Transactions of the American Fisheries Society 138:756–767, 2009

DOI: 10.1577/T08-123.1

[Article]

The Role of Environmental Factors in Determining Early Survival and Invasion Success of Exotic Brown Trout

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Abstract.—Due to significant threats to native species posed by nonnative fishes, it is important to understand how species life history strategies interact with environmental conditions to explain the outcome of nonnative fish invasions. Brown trout *Salmo trutta* are prolific invaders but often exhibit upstream distributional limits in streams of the intermountain western United States. We used redd counts, embryo survival experiments, and temperature modeling to identify limits to brown trout invasion. Brown trout spawned later than previously reported and established spawning areas in high-elevation stream reaches (1,983-m elevation), where adult recruitment is typically very low. While embryo survival was lower in high-elevation, cooler-water areas, these harsh overwinter conditions did not necessarily preclude hatching success ($\geq$36%). However, model predictions based on winter temperature data indicate that during most years, brown trout fry probably would fail to emerge from the gravel before the onset of peak spring flooding in these high-elevation reaches, suggesting that high spring flows could limit invasion success. A better understanding of mechanistic limits to invasion success across multiple life stages is crucial to predicting the future expansion of exotic fish species.

As a result of widespread introductions and dispersal, nonnative fish species pose one of the most significant threats to the persistence of native fishes worldwide (e.g., Wilcove et al. 1998). The establishment of introduced species ultimately depends on reproductive success, which is governed by the relation between life history requirements and environmental conditions (e.g., Moyle and Light 1996; Olden et al. 2006). However, the wide variety of environmental conditions encountered upon introduction, variability in life history strategies among species, and most recently, climate change, make it difficult to make generalizations about invasion success (e.g., Rieman et al. 2007; Leprieur et al. 2008).

Brown trout *Salmo trutta* are native to Eurasia and North Africa and have been introduced widely throughout the world (MacCrimmon and Marshall 1968; Lever 1996). Brown trout introductions have had negative effects on native fish assemblages and aquatic community structure in many countries (see Courtenay and Stauffer 1984 for review), such that this species is listed in the book "100 of the World's Worst Invasive Alien Species" (Lowe et al. 2000). Despite their widespread invasion success in the United States, brown trout often exhibit upstream limits to their distribution in the intermountain western region (e.g., de la Hoz Franco and Budy 2005), indicating some limitation to their expansion into headwater areas. In many cases, these headwater areas represent habitat fragments important for the persistence of imperiled populations of native trout (e.g., Budy et al. 2007). Recent research has eliminated several plausible mechanisms that might limit the upper distribution of brown trout, including the effects of abiotic conditions on summer growth and survival and interspecific and condition-specific competition (McHugh and Budy 2005, 2006; Budy et al. 2008). Thus, by the process of elimination, these studies all indicate limitations to population expansion at the reproductive and early life stages.

A maladapted reproductive strategy offers a potential mechanism for limiting the distribution of brown trout in intermountain western streams (Moyle and Light 1996; Fausch et al. 2001). In contrast to the spring-spawning reproductive strategy of many native salmonids, brown trout spawn in the fall (September–December), their embryos incubate and hatch during the winter (December–May), and fry emerge in the spring (Klemetsen et al. 2003). This fall-spawning strategy may fail in high-elevation stream reaches that

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Received June 26, 2008; accepted January 22, 2009
Published online May 18, 2009

experience extreme winter and spring conditions, including highly variable water temperatures, ice formation, and severe spring flooding resulting from annual snowmelt runoff, all of which occur during a typical year in many intermountain western streams. Such harsh conditions can vary depending on weather-related factors, such as annual snowpack and mean air temperatures, and have the potential to negatively influence reproductive success and egg-to-fry survival through a variety of mechanisms, few of which have been tested in the field. For instance, anchor ice can freeze and kill embryos (Harshbarger and Porter 1979), cool water temperatures can prolong embryo development and fry emergence (Pennell and Barton 1996) beyond suitable environmental periods, and high streamflow events can displace and kill embryos and fry (Lapointe et al. 2000; Cattaneo et al. 2002). Such conditions are avoided by native cutthroat trout *Oncorhynchus clarkii*, which spawn in late spring or early summer (Henderson et al. 2000) on the descending limb of the stream hydrograph (Schmetterling 2000), where incubating embryos and fry experience a relatively warm, stable stream environment.

