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DIFFERENT LIFE HISTORIES OF BROOK TROUT POPULATIONS
INVADING MID-ELEVATION AND HIGH-ELEVATION
CUTTHROAT TROUT STREAMS IN COLORADO

Benjamen M. Kennedy1,2, Douglas P. Peterson1, and Kurt D. Fausch1

ABSTRACT.—Brook trout (Salvelinus fontinalis), native to eastern North America, have invaded many montane cold-water systems of western North America, and these invasions are implicated in the decline of native cutthroat trout (Oncorhynchus clarki). If fisheries biologists are to be effective in managing brook trout invasions, demographic models that predict invasion success will need to incorporate life history variation in different environments. We tested whether brook trout populations invading streams at 2 different elevations varied in life history characteristics that influence population dynamics and potential invasion success. In the high-elevation stream (3195 m), water temperatures were colder and brook trout apparently grew more slowly (i.e., had shorter lengths-at-age), became sexually mature 2 years later, and had life spans 2 to 3 times longer than those in the mid-elevation stream (2833 m). This flexibility in life history may allow brook trout to maximize their chance of establishment and invasion success among elevations. We propose that in mid-elevation streams fast growth and early maturity maximize fitness and can lead to rapid establishment and high population growth rates. In high-elevation streams, slow growth, later maturity, and a long reproductive life span may allow brook trout to successfully establish populations in these marginal habitats where recruitment is often poor.

Key words: brook trout, Salvelinus fontinalis, cutthroat trout, Oncorhynchus clarki, invasion biology, life history, Rocky Mountain streams, otoliths.

Brook trout (Salvelinus fontinalis), native to eastern North America, were introduced widely in western North America starting in the 1870s (MacCrimmon and Campbell 1969) and have invaded many montane cold-water streams where cutthroat trout (Oncorhynchus clarki) were native (Fausch 1989, Adams 1999). These brook trout invasions, along with habitat destruction and hybridization with nonnative rainbow trout (O. mykiss), have contributed to the extinction of 2 subspecies of cutthroat trout in the interior West and the extinction of the other 12 from 95% or more of their original ranges (Behnke 1992, Young 1995). To more effectively manage brook trout invasions and conserve cutthroat trout, it will be necessary to understand the mechanisms of invasion at the population level. This will require detailed information on the life histories of brook trout in populations invading different environments (Moyle and Light 1996).

Like all salmonids, brook trout life history can vary substantially with latitude and elevation (Reimers 1979, Power 1980, Adams 1999). Generally, the waters of southern latitudes and lower elevations are warmer, more productive, and have longer growing seasons. Consequently, brook trout grow faster, become sexually mature earlier, and die at younger ages than those in cold, unproductive waters of northern latitudes and higher elevations. This pattern may be attributed to flexibility in life history characteristics in response to differences in juvenile growth and adult survival (Hutchings 1993).

Although brook trout life history has been documented in other geographic regions (McFadden 1961, Power 1980, Hutchings 1996), there are few published data for mountain streams of the western U.S. Our objective was to provide new information on differences in life histories of brook trout populations invading contrasting environments by comparing length-at-age, length-at-maturity, and longevity of brook trout in 2 Rocky Mountain headwater cutthroat trout streams of different elevations. We predicted that the mid-elevation stream would be warmer, resulting in brook trout with longer lengths-at-age, earlier sexual maturation, and shorter life spans. In contrast, the high-elevation stream was predicted to be colder, resulting in shorter lengths-at-age, later maturation, and longer life spans.

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METHODS

Brook trout were sampled in 2 streams as part of an ongoing, large-scale field experiment to determine effects of invading brook trout on native Colorado River cutthroat trout (O. c. pleuriticus). Both are headwater streams in the central Rocky Mountains in Colorado of similar width (Little Muddy Creek 3.8 m, Willow Creek 2.6 m) and gradient (4.4%, 4.0%). Each receives little or no angling (Peterson and Fausch unpublished data). Long segments of each stream were sampled (Little Muddy Creek 877 m, Willow Creek 1200 m). Elevation at the midpoints of the mid-elevation stream (Little Muddy Creek, 2683 m, range 2659-2695 m) and the high-elevation stream (Willow Creek, 3195 m, range 3189-3220 m) differed by 512 m. Brook trout populations were actively invading and becoming naturalized in both study reaches. In the high-elevation stream, brook trout increased from about 30% of the population in 1988 (Fausch 1989) to 98% in 1998, apparently mainly by upstream movement (Peterson and Fausch unpublished data). In the mid-elevation stream, brook trout rapidly reinvaded the study segment from which they had been removed (Peterson 2000).

