similar to the negative impacts observed elsewhere. However, our data also suggested that habitat complexity may partially offset this negative interaction at some level by affording more niche space for partitioning and adding habitat capacity. If further research showed this pattern to exist more broadly, then protection and restoration of habitat complexity and diversity may play an important role in mediating the negative impacts of Brook Trout on Cutthroat Trout and potentially facilitating sympatry where Brook Trout eradication is not feasible.

RESUMEN.—La presencia de trucha de arroyo no nativa *Salvelinus fontinalis* suele reducir la persistencia a largo plazo de las poblaciones autóctonas de trucha degollada *Oncorhynchus clarkii* en el oeste de EE.UU. Sin embargo, hay casos en los que las dos especies han coexistido durante décadas, y se ha sugerido que condiciones saludables y diversas del hábitat de los arroyos facilitan la simpatría. Nuestro objetivo fue evaluar cómo la diversidad del hábitat puede influir en las interacciones negativas entre la trucha de arroyo y la trucha degollada de Yellowstone *O. c. bouvieri* en la subcuenca de Goose Creek, en el oeste de EE.UU. Determinamos que ninguna de las dos especies fue abundante cuando se encontró en simpatría. La trucha degollada de Yellowstone se encontró en ocho de los 41 sitios muestreados, y fue simpátrica con la trucha de arroyo en cuatro sitios. La regresión por cuantiles mostró que la trucha de arroyo representó un factor limitante para la densidad de truchas degolladas de Yellowstone de edad uno o mayores (peces/100 m²). Una reducida variación en la profundidad del agua reflejó malas condiciones físicas del hábitat, factor que también pareció ser limitante. Las truchas de edad cero se encontraron en peor condición corporal en presencia de la trucha de arroyo. La regresión lineal múltiple mostró que las truchas de arroyo de todos los tamaños tuvieron un efecto negativo, mientras que, la diversidad de elementos de cobertura tuvo un efecto positivo, pero menor, sobre la condición corporal de la trucha degollada de edad cero. La trucha de arroyo pareció influir negativamente en etapas tempranas de la vida de la trucha degollada de Yellowstone en la subcuenca de Goose Creek, de manera similar a los impactos negativos observados en otros sitios. Sin embargo, nuestros datos también sugirieron que la complejidad del hábitat puede compensar parcialmente esta interacción negativa en cierto nivel, al proveer mayor espacio de nicho disponible, añadiendo así capacidad de hábitat. En caso de que investigaciones futuras mostraran que este patrón se observa más ampliamente, entonces la protección y la restauración de la complejidad y la diversidad del hábitat pueden desempeñar un papel importante en la mediación de los impactos negativos de la trucha de arroyo sobre la trucha degollada, y potencialmente facilitar la simpatría donde la erradicación de la trucha de arroyo no es factible.

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The Brook Trout *Salvelinus fontinalis* is native to eastern North America, but it has been intentionally introduced into many western U.S. streams for recreational purposes, where they have displaced native Cutthroat Trout *Oncorhynchus clarkii* populations and played a key role in the extinction of 2 Cutthroat Trout subspecies (Behnke 1992, Dunham et al. 2002a, Peterson et al. 2004). Griffith (1988) suggested that Brook Trout replace Cutthroat Trout after they decline or are extirpated due to habitat degradation or overharvest. However, recent evidence suggests that Brook Trout displace Cutthroat Trout instead of replacing them, and invasion can be either episodic or persistent and is dependent on local habitat conditions (Dunham et al. 2002a, Peterson and Fausch 2003a, 2003b, McGrath and Lewis 2007). Adult Brook Trout often exist in higher densities and exhibit higher production than adult Cutthroat Trout (Benjamin and Baxter 2010, 2012). This is in part because they mature earlier (Kennedy et al. 2003), and they may require less energy to secure dominance hierarchies and thus can allocate more energy towards growth (Green 2015). Additionally, they spawn in fall, which allows them to emerge earlier than Cutthroat Trout and thus affords them competitive and overwinter survival advantages (Gregory and Griffith 2000, Coleman and Fausch 2007). However, both species, when sympatric, show similar use of prey resources and stomach fullness. This suggests a lack of strong interference or exploitative competition between sympatric adults (Dunham et al. 2000, McGrath and Lewis 2007), although competition may only be strong when resources are scarce (Griffith 1988).

Most evidence shows that interactions between Cutthroat Trout and Brook Trout occur in the early life stages. Juvenile Cutthroat Trout abundance is usually lower in the presence of Brook Trout even when adults are healthy, suggesting poor recruitment or juvenile survival (Gregory and Griffith 2000, McGrath and Lewis 2007, Benjamin and Baxter 2010). Experimental studies have shown juvenile Brook Trout to be more aggressive, to occupy more profitable foraging positions, and to consume more food than sympatric juvenile Colorado River Cutthroat Trout *O. c. pleuriticus*, but only at 20 °C and not at 10 °C (De Staso and Rahel 1994). Peterson et al. (2004)

showed that juvenile Colorado River Cutthroat Trout survival, but not adult survival, decreased in the presence of Brook Trout. The Cutthroat Trout recruitment bottleneck that occurs when Cutthroat Trout are sympatric with nonnative Brook Trout is unresolved but believed to be related to age-0 prey resource competition, behavioral interactions that cause age-0 Cutthroat Trout to occupy marginal habitats or to emigrate, predation of age-0 Cutthroat Trout in winter, and predation on Cutthroat Trout eggs (Dunham et al. 2002a, Peterson and Fausch 2003b, McGrath and Lewis 2007).

The Yellowstone Cutthroat Trout *O. c. bouvieri* subspecies is threatened by many factors, including habitat degradation and nonnative species, including Brook Trout (Meyer et al. 2006b, Gresswell 2011). In cage experiments, juvenile Yellowstone Cutthroat Trout overwinter survival was 6% when the 2 species were sympatric but 94% when they were allopatric (Gregory and Griffith 2000). However, Brook Trout were not always thought to have strong, direct interactions with Yellowstone Cutthroat Trout (Thurow et al. 1988). Even recently, Meyer et al. (2014) showed that of 9 sites with sympatric Yellowstone Cutthroat Trout and Brook Trout in the 1980s and 4 sites eventually invaded by Brook Trout in Idaho, Yellowstone Cutthroat Trout were only absent from 2 of those 13 sites when the sites were resurveyed in 2010–2011, whereas Brook Trout were absent at 5 sites; 6 sites still contained sympatric populations after 20 years. The study suggests that there are some situations where the 2 species can co-occur for decades (Meyer et al. 2014). Thus, the negative influence of Brook Trout may take several decades to result in Yellowstone Cutthroat Trout extirpation, and some authors have suggested that the strength of interaction may be dependent on other factors such as habitat quality (Griffith 1988, Thurow et al. 1988).

