Exploring the relative influence of biotic interactions and environmental conditions on the abundance and distribution of exotic brown trout (*Salmo trutta*) in a high mountain stream


Abstract – In the Logan River, UT, USA, exotic brown trout demonstrate a strong allopatric distribution and occur at high densities at low-elevation sites and in tributaries, and in low densities at native trout dominated, high-elevation sites. Summer temperatures and discharge do not appear limiting for growth; adult growth rates were high overall and were greatest when fish were held experimentally at high elevation where they do not occur naturally. Brown trout are superior competitors; competition for space or food was stronger with their own con-specifics than with other species. Evidence of density dependence was not observed at the juvenile life stage; no consistent relationships were detected between brown trout density and age-1 condition or lagged, age-0 weight (g). In contrast, adult brown trout demonstrated density-dependent effects on condition and growth when reared experimentally. Field estimates of adult growth rates (g day\(^{-1}\)), although variable, declined subtly with increasing density, and annual survival was significantly greater in the mainstem sites (mean = 52%) relative to a high-density tributary site (mean = 22%). Annual predicted age-0 brown trout growth potential was four-times greater at the lowermost site, compared with the highest elevation site, although fish lost weight over winter months at all sites. While adult density dependence may influence population abundance at some sites, extreme spring–winter conditions may ultimately limit the upper elevational extent of brown trout in this system. With changing climatic conditions and the potential for habitat degradation in the future, these results have important implications for native fish conservation.

Introduction

Physical factors of natural stream ecosystems typically change along a longitudinal gradient from headwaters to low elevation outlets into larger rivers. This longitudinal arrangement of physical factors is then manifested in the organisation of biological communities in river ecosystems (e.g., Rahel & Hubert 1991; Taniguchi & Nakano 2000). For temperate mountain streams dominated by trout species, two of the most influential physical properties affecting fish species distribution and composition are temperature and flow regime (e.g., Fausch 1989; Poff & Allen 1995; Magoullick & Wilzbach 1998). When stream ecosystems remain largely undisturbed, these physical factors change predictably along the elevational and longitudinal gradient of most streams, with temperatures and discharge increasing with decreasing...
Abiotic and biotic influences on brown trout distribution

The goal of this study was to evaluate the relative influence of environmental variation and biotic interactions on the abundance and distribution of exotic brown trout in the Logan River. Brown trout were introduced into the Logan River in the early 1900s, reproduce naturally, and dominate low-elevation areas historically occupied by native, cutthroat trout (de la Hoz Franco & Budy 2005). We consider four mechanisms hypothesised to limit the abundance and distribution of brown trout in this system using complementary data sources: (i) environmental conditions over the key summer growth period, (ii) interspecific competition with cutthroat trout (discussed here, but previously evaluated in McHugh & Budy 2005, 2006), (iii) density dependence (e.g., growth, survival) and (iv) the effects of extreme winter temperatures. We used vital rates and demographic characteristics measured along an elevational gradient and across several years, as well as model predictions of growth potential over winter, to evaluate the influence of these factors in determining the abundance, distribution and upper elevational extent of brown trout.

Study area

The Logan River runs 64 km from southeast Idaho, through northern Utah, and eventually drains into the Bear River, terminal to the Great Salt Lake. The climate of the area is characterised by cold, snowy winters (January air temperature: low, −9 °C; high, 0 °C; mean precipitation 4.0 cm) and hot, dry summers (July air temperature: low, 15 °C; high, 31 °C; mean precipitation 1.6 cm), yielding a hydrograph dominated by a spring-snowmelt flood (average 16 m³·s⁻¹) followed by base-flow conditions (approximately 3 m³·s⁻¹). In addition to Bonneville cutthroat trout and brown trout (stream resident only), the river is also inhabited by mountain whitefish (Prosopium williamsoni Girard) and mottled sculpin (Cottus Bairdi Girard) as well as a very small number of exotic brook trout (Salvelinus fontinalis Mitchell) and stocked exotic rainbow trout (O. mykiss Walbaum) in isolated areas.