In late summer (8 August to 20 September) 1998, 1999, and 2000, we removed brook trout using 2-pass electrofishing removal (see Riley et al. 1992 for methods). Captured brook trout were euthanized in an overdose of MS-222, measured (fork length, nearest mm), and weighed (nearest g). Sagittal otoliths were removed from fish >100 mm fork length (FL; n = 160) in the field and stored dry in envelopes, whereas fish <100 mm FL (n = 24) were preserved in 70% ethanol and otoliths were later removed in the laboratory. In 2000 we collected additional otoliths from brook trout <178 mm FL (n = 32) in the high-elevation stream because insufficient numbers of small fish were collected in 1998 and 1999.

Sagittal otoliths are more accurate and precise than scales for determining ages of brook trout (Dutil and Power 1977, Reimers 1979, Power 1980). Excised otoliths were cleaned, mounted on microscope slides with thermoplastic cement, and ground along the sagittal plane (horizontal cross section) with 400-grit wet sandpaper to clarify annuli. Hall (1991) found no significant difference between ages determined from vertical versus horizontal cross sections. The senior author counted otolith annuli using a compound microscope at 100X magnification with transmitted light. Otoliths were read without knowledge of stream location or fish length. Annular bands, also referred to as "winter bands," indicate periods of slow winter growth (light translucent bands) between periods of fast summer growth (dark opaque bands; Dutil and Power 1977, Reimers 1979). Fish in their 1st year of life did not have annuli and were classified as age 0. Age estimates were verified by the 2nd author who aged a subset of otoliths randomly selected from each age class, again without knowledge of stream or fish length. An age bias plot and coefficients of variation were used to assess systematic reader bias and precision among age classes as recommended by Campana et al. (1995).

All brook trout captured in the 2 streams were removed to maintain treatments in the larger field experiment that was being conducted simultaneously. Therefore, we could not tag fish and recapture them in subsequent years to validate annuli. Instead, we validated age estimates for brook trout in the mid-elevation stream by aging 13 fish of known age in a control stream of similar elevation (East Fork Parachute Creek, 2530 m) where brook trout were not removed. Twelve fish had been marked at age 0 in 1998 and were recaptured in 2000 at age 2. One was marked at age 0 in 1999 and recaptured in 2000 at age 1. Age estimates for fish in the high-elevation stream could not be validated due to small sample size of marked fish recaptured in a similar high-elevation control stream. Thus, age estimates of brook trout from the high-elevation stream were validated for the first 3 years of life by comparing them to age estimates derived from distinguishable modes in a length-frequency histogram. Brook trout age estimates for the mid-elevation stream were also compared with a length-frequency histogram for the first 2 years of life.

Differences in mean length-at-age between streams were analyzed by 2-way ANOVA on log-transformed data (main effects were stream and age) using PROC CLM (SAS version 8.0, SAS Institute Inc., Cary, NC). Lengths of fish preserved in ethanol were converted to fresh lengths using a 1.9% shrinkage correction factor (fresh length = preserved length * 0.9819 + preserved length, r² = 0.995, P < 0.0001) for
juvenile sockeye salmon from Shields and Carlson (1996).

To estimate length at maturity for brook trout males and females, we examined fish collected in 1998 and 1999 that were preserved in 10% formalin. Females were considered mature when their ovaries contained visible orange eggs and extended ventrally, filling the body cavity. If their ovaries contained small granular white oocytes that were dorsally restricted, we considered the fish immature. Males were considered mature when their testes were large and white and immature when their testes were threadlike and restricted to the dorsal surface of the body cavity (see Lagler 1978, Downs et al. 1997, and Hutchings et al. 1999 for detailed descriptions). Preserved lengths were converted to fresh lengths using a 4.8% shrinkage correction factor (fresh length = preserved length * 0.048 + preserved length, \( r^2 = 0.994, P < 0.0001 \)) derived from a sample of 25 brook trout from the mid-elevation stream where fresh and preserved lengths were measured. We used logistic regression (PROC LOGISTIC) to analyze how maturity depended on fish length and stream. Separate analyses were performed for males and females. All statistical tests were considered significant at \( \alpha = 0.05 \).