Our goal was to evaluate how habitat diversity may interplay in the negative interactions between Yellowstone Cutthroat Trout and Brook Trout in the Goose Creek subbasin (Fig. 1). Specifically, our objectives were to (1) quantify any negative association in density and body condition of Yellowstone Cutthroat Trout when these fish are sympatric with nonnative Brook Trout, (2) identify the life stages when any interactions occur, and (3) explore
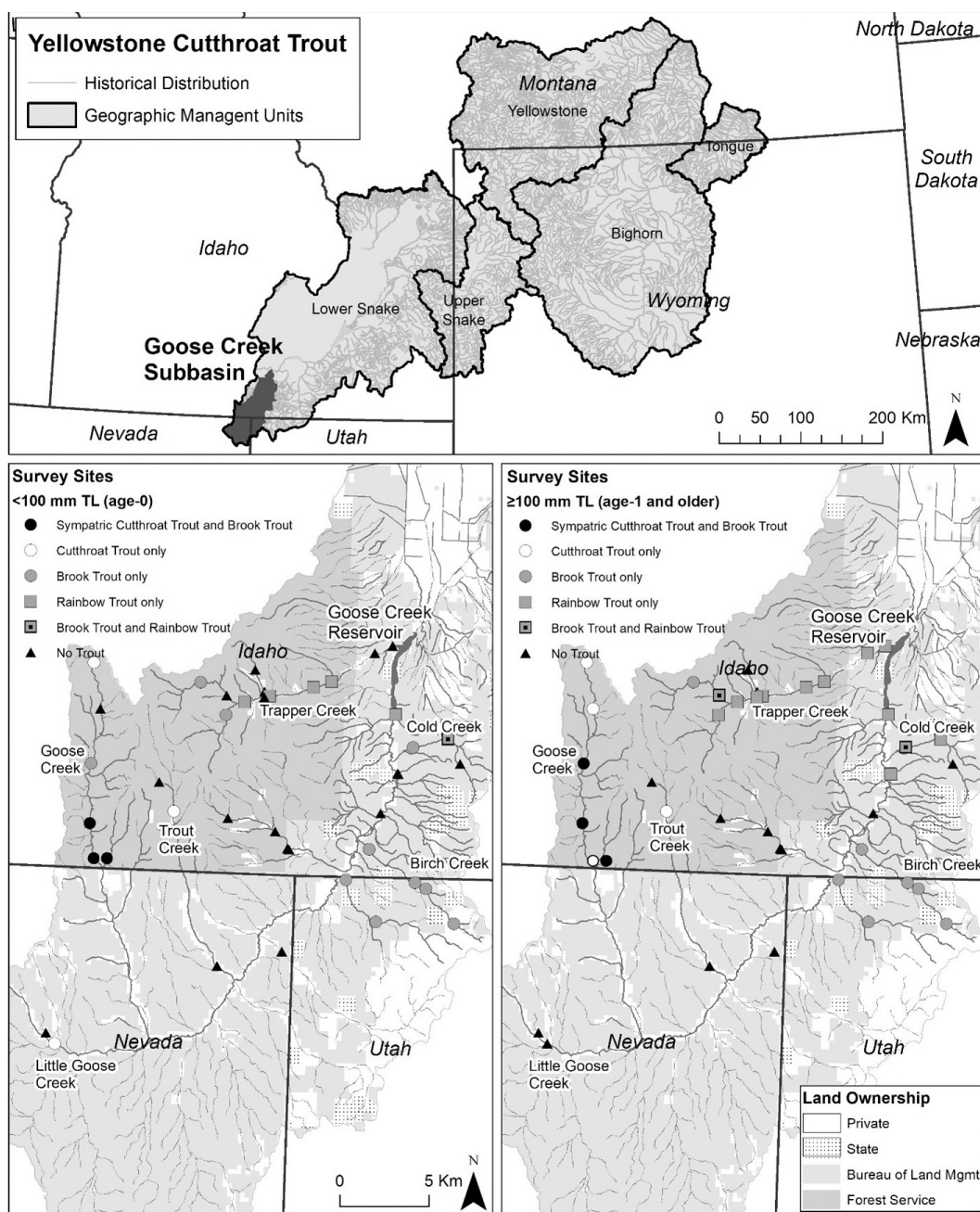
Fig. 1. Yellowstone Cutthroat Trout historical distribution, geographic management units, and Goose Creek subbasin (top panel); Goose Creek subbasin study area and the 41 sites surveyed for fishes from 2013 to 2015 symbolized by salmonid species composition observed at each site (bottom panels). The left bottom panel shows salmonid composition for individuals <100 mm TL (age-0), and the right bottom panel shows salmonid composition of individuals ≥100 mm TL (age-1 and older).

how habitat diversity may offset negative interactions with Brook Trout. The 2 Cutthroat Trout populations that became extirpated in the presence of Brook Trout after 2 decades as reported by Meyer et al. (2014) were in the Goose Creek subbasin (Birch and Cold creeks).

Study Area

The Goose Creek subbasin resides at the boundary between the Great Basin and the Snake River Plain, and it represents the western edge of the geographic range of Yellowstone Cutthroat Trout (Fig. 1). Goose Creek heads in Idaho at approximately 2200 m elevation, flows south into northeast Nevada, into northwest Utah, and then back into Idaho before flowing into Lower Goose Creek (Oakley) Reservoir (1450 m elevation), below which the creek is diverted entirely for irrigation and never reaches the Snake River. Sportfish management on Lower Goose Creek Reservoir is focused on Walleye *Sander vitreus*, Yellow Perch *Perca flavescens*, and Rainbow Trout *Oncorhynchus mykiss*, although many other nonnative sportfish and forage fish and native fishes have been observed during fishery surveys (IDFG 2007a, Meyer et al. 2013). Yellowstone Cutthroat Trout × Rainbow Trout hybrids have also been documented in the subbasin (Meyer et al. 2006b). The Goose Creek basin is a matrix of sage-steppe (*Artemisia tridentata*) and pine-aspen-juniper forest; higher elevations contain pine-aspen forests (*Pinus* spp., *Pseudotsuga* spp., and *Populus tremuloides*), whereas lower elevations contain pinyon–juniper–mountain mahogany forests (*Pinus monophylla*, *Juniperus* spp., and *Cercocarpus ledifolius*). Riparian areas are made up of willows (*Salix* spp.), alders (*Alnus* spp.), cottonwoods (*Populus* spp.), and sedges (Cyperaceae). Average annual precipitation is 18 cm, and streamflow patterns are dominated by snowmelt runoff. Land use is primarily livestock grazing and areas along the Goose Creek main stem are private lands used for hay production and winter grazing (IDFG 2007b). There is a total maximum daily load (TMDL) for the subbasin due to impairments from bacteria (fecal coliform and *Escherichia coli*), dissolved oxygen, total phosphorous, sediment and suspended solids, and temperature (IDEQ 2010, NDEP 2014). These impairments, in part, reflect the impacts of livestock grazing (IDFG 2007b, IDEQ 2010).

METHODS

Fish Sampling

We conducted fish and habitat surveys at 41 sites in the Goose Creek watershed (Fig. 1).