Our studies have been concentrated at eight long-term sites that encompass more than 50 stream kilometre distributed along the longitudinal gradient of the river, and over the time-period 2001–2006. These sites were selected as index sites based on previous sampling throughout the drainage and capture the range of physical and biological characteristics present. The index sites range from 2023 to 1352 m elevation and include two tributaries: (i) Franklin Basin (headwaters); (ii) Red Banks; (iii) Forestry Camp; (iv) Temple Fork (tributary); (v) Twin Bridges; (vi) Right Hand Fork (tributary); (vii) Third Dam and

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(viii) Lower Logan (Fig. 1). Temperature, discharge and other limnological information were collected at each site hourly (e.g., temperature) or monthly (e.g., discharge) when physically possible. More detail on abiotic and biotic site characteristics can be found in de la Hoz Franco & Budy (2005), McHugh & Budy (2005) and Budy et al. (2007). The river can be generally described as high-quality, continuous habitat with the exception of some anthropogenic degradation in upper-elevation tributaries and at low-elevation sites near the city of Logan, Utah (Budy et al. 2007). River water is retained in three small reservoirs; the uppermost of the dams is Third Dam (Fig. 1), and withdrawn via canals at, and downstream from, this point.

Methods

Abundance and distribution

Fish were sampled annually to assess abundance and distribution using electrofishing during summer base-flow conditions (late July to early August) using a backpack-mounted electrofishing unit in smaller tributaries and a canoe-mounted electrofishing unit in larger mainstem reaches. Based on the combination of size–frequency modes, a sub-sample of scale-aged fish sampled across size classes and years (N = 59), and annual growth measurements from a subset of tagged and recaptured fish (N = 345), brown trout were grouped into age (size) classes as: age-1 (100–179 mm total length, TL), age-2 (180–259 mm TL) and age-3 and above (≥260 mm TL). As elsewhere, subadults were determined to be fish age-1 and age-2 that were not sexually mature, and adult brown trout were sexually mature at age-3 and older (Elliott 1994; Alp et al. 2003). In this system, trout <100 mm (age-0) are less efficiently captured using electrofishing techniques, and the minimum size threshold for tagging is 120 mm. Therefore our analyses of population abundance and related measures best reflect fish >100 mm; growth and survival estimates reflect fish >120 mm (the size category for all response variables is provided).

Based on incidental catch during electrofishing, while mountain whitefish densities approach 0.04 fish m$^{-2}$ (but are extremely variable at the lowermost site in elevation; Lower Logan); however, densities of both mountain whitefish and sculpin are extremely low at most mainstem sites (<0.01 and 0.03 fish m$^{-2}$, respectively), and both fishes are virtually absent in the tributaries.

Population abundance was estimated using a three-pass, closed model, generalised maximum-likelihood removal estimator (White & Burnham 1999) for all fish (>100 mm) at each site. Abundance was then scaled up to population density per site (trout m$^{-2}$) based on reach length and width, and estimates were expressed with 95% confidence intervals (CI). Population trend was estimated using the population estimates (2001–2006) based on linear regression of log-transformed annual changes in population growth rate as a function of time step (Morris & Doak 2002). Population trend per site was expressed as lambda ($\lambda$), the annual population growth rate, with 95% CI, and an overall $\lambda$ based on aggregated abundance estimates.
Abiotic and biotic influences on brown trout distribution

Growth, survival and condition

Captured brown trout >120 mm, the minimum size threshold for these tags, were marked at each site with individually-coded, T-bar anchor tags using site-specific colours (2002–2006; Table 1). Site fidelity was assessed by determining the number fish tagged at one location that were subsequently recaptured at that same location; fish were recaptured either: (i) through our annual electrofishing surveys, or (ii) by anglers. Measurements of weight and length for individually marked and recaptured fish were used to estimate mean annual growth rate of brown trout as g-day⁻¹ for each site [(size,₁−size,₄)/days]. In addition, growth rate information from a previous cutthroat trout competition study (e.g., brown trout were a treatment effect; McHugh & Budy 2005) was used to characterise the brown trout growth rate potential along the elevational gradient, particularly for high elevation sites where brown trout are not typically captured. In that study, native cutthroat trout were held in replicated experimental enclosures with and without brown trout, and growth (g-day⁻¹) and condition (see below) of both species was estimated over a 42-day summer period, thus also allowing for an assessment of environmental factors that could limit brown trout growth and survival at high elevation.

