

## Trends in the abundance of Bonneville cutthroat trout and nonnative trout in the Bear River basin of Idaho

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**ABSTRACT.**—Bonneville cutthroat trout (*Oncorhynchus clarkii utah*) have experienced substantial declines in their historical distribution and abundance, and recent status assessments have noted a particular lack of information on abundance trends for the species. From 1993 to 2020, a total of 186 backpack electrofishing surveys were conducted across 34 index reaches to monitor abundance of Bonneville cutthroat trout and nonnative salmonids in southeastern Idaho streams. Trout abundance (all species combined) for fish  $\geq 100$  mm (total length) averaged 7.6 fish/100 m<sup>2</sup> of stream (3.1 fish/100 m). Bonneville cutthroat trout population growth rate ( $\lambda$ ) was generally stable through time (mean  $\lambda = 1.04$  across all reaches; 95% confidence interval, 0.98–1.10), whereas for nonnative trout considered collectively, estimates of  $\lambda$  in general were declining over the entire study period (mean  $\lambda = 0.93$ ; 0.89–0.97). Although mean density of Bonneville cutthroat trout was higher at reaches where nonnative trout were absent ( $\bar{x} = 7.7$  fish/100 m<sup>2</sup>) than where they were present ( $\bar{x} = 4.2$  fish/100 m<sup>2</sup>), estimates of  $\lambda$  for cutthroat trout were not related to the abundance of nonnative trout. Bonneville cutthroat trout  $\lambda$  was also unrelated to all the reach-scale environmental conditions we measured except for conductivity, which was positively associated with  $\lambda$ . Conductivity is normally associated with the productivity of a water body, but it is also correlated to other important cations and anions (e.g., alkalinity and water hardness) that can influence fish populations in a number of ways; thus, we cannot ascertain whether the relationship we observed was causative or correlative. Bonneville cutthroat trout abundance was higher in years when both winter and summer discharge were higher in the previous year, which concurs with a large body of literature demonstrating that reduced baseflow during winter or summer can adversely affect salmonid recruitment, food resources, predatory avoidance, survival, and stream habitat conditions.

**RESUMEN.**—La distribución y abundancia histórica de la trucha degollada de Bonneville (*Oncorhynchus clarkii utah*) ha disminuido de manera sustancial, y la observación de las recientes evaluaciones de su estado muestra una falta de información sobre las tendencias en la abundancia de la especie. Entre 1993 y 2020, se realizaron un total de 186 muestreos a través de electropesca en 34 tramos índice para monitorear la abundancia de truchas degolladas de Bonneville y salmónidos no nativos en los arroyos del sureste de Idaho. La abundancia de truchas (de todas las especies combinadas) de peces  $\geq 100$  mm (de longitud total) fue en promedio de 7.6 peces/100 m<sup>2</sup> de arroyo (3.1 peces/100 m). La tasa de crecimiento de la población ( $\lambda$ ) de trucha degollada de Bonneville se mantuvo generalmente estable a lo largo del tiempo (media  $\lambda = 1.04$  en todos los tramos; intervalos de confianza del 95%, 0.98–1.10), mientras que, para las truchas no nativas consideradas colectivamente, las estimaciones de  $\lambda$  en general disminuyeron durante todo el período de estudio (media  $\lambda = 0.93$ ; 0.89–0.97). Si bien la densidad promedio de la trucha degollada de Bonneville fue mayor en los tramos donde no se encontró truchas no nativas ( $\bar{x} = 7.7$  peces/100 m<sup>2</sup>) comparada con los sitios donde se encontraron presentes ( $\bar{x} = 4.2$  peces/100 m<sup>2</sup>), las estimaciones de  $\lambda$  de la trucha degollada no se relacionó con la abundancia de truchas no nativas. La tasa de crecimiento de la población ( $\lambda$ ) de trucha degollada de Bonneville, tampoco se relacionó con ninguna de las condiciones ambientales a escala de alcance que medimos, excepto con la conductividad, que se asoció positivamente con  $\lambda$ . Generalmente, la conductividad se asocia con la productividad de un cuerpo de agua, pero también se correlaciona con otros cationes y aniones importantes (por ejemplo, la alcalinidad y la dureza del agua) que pueden influir en las poblaciones de peces de varias maneras, por lo que no podemos determinar si la relación que observamos fue causal o correlativa. La abundancia de la trucha degollada de Bonneville fue mayor en los años en que la descarga de invierno y la descarga de verano fueron mayores el año anterior, lo que concuerda con una gran cantidad de literatura que demuestra que el flujo base reducido durante el invierno o el verano puede afectar negativamente el reclutamiento de salmónidos, los recursos alimentarios, la evasión de depredadores, la supervivencia, y las condiciones del hábitat de los arroyos.

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Cutthroat trout that occupy the Bear River drainage of southeastern Idaho and northern Utah are taxonomically designated as Bonneville cutthroat trout *Oncorhynchus clarkii utah* (Behnke 2002). However, recent investigations highlight the fact that they share a phylogenetic relationship with Yellowstone cutthroat trout *O. clarkii bouvieri* in the Snake River basin (e.g., Campbell et al. 2011, 2018, Loxterman and Keeley 2012). The shared phylogeny reflects the historical hydrologic connection between the Bear River and Snake River drainages (Martin et al. 1985, Smith et al. 2002) as well as periods of Bear River hydrologic isolation from the Bonneville Basin (Bouchard et al. 1998). Preserving the unique and diverse genetic, morphologic, and life history characteristics of cutthroat trout in the Bear River basin has been prioritized in several management plans (e.g., UDNR 2018, IDFG 2022).

As with nearly all salmonids, Bonneville cutthroat trout have experienced substantial declines in their historical distribution and abundance, due primarily to habitat loss and fragmentation as well as hybridization and competition with introduced nonnative salmonids (Duff 1988, Hepworth et al. 1997, McHugh and Budy 2006). Such declines were the basis of petitions made in 1998 for listing Bonneville cutthroat trout as threatened under the Endangered Species Act, though their listing was deemed not warranted in 2001 (USFWS 2001) and again (after a lawsuit) in 2008 (USFWS 2008). Nevertheless, it is estimated that Bonneville cutthroat trout currently occupy only 39% of their historical distributional range (UDNR 2018); in the Idaho portion of their range, current occupancy is estimated to be 54% of their historical range (IDFG 2022).

Recent status assessments have noted a particular lack of information on trends in abundance for Bonneville cutthroat trout (Budy et al. 2007, IDFG 2022). To our knowledge, long-term trends have only been reported for southern Utah, where from the 1970s to 1990s, Bonneville cutthroat trout were estimated to occupy only 57 km, with abundance increasing in some streams and declining in others (Hepworth et al. 1997). Without a more thorough and contemporary understanding of trends in population abundance throughout the range of Bonneville cutthroat trout, inferences regarding long-term population persistence cannot be made for the species. The primary objective of the present study was to estimate trends in population abundance for

Bonneville cutthroat trout in the Idaho portion of their range. A secondary objective was to gain a better understanding of what factors might be influencing the status of Bonneville cutthroat trout in Idaho by relating several biotic and abiotic conditions to their abundance and trends in abundance.

## METHODS

### Study Area

The upper Bear River originates in the Uinta Mountains in northeastern Utah, flows north into Wyoming before turning west into Idaho, and eventually turns back south, flowing back into Utah (Fig. 1). The Bear River basin in Idaho is a high desert region of the Intermountain West with streams that range from 1300 to 2500 m in elevation. Riparian vegetation at lower elevation generally consists of native grasses as well as dogwood *Cornus* spp., alder *Alnus* spp., willow *Salix* spp., and cottonwood *Populus* spp., whereas at higher elevation, riparian areas also include mixed conifers including spruce *Picea* spp., fir *Abies* spp., and pine *Pinus* spp.