Sites were surveyed from June to October—8 sites in 2013, 29 sites in 2014, and 4 sites in 2015. Our sites were selected based on the stratified random design used by Meyer et al. (2006b) for Goose Creek, while adding additional sites to increase spatial coverage, represent a range of stream conditions, and increase sample size given constraints on access to private land. Each site, typically 100 m thalweg length (range 50–130 m), was isolated with 6.35-mm bar mesh block nets or by impassable barriers such as beaver dams. Fishes were sampled with multiple-pass electrofishing using one Smith-Root LR-24 electrofishing unit (Smith-Root, Inc., Vancouver, WA) with 1 or 2 netters at 37 sites (Dunham et al. 2009). The lower 4 mainstem Goose Creek sites (mean wetted width from 3.4 to 6.4 m) were sampled with 2 LR-24 backpack electrofishing units and 3 or 4 netters. Two to 4 electrofishing passes were completed when trout were present; sampling was terminated after pass 1 or pass 2 if no trout were captured. Electrofishing was done using pulsed (40-Hz) direct current and 200–450 V (Dunham et al. 2009). All trout were identified and measured for total length to the nearest millimeter. Weights were recorded to the nearest 0.1 g for individuals <10 g, the nearest 0.5 g for individuals between 10 and 50 g, and the nearest 1 g for individuals ≥50 g. Individuals were measured using a spring scale (Pesola®, Schindellegi, Switzerland) attached to the jaw or caudal fin (small fish), and weight measurements were typically taken after length measurements had been completed. Rainbow Trout × Cutthroat Trout hybrids were identified according to Meyer et al. (2003b).

To estimate the abundance of each trout species, we first estimated the abundance of all trout by using the Zippin removal method (Zippin 1958) as implemented in the *FSA* package in R (R Core Team 2015, Ogle 2017). To reduce potential bias due to size-dependent capture efficiency, abundances were estimated separately for 2 trout sizes: <100 mm TL and ≥100 mm TL (age-0 and age-1 and older, respectively; Meyer et al. 2003a, Meyer and High 2011). If >1 trout species was present, then species abundance in each size class was estimated based on the proportion of catch representing each species in each size class; this was done to avoid low precision of species-specific estimates when fish abundance was

low (Meyer and High 2011, Meyer et al. 2014). Trout densities were expressed as the number of individuals per 100 m². Wetted reach areas were computed by multiplying reach length by mean wetted width as measured at 5 to 13 transects spaced 10 m apart (see below).

Habitat Sampling

Habitat surveys were conducted immediately after completion of electrofishing surveys at each site. A transect was established every 10 m along each site perpendicular to the channel at bankfull height (5–13 transects based on site length). 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 60% of water depth using a Hach FH950 velocity meter (HACH Company, Loveland, CO). Cover was classified as 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. Stream substratum at each point was classified according to the dominant class of the modified Wentworth scale: 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). Transect point measurements were summarized (mean [$\overline{x}$], standard deviation [SD], and coefficient of variation [CV]) across all transect points in the reach for each habitat variable, as opposed to summarizing within a transect and then across all transects in the reach where a mean of means, SD of means, and averages of transect proportions would average out important reach-scale heterogeneity. Complexity in water velocity and depth were both calculated as SD, but we used CV (CV = 100 × SD/mean) for velocity because of a high correlation between SD velocity and mean velocity (r = 0.91). Substrate and cover diversity were computed using the Shannon–Wiener index:

$$\mathrm{H}' = -\sum_{i=1}^{n} p_i \cdot \log_e p_i,$$

where p_i represents the proportion of substrate or cover type i, and where n is the number of different types (Legendre and Legendre 2012). Residual pool depth was measured for all pools as maximum pool depth minus water depth at the downstream riffle crest (Armantrout 1998). Stream bank stability was classified at each transect endpoint as fracture, slump, slough, eroding, or absent (Burton et al. 2011). Mean August stream temperature was measured using thermographs (TidbiT v2, Onset Computer Corporation, Bourne, MA) 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 1 (with an elevation correction) or 2 thermographs (distance interpolation) in the subbasin.

Cutthroat Trout Density

We evaluated the influence of Brook Trout and physical habitat conditions as limiting factors on Yellowstone Cutthroat Trout densities using quantile regression (Dunham et al. 2002b). Quantile regression models the quantiles of a response variable distribution instead of the mean response typically modeled in regression analysis. When upper quantiles are modeled, they effectively represent the potential maximum response to one or more variables at different levels of those variables, but other factors may keep some observations of the response variable from reaching the upper quantile (i.e., the full potential of the response variable), which is useful when not all important processes are measured (Cade and Noon 2003). This analysis can thus be viewed as more appropriate for identifying limiting factors than regression analyses focused on the mean distribution of the response variable (Cade et al. 1999).

Single-variable quantile regression models were fit with age-1 and older (>100 mm TL) Cutthroat Trout density as the response variable (fish/100 m²). We focused on age-1 and older Cutthroat Trout because the negative interaction between age-0 Cutthroat Trout and Brook Trout, if driven by competition, would likely reduce age-0 Cutthroat Trout survival, especially in winter, and therefore would not manifest itself in Cutthroat Trout densities until one year later because sampling occurred primarily in summer. Predictors comprised physical habitat and Brook Trout variables, including measures of habitat complexity (CV of velocity, SD depth, cover diversity, and substrate diversity), measures of stream condition (percent fines, channel width-to-depth ratio,

percent stream bank slough/slump, and mean August temperature), and Brook Trout density (age-0, age-1 and older, and all Brook Trout; $\log[(\text{fish}/100 \text{ m}^2) + 1]$). We limited our analysis to single-predictor candidate models to focus on each as a limiting factor alone (Cade et al. 1999, Cade and Noon 2003) and to sites where at least Cutthroat Trout or Brook Trout (or both) of any size were present ($n = 19$, see Results). All quantile regression models were fit to the 90th percentile (0.9 quantile) of the response variable, which was the $\log_e$-transformed age-1 and older Cutthroat Trout density ($[\text{fish}/100 \text{ m}^2] + 1$). Models were fit using the '*quantreg*' package (Koenker 2012, 2020) in R (R Core Team 2015); parameter standard errors were estimated using the xy-bootstrap method; and models were evaluated using the AICc statistic developed for quantile regression (i.e., rqAICc; Cade et al. 2005). The model with the minimum rqAICc was considered the most plausible, and models within <4 rqAICc units were considered plausible as well. Model fit was evaluated using the quantile coefficient of determination (R^1) that represents the proportional reduction in objective function by a model compared to an intercept-only model (Cade et al. 2005).

Cutthroat Trout Body Condition

We evaluated the effect of Brook Trout on juvenile Cutthroat Trout body condition using 2 complementary analyses. First, we used a *t* test to compare the relative condition of Cutthroat Trout at sites with Brook Trout and at sites without Brook Trout. Relative condition (K_n) was computed for each individual fish as the observed weight (W) divided by the length-specific mean weight of all Cutthroat Trout in the watershed (W'):

$$K_n = 100 * (W/W') .$$

W' was predicted from a weight–length equation developed from all Cutthroat Trout sampled:

$$W' = aL^b ,$$

where L is total length, and where a and b are constants estimated by regressing $\log_{10}(W)$ versus $\log_{10}(L)$ (Neumann et al. 2012). Separate *t* tests were computed for Cutthroat Trout age-0 (<100 mm TL) and age-1 and older

(≥100 mm). The significance of each *t* test was evaluated at $\alpha = 0.10$, which was selected to balance type I and type II errors. The same analysis was replicated for Brook Trout to evaluate any reciprocal effect of Cutthroat Trout on Brook Trout.