We hypothesized the fall-spawning reproductive strategy employed by brown trout prevents successful invasion into high-elevation stream reaches because winter habitat conditions cause (1) high rates of embryo mortality due to direct effects (e.g., anchor ice) and (2) a longer incubation time as a function of colder water temperatures, which then prevents fry emergence before the onset of damaging peak spring flows and, thus, increases embryo mortality indirectly. We tested this hypothesis in our combined field and experimental study of the spawning ecology, early life stage survival, and fry-emergence timing of a naturalized population of brown trout in a high mountain stream in northern Utah. We first documented the spatial and temporal extent of brown trout spawning to determine the potential for invasion into high-elevation stream reaches. We then evaluated brown trout embryo survival to determine whether overwinter conditions caused higher mortality in high-elevation stream reaches. Finally, we predicted emergence timing at different stream elevations and related it to the timing of potentially damaging peak streamflow during spring runoff.

Methods

Study Area

Our study area encompassed a large portion (approximately 50 km) of the Logan River and its tributaries in northern Utah. The headwaters of the Logan River originate in the Bear River Mountains in southeastern Idaho, and the river flows about 64 km southwest from the Idaho border (2,590-m elevation) until it joins the Little Bear River in Cache Valley, Utah (1,343-m elevation; Figure 1). Major tributaries to the Logan River include Beaver Creek (river kilometer [rkm] 10.5; 1,997-m elevation), Temple Fork (rkm 22.5; 1,745-m elevation), Right Hand Fork (rkm 36; 1,590-m elevation), and Spawn Creek (1,800-m elevation at mouth), a second-order tributary to Temple Fork. We also considered Franklin Basin (the Logan River's headwaters) a tributary for the purposes of this study because it has physical characteristics similar to those of the other tributaries mentioned. We defined the main stem of the Logan River as beginning at the point where Franklin Basin and Beaver Creek converge. Strong seasonal variation is evident in the river's hydrograph, with fluctuations in discharge (<3 to >30 m^3/s) caused by spring snowmelt and dry summers. Key environmental attributes change notably along the elevation gradient in the Logan River; higher elevation sites typically are characterized by relatively low water temperature, moderate to steep gradient, large substrate size, and high water velocity. Winter ice formation is also prevalent in high-elevation stream reaches, which experience cooler winter water temperature. In contrast, the lower elevation reaches of the Logan River are characterized by warmer water temperature, lower gradient channels with smaller substrate size, and more deposited gravel beds. More detailed information describing physical habitat characteristics in the Logan River can be found in de la Hoz Franco and Budy (2005).

Introduced brown trout and native Bonneville cutthroat trout *O. clarkii utah* exhibit a parapatric distribution in the Logan River, with lower elevation areas occupied by brown trout, higher elevation areas occupied by Bonneville cutthroat trout, and a transition zone where both species exist in sympatry (de la Hoz Franco and Budy 2005; Budy et al. 2007, 2008). Other species present in the river include native mountain whitefish *Prosopium williamsoni* and mottled sculpin *Cottus bairdii*, as well as introduced rainbow trout *O. mykiss* and brook trout *Salvelinus fontinalis*, the latter of which occur only in isolated, upper tributary locations that were not part of our study area.

Brown Trout Spawning

Spawning habitat location.—Before the brown trout spawning season in autumn of 2006, we conducted visual habitat surveys during steady, base streamflow across approximately 50 km of the Logan River and its tributaries and identified all potential patches of spawning habitat. We identified potential habitat using specific literature-derived values (Raleigh et al. 1986)