Water temperature was measured in 1999 and 2000 using TidBit thermographs (Onset Computer Corp., Inc., Pocasset, MA). Thermographs set to record temperature each 24–72 minutes were placed in the deepest pool in each study stream during summer 1999 and retrieved in summer 2000. Water temperature differences between the streams were assessed by comparing mean annual daily temperature, mean July temperature, and warmest mean daily temperature of the summer. To compare length of the growing season between streams, we determined the number of days on which mean daily water temperature equaled or exceeded 4°C. This is a useful measure because feeding and growth of brook trout in aquaculture have been shown to virtually cease below 4°C (Power 1980, Dwyer et al. 1983).

RESULTS

Validation

In the mid-elevation control stream, 12 brook trout marked as age 0 in 1998 and recaptured in 2000 as age 2 (mean 157 mm FL, range 145–166) were determined from otoliths to be age 2. The single age-0 fish marked in 1999 and recaptured in 2000 as age 1 (123 mm FL) was aged to be age 1. In the mid-elevation stream, otolith ages for fish aged 0 and 1 matched ages estimated from distinguishable modes in the length-frequency histogram for 1998 and 1999 combined (Fig. 1). In the high-elevation stream, ages estimated by otoliths for fish ages 0, 1, and 2 also matched ages estimated from distinguishable modes in the length-frequency histogram for 1998 through 2000 combined. Older ages could be neither distinguished from the length-frequency histograms nor validated.

Verification

Visual inspection of the age bias plot of reader 1 versus reader 2 revealed no bias in age estimates for ages 0 through 7 (i.e., minimal deviation from the 1:1 ratio reference line). However, for fish aged 8 and older, ages estimated by reader 2 were lower than those by reader 1. To resolve this discrepancy, the 8 otoliths with the largest difference in age estimates were read again by each reader without knowledge of previous age estimates or stream of origin. The age bias plot revealed no bias until age 9, and estimates of older fish were closer between readers (Fig. 2). Coefficients of variation (CV) of age estimates for ages 0 to 8 were low (mean CV 4.5%, range 0–14). Six of 9 age classes had a CV <4.0%. Coefficients of variation for ages 9 and older were not calculated due to the bias associated with those age classes.

Length-at-Age and Longevity

Means among age groups of brook trout from the high-elevation stream (Willow Creek) was significantly less than brook trout from the mid-elevation stream (Little Muddy Creek) at ages 0, 1, and 2 (\( P < 0.001 \) by \( t \) tests; Table 1). Age-3 trout were also smaller in the high-elevation stream, but the difference was not significant (\( P = 0.51 \)). Two-way ANOVA showed significant interaction of fish age and stream (\( P < 0.001 \)), so \( t \) tests were used to compare simple effects of stream at each age. Brook trout length reached an asymptote after age 5 in the high-elevation stream but did not reach an asymptote in the mid-elevation stream (Fig. 1).
Brook trout from the high-elevation stream had a maximum life span 2 to 3 times longer than trout collected from the mid-elevation stream (Table 1, Fig. 1). Many brook trout removed from the high-elevation stream were ages 8 to 10 and a few were aged to be 11 to 14. Ages of brook trout larger than 200 mm were highly variable, ranging from age 4 to age 14. Most brook trout from the mid-elevation stream reached only age 2 or age 3, and the oldest fish were ages 4 and 5.

**Maturity**

Brook trout males and females from the mid-elevation stream matured at a shorter length and younger corresponding age than those from the high-elevation stream (Fig. 3, Table 2). Both stream (females $\chi^2 = 26.7, P < 0.0001$; males $\chi^2 = 16.9, P < 0.0001$) and FL (females $\chi^2 = 106.3, P < 0.0001$; males $\chi^2 = 62.0, P < 0.0001$) were significant factors in predicting the maturity status of brook trout.
The majority of male brook trout matured at age 1 in the mid-elevation stream and ages 3 and 4 in the high-elevation stream.