We also estimated the effect of Brook Trout presence on Yellowstone Cutthroat Trout weight using a complementary analysis of covariance (ANCOVA) that was an extension and linear version of the standard weight–length equation above. For the ANCOVA, $\log_{10}$ Cutthroat Trout weight was the response variable, $\log_{10}$ total length was the covariate, and the presence of Brook Trout at a site (present = 1, absent = 0) was the main effect. Because we hypothesized that Brook Trout would impact the condition of age-0 Cutthroat Trout only, we included an interaction between the main effect and covariate that, if significant in the direction of our expected response, would show only weight of the smallest Cutthroat Trout to be influenced by Brook Trout presence. Again, the significance of the interaction was evaluated at $\alpha = 0.10$.

Because we hypothesized that Brook Trout would influence the body condition of age-0 Cutthroat Trout only, we used multiple linear regression in a model selection framework to evaluate whether Brook Trout had an effect on age-0 Cutthroat Trout body condition, and whether that effect was stronger than physical habitat variables including measures of habitat complexity. To keep sample size:variable ratios near 10:1, we limited candidate models to all combinations of 3 predictor variables or fewer as main effects only; variables were the same as those described above for the quantile regression models. Akaike's information criterion adjusted for small sample size (AICc) was used to evaluate the plausibility of all candidate models; the model with the lowest AICc value was considered the most plausible. Akaike weights were computed as a measure of the probability that the model is the correct model for models within 4 AICc units (ΔAICc) of the best model (i.e., plausible models; Burnham and Anderson 2002). If multiple models were plausible (ΔAICc < 4), then model averaging with shrinkage (Lukacs et al. 2010) and Akaike weights was performed to estimate parameters and standard errors based on model selection uncertainty in addition to parameter uncertainty. Variable importance
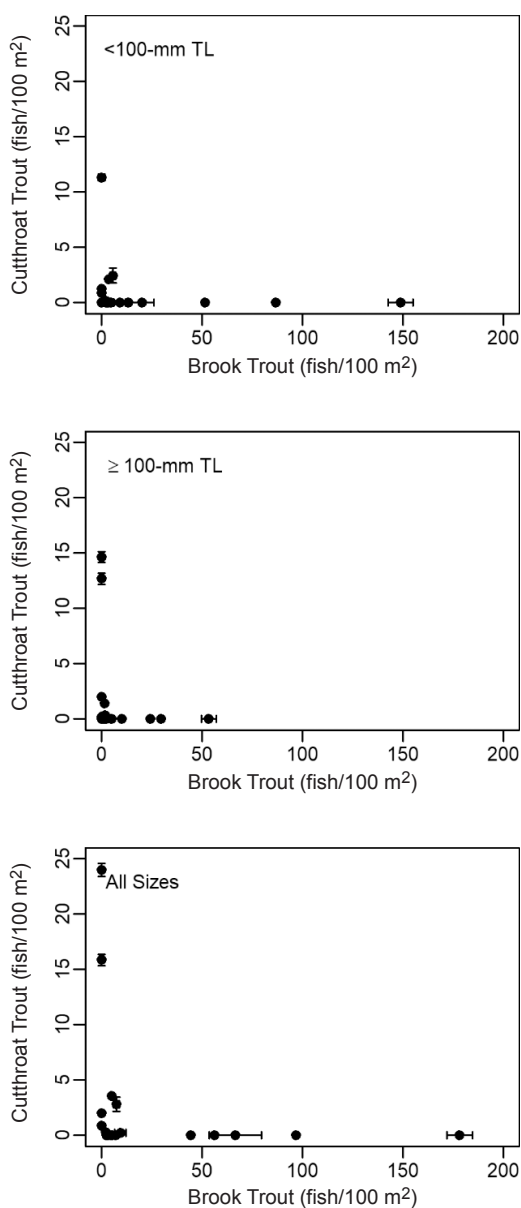
Fig. 2. Scatterplots of Yellowstone Cutthroat Trout and Brook Trout density (±1 SE) for 3 size classes at 41 survey sites in the Goose Creek subbasin.

was evaluated as the sum of Akaike weights for the plausible models in which the variable appeared (Burnham and Anderson 2002). We only used data from sites where age-0 Cutthroat Trout were present, and regression models were fit in Program R (R Core Team 2015).

RESULTS

We were able to acquire access to collect data at 25 of the 31 sites surveyed by Meyer et al. (2006b). We could not acquire access to private land at 4 sites. One site was in the middle of a beaver pond complex and not logistically feasible to sample, and another site was dry. We supplemented those initial sites with opportunistic surveys on accessible perennial streams with the goal of increasing geographic coverage, the range of habitat conditions sampled, and tributary representation; we were denied access to the mainstem Goose Creek on private land in Nevada. Yellowstone Cutthroat Trout were collected at 8 of 41 sites (19.5%), Brook Trout were collected at 15 of 41 sites (36.6%), and the 2 species were sympatric at 4 of the 41 sites (9.8%; Fig. 1). Sympatry occurred only at sites on mainstem Goose Creek in the upper watershed upstream of the Nevada state line. Rainbow Trout, the only other salmonid collected, occupied 14 of 41 sites (34.1%) near Goose Creek Reservoir, but they were never sympatric with Cutthroat Trout. We did observe some Rainbow Trout with Cutthroat Trout characteristics (larger posterior spots and faint red throat slashes) in Trapper Creek that could have been hybrids, but they were primarily Rainbow Trout phenotypes and so were called Rainbow Trout due to the uncertainty in visually identifying hybrids (Meyer et al. 2003b).

Cutthroat Trout Density

Yellowstone Cutthroat Trout densities, when the species was present, ranged from 0.15 to 11.33 fish/100 m^2 for individuals <100-mm TL and from 0.15 to 12.68 fish/100 m^2 for individuals ≥100 mm TL. Sympatry at 4 sites only occurred at the lowest abundances of Cutthroat Trout and Brook Trout we observed, for both age-0 (<100 mm) and age-1 and older (≥100 mm) individuals (Fig 2).

Brook Trout density (all ages) and variation (SD) in water depth both explained the variation in the upper limit of age-1 and older Cutthroat Trout densities and thus appeared to be factors limiting Cutthroat Trout abundance (Table 1). No other candidate models were within 10 rqAICc units of the best model. Quantile coefficients of determination showed both Brook Trout density (all ages) and SD of depth to predict the upper quantile of age-1

TABLE 1. Parameter estimates (b_i) and standardized parameter estimates (b_{i_std}), 90% confidence limits of parameter estimates (in parentheses), log-likelihood, rqAICc, ΔrqAICc, Akaike weights (w_i), and R^1 for candidate quantile regression models, both the initial single-variable candidate models and the exploratory interaction model, predicting age-1 and older Cutthroat Trout density (fish/100 m²) as a function of physical habitat variables or Brook Trout density of all ages (log[(fish/100 m²)+1]; Log BKT). Only candidate models with ΔrqAICc < 12 are shown.

Model	b_i (90% CI)	b_{i_std} (90% CI)	LogLik	rqAICc	ΔrqAICc	w_i	R^1
Log BKT (fish/100 m²)	−0.504 (−0.569 to −0.504)	−0.820 (−0.925 to −0.82)	−25.00	57.60	0.00	0.756	0.46
SD Depth (m)	30.440 (−10.954 to ∞)	1.388 (−0.499 to ∞)	−26.13	59.86	2.26	0.244	0.42
Temperature (°C)	−0.374 (−0.963 to −0.151)	−0.555 (−1.432 to −0.244)	−30.47	68.54	10.94	0.000	0.27
CV Velocity (%)	0.026 (−0.021 to 0.062)	−0.763 (−0.620 to 1.805)	−30.90	69.40	11.80	0.000	0.26

and older Cutthroat Trout density reasonably well (R$^1_{Brook Trout}$ = 0.46; R$^1_{SD Depth}$ = 0.42; Table 1). Brook Trout had a negative effect on the upper limits of age-1 and older Cutthroat Trout densities, and SD of depth had almost twice the effect on densities, albeit positive (Fig. 3A, B), based on standardized parameter estimates, although parameter uncertainty was high and the 90% confidence interval of the estimate included zero (Table 1).