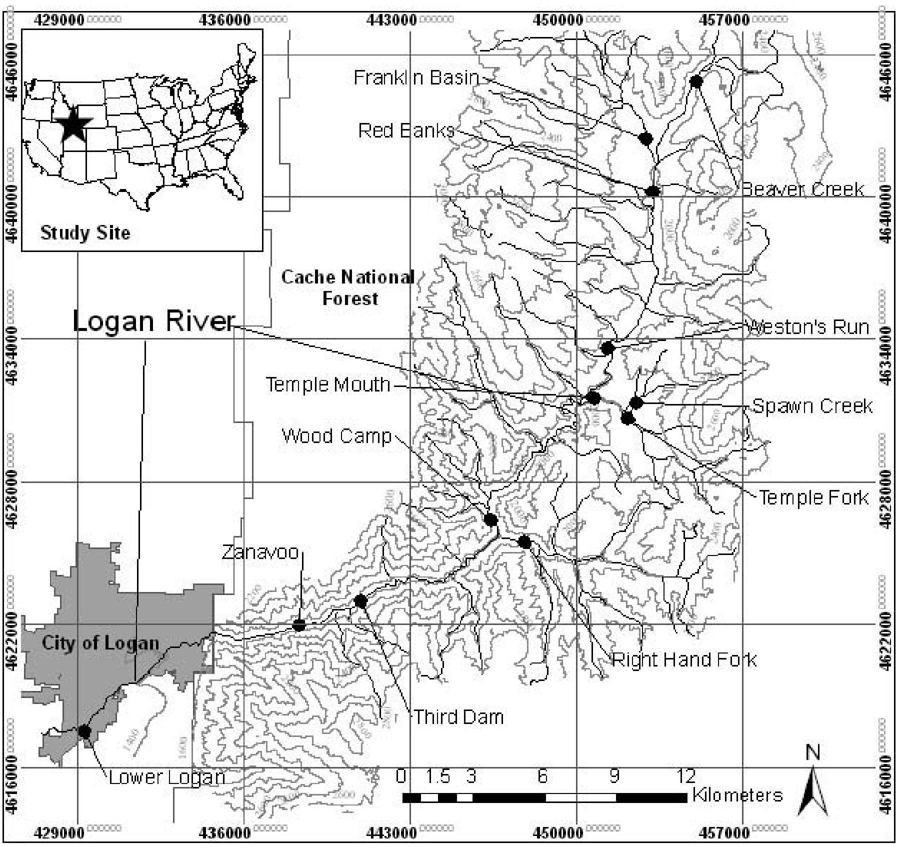

FIGURE 1.—Logan River and its tributaries, northern Utah. Site names represent tributaries and main-stem reaches. See Table 2 for site-specific Universal Transverse Mercator coordinates. Inset shows location of study area in the western United States.

describing the range of substrate size (0.3–10.0-cm diameter), water depth (>6.4 cm), and water velocity (15–90 cm/s) used by spawning brown trout. After determining that an area probably contained suitable spawning habitat, we marked its location (Global Positioning System [GPS] coordinates) with the intention of revisiting the site during the spawning season.

Redd counts.—Upon the first sign of brown trout spawning activity, we began our complete census of redds (weekly in 2006, bi-weekly in 2007) in the main stem of the Logan River and the tributaries and continued surveying until spawning activity ceased. Redd counts consisted of revisiting all identified potential spawning areas and examining them for spawning activity. We also conducted redd counts in areas that were not identified as potential spawning habitat in the main stem of the Logan River to validate our preseason suitable habitat identification. In the tributaries, we counted redds throughout contiguous sections of Right Hand Fork (2.3 km), Temple Fork (1.9 km), and Spawn Creek (750 m).

We defined a redd as an area containing clean substrate in relation to surrounding conditions and a characteristic structure containing a pit and tailspill (Ottaway et al. 1981; Witzel and MacCrimmon 1983). Each individual redd was marked with flagging tape and its location was recorded using GPS receivers. Based on previous research on fish distribution and abundance, abiotic factors, and natural breaks in topography and geomorphology (de la Hoz Franco and Budy 2005), we divided the main stem of the Logan River into five adjacent reaches for redd data analysis purposes and compared redd densities across sites and across years.

Embryo Survival

We evaluated brown trout embryo hatching success along a gradient of elevation in the Logan River and its tributaries in 2006–2007 and again in 2007–2008 by placing a known number of hatchery-reared fertilized eggs in incubation boxes buried in the gravel at likely spawning locations. In autumn 2006, we constructed cylindrical egg boxes with thin, semi-rigid polyvinyl chloride (PVC) mesh material as recommended by Harris (1973) but at a slightly larger size (8.9 cm in diameter, 8.9 cm in height). We located egg box sites randomly within systematically selected reaches in the Logan River (four sites from low elevation to headwaters) and the tributaries (Right Hand Fork, Temple Fork, Spawn Creek, and Franklin Basin). After selecting a site, we measured water depth, water velocity, and substrate size to ensure that the values were within those described for spawning brown trout (Raleigh et al. 1986). If unsuitable, another site was selected randomly and surveyed. Using this approach, we selected four main-stem sites and four tributary sites. At each site, we buried three egg boxes in the gravel, each containing 100 eyed eggs. Eggs were placed in the boxes and boxes were planted using techniques similar to Harris (1973), except that we buried our boxes at a shallower depth to simulate brown trout egg burial depths (approximately 5–10 cm; Crisp and Carling 1989). Each location was accompanied by a temperature logger to predict development-to-hatch time using a model from Crisp (1981). At the predicted hatching time, we revisited each site and verified that embryos had hatched. After all embryos had hatched, we retrieved the egg boxes, counted the number of live yolk sac fry in each box, and calculated mean survival at each site.

In autumn 2007, we conducted the same experiment as in 2006 using an improved egg box design, four additional sites, and twice the number of egg boxes per site. Egg boxes were similar in size to the 2006 boxes, but the new design made them less costly, easier to construct, and more rigid than the boxes constructed in 2006. We constructed boxes by cutting lengths of rigid polypropylene mesh tubing (aperture size, approximately 1 × 5 mm) and capping the ends with low density polyethylene end-caps perforated with small (about 1.5-mm) holes. In addition to the eight 2006 sites, we selected four additional sites randomly within predefined reaches to increase sample size and more effectively evaluate variability among sites, bringing our total to 12 sites (7 in the main stem, 5 in tributaries). We doubled our sample size to six boxes per site in 2007 to increase the precision of our survival estimates within sites. We planted boxes using the same methods as in the 2006 experiment and retrieved them at the predicted hatching time, counted live yolk sac fry, and calculated mean survival at each site. We compared mean survival across years using Student's t-test (SAS Institute 2005; a priori significance level of 0.10).