Annual survival rates were calculated based on individual encounter histories for all tagged brown trout. Survival (Φ) and recapture probability (P) were estimated using a Cormack–Jolly–Seber open survival model based on maximum-likelihood estimation procedures in program MARK (White & Burnham 1999). Known unnatural mortalities (e.g., from sampling) were excluded, and trout were grouped by site and age group at initial capture. A stage-structured survival modelling framework was developed whereby fish in age groups age-1 and age-2 grew (i.e., transitioned) into the next stage each time iteration (representing a year), and fish in the last age group (i.e., age-3 and older) remained in that group. A small set of a priori candidate models were considered based on biological hypotheses of factors affecting survival, and models were ranked according to Akaike’s Information Criteria (AIC; Burnham & Anderson 2002). The best model for recapture probability (P) was first estimated by varying recapture structure (i.e., the PIM global model and then eight reduced versions with a constant survival structure [i.e., S(·)] and combinations of group effects on P were estimated for fish age, site and time (year) as per Franklin et al. (2004). The top survival (Φ) model, that allowed us to compare survival rates across sites, was then estimated based on the best “P” model. Lastly, survival rates were pooled across age and evaluated for statistical differences in survival rates at the mainstem sites (omitting the Lower Logan site because of anthropogenic influences on survival) and compared with the tributary site using a t-test for unequal variance (α = 0.05).

Patterns in condition were assessed across index sites using both experimental and survey data: (i) recrated from small-scale (20 m²) enclosure experiments introduced above (McHugh & Budy 2005) and (ii) from fish measured in the field as part of

Table 1. Relative location, total number of tagged and recaptured fish, mean population abundance and range (range across years by index site), and population growth rates (λ) with 95% confidence intervals for brown trout (>100 mm) at eight index sites over the 6-year period, 2001–2006.

<table>
<thead>
<tr>
<th>Index site</th>
<th>Elevation (m)</th>
<th>River width (m)</th>
<th>Number of fish tagged</th>
<th>Number of unique recaptured fish</th>
<th>Mean abundance (fish/m²)</th>
<th>Range (fish/m²)</th>
<th>λ-value</th>
<th>95% CI</th>
</tr>
</thead>
<tbody>
<tr>
<td>Franklin Basin</td>
<td>2023</td>
<td>9.2</td>
<td>8.4</td>
<td>0</td>
<td>0</td>
<td>0.003</td>
<td>1.000–1.006</td>
<td>0.82–1.31</td>
</tr>
<tr>
<td>Red Banks</td>
<td>1923</td>
<td>13.2</td>
<td>9.8</td>
<td>10</td>
<td>1</td>
<td>0.004</td>
<td>0.000–0.012</td>
<td>–</td>
</tr>
<tr>
<td>Forestry Camp</td>
<td>1855</td>
<td>16.2</td>
<td>11.6</td>
<td>9</td>
<td>2</td>
<td>0.120</td>
<td>0.000–0.349</td>
<td>–</td>
</tr>
<tr>
<td>Temple Fork</td>
<td>1745</td>
<td>22.5</td>
<td>6.7</td>
<td>115</td>
<td>6</td>
<td>0.029</td>
<td>0.020–0.042</td>
<td>0.93–0.107</td>
</tr>
<tr>
<td>Twin Bridges</td>
<td>1691</td>
<td>26.6</td>
<td>13.0</td>
<td>165</td>
<td>60 (46)</td>
<td>0.023</td>
<td>0.017–0.050</td>
<td>0.83–1.24</td>
</tr>
<tr>
<td>Right Hand Fork</td>
<td>1358</td>
<td>36.1</td>
<td>3.7</td>
<td>418</td>
<td>97 (49)</td>
<td>0.623</td>
<td>0.179–1.050</td>
<td>0.67–1.36</td>
</tr>
<tr>
<td>Third Dam</td>
<td>1509</td>
<td>43.0</td>
<td>10.2</td>
<td>516</td>
<td>130 (49)</td>
<td>0.161</td>
<td>0.111–0.223</td>
<td>0.95–1.07</td>
</tr>
<tr>
<td>Lower Logan</td>
<td>1352</td>
<td>56.8</td>
<td>11.3</td>
<td>281</td>
<td>74 (12)</td>
<td>0.087</td>
<td>0.027–0.248</td>
<td>0.70–1.04</td>
</tr>
<tr>
<td><strong>Pooled estimate</strong></td>
<td>1514</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>0.79</td>
<td>0.59–1.08</td>
</tr>
</tbody>
</table>

*: “ signifies that estimate is not available or applicable.