Besides Bonneville cutthroat trout, other salmonids occupying streams in the study area included nonnative brown trout *Salmo trutta*, brook trout *Salvelinus fontinalis*, rainbow trout *Oncorhynchus mykiss*, and cutthroat × rainbow hybrids (hereafter hybrids). Common nongame species occupying streams in the study area include Utah sucker *Catostomus ardens*, mountain sucker *Pantosteus platyrhynchus*, longnose dace *Rhinichthys cataractae*, speckled dace *R. osculus*, mottled sculpin *Cottus bairdii*, and Paiute sculpin *C. beldingii*, none of which are suspected of being important competitors for food and space with salmonids. Bonneville cutthroat trout can be readily (though not perfectly) differentiated from rainbow trout and hybrids using the phenotypic characteristics outlined in Meyer et al. (2022). In short, fish were considered to be Bonneville cutthroat trout when they had (1) few spots on top of the head, (2) no white leading edge on the pelvic, dorsal, or anal fins, (3) spots on the body that were large and concentrated posteriorly and dorsally, and (4) a strong or at least a faint throat slash. Rainbow trout and hybrids were considered one taxon in the present study, and were visually identified by some combination of the presence of white edges on the pelvic, dorsal, or anal fins, smaller spots evenly distributed throughout the body surface,

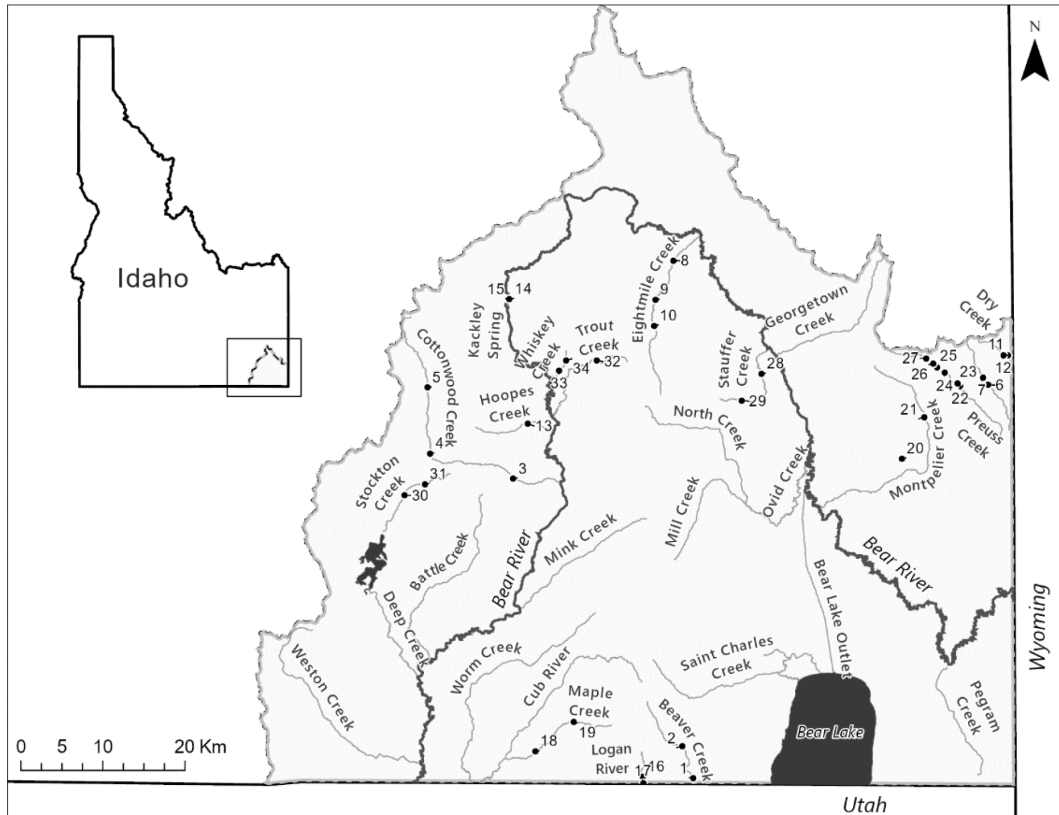


Fig. 1. Location of reaches that were repeatedly electrofished to determine trends in the abundance of Bonneville cutthroat trout (*Oncorhynchus clarkii utah*) and nonnative trout in Bear River tributaries of southeast Idaho. Site numbers correspond to those in Tables 1 and 2.

many spots on the top of the head, or the absence of a throat slash.

#### Fish Sampling

From 1993 to 2020, 34 trend-monitoring reaches in 16 different Bear River tributaries (Table 1, Fig. 1) were repeatedly sampled to assess salmonid occurrence and abundance. These index reaches were established in streams known to contain Bonneville cutthroat trout. They were not drawn from a probability-based design, but rather, they were established near roads, bridges, culverts, or other access points. Latitude and longitude were determined at the lower end of each reach using a Global Positioning System (GPS). Once established, GPS units were used to relocate the lower ends of each index reach prior to each new survey. Reach length sampled by field crews was determined with a tape measure and varied from 34 to 815 m, but average reach length was 120 m and

>90% of the reaches were between 70 and 130 m in length.

Fish were sampled with backpack electrofishing units using pulsed DC, with output generally at 60 Hz and 25% duty cycle; voltage ranged from 200 to 800 V depending on fish response to the electric field. Captured salmonids were identified to species and measured for total length. Nongame species that were encountered were not captured or enumerated.

Fish abundance was estimated based on either single-pass or multipass backpack electrofishing depletions. For multipass depletions, trout abundance was estimated using the maximum-likelihood removal method developed by Zippin (1956, 1958), using the MicroFish software package (Van Deventer 1989). If no trout were captured on the second pass, we considered the catch on the first pass to be the estimated abundance. Using data from all 128 multipass depletion surveys that were conducted across all

TABLE 1. Location and channel characteristics for 34 reaches sampled repeatedly with backpack electrofishing to determine trends in occurrence and abundance of salmonids in Bear River tributaries of southeast Idaho. Site numbers correspond to those on the map in Fig. 1.