Temperature

The high-elevation stream was substantially colder and the growing season much shorter than the mid-elevation stream during summer 1999 to 2000 (27 August 1999 to 26 August 2000). Mean daily water temperature for this year was 1.9°C in the high-elevation stream and 3.8°C in the mid-elevation stream. Mean water temperatures in July were 7.1°C in the high-elevation stream versus 12.5°C in the mid-elevation stream, and mean daily water temperatures for the warmest day were 9.2°C and 13.5°C, respectively. In the high-elevation stream, water temperature averaged 4°C or warmer on only 87 days, whereas in the mid-elevation stream 134 days were at least this warm, a difference in growing season of 47 days.

DISCUSSION

The effect of FL did not vary by stream (i.e., no FL * stream interaction; females $\chi^2 = 2.70, P = 0.10$; males $\chi^2 = 2.54, P = 0.11$), so the interaction term was removed to produce the final equations:

- probability of maturity (females) = 
  \[
  \frac{\exp(-20.0091 + 5.0592 \times \text{stream} + 0.1107 \times \text{FL})}{1 + \exp(-20.0091 + 5.0592 \times \text{stream} + 0.1107 \times \text{FL})}
  \]

- probability of maturity (males) = 
  \[
  \frac{\exp(-12.3065 + 3.7229 \times \text{stream} + 0.0735 \times \text{FL})}{1 + \exp(-12.3065 + 3.7229 \times \text{stream} + 0.0735 \times \text{FL})}
  \]

where stream = 1 for the mid-elevation stream and stream = 0 for the high-elevation stream.

In the mid-elevation stream, logistic regression predicted females 135 mm FL (128–142 mm, 95% fiducial confidence limits) to have a 0.5 (i.e., 50%) probability of being mature versus 181 mm FL (171–187 mm) in the high-elevation stream. Males 117 mm FL (111–123 mm) were predicted to have a 0.5 probability of being mature in the mid-elevation stream versus 169 mm FL (148–179 mm) in the high-elevation stream. Mean length-at-age relationships indicated that the majority of females from the mid-elevation stream matured at age 2 versus age 4 in the high-elevation stream.

Brook trout in the mid-elevation stream had a very different life history from those in the high-elevation stream. As predicted, temperature data showed that the high-elevation stream was much colder than the mid-elevation stream and the growing season was 47 days shorter. In an aquaculture setting, brook trout have lower growth efficiency at colder water temperatures (4–7°C) and achieve maximum growth efficiency at 10–13°C (Dwyer et al. 1983). Brook trout in the mid-elevation stream were longer at ages 0, 1, and 2 relative to brook trout in the high-elevation stream. This suggests that brook trout grew faster as juveniles in the mid-elevation stream than in the high-elevation stream. However, age-3 brook trout were similar in length in both streams, which could have been caused by at least 3 factors. First, growth of brook trout in the mid-elevation stream may have been slowed after first reproduction, which occurred at an early age. Second, brook trout may have been immigrating into the high-elevation study segment from areas downstream where growth is faster. Third, the faster-growing brook trout in the mid-elevation stream may have been dying at younger ages, leaving only the slower-growing fish in the population for our comparison. Overall, we predicted that brook trout in the high-elevation stream would mature later and
Table 1. Length-at-age (mm) of brook trout removed from the high-elevation stream (Willow Creek) and mid-elevation stream (Little Muddy Creek) in late summers of 1998, 1999, and 2000. Ages are based on otoliths read by reader 1. Two-sample t-tests were used to test simple effects of stream at each age.