Number of unique recaptured fish refers to fish encountered once, and the number in parenthesis denotes number of those same unique fish captured on 1–4 additional occasions.
annual surveys described above. Relative weight \( W_r = W/W_s \times 100; \) Anderson & Neumann (1996) was used as a relative measure for comparisons of condition along the elevation gradient and to evaluate inter-specific competition, where: \( W \) is the observed mass (g) of a fish, and \( W_s \) is the predicted mass (g) based on its total length (mm) and a standard length-weight relationship for wild brown trout in the Logan River \( (W_s = 1.708 \times 10^{-5} \text{TL}^{2.905}; \) McHugh & Budy (2005)). Fulton’s \( K \) \( (K_{TL} = W/L^3 \times 100,000) \) was used as a measure of condition to test for density-dependent effects on juvenile fish (below), and facilitated comparison with other studies evaluating density dependence (Anderson & Neumann 1996).

Inter-specific competition and density dependence

Measures of condition described above were used to compare adult brown trout performance in sympathy (with Bonneville cutthroat trout) to allopatry, to assess the relative influence on inter- and intra-specific competitive interactions. In addition, the impacts of density-dependent effects on all life stages were assessed using linear-regression analyses. The relationship between the weight (g) of age-0 brown trout (as the dependent variable) and subadult and adult (all brown trout >100 mm) brown trout density \( (\text{fish}\cdot\text{m}^{-2}) \) as the independent variable – from the previous year), and similarly, the relationship between condition of age-1 brown trout (Fulton’s \( K \) as the dependent variable) and subadult and adult (all brown trout >100 mm) brown trout density \( (\text{fish}\cdot\text{m}^{-2}) \) as the independent variable) were evaluated. Finally, the relationship between subadult and adult brown trout growth \( (g\text{-day}^{-1}) \text{ as the dependent variable}) and subadult and adult brown trout density \( (\text{fish}\cdot\text{m}^{-2}) \) as the independent variable) was independently assessed using an exponential decay function.

Growth potential: winter temperatures

The Elliott growth model (Elliott et al. 1995) was used to predict the relative growth potential of age-0 brown trout during their first year of life for the four index sites for which year-round temperature data were available. Average, maximum and minimum daily temperatures were continuously recorded at the Franklin Basin, Red Banks, Twin Bridges and Lower Logan sites. Growth was assumed to be zero at lower and upper temperature thresholds of 3.56 and 19.48 °C, respectively, and optimal growth was assumed to occur at 13.11 °C as per Jensen et al. (2003). The average weight of an age-0 brown trout in July as the starting weight (3.4 g), and the site-specific potential growth of an average brown trout was estimated for 1 year (July–June), based on the average daily temperature at each site. Growth potential was calculated over monthly intervals for 1 year, and growth rates were expressed as g day\(^{-1}\) for comparison to other studies.

Results

Abundance, distribution and trend

Mean (across 6 years) densities of brown trout ranged from a high of 1.03 fish\(\cdot\text{m}^{-2}\) at a low elevation tributary site (Right Hand Fork) to lows of <0.0025 fish\(\cdot\text{m}^{-2}\) at the uppermost end of their distribution (Red Banks; Table 1). When these data were used to estimate the population growth rate \( (\lambda; \text{i.e., trend}) \), \( \lambda < 1.0 \) at all sites (with one exception; Red Banks) and \(<1.0 \) for the pooled estimate (Table 1). While a \( \lambda < 1.0 \) indicates the population is declining, 95% confidence intervals of \( \lambda \) were consistently wide and overlapped 1.0, because of inter-annual variability and small sample size (only 6 years), indicating we cannot conclude with certainty that the population is declining. The one exception is the trend in brown trout abundance at the lower-most site, Lower Logan, where abundance has demonstrated a substantial and consistent decline over time most likely in response to dam-related activities directly upstream \( (\lambda = 0.70; 95\% \text{ CI } = 0.47–1.04; \text{Table 1}) \).