Stream	Site	Latitude	Longitude	Wetted width (m)	Elevation (m)	Reach gradient (%)
Beaver Creek	1	42.00668	-111.52330	3.42	2342	1.6
Beaver Creek	2	42.04209	-111.53921	3	2438	1.2
Cottonwood Creek	3	42.33583	-111.78822	4.7	1593	2.8
Cottonwood Creek	4	42.36329	-111.91115	4.7	1798	0.9
Cottonwood Creek	5	42.43579	-111.91551	5.2	1950	2.3
Dry Creek	6	42.43843	-111.08034	2	2016	2.2
Dry Creek	7	42.44483	-111.09206	2	2058	3.6
Eightmile Creek	8	42.57513	-111.55017	3.8	1822	0.7
Eightmile Creek	9	42.53210	-111.57719	3.6	1900	1.8
Eightmile Creek	10	42.50363	-111.57875	4.3	1976	2.2
Giraffe Creek	11	42.46874	-111.05453	1.8	2183	2.0
Giraffe Creek	12	42.46919	-111.06061	1.81	2190	2.0
Hoopes Creek	13	42.39604	-111.76631	2.6	1585	5.1
Kackley Spring	14	42.53336	-111.79376	3.2	1536	1.7
Kackley Spring	15	42.53363	-111.79468	3.2	1535	1.7
Logan River	16	42.00854	-111.59756	3.9	2349	2.5
Logan River	17	42.00140	-111.59659	2.62	2319	2.8
Maple Creek	18	42.03643	-111.75569	4	1478	1.8
Maple Creek	19	42.06861	-111.69902	3.68	1791	5.6
Montpelier Creek	20	42.35642	-111.21303	5.32	2055	4.3
Montpelier Creek	21	42.40182	-111.17937	3.5	2024	1.0
Preuss Creek	22	42.43580	-111.12568	1.79	2024	2.6
Preuss Creek	23	42.43858	-111.12993	0.93	2031	1.3
Preuss Creek	24	42.45042	-111.14856	1.37	2093	2.9
Preuss Creek	25	42.45630	-111.15980	2.51	2130	2.2
Preuss Creek	26	42.46056	-111.16570	2.32	2143	2.2
Preuss Creek	27	42.46647	-111.17562	1.22	2185	3.2
Stauffer Creek	28	42.45095	-111.41848	2.34	1800	0.1
Stauffer Creek	29	42.42092	-111.44934	2.4	1866	2.3
Stockton Creek	30	42.31746	-111.94935	2.51	1567	3.2
Stockton Creek	31	42.32958	-111.91892	1.7	1664	3.1
Trout Creek	32	42.46549	-111.66452	3.4	1645	4.7
Whiskey Creek	33	42.45533	-111.72230	8.1	1565	0.5
Whiskey Creek	34	42.46587	-111.70975	5.4	1575	1.1

years, we developed a linear relationship (with the origin through zero) between the numbers of trout captured in first passes and the subsequent maximum-likelihood abundance estimates ( $F = 2877.3$ ,  $P < 0.001$ ,  $r^2 = 0.88$ ). From this relationship, we predicted trout abundance for 58 additional surveys in which only a single removal pass was conducted (cf. Lobón-Cerviá et al. 1994; Kruse et al. 1998). Abundance was standardized to fish/100 m<sup>2</sup> of stream surveyed, but fish/100 m of stream was also included for reference.

The length of age-0 fish was inconsistent across reaches and among species, and age-0 fish were difficult to sample effectively; therefore, we did not include fish <100 mm in any of our estimates of trout abundance. We assumed this cutoff effectively separated age-0 and age-1 fish (cf. Budy et al. 2007), but the smallest of the

age-1 trout were also likely excluded by this cutoff. Separating abundance estimates for each species was often not possible because low abundance or limited catch precluded such partitioning at some index reaches. Therefore, in order to maintain consistency in methodology across reaches and time periods, all trout species were pooled for an overall estimate of trout abundance at the reach scale (e.g., Mullner et al. 1998, Isaak and Hubert 2004, Carrier et al. 2009), and point estimates for each species were calculated based on the proportion of the catch that each species composed (cf. Meyer and High 2011).

#### Estimating Finite Population Growth Rates

To estimate trends in fish abundance at individual reaches, we used linear regression with sample year as the independent variable and log<sub>e</sub>

transformations of trout abundance as the dependent variable. Because the natural logarithm is undefined for zero, we added 0.1 fish/100 m<sup>2</sup> to each estimate of abundance. The slope of the regression line is equivalent to the intrinsic rate of change ( $r$ ) for the population (Gerrodette 1987, Morris and Doak 2002); this approach to monitoring trend assumes that the population changes in an exponential manner and that the rate of population change is constant over the sampling period. Confidence intervals (CIs) around the slope estimates were obtained from the linear regression models. Each estimate of  $r$  was exponentiated to convert it to the finite population growth rate ( $\lambda$ ).

Estimates of  $\lambda$  were calculated for Bonneville cutthroat trout at each reach because they occupied every reach. Because all of the non-native trout in the study area—brook trout, brown trout, and rainbow trout—have been previously demonstrated to have a negative effect on cutthroat trout (e.g., Dunham et al. 2002, McHugh and Budy 2006, Seiler and Keeley 2009), and because the species composition of non-native trout varied through time and among reaches, we grouped the abundance of all non-native trout together to estimate  $\lambda$  for nonnative trout where they occurred. Estimates of  $\lambda$  with 90% CIs that overlapped unity (i.e., 1.00) were assumed to be stable populations, whereas those populations with  $\lambda < 1.00$  or  $> 1.00$  were assumed to be declining or increasing in abundance, respectively. We used a significance level of  $\alpha = 0.10$  for individual estimates of  $\lambda$ , and for overall mean estimates across all reaches, to increase the power of detecting trends in population abundance (Peterman 1990, Maxell 1999, Dauwalter et al. 2009).

#### Relating Reach-scale Stream Conditions to Population Growth

To assess whether population growth rate at each index reach was associated with various stream conditions at that reach, we treated each reach as the sample unit and related several predictor variables to  $\lambda$  using multiple linear regression. Elevation (often a surrogate for stream temperature: Isaak et al. 2010, Wenger et al. 2011, Eby et al. 2014), wetted width, and stream gradient can influence nonnative salmonid invasion success, mediate competitive interactions among salmonids, and explain partitioning of salmonids along stream networks (e.g., Fausch 1989, Bozek and Hubert 1992, Rahel and Nibbelink 1999,

Peterson et al. 2004, Torgersen et al. 2006). Elevation (m) was determined from digital U.S. Geological Survey (USGS) 1:24,000-scale topographic maps based on GPS-acquired latitude/longitude coordinates obtained in the field at the lower end of the reach. Mean wetted width (m) was calculated from the average of 10 transects spaced equally throughout each reach. Gradient (%) was determined using the same digital topographic maps; the distance (m) between the 2 contour lines that bounded the study site latitude/longitude coordinates was traced, and gradient was calculated as the elevational increment between those contours divided by the traced distance (converted to a percentage). These stream conditions varied substantially among reaches (Table 1), with averages of 1918 m for elevation, 2.3% for channel gradient, and 3.2 m for wetted width.

Using the GIS model constructed by Olson and Cormier (2019), conductivity was estimated for each index reach and was included in our analyses as a measure of stream productivity (McFadden and Cooper 1962, Scarnecchia and Bergersen 1987). Road density was included because western native trout are usually negatively impacted by roads that are near streams (Eaglin and Hubert 1993, Valdal and Quinn 2011). The 2019 Topologically Integrated Geographic Encoding and Referencing (TIGER) database (United States Census Bureau 2019) was used to map all the roads in Idaho, and road density was estimated by summing the total kilometers of road within a 1.78-km radius (i.e., a 10-km<sup>2</sup> area) of each index reach. We assumed that conductivity and road density in 2019 was representative of those characteristics throughout the study period. A final predictor variable included the mean abundance of nonnative trout at the reach (across all surveys), which was Log<sub>e</sub> transformed.

#### Relating Broad-scale Environmental Conditions to Population Abundance

In addition to the reach-scale evaluation previously described, we used multiple linear regression to assess whether annual Bonneville cutthroat trout abundance across the landscape was influenced by broad-scale bioclimatic predictor variables, including those representing stream flow, thermal regime, and drought. For this analysis, we treated each year as the sample unit.