Because temperature can be considered an indicator of conditions affecting brown trout embryos (i.e., temperature influences ice conditions and embryo development time), we evaluated the relation between mean water temperature during the months of December and January (consistently the two coldest months of the year; independent variable) and percent embryo survival to hatch (dependent variable) for both years using linear regression analysis (SAS Institute 2005; a priori significance level of 0.10).

Predicting Emergence

We used 2006 temperature data collected at low- (1,420 m), mid- (1,600 m), and high- (2,030 m) elevation sites in the Logan River to predict the timing of brown trout fry hatching and emergence from the gravel in each of these areas. Temperature data were available from 19 November 2006 through emergence in 2007; we used 19 November as a starting date to model peak emergence, as peak spawning occurred close to this date at most sites. We used average daily water temperature taken from hourly temperature logger readings for each day combined with two models for brown trout development to estimate the proportion of total development that would have taken place given the average temperature on a specific day. We used brown trout model 1b from Crisp (1981) to calculate the number of days required to reach 50% hatch at each daily temperature. This model was developed using results from experiments that evaluated time to 50% hatch of brown trout embryos incubating at a variety of constant temperatures in the laboratory. We predicted the number of days from fertilization to 50% hatch (D) using the following equation:

$$\log D = b\log(T - \alpha) + \log a, \qquad (1)$$

where T is water temperature (°C), α is a temperature correction (°C), and a and b are constants given in Table 2 of Crisp (1981).

We then used the model from Crisp (1988) to convert time to 50% hatch into time to 50% emergence. This model was based on the comparison between time required to reach 50% hatch and time required to reach 50% emergence, or swim-up, derived from laboratory experiments where brown trout embryos and fry were incubated over a range of constant water temperatures. We evaluated time to 50% emergence (D_3) using the following equation:

$$D_3 = 1.66D_2 + 5.4, \qquad (2)$$

where D_2 is the number of days from fertilization to 50% hatch, calculated using equation (1) as described here.

Using these requirements, we estimated the percent of total development (from fertilization to emergence) likely achieved during each day (1/x where x = the number of days required for emergence, based on the average temperature at each daily time step), and we added percent development for each day to the accumulated total percent development from each of the previous days. When percent development reached 100%, we assumed that brown trout had reached the period of peak emergence at that time. We then used Logan River streamflow data from the U.S. Geological Survey (USGS) National Water Information System (available at: waterdata.usgs.gov/nwis/rt; USGS site 10109000) to calculate the median date and range of dates on which peak streamflow occurred over the 37-year period (1971–2007) of available daily streamflow data, and we compared our predicted emergence dates with the streamflow data. We assumed that peak streamflow had the potential to affect brown trout egg-to-fry survival if it occurred before predicted peak emergence times.

Results

Brown Trout Spawning

We observed the first brown trout redds on 3 November 2006 and on 22 October 2007. Spawning activity continued until around mid-December of both years at most sites. We observed a typical "bell-shaped" pattern of spawning activity in 2007, with an apparent peak near the end of the third week in November (Figure 2). Overall, we counted a total of 1,775 redds (1,506 in the main stem, 269 in tributaries) in 2006 and 1,662 redds (1,285 in the main stem, 377 in tributaries) in 2007. All redds in the main stem of the Logan River were observed in areas previously identified as potentially suitable for spawning in our habitat surveys. We observed brown trout spawning at elevations as high as 1,983 m but at very low densities, despite our observations of adequate spawning habitat in these areas. Redd densities varied widely across reaches (4–147 redds/ha in 2006, 4–242 redds/ha in 2007) and declined with increasing elevation in both the main stem and tributaries of the Logan River during both years (Figure 3). Redd densities were higher in the tributaries (Figure 3), which contain a higher proportion of apparent spawning substrate per unit area. Within sites, redd densities were very similar across years in the main stem of the Logan River (mean difference = 0.61%) but increased by an average of 74% in the tributaries in 2007.

