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Relative Effects of Biotic and Abiotic Processes: A Test of the Biotic–Abiotic Constraining Hypothesis as Applied to Cutthroat Trout

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Abstract.—The Biotic–Abiotic Constraining Hypothesis (BACH) suggests that biotic interactions can have an overriding negative influence on a fish species, even when abiotic conditions are suitable. The abundance of a fish species is predicted to be largely regulated by abiotic habitat characteristics when densities of predators or competitors are low. However, when predator or competitor densities are high, the abundance of the fish species is suppressed by biotic interactions regardless of environmental conditions. We used data from the Salt River basin (Idaho–Wyoming) to investigate whether the BACH could be used to explain patterns in the density of cutthroat trout *Oncorhynchus clarkii* across a watershed. Using a combination of principal components and nonlinear multiple-regression analyses, we determined that the BACH was useful for explaining patterns in cutthroat trout density. When brown trout *Salmo trutta* and brook trout *Salvelinus fontinalis* densities were low, cutthroat trout density was highly variable and was best explained by habitat characteristics. High cutthroat trout densities were found in high-gradient reaches with little fine substrate and a low proportion of deep-pool habitat (i.e., reaches with a diversity of pools, riffles, and runs). When brown trout and brook trout densities were high, cutthroat trout density was always low despite favorable habitat conditions. Brown trout density was highest in low-elevation reaches with warm water temperatures and abundant instream cover, whereas brook trout density was highest in high-elevation reaches with low water temperatures. This study suggests that the influence of brown trout and brook trout densities overrode the influence exerted by habitat conditions on cutthroat trout density in the Salt River basin and that the BACH is useful for explaining biotic and abiotic influences on lotic cutthroat trout populations.

A goal in aquatic ecology is to understand the relative influence of biotic (e.g., predation, competition) and abiotic (e.g., environmental characteristics) factors on the structure and function of aquatic systems (Persson 1997; Matthews 1998; Jackson et al. 2001). Consequently, much research in fish ecology attempts to disentangle the relative effects and magnitudes of biotic and abiotic features on fish population dynamics and assemblage structure. One dichotomy that has resulted from these efforts suggests that animal populations are predominately controlled by either biotic or abiotic factors. Schoener (1987) identified the relative importance of biotic and abiotic factors as a major axis of polarization among ecologists. While the controversy over biotic and abiotic influences may be considered antiquated by many, questions and debates regarding the relative roles of biotic and abiotic factors remain important in contemporary ecology. For instance, Sumari (1971) identified factors affecting the biomass of Eurasian perch *Perca fluviatilis* in Finnish lakes and concluded that biotic interactions were the most important factors regulating perch populations. The primary mechanisms suggested were competition from roach *Rutilus rutilus* and predation by northern pike *Esox lucius*, burbot *Lota lota*, roach, and Eurasian perch. Later, Persson (1997) reanalyzed these data and argued that while biotic interactions were important, abiotic features (e.g., conductivity, pH) played a role in mediating biotic effects. Thus, the identity, relative occurrence, and magnitude of biotic and abiotic controls remain important questions in fish ecology.

Most ecologists recognize that biotic and abiotic factors may act synergistically to affect animal populations (Tonn and Magnuson 1982; Persson 1997; Matthews 1998; Jackson et al. 2001). This contention is supported by a large body of research across a variety of aquatic systems. For instance, Schlosser and Ebel (1989) showed that invertebrate and fish assemblages in a Minnesota stream were influenced by both the flow regime and predation by cyprinids. Harvey (1991) found that channel morphology and predation interacted to regulate larval fish density in an Oklahoma stream.

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In a study of Wisconsin lakes, Tonn and Magnuson (1982) illustrated the interactive effects of abiotic habitat characteristics and predation on fish assemblage structure.

One hypothesis attempting to explain biotic and abiotic interactions is the Biotic–Abiotic Constraining Hypothesis (BACH), which hypothesizes that biotic interactions can have an overriding influence on a species even when abiotic characteristics are suitable (Quist et al. 2003). The abundance of a species is predicted to be largely regulated by abiotic characteristics when densities of predators or competitors are low. However, when predator or competitor densities are high, a species is suppressed by biotic interactions regardless of environmental conditions. The BACH was outlined by Quist et al. (2003) as a result of observations involving white crappies *Pomoxis annularis*, walleyes *Sander vitreus*, and habitat characteristics in Kansas reservoirs. Specifically, when juvenile white crappie density was low, recruitment of walleyes was highly variable and was explained by environmental characteristics. However, when juvenile white crappie density was high, walleye recruitment was always low despite favorable environmental conditions. Quist et al. (2004) similarly reported that nonnative centrarchids and percids had an overriding influence on native cyprinids in the Missouri River drainage of Wyoming. Studies illustrating the BACH have focused on warmwater fish assemblages, and the applicability of the BACH to coldwater systems is unknown. Systems containing cutthroat trout *Oncorhynchus clarkii* are appropriate for tests of the BACH because nonnative salmonids may have a deleterious effect on both the distribution and abundance of cutthroat trout (Behnke 2002). Therefore, the purpose of this study was to examine the interaction among abiotic and biotic characteristics and the generality of the BACH to coldwater stream systems. Specifically, we sought to determine relations among cutthroat trout density, habitat characteristics (e.g., substrate, cover, channel morphology), and densities of nonnative salmonids (brown trout *Salmo trutta* and brook trout *Salvelinus fontinalis*) across a watershed where cutthroat trout are native.