Stream flow was included as a predictor variable because it is important for all life stages of stream-dwelling salmonids, including migration,

spawning, and rearing (reviewed *in* Bjornn and Reiser 1991), and because both summer and winter stream flow can affect salmonid abundance (Bell et al. 2000, Mitro et al. 2003, Kanno et al. 2016). To characterize annual stream flow across the entire study area, we used mean daily discharge ( $\text{m}^3/\text{s}$ ) from 3 U.S. Geological Survey (USGS) stream gaging stations that (1) bounded the study area, (2) had similar magnitude of daily and mean annual flow, (3) were located in smaller streams not subject to intense upstream water management, and (4) were strongly correlated with each other (mean correlation coefficient [ $r$ ] between these stations for average daily discharge = 0.82). The stations included the Logan River (USGS station 10109000), Blacksmith Fork (USGS station 10113500), and the Portneuf River (USGS station 13073000). We averaged the mean daily discharge from these 3 stations, from which mean summer (Jun–Aug) and mean winter (Dec–Feb) discharge were calculated for each year.

Temperature was included as a predictor variable because the severity of both summer and winter water temperatures can affect the survival and abundance of stream-dwelling salmonids (e.g., Jowett 1992, Isaak and Hubert 2004, Meyer et al. 2010). Long-term stream temperature data were generally lacking across the study area. However, air temperature is often strongly correlated to stream water temperature (Crisp and Howson 1982), and summer air temperature is often correlated to the distribution and abundance of salmonids in Rocky Mountain streams (e.g., Dunham et al. 1999, Rahel and Nibbelink 1999) and elsewhere (Kanno et al. 2016). We therefore used annual air temperature variation to index annual water temperature variation. Accordingly, mean daily air temperature data were obtained from the National Oceanic and Atmospheric Administration's (NOAA) Global Historical Climatology Network for 3 stations that bounded the Bear River basin in Idaho (Emigrant Summit, station USS0011G06S; Franklin Basin, station USS0011G32S; and, Giveout, station USS0011G33S). We averaged the mean daily values from these 3 stations, from which mean summer (Jun–Aug) and mean winter (Dec–Feb) air temperatures were calculated for each year.

While stream flow and water temperature are experienced directly by salmonids in lotic habitats, drought can have a more nuanced impact on stream-dwelling salmonids. For instance, although drought may directly affect stream flow and

water temperature, it may also indirectly affect stream-dwelling salmonids by influencing conditions such as riparian vegetation, fire, bank stability, and food resources (Lynn Zong et al. 1996, Dwire and Kauffman 2003, Boulton 2003, Garssen et al. 2014). Consequently, drought is often associated with fluctuations in the abundance of stream-dwelling salmonids (Elliott et al. 1997, Hakala and Hartman 2004, Meyer et al. 2014), including Bonneville cutthroat trout (White and Rahel 2008).

To characterize an annual drought index for the study area, estimates of the Palmer Drought Severity Index (PDSI) were obtained from NOAA's National Center for Environmental Information for the Southeast Division of Idaho. The PDSI is a monthly measure of dryness that is based on recent moisture supply, soil characteristics, and evapotranspiration (Palmer 1965). Negative PDSI values of 0 to  $-0.5$  are normal,  $-0.5$  to  $-1$  indicate incipient drought,  $-1$  to  $-2$  indicate mild drought,  $-2$  to  $-3$  indicate moderate drought,  $-3$  to  $-4$  indicate severe drought, and less than  $-4$  indicate extreme drought. Positive PDSI values follow a similar qualitative categorization for wet weather. We averaged the 12 monthly values to compute a mean PDSI for each year.

To characterize annual variation in Bonneville cutthroat trout abundance, estimates for all sampling events at a reach were normalized to a  $Z$  score based on the mean abundance at the reach across all sampling periods, so that each reach had a mean abundance  $Z$  score of zero and a standard deviation of one. Normalizing the cutthroat trout abundance data had the effect of making all reaches contribute equally to the abundance-bioclimate relationships rather than hinging more heavily on the reaches with the highest abundance. For each year of fish sampling, we estimated a mean  $Z$  score for all reaches surveyed in that year. Since we surveyed fish abundance in 17 separate years, this gave us a sample size of 17 for this analysis. Because broad-scale bioclimatic conditions such as stream flow, temperature, and drought are likely to affect recruitment or have other delayed effects that outweigh influences on within-year abundance (e.g., Bell et al. 2000, Copeland and Meyer 2011), we related bioclimatic conditions to Bonneville cutthroat trout abundance at a one-year time lag.

#### Data Analyses

For both the reach-scale and broad-scale modeling exercises described above, we considered

all combinations of predictor variables during model construction, but interaction terms were not considered due to small sample size for both data sets. Models were ranked using Akaike's information criterion corrected for small sample size (AICc; Burnham and Anderson 2002), and we considered the most plausible models to be those with AICc scores within 2.0 of the best model (Burnham and Anderson 2004). AICc weights ( $w_i$ ) were used to assess the relative plausibility of each of the most plausible models, and coefficients of determination ( $r^2$ ) or adjusted  $r^2$  (for models with more than one predictor variable) were used to describe the amount of the variation in the response variables that was explained by the parameters in the models. Coefficient estimates are reported only for the most plausible models, and only those coefficients with 95% CIs that did not overlap zero were considered influential in a model, regardless of their inclusion. In addition, we assessed whether Bonneville cutthroat trout abundance was higher in allopatry than in sympatry with nonnative trout by using a simple  $t$  test. All analyses were conducted using the SAS statistical software package (SAS Institute 2009).

## RESULTS

Bonneville cutthroat trout >100 mm TL were captured during 171 of the 186 electrofishing surveys conducted. At 3 index reaches, Bonneville cutthroat trout were present during the initial survey but absent during the final survey, but there were also 3 reaches where they were absent during the initial survey (though they were known to be present in the stream) but present during the final survey (Table 2).

Nonnative trout were captured during 80 surveys and occurred at 20 of the 34 index reaches. Rainbow trout and hybrids were the most common nonnative salmonid encountered (captured in 43 surveys at 16 reaches), followed by brook trout (35 surveys at 8 reaches), and brown trout (26 surveys at 5 reaches). At 11 of the 34 reaches, at least one nonnative trout either appeared at or disappeared from the reach from the beginning to the end of the time period, and all 3 nonnative species experienced appearance and disappearance at one or more index reaches (Table 2).

Across all surveys conducted, Bonneville cutthroat trout density averaged 5.6 fish/100 m<sup>2</sup> (or 2.5/100 m) and ranged from 0 to 25.3 fish/100 m<sup>2</sup> (0 to 19.4/100 m). In comparison,

nonnative trout density averaged 2.1 fish/100 m<sup>2</sup> (or 0.5/100 m) and ranged from 0 to 29.9 fish/100 m<sup>2</sup> (0 to 9.1/100 m). Mean density of Bonneville cutthroat trout was higher ( $t = 4.61$ ,  $df = 184$ ,  $P < 0.001$ ) at reaches where nonnative trout were absent ( $\bar{x} = 7.7$  fish/100 m<sup>2</sup>;  $SE = 0.7$ ) than where they were present ( $\bar{x} = 4.2$  fish/100 m<sup>2</sup>,  $SE = 0.4$ ). Of the 111 surveys conducted at the 20 reaches where Bonneville cutthroat trout and nonnative trout were sympatric, density was >3.0 fish/100 m<sup>2</sup> for both taxa on only 12 occasions (Fig. 2).

Across all 34 index reaches combined, mean  $\lambda$  was 1.04 for Bonneville cutthroat trout, and the 90% CI on this overall average overlapped unity (0.98–1.10; Table 2). Within individual reaches, Bonneville cutthroat trout population growth rate was generally stable, with statistically significant declines in  $\lambda$  at 3 reaches, statistically significant increases in  $\lambda$  at 3 other locations, and stable estimates of  $\lambda$  (i.e., nonsignificant changes) at the remaining reaches. In comparison, mean  $\lambda$  for all reaches combined averaged 0.93 for nonnative trout, and the 90% CI on this overall average did not overlap unity (0.89–0.97), suggesting that nonnative trout in general were declining in the long-term monitoring reaches over the entire study period. However, few estimates of  $\lambda$  were statistically significantly declining at individual reaches (Table 2).