<table>
<thead>
<tr>
<th>Age</th>
<th>High-elevation stream</th>
<th>Mid-elevation stream</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>n</td>
<td>Mean</td>
<td>Range</td>
</tr>
<tr>
<td>0</td>
<td>10</td>
<td>45</td>
<td>38-58</td>
</tr>
<tr>
<td>1</td>
<td>11</td>
<td>77</td>
<td>70-88</td>
</tr>
<tr>
<td>2</td>
<td>22</td>
<td>151</td>
<td>103-170</td>
</tr>
<tr>
<td>3</td>
<td>6</td>
<td>158</td>
<td>134-177</td>
</tr>
<tr>
<td>4</td>
<td>7</td>
<td>175</td>
<td>135-210</td>
</tr>
<tr>
<td>5</td>
<td>5</td>
<td>198</td>
<td>159-209</td>
</tr>
<tr>
<td>6</td>
<td>10</td>
<td>201</td>
<td>122-222</td>
</tr>
<tr>
<td>7</td>
<td>5</td>
<td>197</td>
<td>194-203</td>
</tr>
<tr>
<td>8</td>
<td>11</td>
<td>209</td>
<td>194-211</td>
</tr>
<tr>
<td>9</td>
<td>18</td>
<td>211</td>
<td>190-236</td>
</tr>
<tr>
<td>10</td>
<td>8</td>
<td>216</td>
<td>200-222</td>
</tr>
<tr>
<td>11</td>
<td>2</td>
<td>212</td>
<td>208-216</td>
</tr>
<tr>
<td>12</td>
<td>4</td>
<td>213</td>
<td>187-226</td>
</tr>
<tr>
<td>13</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>14</td>
<td>1</td>
<td>246</td>
<td>-</td>
</tr>
</tbody>
</table>

Brook trout invading cutthroat trout streams in Colorado could be accurately aged using otoliths. Ages derived from otoliths matched known ages from marked fish, indicating that brook trout otoliths formed a single distinguishable annulus each winter. Age estimates for brook trout up to age 8 were precise and highly reproducible as indicated by the minimal deviation between readers and low coefficients of variation. Precision of age estimates for older fish depended on the readability of annuli. For example, one otolith with obscure, closely spaced annuli was aged 11 by reader 1 and aged 8 by reader 2. In contrast, another otolith with clearly distinguishable annuli was aged 12 by both readers. Reimers (1979) validated otolith age estimates for old brook trout in stunted populations (up to 24 years old) in unproductive high-elevation lakes by comparing otolith age estimates with known ages based on stocking records and found that the estimates matched. Hall (1991) marked fish with oxytetracycline to validate the formation of annuli on otoliths of older brook trout (5–10 years old) in stunted populations and found that one distinguishable annulus was formed each winter. Kruse et al. (1997) found otolith age estimates for Yellowstone cutthroat trout to be very precise when comparing age estimates from 3 readers who read each otolith 3 different times.

Fig. 3. Probability of sexual maturity as a function of length for male and female brook trout removed from the high-elevation stream (Willow Creek) and mid-elevation stream (Little Muddy Creek) estimated by logistic regression. The left 2 curves are for the mid-elevation stream, the right 2 curves for the high-elevation stream. Arrows indicate lengths of females with a 0.5 probability of being mature (134 mm FL in the mid-elevation stream, 181 mm FL in the high-elevation stream). Probabilities are based on a sample of 402 brook trout removed in early fall 1998 and 1999.
TABLE 2. Percent of male and female brook trout that were sexually mature by size class in the high-elevation (Willow Creek) and mid-elevation (Little Muddy Creek) streams (sample sizes are in parentheses). Data are based on 405 fish removed during August and September 1998 and 1999 from the high-elevation stream and during September 1999 from the mid-elevation stream.