Embryo Survival

Mean embryo survival to the time of hatching generally declined with increasing elevation in the Logan River and tributary sites during both study years, but the trend was not consistent across all sites (Figure 4). Survival was lower in 2007–2008 than in 2006–2007 (t = 2.84, P = 0.01, df = 18; Figure 4). Variability in our survival estimates was considerably lower in the second year of the study, probably in response to our increased sample size (Figure 4). Mean embryo survival never fell below 47% in the main stem and 36% in the tributaries (Table 1). While water temperature declined with increasing elevation, this trend was not always consistent (Table 1). Mean embryo survival increased with mean winter water temperature during both 2006–2007 ($y = 5.354x + 75.884$, $r^2 = 0.51$, $P = 0.289$) and 2007–2008 ($y = 14.565x + 49.224$, $r^2 = 0.76$, $P = 0.010$; Figure 5), but this relation was only statistically significant in 2007–2008. Note also that the extremely low temperature and survival values at one of our 2007–2008 sites (Weston's Run, Table 1) had a strong influence on our analysis. Our predictions of hatching times based on temperature data were consistently accurate, which elevated confidence in our ability to predict brown trout fry emergence from the gravel.

Predicting Emergence

The timing of predicted peak emergence from the gravel varied substantially across elevations (Table 2; Figure 6). Peak brown trout emergence in low-elevation areas was predicted to occur more than 1 month earlier than emergence in high elevations and before both the median and range of dates of peak spring discharge based on 37 years of Logan River streamflow data (Table 2). In contrast, predicted peak brown trout emergence from mid-elevation reaches occurred before the median date of peak spring discharge but within the range of peaks experienced during this time period, indicating that during some years fish in these areas would not emerge before peak flows occurred. Finally, predicted peak brown trout emergence in high-elevation stream reaches did not occur before the median date of peak discharge, indicating that during most years brown trout in these areas would still be in the gravel at the onset of spring runoff and could be subject to mechanical damage resulting from streambed scour.

Discussion

Life history strategy is often a crucial determinant in the invasion success of nonnative fishes (Moyle and Light 1996; Fausch et al. 2001). Our investigation of the fall-spawning life history strategy of brown trout in an intermountain western stream may better explain the distributional limits of these ubiquitous invaders. Budy et al. (2008) explored a wide range of potential