The estimated finite population growth rates for Bonneville cutthroat trout at individual stream reaches were most strongly associated (positively) with conductivity at the reach, followed by road density (also a positive association); the remaining stream conditions included in our analyses (nonnative trout density, wetted width, elevation, and stream gradient) were weakly associated with estimates of  $\lambda$  (Fig. 3). All of the plausible models relating reach-scale stream conditions to estimates of  $\lambda$  at each reach included conductivity (Table 3), and none of the coefficient estimate 95% CIs included zero (Table 4); estimates indicated that Bonneville cutthroat trout population growth was higher at reaches with higher conductivity. All of the remaining stream conditions appeared in some of the most plausible models (Table 3), but in nearly all instances, the 95% CIs around these parameter estimates included zero (Table 4), indicating that none of the remaining variables were very influential in the models in which they appeared. These models explained 19% to 29% of the variation we observed in Bonneville

TABLE 2. Mean abundance with associated coefficient of variation (CV), along with finite population growth rates ( $\lambda$ ) and their associated 90% confidence intervals (CIs) for Bonneville cutthroat trout and nonnative trout at 34 long-term monitoring reaches in Bear River tributaries of southeast Idaho. Nonnative trout species (spp.) included brook trout (BKT), brown trout (BNT), and rainbow trout and hybrids (RBT). Bold text highlights estimates for which CIs do not overlap zero. Arrows indicate where a species appeared at (up arrow) or disappeared from (down arrow) the reach over the study period. Site numbers correspond to those on the map in Fig. 1.

Site	Stream	Time period	Number of surveys	Bonneville cutthroat trout				Nonnative trout				
				Fish/100 m <sup>2</sup>		$\lambda$		Fish/100 m <sup>2</sup>		$\lambda$		
				Mean	CV	Est.	90% CI	Mean	CV	Est.	90% CI	
1	Beaver Creek	2006–2017	6	3.62	0.80	0.95	0.77–1.16	1.19	1.47	<b>0.72</b>	<b>0.53–0.96</b>	BCT, BKT $\uparrow$ , RBT
2	Beaver Creek	2009–2017	5	1.81	1.30	1.22	0.66–2.28	5.24	0.49	0.95	0.81–1.11	BCT, BKT, RBT $\downarrow$
3	Cottonwood Creek	2006–2019	8	8.83	0.56	<b>0.90</b>	<b>0.82–0.99</b>	1.14	0.99	0.92	0.71–1.19	BCT, RBT
4	Cottonwood Creek	2006–2019	6	1.79	0.48	0.96	0.88–1.04	0.05	2.45	0.97	0.87–1.09	BCT, RBT
5	Cottonwood Creek	2011–2017	4	8.05	0.41	0.96	0.67–1.38	0.47	1.40	0.78	0.37–1.63	BCT, RBT $\downarrow$
6	Dry Creek	2008–2020	5	4.07	1.09	1.11	0.84–1.48	—	—	—	—	—
7	Dry Creek	2012–2020	5	6.02	0.69	0.92	0.70–1.21	—	—	—	—	—
8	Eighthmile Creek	2010–2018	3	1.58	0.27	1.05	0.81–1.37	9.07	0.43	<b>0.89</b>	<b>0.86–0.92</b>	BCT, BKT
9	Eighthmile Creek	2006–2018	7	0.55	1.60	0.87	0.69–1.10	8.96	0.39	0.98	0.90–1.08	BCT $\downarrow$ , BKT
10	Eighthmile Creek	2010–2020	6	1.03	0.60	1.18	0.92–1.52	17.45	0.47	0.98	0.80–1.19	BCT, BKT, RBT $\uparrow$
11	Giraffe Creek	2008–2020	6	14.48	0.29	0.99	0.92–1.06	—	—	—	—	—
12	Giraffe Creek	2004–2020	7	14.25	0.47	<b>1.08</b>	<b>1.02–1.15</b>	—	—	—	—	—
13	Hoopes Creek	2009–2019	5	2.73	0.87	1.13	0.92–1.38	—	—	—	—	—
14	Kackley Spring	2009–2018	5	7.05	0.92	<b>1.71</b>	<b>1.28–2.28</b>	3.86	0.59	0.94	0.77–1.17	BCT $\downarrow$ , BNT $\downarrow$ , RBT $\uparrow$
15	Kackley Spring	2009–2018	6	5.46	0.53	<b>1.58</b>	<b>1.20–2.08</b>	4.53	0.40	0.95	0.86–1.07	BCT $\downarrow$ , BNT $\downarrow$ , RBT $\uparrow$
16	Logan River	2011–2019	3	9.66	0.25	1.04	0.80–1.34	0.11	1.73	0.82	0.60–1.12	BCT, RBT $\downarrow$
17	Logan River	2001–2019	7	4.2	0.56	0.98	0.89–1.09	0.28	1.89	0.99	0.83–1.17	BCT, RBT
18	Maple Creek	2009–2019	6	7.47	0.49	<b>0.88</b>	<b>0.80–0.97</b>	1.77	1.02	1.14	0.71–1.82	BCT, BNT $\downarrow$ , RBT $\downarrow$
19	Maple Creek	2006–2017	6	6.41	0.38	0.96	0.84–1.09	0.26	2.45	0.91	0.68–1.21	BCT, RBT
20	Montpelier Creek	2006–2020	6	0.23	2.04	<b>0.83</b>	<b>0.75–0.90</b>	2.75	0.48	0.95	0.83–1.08	BCT $\downarrow$ , BKT $\downarrow$ , BNT $\downarrow$ , RBT $\uparrow$
21	Montpelier Creek	2006–2020	7	3.8	0.56	1.04	0.96–1.11	6.82	0.40	1.04	0.97–1.11	BCT, BKT, BNT $\downarrow$ , RBT
22	Preuss Creek	1993–2010	4	5.68	0.69	1.06	0.94–1.20	—	—	—	—	BCT
23	Preuss Creek	2004–2020	7	4.43	0.79	0.98	0.89–1.08	—	—	—	—	BCT
24	Preuss Creek	1993–2020	6	7.92	0.76	0.93	0.77–1.11	—	—	—	—	BCT
25	Preuss Creek	1993–2008	3	10.47	1.24	1.06	0.33–3.37	—	—	—	—	BCT
26	Preuss Creek	1993–2008	3	9.91	0.76	1.16	0.81–1.67	—	—	—	—	BCT
27	Preuss Creek	1993–2020	8	10.3	0.60	0.98	0.93–1.04	—	—	—	—	BCT
28	Stauffer Creek	2012–2020	4	4.16	0.65	0.99	0.69–1.42	—	—	—	—	BCT
29	Stauffer Creek	2012–2020	5	9.06	0.64	0.94	0.74–1.19	—	—	—	—	BCT
30	Stockton Creek	2009–2019	7	2.9	0.71	1.06	0.94–1.19	—	—	—	—	BCT
31	Stockton Creek	2010–2019	6	6.52	0.43	0.96	0.85–1.08	0.14	2.45	0.86	0.69–1.07	BCT, RBT $\downarrow$
32	Trout Creek	2011–2019	4	6.35	0.42	1.07	0.85–1.35	1.87	0.37	1.01	0.80–1.29	BCT, BKT
33	Whiskey Creek	2011–2019	5	0.86	1.13	1.17	0.73–1.88	0.39	0.91	0.95	0.72–1.26	BCT $\downarrow$ , RBT
34	Whiskey Creek	2011–2019	5	0.36	1.28	0.81	0.56–1.19	0.122	0.74	0.89	0.66–1.20	BCT $\downarrow$ , RBT