Methods

The Salt River is a fifth-order stream that originates in the Salt River Range of Wyoming and flows north for approximately 45 km to its confluence with the Snake River at Palisades Reservoir on the Idaho–Wyoming border (Isaak 2001). Numerous spring streams emerge from the alluvium adjacent to the Salt River and flow a short distance before joining the river. Mountain ranges surrounding the basin differ in morphology, which affects valley form, channel morphology, and instream habitat characteristics. The Salt River Range on the east side of the watershed is rugged, characterized by elevations exceeding 3,300 m and narrow, constrained valleys. Streams on the east side of the basin have straighter channels, steeper channel slopes, and lower stream temperatures than those in other portions of the drainage. The Gannet Hills to the south and the Caribou and Webster ranges to the west are less rugged, and elevations are less than 3,000 m. Valleys are wide and streams are unconstrained in the southern and western portions of the watershed.

Eleven fish species are native to the Salt River drainage, including the mountain whitefish *Prosopium williamsoni*, Utah sucker *Catostomus ardens*, mountain sucker *C. platyrhynchus*, longnose dace *Rhinichthys cataractae*, speckled dace *R. osculus*, Utah chub *Gila atraria*, leatherside chub *Snyderichthys copei*, redside shiner *Richardsonius balteatus*, mottled sculpin *Cottus bairdii*, Paiute sculpin *Cottus beldingii*, and cutthroat trout (Baxter and Stone 1995). Brown trout, rainbow trout *O. mykiss*, and brook trout were introduced and have become naturalized in the watershed. Brown trout and brook trout are widespread, but rainbow trout are relatively rare in the watershed (Isaak 2001).

Fish and habitat were sampled from 83 reaches during 1996 and 1997. Sampling began in early July after snowmelt runoff subsided, and continued until mid-September of each year. We sampled fish by deploying a downstream block net and then using a backpack electrofishing unit (model 15-C, Smith-Root, Vancouver, Washington) to conduct multiple removal efforts within a reach (Isaak 2001). An effort was made to capture 35 age-1 or older trout during the first pass through a reach, but this was not always possible when densities were low. In such cases, sampling stopped when 300–400 m of stream had been sampled. When fish were abundant, at least 100 m of stream was sampled. Because the endpoint of sampling was not predetermined, the upstream block net was not set until a criterion for stopping was met. The block net was then deployed a short distance upstream and the remainder of the reach was electrofished. Trout were identified to species, and each fish was measured to the nearest millimeter (total length). Weights were estimated from speciesspecific length–weight regressions (r^2 = 0.96–0.99) developed for lotic trout populations in Wyoming (W. A. Hubert, unpublished data).

After three removal passes, additional removal efforts (1–4) were conducted until the width of the confidence interval associated with the population estimate was less than 30% of the population estimate. Population estimate precision was calculated in the field after the second and subsequent removal efforts by use of a graph from MicroFish 3.0 (Van Deventer and Platts 1989) in conjunction with approximate estimates of population size and removal efficiency derived from the following equations:

$$S = x_1/[1 - (x_2/x_1)] \text{ and}$$

$$E = (x_1 - x_2)/x_1,$$

where S is the estimate of population size, E is electrofishing efficiency, x_1 is the number of trout captured during the first removal effort, and x_2 is the number of trout captured during the second removal effort. In an attempt to minimize heterogeneity of capture probabilities (e.g., due to sampling or temperature), removal efforts were spaced at 1-h intervals, electrofishing equipment was operated by the same person, and electrofishing only occurred when the water temperature exceeded 7°C.