Cutthroat Trout Body Condition

One hundred thirty-three Yellowstone Cutthroat Trout were collected across the 8 sites at which they were present; 55 individuals were <100 mm TL (10 individuals at 4 sites sympatric with Brook Trout), 78 were ≥100 mm TL (5 individuals at 4 sites sympatric with Brook Trout). The weight–length equation was estimated as

$$W = 0.000005 \times L^{3.1337},$$

(df = 130, r^2 = 0.991). Yellowstone Cutthroat Trout relative condition, K_n, ranged from 38 to 138 ($\bar{x}$ = 101.0, SD = 12.6), and it was significantly higher in the absence of Brook Trout for individuals <100 mm TL (t = 2.97, df = 8.42, P = 0.02) but was not different where Brook Trout were present (versus absent) for individuals ≥100 mm TL (t = −0.25, df = 3.07, P = 0.82; Fig. 4) where statistical power to detect change was low due to small sample size when Brook Trout were present (power = 6%); relative condition of Brook Trout <100 mm TL did not differ when Cutthroat Trout were and were not present (t = −0.29, df = 96.9, P = 0.78).

Only the smallest Yellowstone Cutthroat Trout were shown to be of lower weight per unit length in the presence of Brook Trout, as shown by the significant Brook Trout × total length interaction term in the ANCOVA (t = 8.98, df = 127, P < 0.001). Prediction intervals (90%) on the weight–length plot for Cutthroat Trout with Brook Trout present versus absent did not overlap for the smallest individuals (Fig. 5). Four of 5 of the smallest Cutthroat Trout sympatric with Brook Trout had high influence on this model (Cook's distance 0.93–1.53). A model refit excluding those 4 observations (leaving 1 small Cutthroat Trout <40 mm TL) still showed a significant Brook Trout × total length interaction (P < 0.001).
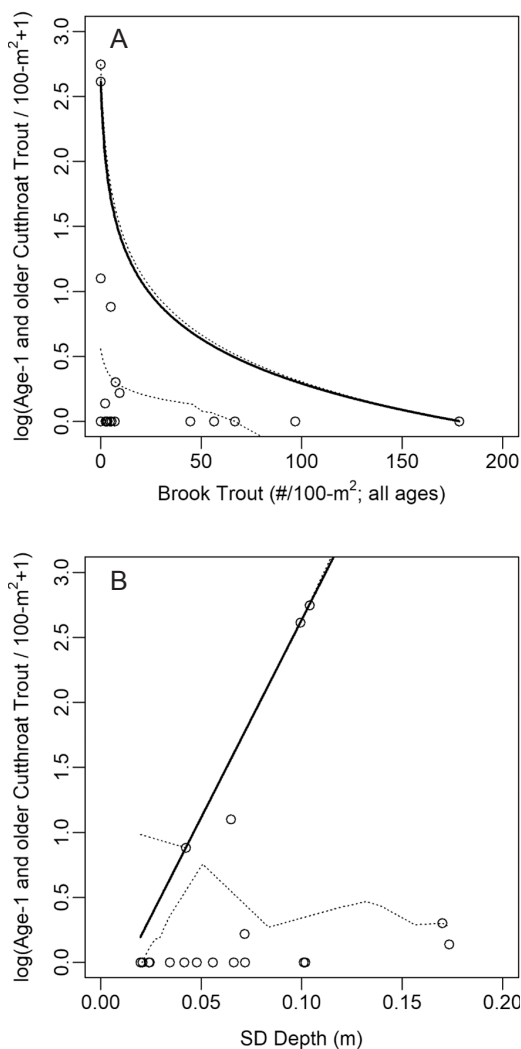
Fig. 3. Observed and predicted densities of age-1 and older Cutthroat Trout from a quantile (τ = 0.9) regression model as a function of (A) Brook Trout density (all sizes), and (B) SD of Water Depth. The dashed lines represent 90% bootstrapped confidence intervals.
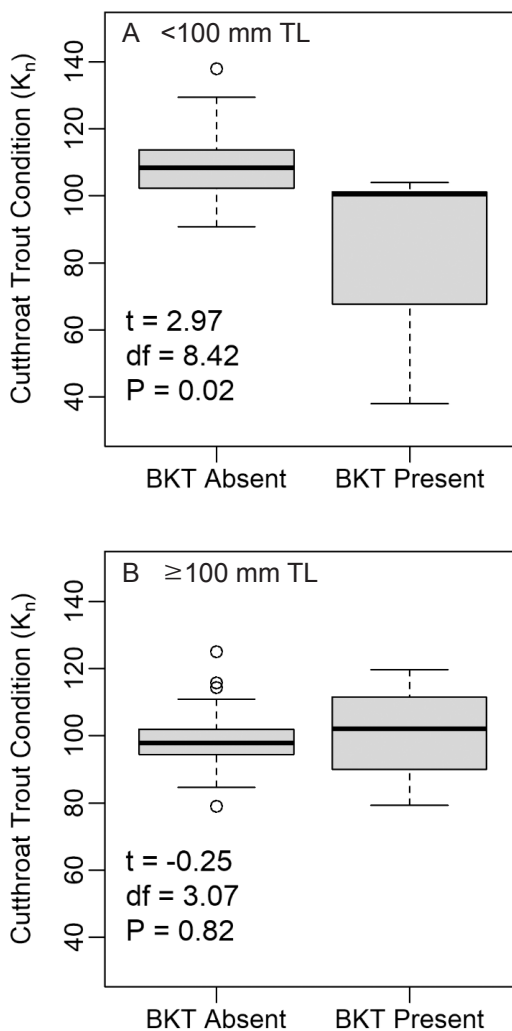

Fig. 4. Boxplots of Yellowstone Cutthroat Trout relative condition (K_n) at sites with Brook Trout (BKT) present and absent for 2 size classes: <100 mm TL and ≥100 mm TL.

Model selection showed 10 candidate multiple regression models to be plausible when explaining the body condition of age-0 Cutthroat Trout as a function of Brook Trout density and habitat covariates (ΔAICc < 4; Table 2). Cover diversity (H′) and Brook Trout density, either age-0 or age-1 and older density, appeared in all 10 top models; however, models with age-1 and older Brook Trout (≥100 mm TL) had more support and higher importance values than did models with age-0 Brook Trout (<100 mm TL; Tables 2, 3).