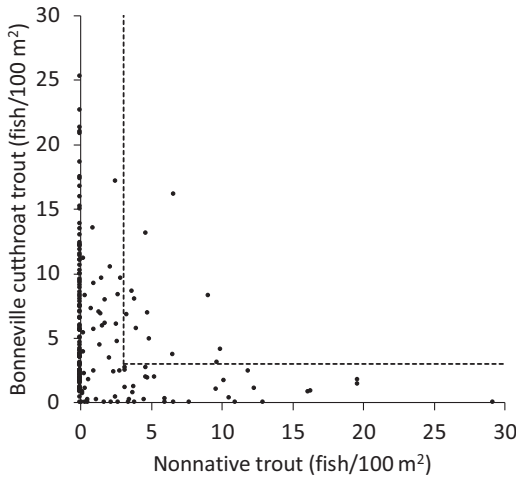


Fig. 2. Scatterplot of the density of Bonneville cutthroat trout versus density of nonnative trout for individual electrofishing surveys conducted at long-term monitoring reaches in Bear River tributaries of southeast Idaho. Dashed lines delineate a density of 3.0 fish/100 m<sup>2</sup>.

cutthroat trout estimates of  $\lambda$  among index reaches (Table 3).

The mean annual Z scores of Bonneville cutthroat trout abundance at individual stream reaches were most strongly associated with annual variation in mean daily discharge at nearby USGS gaging stations the previous winter and the previous summer and were weakly associated with annual variation in nearby daily air temperatures the previous summer and previous winter and with mean annual PDSI for southeast Idaho the previous year (Fig. 4). The most parsimonious model relating bioclimatic factors to normalized cutthroat trout abundance included only winter discharge (Table 5), with the parameter estimate (and associated 95% CIs) indicating that Bonneville cutthroat trout abundance was generally higher in years when winter discharge was higher the previous year (Table 6). There was also some support for 2 additional models, one including both winter and summer discharge, and the other including summer air temperature and discharge (Table 5). Based on parameter estimates and their 95% CIs (Table 6), the second-best model indicated that winter and summer flow the previous year did not influence annual variation in cutthroat trout abundance, whereas the third-best model indicated that cutthroat trout abundance was generally higher in years with higher summer discharge the previous year. The most plausible models (i.e., those

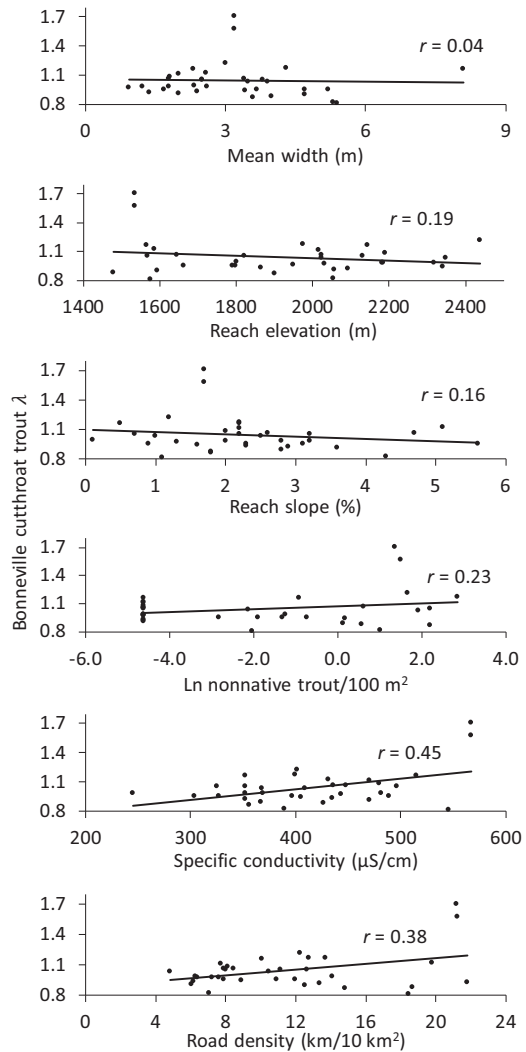


Fig. 3. Scatterplots of Bonneville cutthroat trout finite population growth rate ( $\lambda$ ) versus various abiotic stream conditions at 34 long-term monitoring reaches in Bear River tributaries of southeast Idaho.

with AICc scores within 2.00 of the best model) explained from 24% to 31% of the annual variation we observed in normalized Bonneville cutthroat trout abundance across the landscape (Table 5).

## DISCUSSION

Bonneville cutthroat trout have unequivocally experienced a range-wide reduction in occupancy and abundance from historical levels, though much of this range contraction occurred decades ago,

TABLE 3. Top models relating reach-scale conditions to Bonneville cutthroat trout finite population growth rate ( $\lambda$ ) at 34 long-term monitoring reaches in Bear River tributaries of southeast Idaho. Akaike's information criteria (AICc), change in AICc ( $\Delta$ AICc), and AICc weights ( $w_i$ ) were used to assess model plausibility, and coefficients of determination ( $r^2$ ) indicate the amount of variation explained in the models.

Model	AICc	$\Delta$ AICc	$w_i$	$r^2$
Conductivity + road density	-121.54	0.00	0.10	0.24
Conductivity + road density + Ln(nonnative trout density) + width	-121.20	0.35	0.08	0.29
Conductivity + road density + Ln(nonnative trout density)	-120.51	1.04	0.06	0.24
Conductivity + road density + elevation	-120.32	1.22	0.05	0.24
Conductivity	-120.22	1.32	0.05	0.20
Conductivity + road density + gradient	-120.19	1.36	0.05	0.23
Conductivity + Ln(nonnative trout density)	-120.02	1.52	0.05	0.20
Conductivity + road density + width	-119.83	1.71	0.04	0.23
Conductivity + road density + Ln(nonnative trout density) + width + gradient	-119.77	1.78	0.04	0.29
Conductivity + Ln(nonnative trout density) + width	-119.56	1.99	0.04	0.22
Conductivity + gradient	-119.50	2.04	0.03	0.19

due primarily to habitat alterations resulting from land-use practices and the introduction of nonnative salmonids (Duff 1988). Our results suggest that in the last several decades, the distribution and abundance of Bonneville cutthroat trout at index reaches in southeastern Idaho are generally stable. Whether this is true in other portions of their range is unknown because additional published long-term trend data are lacking. Considering that Bonneville cutthroat trout occupy a higher proportion of their historical range in Idaho (54%; IDFG 2022) than elsewhere, and that the Bear River basin is known to be a stronghold for Bonneville cutthroat trout (UDNR 2018), the index reaches in our study likely represent some of the best remaining lotic habitat for the species, and thus may not accurately represent trends in abundance across their range. Additional trend monitoring is clearly needed to better characterize the status of Bonneville cutthroat trout at a broader scale.