Similar to the pattern documented in isolated years as part of other studies, the 5-year mean abundance of brown trout and cutthroat trout demonstrated a distinct allopatric pattern of species segregation along an elevational gradient (Fig. 1). Cutthroat trout dominate upper (>1800 m) elevation areas, brown trout dominate lower elevation areas (<1700 m), and there is a zone in the middle where both species are present albeit at low density (Fig. 2). Although there is some inter-annual variability, the overall pattern of species distribution was generally consistent across years \( (N = 6) \).

Environmental conditions: spring to summer growth period

The range of temperature and discharge measured across each index site, over the spring to summer period in the Logan River, does not appear to be limiting for brown trout growth. Mean stream temperatures over this period ranged from lows of approximately 8–10 °C at high elevation sites and in spring-fed tributaries to a high of approximately 16 °C at the lowermost site (Fig. 3). Post-spring spate and summer (i.e., base-flow) discharge generally remains <3 m\(^{3}\text{-s}^{-1}\) (Fig. 3). Spring maximum discharge typically occurs in late May or June, as a function of snow melts, and approaches 35 m\(^{3}\text{-s}^{-1}\).
Growth, survival and condition

From July 2002 through August 2006, 1514 brown trout were tagged and 559 brown trout were recaptured (Table 1). Based on mark-recapture estimates of annual growth, on average, brown trout (>100 mm) demonstrated the highest growth rates at the Red Banks and Lower Logan sites (up to 0.6 g day$^{-1}$) and the lowest growth rates in the tributaries; however, growth rates were extremely variable across years at some sites (Fig. 4). When brown trout were reared experimentally in enclosures at five of the index sites, the greatest growth rates (and condition; not shown here) were observed at the three sites highest in elevation (Fig. 4; see McHugh & Budy 2005 for details). Growth rates were as high as 0.6 g day$^{-1}$ at the uppermost site, an area where wild brown trout are typically not captured during annual surveys.

Recapture probability ($P = 0.73$; 95% CI = 0.65–0.80) and site fidelity (approximately 100%) were relatively high and many fish were recaptured repeatedly at the same location; only one tagged fish (1 of 1514; 0.07%) was detected at a location different from the site where it was tagged. The only exception was the tributary Temple Fork site, where despite relatively high densities of fish sampled, only six tagged fish were recaptured (Table 1). The low recapture probability ($P$) at this site is unsurprising because: (i) it is a transition zone between major river zones for brown trout and cutthroat trout, and between brown trout moving in and out of the tributary, perhaps associated with spawning, and (ii) the site experiences frequent habitat changes of large magnitude when beaver (Castor canadensis) dams are constructed and subsequently breached under high flows.

Mean annual estimates of survival rate were generally similar across age classes, yet declined with decreasing elevation (model = $\Phi$ (age + site); $p$-value); Fig. 5). Estimates of survival could not be obtained for high elevation sites because of their naturally low sample sizes, and the low survival rates at the Lower Logan site were caused by sporadic dam sluicing operations upstream, and associated fish kills, and likely do not reflect natural survival rates. When pooled across age classes, survival rates were significantly greater in the mainstem sites (Twin Bridges and Third Dam; $N = 6$, mean = 52%) relative to the tributary (Right Hand Fork; $N = 3$; mean = 22%) ($P = 0.03$, d.f. = 3). The lowest and most variable annual survival rates observed (mean = 10%) were for age-3 and older fish in the Right Hand Fork tributary, where the highest average adult fish densities occur in the river.

Inter-specific competition

Based on earlier field experiments, brown trout consistently out-competed cutthroat trout when reared...
in enclosures (Fig. 4). Specifically, adult brown trout suppressed cutthroat trout growth and condition, and the pattern was generally consistent across the elevational gradient of the Logan River. Furthermore, brown trout were unaffected by the presence of cutthroat trout and temperature did not appear to be a strong mediator of competition during this life stage or time of year.

Density dependence

No evidence of density dependence was observed at early life stages of brown trout, despite the relatively high densities of brown trout at some sites (see above). Similarly, no consistent relationships were detected between condition (Fulton’s $K$) of age-1 brown trout and density ($R^2 = 0.00006$, d.f. = 28, $P = 0.97$) of brown trout (>100 mm; Fig. 6) or age-0 brown trout weight (g) and brown trout density in the previous year ($R^2 = 0.001$, d.f. = 19, $P = 0.88$; Fig. 6).