Final population estimates were calculated for age-1 and older trout by use of the maximum likelihood estimator in MicroFish 3.0 (Van Deventer and Platts 1989). Age-0 trout (determined by the timing of appearance in samples and examination of length frequency distributions) were removed from the population estimates. To account for differences in catchability, we calculated separate population estimates for trout less than 135 mm and trout greater than or equal to 135 mm. The 135-mm breakpoint was selected based on observations made while sampling and based on a previous study suggesting changes in fish catchability at this length (Anderson 1995). Density estimates were obtained by adding population estimates for both length categories and dividing the total by the estimated surface area of the reach. Biomass estimates were calculated by multiplying the population estimate by the estimated mean weight of trout in the sample.

Elevation (meters above mean sea level) of the study reaches was determined from 1:24,000-scale U.S. Geological Survey topographic maps. Water temperature (°C) was recorded every 30 min by use of digital thermographs (model WTA32, Onset Computer Corp., Pocasset, Massachusetts) deployed at opposite ends of each study stream. Stream temperatures were summarized as the mean temperature for July and August (i.e., mean summer temperature). Mean temperatures for reaches without thermographs were interpolated based on stream-specific rates of water temperature change that were calculated by dividing the difference in elevation between upstream and downstream thermographs into the difference in mean water temperature at those sites. Channel slope (%) was estimated with an Abney level by the method of Isaak and Hubert (1999). Wetted width was measured to the nearest centimeter along transects placed perpendicular to the streamflow at 10-m intervals along the length of each reach. Depth was measured to the nearest centimeter and substrate characteristics were identified at points spaced at 25, 50, and 75% of the transect length. Substrate categories included fine ($<$2 mm in diameter), gravel (2–64 mm), cobble (65–256 mm), and boulder ($>$256 mm) substrate (modified from Armantrout 1998). Length and width were measured for all cover patches that were within 1 m of each transect. Instream cover was defined as overhanging cover, woody debris, or aquatic vegetation in water at least 15 cm deep (Wesche 1980). Habitat characteristics in a reach were summarized as the mean of measurements for each variable across all transects.

Because reaches within the same stream were highly variable with regard to stream geomorphology, instream habitat, and fish assemblage structure, and because one of the primary objectives of the study was to evaluate patterns in cutthroat trout density among reaches, reaches were treated as the experimental unit in the analysis. Habitat data were examined and simplified by use of principal components analysis (PCA). Variables included in the analysis were selected to represent the position of a reach in the watershed (elevation), reach morphology (channel slope), thermal characteristics (mean summer temperature), channel morphology (mean width, proportion of the reach classified as deep pool habitat [pools $>$ 0.5 m deep]), instream cover, and substrate composition (proportion of fine substrate). These variables were selected based on their correlation with other variables in each category and their importance to salmonids (e.g., Kozel and Hubert 1989; Bozek and Hubert 1992). For example, we used the proportion of fine substrate to reflect substrate composition because it was highly correlated ($r > |0.60|$) with all other substrate categories. Using these variables, we conducted PCA on the correlation matrix rather than the variance–covariance matrix because the habitat variables were measured on different measurement scales (Johnson 1998). All proportional data were arcsine square-root transformed prior to analysis (Sokal and Rohlf 1995). Only axes with eigenvalues greater than 1 were retained for further analysis (Johnson 1998). Contribution of each variable to the principal component (PC) axis was examined by use of factor loadings and Pearson's correlation between PC scores and habitat variables. The PC scores were calculated for each reach and used as independent variables in a multiple-regression analysis.

Multiple-regression analysis was used to examine relationships of cutthroat trout density with physical habitat (i.e., PC scores) and densities of brown trout and brook trout. We focused our analysis on brown trout and brook trout because both species were common in the watershed and may negatively influence cutthroat trout in the Rocky Mountain region through either predation (brown trout) or competitive mechanisms (brown trout or brook trout; Behnke 2002). Because relationships of cutthroat trout density with biotic and abiotic characteristics were curvilinear, and to enable comparison with previous studies (e.g., Quist et al. 2004), nonlinear regression techniques were used, namely,

$$Y = \beta_0 \times \exp(\beta_1 X_1 + \beta_2 X_2 + \ldots + \beta_k X_k),$$

where Y is cutthroat trout density, β_0 is the intercept, β_k is the coefficient estimate for the kth independent variable, and X_k represents the kth independent variable. Multiple-regression analysis was also conducted for brown trout and brook trout by use of scores from each PC axis and density of either brown trout (brook trout models) or brook trout (brown trout models) as independent variables. The same analysis was performed with biomass of each species as the dependent variable. Because the results for biomass were nearly identical to those for density, results for biomass are not presented here.