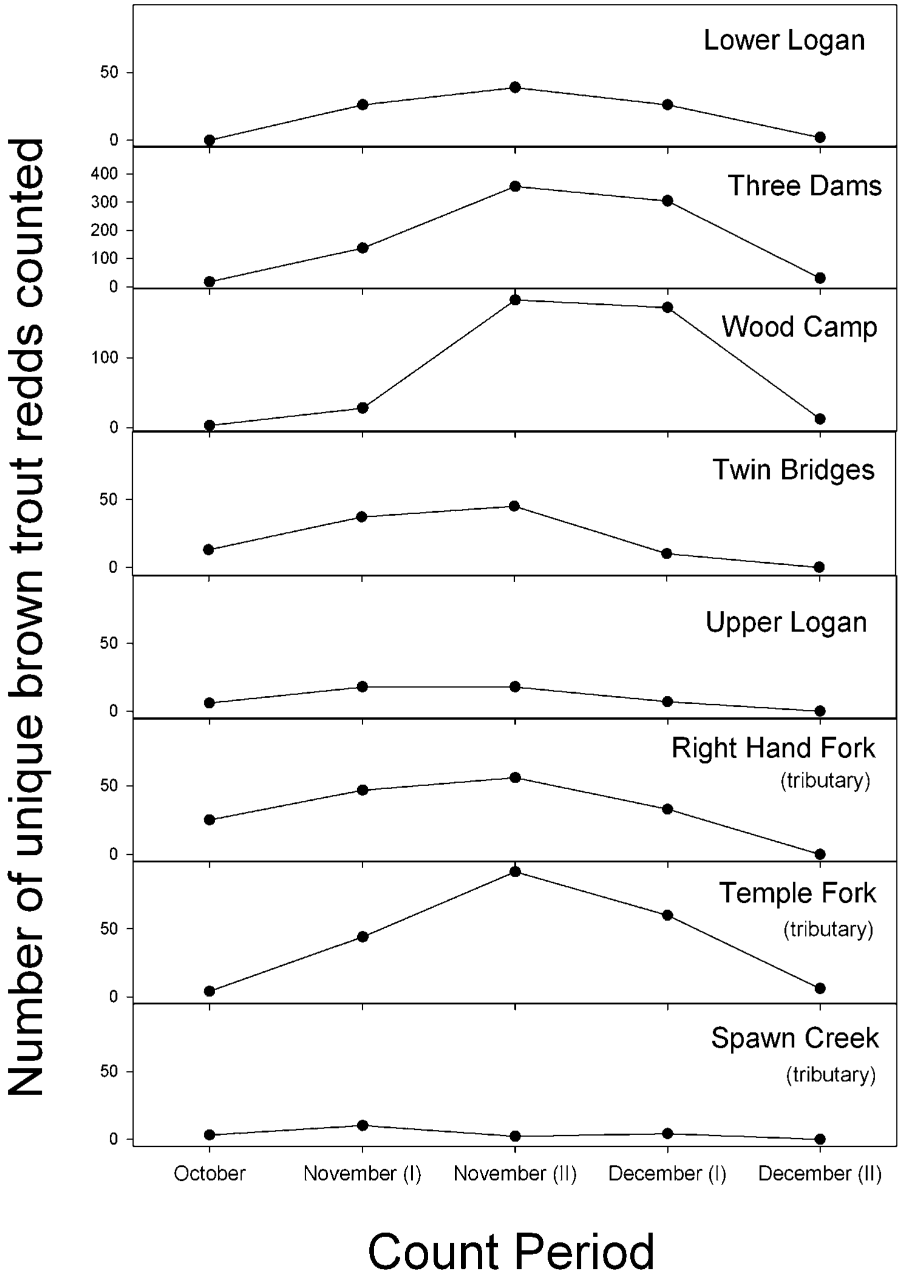

FIGURE 2.—Number of brown trout redds counted by period at five main-stem Logan River (Utah) sites and three tributary sites in 2007. Count periods began near the end of October and were separated by approximately 2 weeks at each site. Note scale changes on y-axis.

limitations to the distribution of brown trout in our study stream and concluded, by process of elimination, that overwinter conditions and spring runoff probably influenced these fall-spawning fish and warranted further consideration. In this study, we documented brown trout spawning in high-elevation stream reaches up to 1,980-m elevation, higher than where we typically encounter brown trout during summer electrofishing surveys (Budy et al. 2008), which indicates the potential for upstream invasion. As hypothesized, we observed a decline in embryo survival at higher elevation and cooler-water sites but

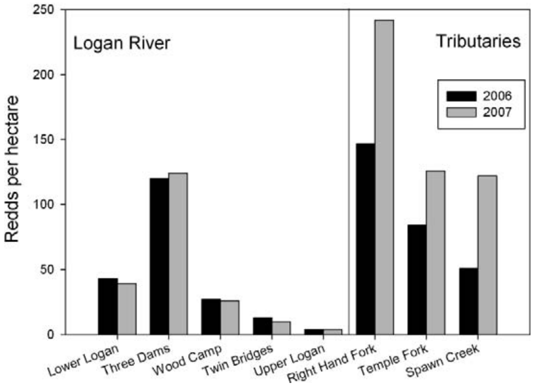

FIGURE 3.—Brown trout redd densities calculated from the census of redds in 2006 and 2007 at five adjacent reaches on the main stem of the Logan River, Utah, and three tributary reaches. Sites are arranged from low to high elevation (left to right) on the x-axis within main-stem and tributary groupings.

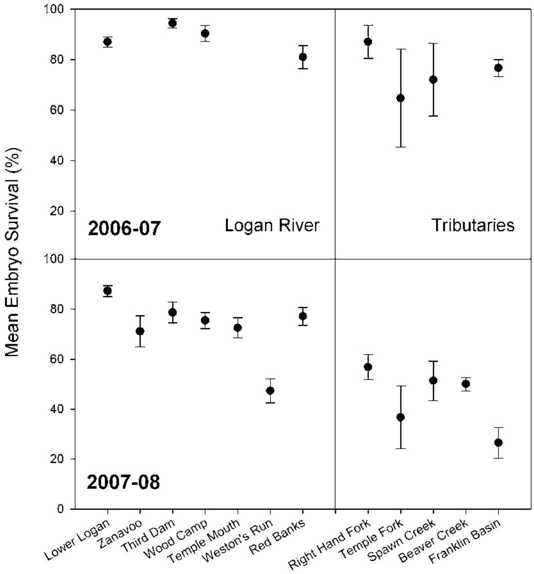

FIGURE 4.—Mean (±SE) brown trout embryo survival to hatching at Logan River (Utah) main stem and tributary sites in 2006–2007 and 2007–2008. Sites are arranged from low to high elevation on the x-axis within main-stem and tributary groupings.

did not document complete recruitment failure at these high sites, again indicating the potential for successful invasion at this life stage. Given that our combined spawning and embryo survival data indicate brown trout have the potential to successfully reproduce and invade farther upstream (to the embryo hatching stage), our predictions of emergence timing indicate that conditions between the embryo hatching and emergence periods could possibly have the greatest influence on brown trout survival in high-elevation stream reaches. While direct evidence for the effect of streamflow on egg-to-fry survival is lacking (but see Crisp 1989), this factor may be an important determinant of recruitment and ultimately invasion success.