In contrast, adult brown trout demonstrated evidence of density dependence when reared in experimental enclosures in the presence of cutthroat trout ($N = 4$ brown trout, $N = 4$ cutthroat trout) as compared with when reared alone at the same density ($N = 8$ brown trout; Fig. 4; see McHugh & Budy 2005).
Condition was greater when brown trout were raised at a lower density of their own species but also in the presence of their competitive inferior (cutthroat trout; see above), indicating brown trout experience negative effects of intra-specific interactions at higher densities and the potential for density-dependent effects (McHugh & Budy 2005). Further, growth rates (g day⁻¹) of subadult and adult brown trout observed in the field demonstrated a weak, albeit insignificant, negative relationship with increasing brown trout density (R² = 0.15, d.f. = 13, P = 0.17; Fig. 6).

Growth potential: winter temperatures
A wide range of growth potential was observed across four of the index sites based on predictions of annual growth of age-0 brown trout using the Elliott growth model (Fig. 7). After 1 year of growth, age-1 brown trout at the Lower Logan site were 22.0 g (Gᵢ = 1.6), whereas at the highest elevation site, Franklin Basin, age-1 brown trout achieved only 6.0 g (Gᵢ = 0.3). The pattern in these predicted growth rates parallels our observations of age-0 brown trout growth based on limited size-at-age data available for lower elevation sites. Although age-0 brown trout lost weight over the winter months at a similar rate at all sites, the total amount of weight loss was greatest at the second highest elevation site (Red Banks), and age-0 brown trout recovered the least amount of weight by July of the next year at the upper-most site (Franklin Basin).

Discussion
The goal of this study was to explore factors potentially limiting the distribution and abundance of exotic brown trout in a stream currently home to one of the largest remaining metapopulations of endemic Bonneville cutthroat trout (Budy et al. 2007). A distinct allopatric pattern of species distribution was observed, a pattern that appeared to fluctuate little across years; native cutthroat trout dominate high elevation (>1800 m) sites and exotic brown trout dominate low elevation (<1700 m) sites with an intermediate zone of low abundance of both species. We evaluated four hypothesised mechanisms that could explain this pattern, and discuss evidence for and against each of these factors. Factors with the potential to limit the upper elevational extent of brown trout, where they may interact with or exclude native trout from remaining habitat fragments, were of notable interest.

Environmental conditions: spring to summer growth period
Temperature and discharge are perhaps two of the most influential abiotic factors determining fish distribution in streams; both physical variables change predictably along the longitudinal and elevational gradient of the Logan River and may be important in structuring the fish community (de la Hoz Franco & Budy 2005). In this system, summer (base flow) discharge generally remains <3 m³s⁻¹, within the range thought to be acceptable for brown trout age-1 and older (Heggenes & Traaen 1988; Jensen & Johnsen 1999). Similarly, spring-to-summer temperatures during this important time period for growth were generally within the range considered optimal or suitable for brown trout growth and consumption across all index sites (12.8–16.9 °C) and were never outside the physiological thresholds for survival (Elliott & Hurley 2000; Ojanguren et al. 2001; Jensen et al. 2003).

Accordingly, across the sites where brown trout occur (only up to 1800 m elevation), the patterns of growth, survival rates and population trend (λ) observed in the Logan River did not correspond to longitudinal and elevational changes in temperature and discharge. Annual survival rates of brown trout in the Logan River ranged 10–66% across sites and age classes, but were high at mid-elevation sites and lower in the low-elevation tributary (Right Hand Fork). Others have documented comparable survival rates in introduced populations of brown trout in the USA (e.g., 19–56%, McFadden & Cooper 1962; approximately 30–50%, Carlson & Letcher 2003) and native populations in Norway (juvenile survival across three streams, 41%; Lund et al. 2003) and Scotland (juvenile survival 70%; Egglishaw & Shackley 1977). In addition, growth rates of wild brown trout at colder, higher-elevation sites were similar to rates observed at low-elevation warmer sites; however, when reared
experimentally at colder, high-elevation sites where they do not occur naturally, brown trout grew faster as compared with low-elevation sites (this study; McHugh & Budy 2005). Further, although direct comparisons are difficult to find, growth rates of wild brown trout in the Logan River generally exceeded rates documented in other published studies from other countries (Greenberg & Dahl 1998; Lobon-Cervia & Rincon 1998; Johnson et al. 2006; but see Jensen et al. 2006). In temperate streams like the Logan River, temperatures are within the range suitable for growth over a limited time period from spring through early autumn (May–September), and most of the annual fish growth occurs over this time period (this study; Lobon-Cervia & Rincon 1998). As a result, we conclude that environment conditions over the spring to summer growth period alone do not limit the upper elevational extent of brown trout.