We used the information-theoretic method to choose among competing multiple-regression models (Burnham and Anderson 2002). The information-theoretic method relies on an accumulation of evidence for a priori hypotheses and fosters the concept of statistical evidence and level of support for each model and its alternatives. We developed 14 models for cutthroat trout and 7 models each for brown trout and brook trout. The models contained various combinations of independent variables that we considered biologically relevant based on current knowledge of salmonid ecology. Akaike's information criterion corrected for small-sample bias (AIC_c) was used to compare candidate models; the best candidate model is the one with the lowest AIC_c (Burnham and Anderson 2002). Akaike weights (w_i) were used to assess the relative plausibility of each candidate model, as described by Burnham and Anderson (2002). Evidence ratios were calculated for each model as the maximum observed w_i (i.e., lowest AIC_c) divided by the model's w_i to provide strength of evidence for the model with the lowest AIC_c. Although the information-theoretic method selects the best model from a series of competing models, the competing models could all be poor. Therefore, we calculated the coefficient of determination (R^2) for each model to provide an indication of model fit.

We computed an averaged multiple-regression equation for cutthroat trout by weighting coefficient estimates from each regression model by their associated w_i (Burnham and Anderson 2002). Use of averaged coefficients from competing models reduces bias associated with the uncertainty of model selection and therefore provides a more precise inference than does the use of only one model (Burnham and Anderson 2002; Harig and Fausch 2002; Weigel et al. 2003). Model-averaged coefficients were only calculated for independent variables that were present in at least one model where w_i was within 10% of the maximum (Weigel et al. 2003). For example, if the best model (i.e., lowest AIC_c) had a w_i of 0.550, only models with w_i greater than 0.055 were used to calculate an averaged model. The PCA and multiple-regression analyses were conducted in the Statistical Analysis System (SAS Institute 1996).

Results

Cutthroat trout were the most common salmonid species in the watershed and occurred in 95% of the reaches (Table 1). Brown trout (31% of reaches) and brook trout (24% of reaches) were also relatively common in the watershed. Cutthroat trout density varied from 0 to 0.56 fish/m^2, averaged (mean ± SE = 0.08 ± 0.01 fish/m^2, and was highest in reaches without brown trout or brook trout (Table 1). Brown trout (0.01 ± 0.01 fish/m^2) and brook trout (0.02 ± 0.01 fish/m^2) had similar mean densities across all reaches, but maximum density was higher for brook trout (maximum = 0.39 fish/m^2) than for brown trout (0.10 fish/m^2).

TABLE 1.—Number of reaches (N) and mean density (fish/m^2) of sympatric and allopatric cutthroat trout (CUT), brown trout (BNT), and brook trout (BKT) in the Salt River watershed of Idaho–Wyoming (1996–1997). Allopatric BKT and sympatric BNT and BKT (i.e., in the absence of CUT) were not observed in the watershed.

Species	N	Density (SE)		
		CUT	BNT	BKT
CUT	43	0.12 (0.02)		
BNT	1		0.05[a]	
CUT and BNT	16	0.04 (0.01)	0.03 (0.01)	
CUT and BKT	11	0.05 (0.02)		0.12 (0.04)
CUT, BNT, and BKT	9	0.04 (0.02)	0.03 (0.01)	0.01 (0.01)

[a] Standard error not estimable.

Rainbow trout were sampled from only two reaches and had a maximum density of 0.01 fish/m^2. Consequently, rainbow trout were excluded from further analysis.

The first three PC axes had eigenvalues greater than 1 and cumulatively explained 81% of the variation in habitat characteristics among reaches (Table 2). All habitat variables were significantly ($P \leq 0.05$) correlated with PC scores from the first axis. The most important variables with respect to the first PC axis were interpreted to be channel slope, proportion of fine substrate, and amount of deep pool habitat in the reach. The second axis explained 17% of the variation among reaches and primarily comprised elevation, instream cover, and mean summer temperature. The third axis explained 15% of the variation in habitat characteristics among reaches and was dominated by stream width and instream cover.

Cutthroat trout density was best explained by scores from the first PC axis and by densities of brown trout and brook trout (Table 3). The model containing all three of these variables had the lowest AIC$_c$ and explained 63% of the variation in cutthroat trout density among reaches. Therefore, we calculated an averaged model from the models that had w_i within 10% of the maximum w_i (Figure 1). When brown trout and brook trout densities were low (i.e., <0.10 fish/m^2), cutthroat trout density was highly variable (Figure 1A). Variation in cutthroat trout density was largely explained by scores from the first PC axis, suggesting that high densities of cutthroat trout occurred in high-gradient reaches with large substrate and a low proportion of deep pool habitat (Figure 1B, C). Reaches with a low proportion of pool habitat and a high cutthroat trout density were generally characterized as having a diversity of channel units (i.e., pools, riffles, and runs). Despite the effects of habitat characteristics on cutthroat trout, brown trout and brook trout densities appeared to have an overriding influence on cutthroat trout density (Figure 1). High densities of cutthroat trout were observed in reaches that contained few or no brook trout or brown trout. In reaches where brook trout or brown trout were abundant, moderate to high densities of cutthroat trout were expected based on the habitat features of the reach. However, high densities of nonnative salmonids were always associated with low densities of cutthroat trout.