Model-averaged parameter estimates (with shrinkage) showed a positive effect of cover diversity and a negative effect of Brook Trout of both sizes on age-0 Cutthroat Trout body condition, although age-1 and older Brook Trout had a stronger negative effect than age-0 Brook Trout did (Fig. 6, Table 3). Parameter estimates from models refit with scaled and centered data showed Brook Trout to have about 2.5 times the effect on age-0 Cutthroat Trout body condition than did cover diversity within the range of conditions observed (Table 3).
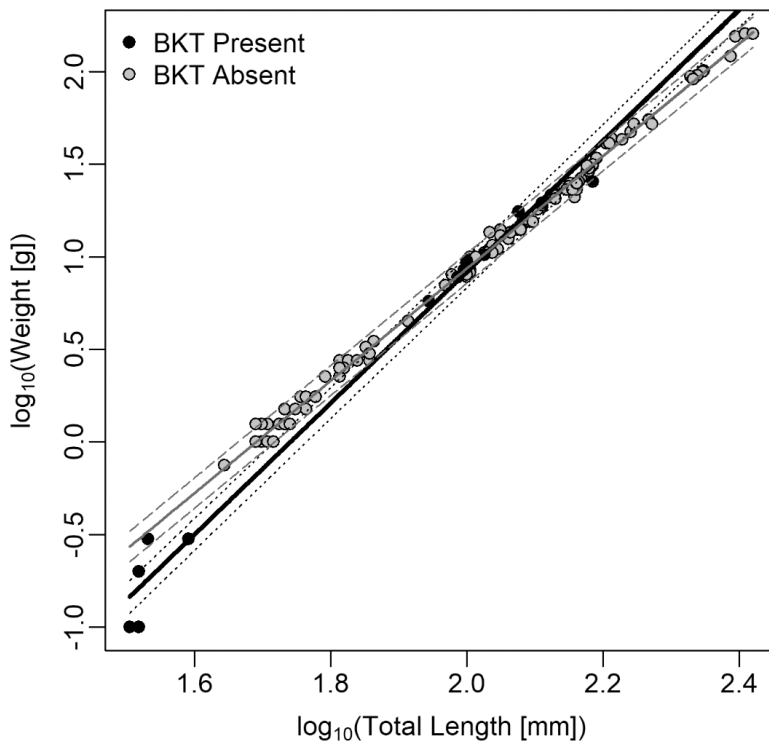
Fig. 5. Yellowstone Cutthroat Trout length–weight plots at sites with and without Brook Trout (BKT). Thicker lines indicate best fit, and thinner lines represent 90% prediction intervals (gray and dashed = Brook Trout present; black and dotted = Brook Trout absent).

DISCUSSION

We found that Yellowstone Cutthroat Trout rarely occurred, and were never abundant if they did occur, in the presence of Brook Trout in the Goose Creek subbasin. We found them to be abundant at only 2 sites where Brook Trout were absent; these 2 sites had areal densities (16–24 per 100 m²) that were above average for subbasins in the upper Snake River Basin (Meyer et al. 2006b). The negative interaction we observed appeared to be strongest at the age-0 life stage of Yellowstone Cutthroat Trout, as shown in other studies that included other Cutthroat Trout subspecies (reviewed by Dunham et al. 2002a). This suggests that some of the negative interactions between age-0 Cutthroat Trout and Brook Trout are similar to those studied elsewhere. In addition to this commonality, our study was revealing in 3 ways. First, a synthesis of studies suggested that age-0 Cutthroat Trout are impacted most by age-0 Brook Trout (Dunham et al. 2002a). However, we observed that

Brook Trout of all sizes had a negative effect on age-1 and older Cutthroat Trout densities, suggesting that age-0 Cutthroat Trout are affected, in part, by negative interactions with larger Brook Trout and not just age-0 Brook Trout. Second, our study provides data-based evidence that suggests that habitat diversity plays a role in the abundance and body condition of age-0 Cutthroat Trout and may offset, at least partially, the negative interaction with Brook Trout. Third, we observed these responses on the geographic range periphery, where some researchers have posited that habitat may differ from the range core and that populations may have unique genetics resulting from founding events, drift, or local adaptation, each of which has the potential to influence ecological interactions between native and nonnative species (Southwood 1977, Lesica and Allendorf 1995, Bunnell et al. 2004). The negative interaction with nonnative Brook Trout does not seem to be unique with regard to the peripheral nature of populations in the Goose Creek subbasin.

TABLE 2. Number of parameters (df), log-likelihood, AICc, ΔAICc, and Akaike weights (w_i) for plausible (ΔAICc < 4) and nearly plausible (ΔAICc = 4–6) candidate linear regression models predicting relative condition (K_n) of age-0 Yellowstone Cutthroat Trout as a function of physical habitat variables and age-0 and age-1 and older (Age 1+) Brook Trout density (log[(fish/100 m²) + 1]). Candidate models represented all combinations of predictor variables limited to a maximum of 3 terms in a single model. Akaike weights (w_i) computed for plausible models (ΔAICc < 4) only.

Model	df	logLik	AICc	ΔAICc	w_i
Cover Diversity + Age-1+ Brook Trout + Substrate Diversity	5	−207.83	426.92	0.00	0.195
Cover Diversity + Age-1+ Brook Trout	4	−209.08	426.97	0.05	0.191
Cover Diversity + Age-1+ Brook Trout + SD Velocity	5	−207.97	427.19	0.27	0.171
Cover Diversity + Age-1+ Brook Trout + % Fines	5	−208.72	428.69	1.77	0.081
Cover Diversity + Age-1+ Brook Trout + Age-0 Brook Trout	5	−208.72	428.70	1.78	0.080
Cover Diversity + Age-1+ Brook Trout + Temperature	5	−208.75	428.76	1.84	0.078
Cover Diversity + Age-0 Brook Trout	4	−210.19	429.21	2.29	0.062
Cover Diversity + Age-1+ Brook Trout + Width:Depth Ratio	5	−208.99	429.23	2.31	0.062
Cover Diversity + Age-0 Brook Trout + Temperature	5	−209.17	429.60	2.68	0.051
Cover Diversity + Age-0 Brook Trout + SD Velocity	5	−209.73	430.72	3.80	0.029
Cover Diversity + Age-0 Brook Trout + % Fines	5	−209.88	431.01	4.09	—
Age-0 Brook Trout + SD Velocity + Temperature	5	−210.04	431.32	4.41	—
Cover Diversity + Age-0 Brook Trout + Width:Depth Ratio	5	−210.17	431.58	4.66	—
Cover Diversity + Age-0 Brook Trout + Substrate Diversity	5	−210.17	431.60	4.68	—
% Fines + SD Velocity + Width:Depth Ratio	5	−210.71	432.66	5.74	—

The lower body condition of age-0 Cutthroat Trout in the presence of Brook Trout in our study suggests a negative interaction at that life stage; however, our data suggested that in the Goose Creek subbasin this interaction was not limited to age-0 Brook Trout but rather age 1 and older Brook Trout had a stronger effect. Unfortunately, our study does not elucidate the mechanism of the interaction, and future studies are needed to reveal it. Dunham et al. (2002a) reviewed studies evaluating Cutthroat Trout–Brook Trout interactions, and most studies concluded, despite a lack of clear evidence, that interspecific competition is the mechanism driving the negative impacts of Brook Trout. Peterson et al. (2004) found that juvenile Colorado River Cutthroat Trout had higher survival when Brook Trout were removed from midelevation Colorado streams (2500–2700 m elevation) and that Cutthroat Trout recruitment failed regardless of whether Brook Trout were present in high elevation cold streams (3150–3250 m). McGrath and Lewis (2007) suggested that studies on feeding, growth, and lipid levels of age-0 Cutthroat Trout would provide insights into the mechanisms of the negative impacts of Brook Trout. That the density of age-1 and older Brook Trout explained more variation in age-0 Cutthroat Trout body condition in our study is yet another example that suggests that interference competition, aggressive behavior, or possibly predation underlies some of the negative interaction we observed, but this result should be followed up with behavioral field or lab experiments (De Staso and Rahel 1994).