Brown trout spawned from late October or early November through mid-December in the Logan River, which is considerably later than for many established brown trout populations in North America (Pender and Kwak 2002; Zimmer and Power 2006; but see Beard and Carline 1991). Spawning timing appeared to be similar across the Logan River's elevation gradient, despite lower water temperatures (which delay incubation time; Stonecypher et al. 1994) at higher elevations. The onset of brown trout spawning is believed to be triggered by a combination of water temperature and day length (Raleigh et al. 1986; Crisp 2000), and spawning timing can vary considerably depending on geographic area and stock origin (Shields et al. 2005). Given that most North American brown trout probably originated from stocks adapted to relatively mild climates in Germany and Scotland (MacCrimmon and Marshall 1968; Lever 1996) and may not have had sufficient time to adopt a more favorable spawning strategy, their timing for spawning appears to be maladapted to the cold temperatures and highly variable hydrologic conditions of high-elevation mountain stream reaches (e.g., rainbow trout; Fausch et al. 2001).

Another fall-spawning invader, the brook trout, has been extremely successful in colonizing headwaters of intermountain western streams, potentially confounding the idea that this life history strategy is poorly adapted to environmental conditions. However, there are a number of differences between the two species that may explain the high-elevation invasion success of brook trout. Brook trout typically occupy smaller, higher elevation stream reaches than do brown trout (Vincent and Miller 1969; Bozek and Hubert 1992) and spawn exclusively in areas with much lower water velocity and higher groundwater seepage than do brown trout (Witzel and MacCrimmon 1983). Furthermore, brown trout do not appear to select groundwater areas for spawning (Hansen 1975; Witzel and MacCrimmon 1983). The relative warming influence of groundwater in these cold, high-elevation streams can be expected to facilitate earlier emergence timing, allowing brook trout fry to seek out slow-water refugia before spring runoff occurs. We did not observe any brook trout redds in our study; brook trout are only present in the Logan River system in isolated headwater and tributary areas above the highest

TABLE 1.—Site location (Universal Transverse Mercator [UTM] coordinates) and characteristics of 2007–2008 brown trout embryo survival experiment sites in the Logan River, Utah, and tributaries.

Site name	UTM E	UTM N	Elevation (m)	Winter temperature, mean (°C)	Egg survival, mean (%)
Main stem					
Lower Logan River	429346	4617513	1,364	2.18	87.17
Zanavoo	438367	4621929	1,510	1.73	71.17
Third Dam	440940	4622944	1,533	1.94	78.67
Wood Camp	446461	4626377	1,604	2.44	75.50
Temple Mouth	450805	4631476	1,756	1.50	72.50
Weston's Run	451357	4633599	1,821	0.16	47.33
Red Banks	453286	4640167	1,979	1.37	77.17
Tributaries					
Right Hand Fork	447869	4623463	1,646	8.20	56.83
Temple Fork	452208	4630645	1,814	1.69	36.67
Spawn Creek	452538	4631290	1,839	2.22	51.33
Franklin Basin	452982	4642423	2,032	1.22	26.50
Beaver Creek	455066	4644879	2,086	−0.05	50.00

elevation at which we encountered brown trout redds. The differences between brook trout and brown trout spawning strategies may partially account for the differential distribution of these two species.

Because of the colder water and associated habitat conditions, we expected brown trout embryo hatching success to be lower in high-elevation areas and to be near zero in areas where we do not observe brown trout spawning activity or natural recruitment. Although water temperature (within the ranges we encountered) is not expected to influence brown trout embryo survival directly (Stonecypher et al. 1994), we considered it a surrogate for identifying the effect of other potentially limiting factors, such as anchor ice (Hirayama et al. 2002), which is difficult to quantify in the field (Doering et al. 2001) and believed to significantly influence incubating embryos (cited by Kerr et al. 2002). Embryo survival declined somewhat with increasing elevation, but this pattern may have been partially masked by the fact that water temper-