TABLE 2.—Loadings from the principal components (PC) analysis of physical habitat information from reaches in the Salt River watershed of Idaho–Wyoming (1996–1997). Abiotic variables include elevation (meters above mean sea level), mean width (m), channel slope (%), proportion of the reach with instream cover (%), proportion of fine substrate (%), proportion of the reach with deep pool habitat (%), and temperature (°C). Numbers in parentheses are Pearson correlation coefficients between habitat variables and PC scores. Correlation coefficients greater than $|0.50|$ were statistically significant ($P \leq 0.05$). Eigenvalues (λ) and the proportion of the variation explained by the first three PC axes (i.e., PC1–PC3 are provided).

Variable	PC1	PC2	PC3
Elevation	−0.35 (−0.65)	−0.49 (−0.54)	−0.15 (−0.16)
Width	0.29 (0.55)	−0.29 (−0.31)	0.69 (−0.70)
Slope	−0.43 (−0.80)	0.14 (0.15)	0.28 (0.28)
Cover	−0.28 (−0.52)	0.51 (0.56)	0.52 (0.53)
Fine	0.44 (0.83)	−0.01 (−0.02)	−0.12 (−0.12)
Deep pool	0.47 (0.87)	−0.14 (−0.15)	0.28 (0.28)
Temperature	0.30 (0.58)	0.60 (0.65)	−0.24 (−0.22)
λ	3.44	1.18	1.04
Variation	0.49	0.17	0.15

TABLE 3.—Nonlinear multiple-regression models predicting densities (fish/m^2) of cutthroat trout, brown trout (BNT), and brook trout (BKT) in the Salt River watershed of Idaho–Wyoming (1996–1997). Habitat characteristics were modeled based on principal component (PC) scores from the first three PC axes. Akaike's information criterion corrected for small sample size (AIC$_c$), Akaike weight (w_i), percent of the maximum w_i (% Max w_i), and the evidence ratio (ER = [Max w_i]/w_i) were used to select the top models from each set of a priori candidate models. The AIC$_c$ values were calculated from the number of model parameters, sample size (N = 83), and the residual sum of squares (RSS). The direction of influence (i.e., positive or negative) is provided for each variable. The coefficient of determination (R^2) is provided as an indication of model fit.

Variable(s)	RSS	AIC$_c$	w_i	% Max w_i	ER	R^2
Cutthroat trout						
−BNT, −BKT, −PC1	0.580	−174.196	0.737	100	1.000	0.63
−BNT, −PC1	0.651	−171.274	0.171	23.2	4.309	0.59
−BKT, −PC1	0.711	−168.096	0.035	4.7	21.112	0.55
−BNT, −BKT, +PC3	0.710	−166.906	0.019	2.6	38.281	0.55
−PC1	0.772	−166.322	0.014	1.9	51.264	0.51
−BNT, −PC2	0.772	−165.129	0.008	1.1	93.072	0.51
−BNT, +PC3	0.772	−165.129	0.008	1.1	93.072	0.51
−BNT, −BKT, −PC2	0.761	−164.406	0.006	0.8	133.647	0.52
−PC2	0.897	−160.913	0.001	0.1	766.441	0.43
−BKT, +PC2	0.892	−159.921	0.001	0.1	1,258.150	0.44
−BNT	0.950	−158.843	0.001	0.1	2,156.842	0.40
+PC3	0.959	−158.503	0.001	0.1	2,556.369	0.40
−BKT, +PC3	0.941	−157.994	0.001	0.1	3,298.509	0.40
−BKT	1.021	−156.245	0.001	0.1	7,906.489	0.36
Brown trout						
+PC2	0.036	−276.821	0.687	100	1.000	0.27
−BKT, +PC2	0.039	−272.743	0.089	12.9	7.683	0.21
−PC1	0.041	−272.133	0.065	9.5	10.423	0.17
−BKT	0.042	−271.265	0.043	6.3	16.092	0.15
+PC3	0.042	−271.265	0.043	6.3	16.092	0.15
−BKT, +PC3	0.041	−270.940	0.036	5.2	18.923	0.17
−BKT, −PC1	0.041	−270.940	0.036	5.2	18.923	0.17
Brook trout						
−PC2	0.247	−207.400	0.429	100	1.000	0.21
−BNT, −PC2	0.244	−206.648	0.295	68.8	1.457	0.22
−BNT	0.260	−205.552	0.170	39.6	2.521	0.17
−BNT, +PC3	0.278	−201.946	0.028	6.5	15.292	0.11
−PC3	0.288	−201.865	0.027	6.3	15.925	0.08
−PC1	0.289	−201.739	0.025	5.8	16.951	0.08
−BNT, −PC1	0.280	−201.687	0.024	5.6	17.401	0.11