It is not surprising that we observed Brook Trout limiting the abundance of age-1 and older Cutthroat Trout (Dunham et al. 2002a). However, we also observed that low variation (SD) in water depth, one measure of habitat complexity that reflects poor stream conditions, may also limit Cutthroat Trout abundance. Variation in water depth as we measured it reflects both lateral and longitudinal variation in stream channel bed form. Lateral variation is expected to increase in deeper, larger streams as well as in streams with lower width-to-depth ratios. Longitudinal variation is expected to be higher in streams with well-structured riffle-pool sequences (Knighton 1998). Both width-to-depth ratio and riffle-pool structure reflect the condition of physical habitat in streams (Kauffman and Krueger

Table 3. Model-averaged parameter estimates ($b \pm 1$ SE), importance values ($\sum w_i$ for models in which the parameter appears), and number of models in which the parameter appears (N) for plausible models predicting relative condition (K_n) of age-0 Cutthroat Trout as a function of physical habitat variables and age-0 or age-1 and older (Age-1+) Brook Trout density ($\log[(\text{fish}/100 \text{ m}^2) + 1]$).

Variable	Unstandardized b_i (1 SE)	Standardized b_i (1 SE)	Importance	N
Intercept	93.88 (24.53)	−0.47 (0.12)	1.00	10
Cover Diversity	48.41 (15.73)	0.59 (0.19)	1.00	10
Age-1+ Brook Trout	−44.03 (20.90)	−1.41 (0.74)	0.86	7
Age-0 Brook Trout	−4.55 (10.07)	−0.32 (0.64)	0.22	4
SD Velocity (m/s)	31.66 (82.23)	0.04 (0.09)	0.20	2
Substrate Diversity	−3.19 (8.01)	−0.04 (0.10)	0.20	1
Temperature	0.34 (1.30)	0.02 (0.07)	0.13	2
% Fines	−0.02 (0.08)	−0.01 (0.05)	0.08	1
Width:Depth Ratio	−0.01 (0.11)	−0.002 (0.03)	0.06	1

1984, Walrath et al. 2016). Streams in poor condition from land use (e.g., agriculture, livestock production) often have wide, shallow stream channels that lack physical habitat complexity (Kauffman and Krueger 1984). Thus, our data from the Goose Creek Subbasin suggest that more habitat complexity, a common attribute of healthy streams, results in increased habitat capacity for age-1 and older Yellowstone Cutthroat Trout. Increased capacity may partially offset the negative impacts of Brook Trout and facilitate sympatry as suggested by others (Thurow et al. 1988, Gresswell 2011).

We also found that habitat diversity, and thus quality, may partially offset the negative effects of Brook Trout on age-0 Cutthroat Trout. Habitat diversity is thought to provide more niche space and increase the likelihood that all required habitats exist in a smaller unit area for Cutthroat Trout persistence (Horan et al. 2000). Our data suggest that more forms of cover improve living conditions, and thus body condition, for age-0 Cutthroat Trout, although the mechanisms again remain elusive. Diverse forms of cover may create refuge from predators or provide more space for coexistence with congeners such as Brook Trout (Penaluna et al. 2016). Thus, when Brook Trout are present, diverse forms of cover may allow sufficient habitat availability and partitioning to limit behavioral interactions that have been suggested to cause stress, low survival, and/or emigration of age-0 Cutthroat Trout and allow the 2 species to coexist at some level (McGrath and Lewis 2007). Thurow et al. (1988) noted that Yellowstone Cutthroat Trout may persist when they are sympatric with nonnative salmonids, including Brook Trout, in high-quality habitats, but that

research provided no data-based evidence as we have here. Habitat quality and complexity have been shown to positively influence the persistence of other Cutthroat Trout subspecies (Horan et al. 2000, Peterson et al. 2014). This portends that improving instream cover diversity is another management action that should be considered by managers attempting to conserve Cutthroat Trout populations faced with Brook Trout invasions. However, our standardized parameter estimates suggest that Brook Trout have approximately 2.5 times the [negative] effect on body condition of age-0 Cutthroat Trout than cover diversity does within the range of conditions we observed, which begs the question: how much habitat complexity is enough to facilitate long-term persistence in the face of a Brook Trout invasion?

The role that diverse instream cover plays in facilitating coexistence of Cutthroat Trout and Brook Trout could be further evaluated through underwater observation and field enclosure studies where cover diversity, food availability, and fish densities are manipulated (Meyer and Griffith 1997). The Goose Creek subbasin does have a TMDL with listed impacts of nutrients, sedimentation, and temperature related to livestock grazing (IDFG 2007b, IDEQ 2010). Riparian exclosures could be used in areas where the 2 species are sympatric to improve habitat conditions through passive restoration, and age-0 Cutthroat Trout interactions with Brook Trout, condition, survival, and movement could be monitored concurrently with changes in habitat condition and complexity (Platts and Rinne 1985, Peterson and Fausch 2003a, Quist et al. 2006, Dauwalter et al. 2018). In addition to field experiments, a larger and geographically
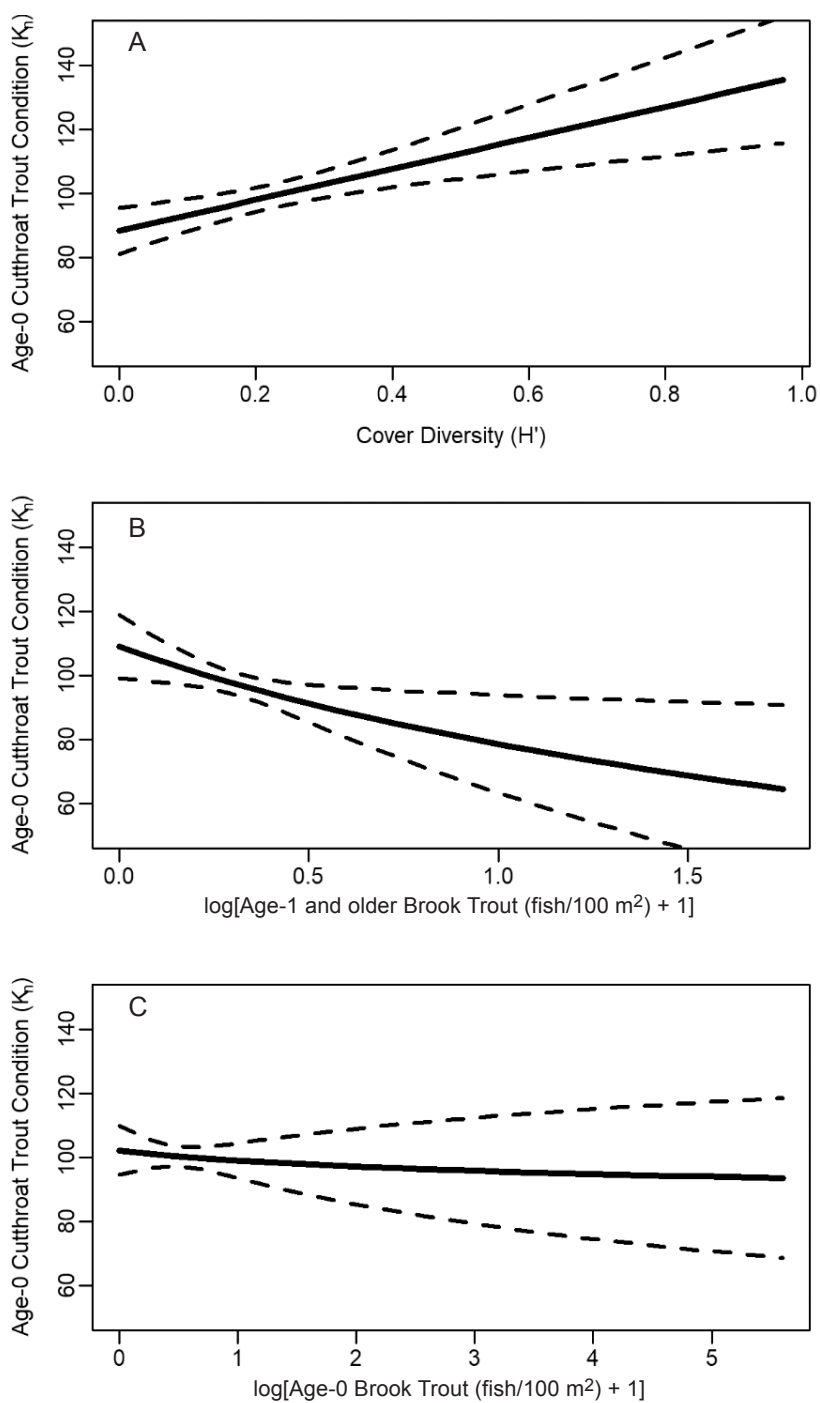
Fig. 6. Model-averaged predictions (90% confidence interval) of age-0 Yellowstone Cutthroat Trout relative condition (K_n) as a function of (A) instream cover diversity (H'); (B) density of age-1 and older Brook Trout (<100 mm TL); and (C) density of age-0 Brook Trout (≥100 mm TL).