Inter-specific competition

Inter-specific competition has the potential to limit the distribution of fishes and to interact with abiotic factors along an elevational stream gradient through processes such as temperature-mediated competition (Fausch 1989; Fausch et al. 1994) and shifts in habitat use (Gatz et al. 1987). Densities of nontrout fishes (sculpin and whitefish) in the Logan River are extremely low with distributions that do not suggest evidence for inter-specific competition with brown trout [e.g., contrast with sculpin densities reported by Hesthagen & Heggenes (2003)]. Sculpin densities are similar both at sites where brown trout occur in high density and sites where brown trout occur only in low abundance; note however, that these data are limited as they are based on incidental catch. Inter-specific competition between brown trout and cutthroat trout in the Logan River was evaluated previously as part of other studies (de la Hoz Franco & Budy 2005; McHugh & Budy 2005, 2006). These studies and others (e.g., Wang & White 1994; Shemai et al. 2007) demonstrate that brown trout consistently out-compete cutthroat trout. Although, the overall distribution of brown trout was negatively associated with increased diel temperature fluctuation (de la Hoz Franco & Budy 2005), their interactions with cutthroat trout did not appear to be temperature-dependent (McHugh & Budy 2005). Quist & Hubert (2005) similarly demonstrated that the influence of brown trout on cutthroat trout density overrode the effects of physical habitat conditions. We conclude that while brown trout likely exclude cutthroat trout at lower elevations, inter-specific competition between brown trout and cutthroat trout does not limit the upper distribution and abundance of brown trout (but see density dependence below) in the Logan River.

Density dependence

In contrast to inter-specific interactions, there are numerous examples identifying the importance of density dependence (intra-specific interactions) in regulating brown trout populations through intra-specific effects on recruitment, growth, and survival or mortality (e.g., Elliott 1984, 1994; Lobon-Cervia 2004). Despite the relatively high densities of brown trout at some sites (1.03 fish m$^{-2}$), little evidence of density dependence was observed operating at the early life stages of brown trout, nor was there a relationship between age-0 or juvenile brown trout size and condition and total brown trout density. Jenkins et al. (1999) warn that density-dependent effects can be difficult to detect based on observational data in high-density streams and given the influence of both scale and inter-annual variation in growth; these factors could obscure the effects of density dependence at early life stages in our study. However, across several years and three scales of evaluation (site, stream and river drainage), Lobon-Cervia (2007) similarly observed no evidence for density dependence as a driver of population size.

Conversely, several patterns were observed indicating the potential for density dependence operating at the subadult and adult life stages. First, brown trout reared in sympathy with cutthroat trout demonstrated higher growth rates than when raised at the same densities of brown trout only, indicating that brown trout compete more strongly for space or food with their own con-specifics than with other species (McHugh & Budy 2005, 2006). Second, albeit variable, adult growth rates appear to decline non-linearly with increased brown trout density, and mean annual survival and growth rates were generally lowest at the sites with the highest brown trout density (but see growth discussion below). Density-dependent effects on subadult and adult fish growth and survival could be manifested through a variety of mechanisms including the reduction in the availability of food (Lobon-Cervia 2005) and territorial behaviour, the later of which has been demonstrated to be both density- and size-dependent (Elliott 1990, 1994). Based on the observations from our study, we conclude that density dependence has the potential to influence adult brown trout abundance; however, this factor alone appears insufficient to explain the observed distribution of brown trout in the Logan River.