Unlike cutthroat trout density, the densities of brown trout and brook trout were best related to scores from the second PC axis (Table 3). Brown trout density was generally highest in low-elevation reaches (<2,000 m) with abundant instream cover (>40% of the reach with cover) and relatively high mean summer water temperatures (11–16°C). Brook trout density was highest in high-elevation reaches (>2,100 m) with low mean summer water temperatures (5–8°C) and little instream cover (<25% of the reach with cover). Although relationships were developed for brook trout and brown trout, the best models explained less than 30% of the variation in density for both species.

Discussion

Densities of each salmonid species were related to differing habitat characteristics. Brown trout in the Salt River watershed were most abundant in low-elevation reaches with relatively warm water temperatures. Bozek and Hubert (1992) reported that brown trout were most common in low-elevation reaches in Wyoming, and similar results have been reported throughout the Rocky Mountain region (e.g., Vincent and Miller 1969; Gard and Flittner 1974; Larscheid and Hubert 1992). High densities of brown trout were also related to abundant instream cover in the Salt River drainage. Instream cover is often associated with brown trout abundance in lotic systems (e.g., Bachman 1984; Larscheid and Hubert 1992). In contrast to brown trout, brook trout are often most abundant in high-elevation streams (Vincent and Miller 1969; Gard and Flittner 1974; Bozek and Hubert 1992). Brook trout density in the Salt River watershed was generally highest in small, high-elevation reaches. The