broader data set throughout the range of Yellowstone Cutthroat Trout or Cutthroat Trout more broadly could be used to explore how habitat condition and diversity interacts with, or potentially offsets, the negative interaction between Brook Trout and Cutthroat Trout.

The Goose Creek subbasin is the southern and western geographic range extent for Yellowstone Cutthroat Trout (Haak et al. 2010). Peripheral populations on the range margin have conservation value because they often experience genetic drift, occupy marginal habitat (compared to the range core), and thus experience unique selective pressures leading to local adaptations. They also can harbor unique genetic legacies from colonization and isolation events (Lesica and Allendorf 1995, Haak et al. 2010). The contemporary Yellowstone Cutthroat Trout populations in the Upper Snake River represent 2 major genetic lineages that reflect a diverse geologic and colonization history (Cegelski et al. 2006, Campbell et al. 2011, 2018). But our habitat data did not suggest that habitat was, in fact, marginal in our peripheral study subbasin. Temperature was not limiting to our stenothermal study species as might be expected for salmonids at the lower elevation range periphery (corroborated by Al-Chokhachy et al. 2013). That thermal habitat is not marginal is not surprising because the western distribution of Yellowstone Cutthroat Trout is limited instead by a biogeographic barrier where Interior Redband Trout *O. mykiss* spp. occupy Snake River subbasins farther west below Shoshone Falls (Muhlfeld et al. 2015). Thus, the peripheral nature of the Goose Creek subbasin does not appear to have altered the commonly observed negative interaction between nonnative Brook Trout and Yellowstone Cutthroat Trout. However, it remains intriguing why over 2 decades Meyer et al. (2014) only observed Yellowstone Cutthroat Trout extirpations in the Goose Creek subbasin and not elsewhere in the Upper Snake River basin. Instead, our habitat data suggested that habitat complexity is limiting in the Goose Creek subbasin, which is likely due to livestock grazing and other uses that are pervasive across the range of Yellowstone Cutthroat Trout (IDFG 2007b, Gresswell 2011).

Our study suggests that Brook Trout negatively influence the distribution, abundance, and condition of Yellowstone Cutthroat Trout at early life stages, suggesting a similar interaction that has been repeatedly observed in other studies that have included other Cutthroat Trout subspecies. Thus, removal of Brook Trout from Cutthroat Trout habitats should remain a conservation focus just as it has been throughout the range of Cutthroat Trout across subspecies (Thompson and Rahel 1996, Gresswell and Vondracek 2010). In a subbasin adjacent to Goose Creek, Thompson and McKell (2021) demonstrated use of a temporary barrier that allowed them to employ electrofishing removal of Brook Trout where they were sympatric with Yellowstone Cutthroat Trout above the temporary barrier, but then the researchers used more effective piscicides to remove Brook Trout below the temporary barrier where Cutthroat Trout were absent; the temporary barrier was removed to reconnect the 2 stream segments once Brook Trout were eradicated. Brook Trout removal, coupled with intentional isolation of populations above barriers, is a common conservation action implemented for Cutthroat Trout (Thompson and Rahel 1996, Dunham et al. 2002a, Gresswell and Vondracek 2010). A temporary barrier design can improve the logistical feasibility of Brook Trout removal without committing to long-term isolation of Cutthroat Trout in small habitat patches where long-term persistence is less likely (Roberts et al. 2013, Peterson et al. 2014).

A novel finding from our study showed that physical habitat complexity is positively associated with Yellowstone Cutthroat Trout independent of Brook Trout, which suggests that complex, and therefore healthy, physical habitat may partially offset the negative effects of Brook Trout. Thus, increasing habitat complexity should be considered in cases when managers attempt to conserve Cutthroat Trout populations invaded by Brook Trout when eradication is not feasible (Meyer et al. 2006a, Peterson et al. 2008, Shepard et al. 2014). Improving habitat complexity (a.k.a. heterogeneity or diversity) is a common goal for stream habitat restoration and enhancement (Roni et al. 2013b). For example, Billman et al. (2013) showed that habitat enhancements increased habitat complexity in the Provo River, Utah, and the complexity then allowed native fishes to coexist with nonnative and piscivorous Brown Trout *Salmo trutta*. Pierce et al. (2013) also showed that stream restoration

increased the capacity for both native West-slope Cutthroat Trout *O. c. lewisi* and nonnative trout to coexist in the Blackfoot River watershed in Montana. In some streams, restoration shifted the salmonid composition more toward native Cutthroat Trout. Habitat complexity, however, was not measured in the study. The use of restoration to facilitate sympatry needs to be explored more broadly in an experimental or adaptive management context across Cutthroat Trout subspecies and different habitat types (Anderson et al. 2003, Roni et al. 2013a). Habitat complexity and quality may explain why some populations of Cutthroat Trout and Brook Trout have coexisted for decades (Meyer et al. 2014). Thus, habitat protection and restoration, along with Brook Trout suppression, should receive increased consideration as a complementary action for Cutthroat Trout conservation when Brook Trout eradication is not feasible (Meyer et al. 2006a, Peterson et al. 2008).

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