Bonneville cutthroat trout population growth rates were generally stable even at reaches where nonnative trout were present, and nonnative trout (taken collectively) showed declining population growth rates in the Bear River basin. This was unexpected, since all 3 nonnative trout generally have adverse effects on cutthroat trout populations (e.g., Dunham et al. 2002, McHugh and Budy 2006, Seiler and Keeley 2009). In addition, we found that the occurrence of nonnative salmonids was temporally inconsistent, as evidenced by the fact that 13 of the 20 index reaches where nonnative salmonids occurred experienced either contractions or expansions in species occupancy. This concurs with a recent

study in western Montana, which revealed that brook trout, brown trout, and rainbow trout were all undergoing contractions and expansions in their occurrence in some watersheds (Bell et al. 2021). The temporal stability of stream fish assemblages varies dramatically among taxa and ecosystems but is generally thought to be driven by variation in density-dependent and density-independent factors (Gido and Jackson 2010). Although Bonneville cutthroat trout trends in abundance were as stable at reaches where they were sympatric with nonnative trout as they were in allopatric reaches, their abundance was generally higher at reaches where nonnative trout were absent than where they were present. Despite the indication of some population resilience by Bonneville cutthroat trout to the presence of nonnative trout, the nearly ubiquitous negative relationship nonnative trout have on native trout (Krueger and May 1991, Buoro et al. 2016) suggests that management actions designed to curtail the spread or abundance of nonnative trout may eventually be needed for the long-term persistence of Bonneville cutthroat trout in Idaho.

Our results suggest that reduced baseflow in summer or winter months may have had an adverse influence on Bonneville cutthroat trout abundance the following year. Considering that age-0 fish in one year were large enough the following year to be included in our abundance estimates—and they would likely have constituted the most abundant age class in most instances—the negative relationship between summer or winter baseflow levels and Bonneville cutthroat trout abundance is perhaps the result of poor survival or production of age-0 fish

TABLE 4. Parameter estimates and 95% confidence intervals (LL = lower limit, UL = upper limit) for the top models relating reach-scale conditions to Bonneville cutthroat trout finite population growth rates ( $\lambda$ ) at 34 long-term monitoring reaches in Bear River tributaries of southeast Idaho. Bold text highlights estimates for which the 95% confidence intervals do not overlap zero.

Model and parameter	Estimate	SE	95% Confidence interval	
			LL	UL
Model 1				
Intercept	0.53	0.16	0.22	0.85
Conductivity	<b>0.0009</b>	0.0004	<b>0.0002</b>	<b>0.0017</b>
Road density	0.011	0.006	-0.001	0.022
Model 2				
Intercept	0.70	0.17	0.36	1.04
Conductivity	<b>0.0009</b>	0.0004	<b>0.0002</b>	<b>0.0016</b>
Road density	0.011	0.006	-0.001	0.023
Ln(nonnative trout density)	0.023	0.012	-0.001	0.046
Wetted width	-0.038	0.022	-0.081	0.006
Model 3				
Intercept	0.57	0.16	0.25	0.88
Conductivity	<b>0.0009</b>	0.0004	<b>0.0002</b>	<b>0.0017</b>
Road density	0.010	0.006	-0.002	0.021
Ln(nonnative trout density)	0.012	0.010	-0.001	0.032
Model 4				
Intercept	0.18	0.38	-0.57	0.92
Conductivity	0.0011	0.0004	<b>0.0003</b>	<b>0.0018</b>
Road density	0.015	0.007	<b>0.001</b>	<b>0.028</b>
Elevation	0.000	0.000	-0.0001	0.0004
Model 5				
Intercept	0.59	0.16	0.27	0.91
Conductivity	0.0011	0.0004	<b>0.0003</b>	<b>0.0018</b>
Model 6				
Intercept	0.58	0.17	0.25	0.90
Conductivity	0.0010	0.0004	<b>0.0002</b>	<b>0.0017</b>
Road density	0.010	0.006	-0.002	0.022
Gradient	-0.022	0.022	-0.007	0.022
Model 7				
Intercept	0.62	0.16	0.31	0.94
Conductivity	0.0011	0.0004	<b>0.0003</b>	<b>0.0018</b>
Ln(nonnative trout density)	0.015	0.011	-0.006	0.035
Model 8				
Intercept	0.57	0.17	0.25	0.90
Conductivity	<b>0.0009</b>	0.0004	<b>0.0002</b>	<b>0.0017</b>
Road density	0.0120	0.0061	<b>0.0001</b>	<b>0.0238</b>
Wetted width	-0.015	0.019	-0.054	0.023
Model 9				
Intercept	0.75	0.18	0.40	1.10
Conductivity	<b>0.0009</b>	0.0004	<b>0.0002</b>	<b>0.0017</b>
Road density	0.011	0.006	-0.001	0.022
Ln(nonnative trout density)	0.022	0.012	-0.002	0.045
Wetted width	-0.041	0.022	-0.084	0.003
Gradient	-0.023	0.022	-0.065	0.020
Model 10				
Intercept	0.64	0.17	0.32	0.97
Conductivity	0.0011	0.0004	<b>0.0004</b>	<b>0.0019</b>
Gradient	-0.027	0.023	-0.071	0.017

during low-flow years (Jespersen et al. 2021). Alternatively, reduced baseflow may have had negative effects on multiple age classes (Elliott et al. 1997, Hakala and Hartman 2004). Such an effect of reduced summer or winter baseflow on the abundance of age-0 fish or all age classes

could be the result of (1) reduced reproductive success (Elliott et al. 1997); (2) reduced habitat quality and availability (Hakala and Hartman 2004); (3) diminished food resources (Cowx et al. 1984); (4) intensified predation as subadults are forced into closer proximity to predators

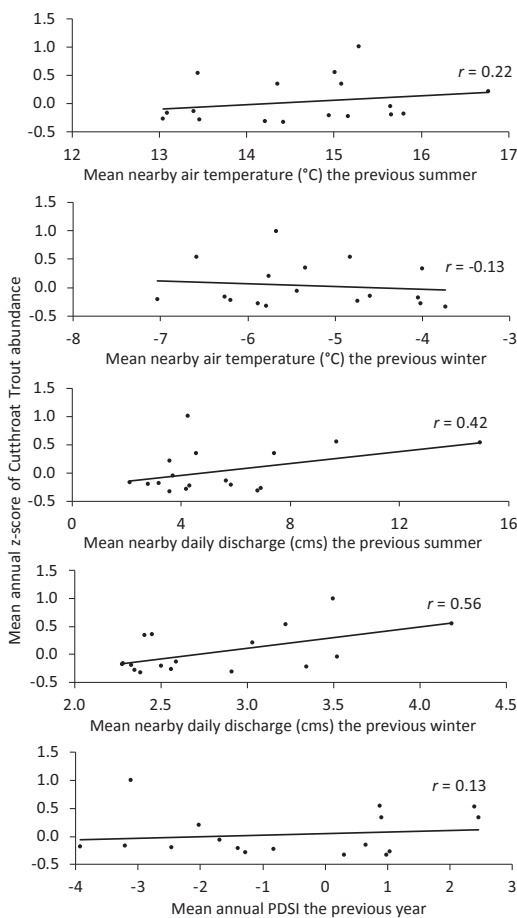


Fig. 4. Scatterplots of mean annual Z scores of Bonneville cutthroat trout abundance in a given year versus nearby air temperature, stream discharge, and Palmer drought severity index (PDSI) the previous year for Bear River tributaries of southeast Idaho from 1993 to 2020.

because of less available space (Larimore et al. 1959); and (5) reduced overwinter habitat, and ultimately, survival of age-0 trout (Hakala and Hartman 2004) or older age classes (Maciolek and Needham 1952). Regardless of the mechanism(s), the negative effects of reduced stream flow on cutthroat trout abundance observed here portends that if climate change continues to diminish baseflow conditions in streams across the west (Luce and Holden 2009), the likelihood of long-term persistence for many Bonneville cutthroat trout populations in Idaho may be reduced.