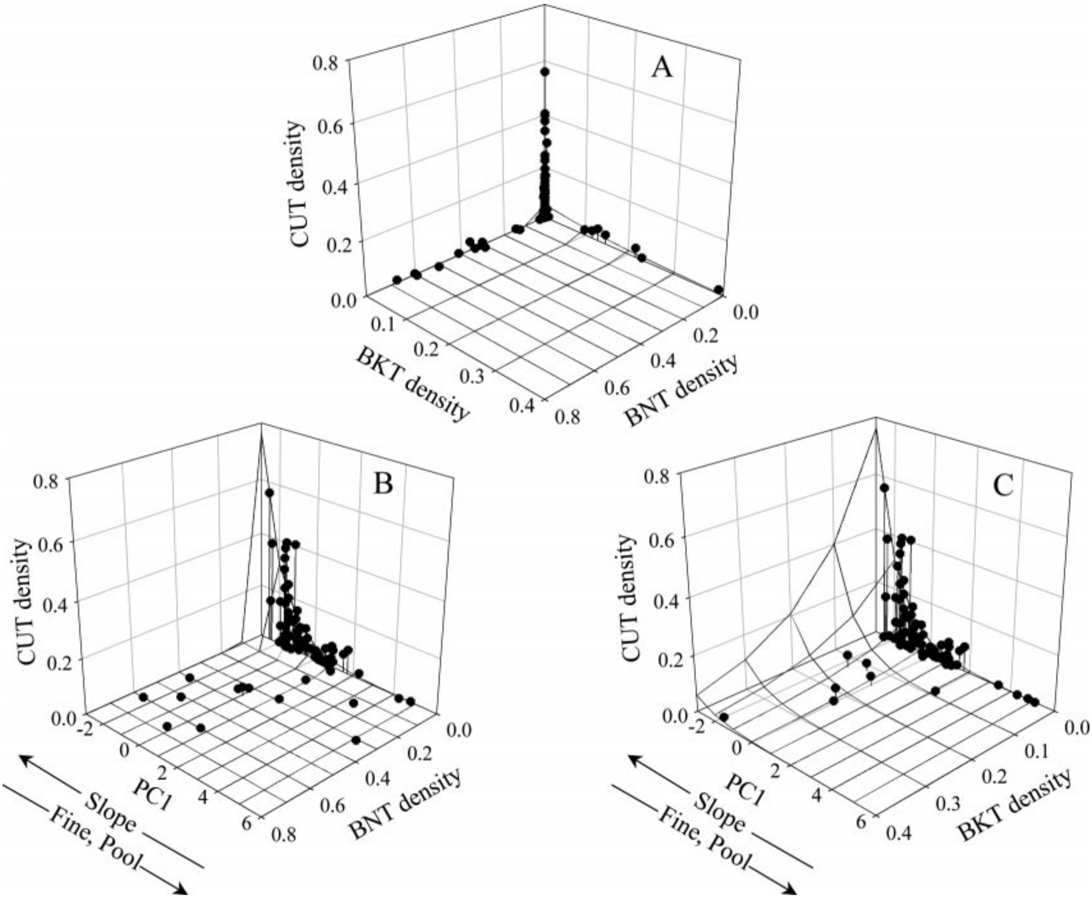

FIGURE 1.—Relationship between cutthroat trout (CUT) density (fish/m^2) in the Salt River watershed of Idaho–Wyoming (1996–1997) and (A) brown trout (BNT) and brook trout (BKT) densities, (B) BNT density and scores from the first principal component axis (PC1) and (C) BKT density and PC1 score. The plane on each panel represents the nonlinear multiple-regression model $\text{CUT} = 0.051 \times e^{(-0.902 \cdot \text{PC1} - 44.150 \cdot \text{BNT} - 6.436 \cdot \text{BKT})}$. Because each graph is missing one of the variables, the plane was developed by inputting zero for that variable and then predicting CUT density.

only exceptions were small spring streams adjacent to the Salt River that had low water temperatures and moderate to high densities of brook trout. Many studies have shown that cutthroat trout occur across a wide range of habitat conditions (e.g., Bozek and Hubert 1992; Kruse et al. 2000; Behnke 2002). Although cutthroat trout occurred throughout the Salt River watershed, cutthroat trout density was related to substrate characteristics, channel slope, and channel morphology. Specifically, high densities of cutthroat trout were observed in reaches with high gradients, low proportions of deep pool habitat, and little fine sediment. While some reaches with high densities of cutthroat trout were at high elevations (probably unsuitable for brown trout but suitable for brook trout), many reaches with high densities were at low elevations.

The habitat associations observed in this study provide insight, but our primary objective was to explore the application of the BACH to a coldwater stream system. Based on the observed patterns, the BACH provided a reasonable explanation of patterns in cutthroat trout density in the Salt River watershed. Specifically, a high cutthroat trout density was only observed when brown trout and brook trout densities were low. High densities of nonnative salmonids were limited to a small number of reaches (12 reaches for brown trout and 7 for brook trout) in the watershed. However, cutthroat trout density was always low in those reaches, even though moderate to high densities of cutthroat trout were expected given the habitat conditions. Thus, brown trout and brook trout densities appeared to have an overriding influence on cutthroat trout in the watershed. The negative association of nonnative salmonids with cutthroat trout in the Salt River watershed was consistent with research across the western United States. Our results support the contention that interactions with nonnative salmonids, including brown trout and brook trout, are the primary cause of cutthroat trout declines and the greatest threat to cutthroat trout conservation in the future (Behnke 2002; Quist and Hubert 2004).

Brown trout and brook trout densities were negatively associated with cutthroat trout density in the Salt River watershed, but the mechanisms affecting these patterns likely differed between brown trout and brook trout. Brown trout are important piscivores that can consume and compete with small cutthroat trout (Wang and White 1994; Behnke 2002), whereas brook trout influence juvenile cutthroat trout through competitive interactions (Griffith 1988; DeStaso and Rahel 1994; Behnke 2002). In our study, high-density populations of brown trout (i.e., >0.15 fish/m^2) had a relatively high proportion of fish greater than 300 mm in length (mean $\pm$ SE $=$ 34.1% $\pm$ 9.4%). Conversely, high-density brook trout populations (i.e., >0.10 fish/m^2) were dominated by fish smaller than 200 mm (59.1% $\pm$ 8.6%). Reaches with a high density of brown trout or brook trout always had a low density of cutthroat trout (i.e., <0.05 fish/m^2). Although cutthroat trout densities were low in such reaches, the fish that were present were relatively large (i.e., proportion of cutthroat trout larger than 200 mm was 85–96%) and probably had the ability to escape predation (e.g., large brown trout) or competition (e.g., small brook trout or brown trout).

The idea that biotic and abiotic factors (i.e., extrinsic mechanisms) influence organisms is not new and has resulted in the development of numerous hypotheses and concepts in ecology. Two concepts most applicable to the BACH are keystone species (Paine 1969; Power et al. 1996) and fundamental versus realized niches (Hutchinson 1959). Dominant species in a system often have a major role in controlling community and ecosystem processes; however, some species (i.e., keystone species) have an influence on other species and ecosystem processes that is disproportionate to their abundance (Power et al. 1996). Although we do not suggest that nonnative salmonids are keystone species in the Salt River drainage, low densities of both brown trout and brook trout appeared to have a substantial influence on cutthroat trout. The concept of fundamental and realized niches also plays a major role in ecology (Hall et al. 2003). With regard to our study, cutthroat trout historically had fundamental and realized niches that encompassed the entire watershed (i.e., except for the highest elevations). However, introduction of nonnative salmonids has truncated the distribution of cutthroat trout, resulting in a constrained realized niche. Although the niche concept can be invoked to explain the patterns observed in our study, the concept of fundamental and realized niches can be used to explain most observations in ecology (e.g., Hall et al. 2003). The concept of keystone species emphasizes biotic interactions, while the niche concept considers that both biotic and abiotic factors synergistically regulate population dynamics.