<table>
<thead>
<tr>
<th>Fork length class (mm)</th>
<th>Male</th>
<th>Female</th>
<th>Male</th>
<th>Female</th>
</tr>
</thead>
<tbody>
<tr>
<td>&lt;101</td>
<td>-</td>
<td>0 (2)</td>
<td>18.2 (11)</td>
<td>0 (14)</td>
</tr>
<tr>
<td>101-110</td>
<td>0 (1)</td>
<td>0 (1)</td>
<td>33.3 (24)</td>
<td>0 (10)</td>
</tr>
<tr>
<td>111-120</td>
<td>0 (1)</td>
<td>-</td>
<td>65.2 (23)</td>
<td>22.2 (9)</td>
</tr>
<tr>
<td>121-130</td>
<td>100 (1)</td>
<td>0 (2)</td>
<td>66.7 (6)</td>
<td>60.0 (5)</td>
</tr>
<tr>
<td>131-140</td>
<td>0 (2)</td>
<td>0 (1)</td>
<td>100 (2)</td>
<td>87.5 (9)</td>
</tr>
<tr>
<td>141-150</td>
<td>-</td>
<td>0 (1)</td>
<td>100 (5)</td>
<td>66.7 (6)</td>
</tr>
<tr>
<td>151-160</td>
<td>0 (1)</td>
<td>0 (1)</td>
<td>100 (6)</td>
<td>100 (6)</td>
</tr>
<tr>
<td>161-170</td>
<td>66.7 (3)</td>
<td>33.3 (3)</td>
<td>100 (6)</td>
<td>100 (6)</td>
</tr>
<tr>
<td>171-180</td>
<td>88.9 (9)</td>
<td>50.0 (6)</td>
<td>100 (5)</td>
<td>100 (2)</td>
</tr>
<tr>
<td>181-190</td>
<td>91.7 (12)</td>
<td>88.5 (20)</td>
<td>-</td>
<td>100(2)</td>
</tr>
<tr>
<td>191-200</td>
<td>95.0 (21)</td>
<td>95.0 (40)</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>201-210</td>
<td>93.9 (33)</td>
<td>95.0 (25)</td>
<td>100 (1)</td>
<td>-</td>
</tr>
<tr>
<td>211-220</td>
<td>100 (20)</td>
<td>100 (10)</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>221-230</td>
<td>100 (5)</td>
<td>100 (1)</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>&gt;230</td>
<td>100 (1)</td>
<td>0 (1)</td>
<td>-</td>
<td>-</td>
</tr>
</tbody>
</table>

America. Power (1980) described life history of brook trout in productive southern-latitude streams, where 2-year-old females provide most of the egg production but rarely reach their 4th year of life (McFadden 1961). Power (1980) also described life history in unproductive northern-latitude and alpine waters, where brook trout grow slowly, males mature at age 3 or older and females at age 4 or older, and trout live to be 8 to 12 years old. In the Rocky Mountains of the northwestern U.S., Mullan et al. (1992) reported that brook trout in warm, mid-elevation streams grow quickly, mature between ages 2 and 3, and live to age 4, whereas brook trout in cold, high-elevation streams grow slowly, mature at age 3, and live to age 8. Within a single Montana stream, Adams (1999) found longer lengths-at-age and earlier maturity in a warmer, mid-elevation reach than in a high-elevation reach, but found little difference in life spans.

Life history theory of teleosts and brook trout presented by Power (1980), Roff (1984), and Hutchings (1993, 1994, 1996) can help explain observed differences in life histories between streams in our study. Varying environmental conditions that result in different juvenile growth and adult survival rates can alter the life history strategy required to maximize fitness. Hutchings (1996) found that brook trout with the fastest growth rates will maximize fitness by maturing early with great reproductive effort (e.g., in the mid-elevation stream). This maximizes the chance of successful reproduction before death, but energy spent during reproduction at this size causes high post-reproductive mortality, resulting in shorter life spans (Roff 1984). In contrast, brook trout with the slowest growth rates will maximize fitness by delaying maturity to larger sizes and older ages (e.g., the high-elevation stream). This delay will decrease post-reproductive mortality (Hutchings 1994), resulting in longer life spans, and enables fish to spawn in multiple years with increased total fecundity.

If fisheries biologists are to be effective in managing brook trout invasions in Rocky Mountain streams, demographic models that predict invasion success will need to be developed at landscape scales (Fausch et al. 2002). However, such models will be sensitive to life history variation associated with different environments, making empirical data such as we present necessary to increase their robustness (Adams 1999). Differences in apparent growth, sexual maturity, and longevity between streams suggest that flexibility in life history is one mechanism whereby brook trout maximize the chance of establishment and promote successful invasions across a wide range of environments in the western U.S. In mid-elevation streams, fast growth and early maturity will favor rapid establishment and high population growth rates (Vermeij 1996). In turn, this may lead to high dispersal and high colonization rates elsewhere, often farther upstream (Gowan...
and Fausch 1996). In contrast, in cold, unproductive, high-elevation streams, later maturity and long reproductive life spans caused by slow growth may allow brook trout to successfully establish populations even in these marginal habitats, where probability of successful recruitment is relatively low among years. Thus, landscape-scale models predicting brook trout invasion rates, distribution, and population growth rates should incorporate data from multiple elevations to account for differences in life history characteristics.

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