Population growth rates for vertebrate species are clearly affected by density-dependent processes (Morris and Doak 2002), but estimates of  $\lambda$  for stream-dwelling trout populations have rarely

been directly linked to other biotic or abiotic stream conditions. Of the factors we investigated, only conductivity (taken from a GIS layer, not field measurements) appeared to influence estimates of  $\lambda$  for Bonneville cutthroat trout. Conductivity is often associated with the productivity of a water body (Rawson 1951, Welch 1952) and has been previously shown to be positively associated with trout abundance in streams (e.g., McFadden and Cooper 1962, Scarnecchia and Bergersen 1987). In the present study, conductivity was estimated to range from 240 to 580  $\mu\text{S}/\text{cm}$ , which are moderate to high values for flowing waters in western North America (Griffith 2014). Conductivity is also correlated to other important cations and anions (e.g., alkalinity and water hardness) that can influence fish populations in several ways (Scarnecchia and Bergersen 1987), so we cannot ascertain whether the relationship we observed was causative or correlative. Although other factors such as road density, elevation, gradient, stream size, and nonnative trout density were not important predictors of Bonneville cutthroat trout population growth, it should be noted that limiting factor analysis is notoriously challenging because such biotic and abiotic conditions can interact in complex ways to affect animal populations (Cade et al. 1999, Townsend et al. 2008). Nevertheless, continued monitoring of these and other Bonneville cutthroat trout populations should include limiting factor analysis whenever feasible to reveal environmental conditions that could be targeted by management or conservation activities.

We expected that drought conditions might adversely affect Bonneville cutthroat trout abundance in the study area, but we observed no such effect. In general, drought reduces the volume and complexity of stream habitat, resulting in diminished food resources (Cowx et al. 1984), reduced reproductive success (Elliott et al. 1997, White and Rahel 2008), shifts in species assemblages (Matthews and Marsh-Matthews 2003), and increased predation (Larimore et al. 1959). Not surprisingly, drought conditions have repeatedly been shown to negatively affect cutthroat trout populations (Dunham et al. 1999, White and Rahel 2008, Gresswell 2011, Meyer et al. 2014). Contemporarily, Bonneville cutthroat trout are closely associated with headwater habitats (Kershner 1995), which are typically more stochastic in nature (Richardson et al. 2005) and less prone to climate-altered conditions (Isaak et al. 2016) than downstream reaches. As such, the

TABLE 5. Top models relating broad-scale bioclimatic conditions to basin-wide Bonneville cutthroat trout abundance in Bear River tributaries of southeast Idaho from 1993 to 2020. Akaike's information criteria (AICc), changes in AICc ( $\Delta$ AICc), and AICc weights ( $w_i$ ) were used to assess model plausibility, and coefficients of determination ( $r^2$ ) indicate the amount of variation explained in the models.

Bioclimatic predictor models	AICc	$\Delta$ AICc	$w_i$	$r^2$
Winter flow	-35.11	0.00	0.22	0.31
Winter flow + summer flow	-33.65	1.46	0.11	0.26
Summer air temperature + summer flow	-33.16	1.95	0.08	0.24

TABLE 6. Parameter estimates and 95% confidence intervals (LL = lower limit, UL = upper limit) for the top models relating broad-scale bioclimatic conditions to basin-wide Bonneville cutthroat trout abundance in Bear River tributaries of southeast Idaho from 1993 to 2020. Bold text highlights estimates for which CIs do not overlap zero.

Model and parameter	Estimate	SE	95% Confidence interval	
			LL	UL
Best model				
Intercept	-1.045	0.425	-1.878	-0.211
Winter flow	0.385	0.149	<b>0.093</b>	<b>0.676</b>
Second-best model				
Intercept	-1.018	0.427	-1.855	-0.182
Winter flow	0.319	0.164	-0.002	0.639
Summer flow	0.029	0.030	-0.029	0.087
Third-best model				
Intercept	-2.585	1.295	-5.123	-0.046
Summer air temperature	0.152	0.084	-0.012	0.316
Summer flow	0.072	0.029	<b>0.015</b>	<b>0.129</b>

headwater stream reaches we included in our study may have been less likely to be influenced by drought.

The primary limitation in our study was that sites selected for long-term monitoring were not originally drawn at random. Consequently, our results may not accurately depict trends in the distribution and abundance of Bonneville cutthroat trout and nonnative trout in streams within the Bear River and Bear Lake tributaries in Idaho that were not sampled. Despite the well-known importance of random sampling to ensure that ecological observations are drawn from the population of interest (Garton et al. 2012), it is common in long-term monitoring programs tracking changes in stream-dwelling salmonid populations to use data from index reaches that were established long ago in a nonprobabilistic manner (e.g., Gowan and Fausch 1996, Ham and Pearsons 2000, Cook et al. 2010). Courbios et al. (2008) highlight the importance of such index reaches because the temporal extent of the data allows examination of long-term population dynamics that would otherwise be unattainable. While our results are promising regarding Bonneville cutthroat trout conservation, we recommend that future efforts combine these index reaches with additional

sites drawn probabilistically to augment the rigor of the current study design.

Nonprobabilistic sampling is not the only limitation of our study. A second shortcoming was our reliance on surrogate data for stream temperature (using elevation and air temperature) and stream flow (using nearby stream gages on larger nearby rivers). Using surrogates rather than direct field measurements for stream temperature and flow are common in fish-stream habitat studies (e.g., Dunham et al. 1999, Rahel and Nibbelink 1999, Kanno et al. 2016) because long-term water temperature and stream flow data are rarely available in headwater streams, but they are not always effective proxies (Isaak et al. 2016). Third, we used geospatial covariates to characterize reach conductivity and road density, and we assumed these conditions were relatively stable throughout the study. This assumption is supported for conductivity by Olson and Cormier (2019) who observed that conductivity, though not constant, was relatively stable through time. For road density, the correlation between point estimates from 2019 TIGER data alone compared to averaging point estimates from the beginning and end of the study (i.e., 2000 and 2019) was very high (Pearson correlation coefficient [ $r$ ] = 0.96). Fourth,

sampling was conducted only at summer baseflows, but salmonid distribution and abundance inherently changes seasonally; thus, sampling at other times of the year during baseflow conditions (e.g., late fall or winter) may have produced different results. Fifth, our estimates of cutthroat trout and rainbow trout and hybrid distribution and abundance may have been slightly biased because phenotype imperfectly differentiates these taxa; however, recent evidence suggests phenotype is quite accurate to differentiate these taxa (Meyer et al. 2022), so this source of bias is likely inconsequential to our general conclusions. Finally, none of the most plausible models we presented explained a large portion of the variation we observed in Bonneville cutthroat trout population growth rates or abundance, implying that other environmental or biological conditions not accounted for in our study (e.g., disease, land-use activities, disturbance events) may have been important predictors.

Notwithstanding study limitations, our results suggest that in the Idaho portion of the Bear River basin, Bonneville cutthroat trout are more stable than are nonnative salmonids. However, considering that we observed reduced summer and winter stream baseflow conditions in a given year leading to reduced Bonneville cutthroat trout abundance in the following year, the projection of further reductions in stream baseflow levels in western North America as the climate continues to warm (Luce and Holden 2009) is concerning. This is especially true in streams containing nonnative trout that may be better adapted to warmer streams (Shepard 2004, Peterson et al. 2004) or lower stream flows. Periodic revisitation of these long-term monitoring reaches will continue to provide valuable information on the status of Bonneville cutthroat trout in Idaho. Expansion of these monitoring reaches to include all areas occupied by Bonneville cutthroat trout (in Idaho and elsewhere) would help confirm or refute the narrower conclusions that can be drawn from this trend-monitoring program.

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