The relative importance of biotic and abiotic factors has been a point of contention among ecologists (e.g., Schoener 1987; Persson 1997). However, numerous studies have shown that abiotic conditions often mediate biotic interactions, illustrating the importance of considering both biotic and abiotic factors (e.g., Anderson et al. 2001; Jackson et al. 2001; Micheli et al. 2002; Meyer 2003). The BACH recognizes that both biotic and abiotic factors influence fish populations, but it is fundamentally different from studies illustrating how abiotic conditions mediate biotic interactions. In contrast to other concepts (e.g., keystone species, fundamental versus realized niches), the BACH hypothesizes that biotic interactions mediate the influence of abiotic conditions because predator or competitor densities must first be low before habitat features can act on a species. Moreover, the BACH predicts a threshold rather than a linear response to biotic interactions. Recognition of a threshold has significant applications to conservation and management of fishes, particularly those efforts aimed at reducing the abundance of nonnative species. For example, in the Salt River watershed, few or no cutthroat trout were present when brown trout density was greater than 0.15 fish/m^2. Based on this relationship, restoring cutthroat trout would require a reduction in brown trout density below this threshold. Similarly, managers may erroneously conclude that habitat is limiting a species in areas where densities of predators or competitors are low. Predator or competitor densities may be low, but they may be above the threshold.

Two aspects of our study warrant comment.

First, the study was conducted across a relatively large spatial scale. Hinch et al. (1991) suggested that large-scale studies are required to develop a ‘‘more balanced view’’ of the relative importance of biotic interactions versus abiotic determinants. If studies are limited in scale, patterns may not be evident. For example, if sampled reaches in the Salt River watershed occurred only in areas with low brown trout or brook trout densities, the conclusion would be that only abiotic factors were regulating cutthroat trout density. The second aspect of this study is that we examined a system where one or more species was introduced. In addition to the current study, the BACH has also been found to be applicable for assessing the influence of white crappies (a native species) on walleyes (a nonnative species) in Kansas reservoirs (Quist et al. 2003) and the influence of nonnative piscivorous fishes on turbid-river cyprinids in the Missouri River system of Wyoming (Quist et al. 2004). Nonnative species are at the forefront of issues facing native species conservation and management (e.g., Behnke 2002; Minckley et al. 2003), suggesting that the BACH is applicable in an array of aquatic systems. For instance, stream gradient was the dominant factor influencing brook trout abundance in streams of the Snowy Range of southeastern Wyoming (Chisholm and Hubert 1986). However, Kozel and Hubert (1989) conducted a similar study in another portion of the same mountain range and found that brook trout abundance was not related to gradient. Because brown trout were highly abundant in the streams studied by Kozel and Hubert (1989), the authors hypothesized that ‘‘. . . brown trout competition probably overwhelmed the effect of gradient in our study reaches.’’ Introduced species often have a dramatic influence on native fish assemblages (e.g., Richter et al. 1997; Minckley et al. 2003), whereas the effects of native predators and competitors may be less evident because interacting species have coevolved. Consequently, future studies should focus on the utility of the BACH in systems without introduced species.

Throughout the Rocky Mountain region, cutthroat trout populations have been substantially reduced or completely replaced by nonnative salmonids (e.g., Behnke 2002). Although habitat alterations have undoubtedly had a detrimental effect on cutthroat trout, biotic influences can have an overriding effect because nonnative salmonids often dominate in areas with suitable habitat. This notion is supported by current restoration activities in which nonnative salmonids are removed and cutthroat trout are reestablished (e.g., Novinger and Rahel 2003). If habitat was the sole mechanism affecting cutthroat trout, the success of such efforts would not be realized. Consequently, this study provides support for the BACH and suggests that the hypothesis can be used to explain the influence of abiotic and biotic constraints on cutthroat trout in the Salt River watershed.

Coupled with results and insights from other studies, the BACH appears to be relevant in both warmwater and coldwater systems and to a variety of fishes. Future application of the BACH should focus on different systems and species, particularly systems lacking nonnative species. Such efforts will help to determine the ultimate utility and generality of the hypothesis.

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