Growth potential: winter temperatures

Quite the opposite to the near-optimal abiotic conditions present over the spring-to-summer growth period, spring spate and winter conditions in the
Logan River are much more severe and potentially limiting for brown trout. We predicted annual growth potential at four of our sites with the most complete temperature data (temperature loggers are frequently blown out and lost during the spring spate) using the Elliott growth model (Elliott et al. 1995). Based on these model predictions, age-0 brown trout lost weight over winter months at all sites; however, after 1 year, age-1 brown trout at the warmer, low-elevation sites were as much as four-times larger than juvenile brown trout at the upper-most site. There are populations of brown trout that appear to demonstrate enhanced local thermal adaptation resulting in relatively high growth rates at extremely low (e.g., in Norway; Jensen et al. 2003) or high temperatures (e.g., northern Spain; Lobon-Cervia & Rincon 1998). The original source population of brown trout stocked into Utah rivers remains unknown and most likely originated in more moderate temperate streams of Europe (MacCrimmon & Marshall 1968; Lever 1996). It should be noted that these Elliott-model growth rates are based on theoretical model predictions with some simplified assumptions about excess ration, feeding behaviour and fish size (Hayes et al. 2000; Rincon & Lobon-Cervia 2002; de la Hoz Franco & Budy 2005). Nevertheless, these model simulations highlight the importance of extreme winter temperatures, conditions that may be especially influential during early life-history stages of brown trout – life stages that can be extremely sensitive and influential in determining the abundance and distribution of stream fishes (Milner et al. 2003). In related research, we are evaluating the spawning density and distribution of redds, egg-to-fry survival, and the factors that influence these life stages along the elevational gradient of the Logan River (Wood and Budy in press).

In addition to extreme winter temperatures, the timing and magnitude of the spring spate also has the potential to limit brown trout. The Logan River is a high gradient and steep-sided stream, composed primarily of riffles and runs with few pools. In addition, spring spates (May–June) in the Logan River are typically large in magnitude and occur over a relatively concentrated time period as a function of rapid snow melt (approximately 2–4 weeks); discharge during this time period often approaches 35 m$^3$s$^{-1}$, a level at which water velocity and bed scour can be detrimental to brown trout fry (Latterell et al. 1998). Brown trout in the Logan River spawn during autumn at base flow and demonstrate variable emergence timing, ranging from early May at the low-elevation sites to early July at upper elevation sites (Wood and Budy in press). High water velocity and/or discharge during the spring spate could result in direct mortality through bed scour while fry are still in the gravel and lethal displacement during emergence (e.g., Heggenes & Traaen 1988; Montgomery et al. 1996; Jensen & Johnsen 1999); high flows may also have indirect negative effects on fry and juvenile growth and survival via dislocation into sub-optimal, high energy habitat (e.g., reduction of available food or space; Elliott 1990; Cattaneo et al. 2002), or because of the synergistic effect of temperature and discharge on fry swimming ability at low temperatures (Heggenes & Traaen 1988; Jensen & Johnsen 1999). Lobon-Cervia (2007) recently demonstrated that a large amount of spatiotemporal variability in recruitment could be explained by merely two factors: discharge during emergence and site depth. In light of these findings and given that brown trout may not be adapted to the timing and magnitude of the spring spate in these high elevation, mountain rivers relative to their native habitat (Fausch et al. 2001), the effects of spring conditions warrant further research and consideration.

Implications

Within the context of native fish conservation and recovery, there is an urgent need to understand the factors that limit the distribution of exotic brown trout within native trout habitat (McHugh & Budy 2005, 2006; Budy et al. 2007). Both natural (e.g., climate variability) and anthropogenic impacts to stream ecosystems (e.g., habitat degradation, global warming) have the potential to alter habitat conditions in the future such that the habitat may become more, or less susceptible, to brown trout invasion and range expansion (Moyle & Light 1996a,b; Hari et al. 2006; Riemann et al. 2007). In this study, we demonstrated that inter-specific competition and abiotic conditions over the spring-to-summer growth period do not limit the upper extent of brown trout in a native cutthroat trout stream. Rather, density dependence at the subadult and adult life stages appears to be influential in determining the abundance and spring/winter conditions appear important in determining the distribution (and upper elevational extent) of brown trout. Alterations to natural temperature regimes, whether natural or anthropogenic, could result in a further expansion of exotic brown trout into native trout habitat (e.g., Borgstrom & Museth 2005). Conversely, habitat restoration may offer a management strategy for reducing brown trout growth based on lower stream temperatures achieved through the re-establishment of riparian vegetation and, potentially, hyporheic exchange (Hancock 2002; Hansen 2007).

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Budy et al.

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