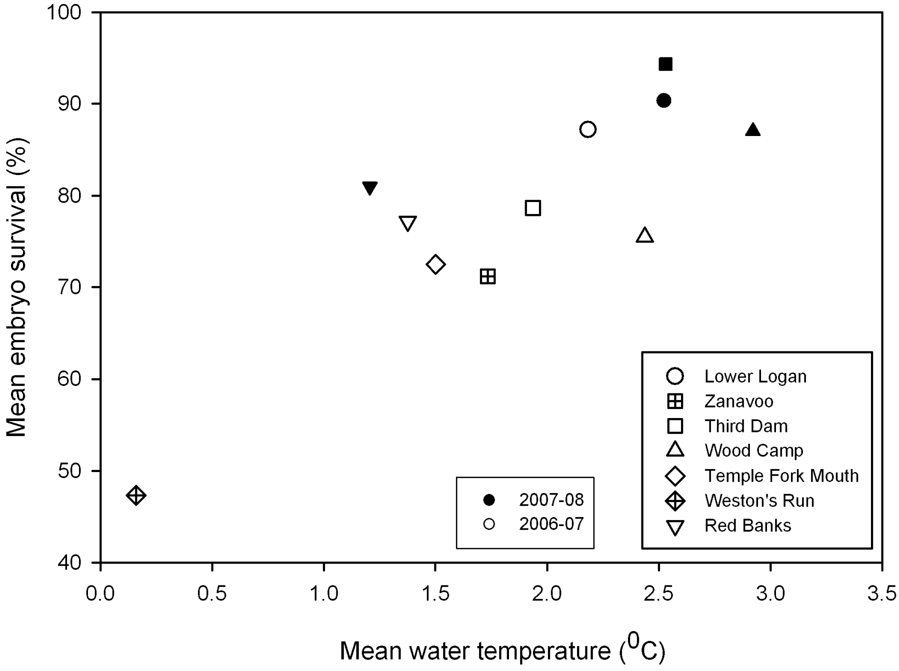

FIGURE 5.—Relation between mean winter water temperature and mean brown trout embryo survival in the Logan River, Utah, in 2006–2007 (black symbols; $y = 5.354x + 75.884$, $r^2 = 0.51$, $P = 0.289$) and 2007–2008 (open symbols; $y = 14.565x + 49.224$, $r^2 = 0.76$, $P = 0.010$).

TABLE 2.—Predicted brown trout emergence times at three Logan River (Utah) sites of varying elevation based on 2006–2007 water temperature data and a peak spawning date of 19 November, compared with the median and range of peak discharge (1971–2007).

		Incubation period		Peak discharge	
Site	Elevation (m)	Peak spawning	Peak emergence	Median	Range
Low	1,420	19 Nov	30 Apr	28 May	1 May–16 Jun
Mid	1,600	19 Nov	7 May	28 May	1 May–16 Jun
High	2,030	19 Nov	2 Jun	28 May	1 May–16 Jun

ature and other fluvial characteristics (e.g., water velocity) (1) generally differ among the tributaries and main-stem areas independent of elevation and (2) did not necessarily change consistently with increasing elevation in the main stem alone. In addition to elevation, sunlight and groundwater inputs, for example, probably influenced site-specific water temperature. However, while embryo survival did decline with decreasing water temperatures and generally declined with increasing elevation, the difference between low- and high-elevation areas was not as dramatic as we hypothesized. In fact, mean survival was well above zero at most sites during both years, indicating that conditions such as anchor ice are unlikely to influence overwinter embryo survival at our sites. Similarly, Nuhfer et al. (1994) hypothesized minimal ice effects on recruitment when comparing winter conditions with influences of peak streamflow. The decline in hatching success we observed at low temperature, high-elevation sites is probably due to longer incubation times, which

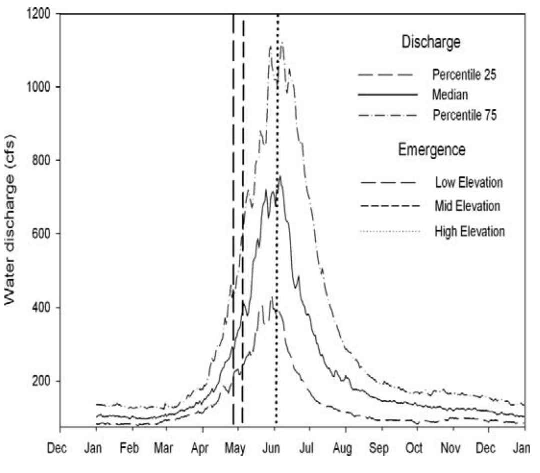

FIGURE 6.—Predicted timing of peak brown trout fry emergence from the gravel at low-, mid-, and high-elevation sites in the Logan River, Utah, based on 2006–2007 temperature data in relation to the 25th-percentile, median, and 75th-percentile values of discharge (cubic feet per second [cfs]; 1 cfs = 0.028 m^3/s) measured over a 37-year period (1971–2007).

result in longer exposure to other potentially lethal factors (e.g., egg displacement and oxygen depletion) aside from temperature alone (Ojanguren and Brana 2003).

Although a number of studies have investigated the egg-to-fry survival of stream salmonids, most have focused on the effects of deposited sediment (Hausle and Coble 1976; Olsson and Persson 1988; Levasseur et al. 2006) and water chemistry (Lacroix 1985; Rubin and Glimsater 1996; Geist et al. 2006). To our knowledge, ours is the only study investigating differential embryo survival along an elevational stream gradient. Our methodology allowed us to make useful comparisons across sites based on water temperature alone. Despite our attempt to isolate other potential sources of embryo mortality (by selecting physically similar sites among reaches), fine sediment deposition probably influenced survival at some of our sites, particularly in the tributaries. At these sites, sediment would sometimes accumulate in one or two boxes and appear to cause low survival, while not affecting others situated only centimeters away. We addressed this potential problem somewhat by doubling our sample size in 2007–2008, which resulted in more precise estimates within sites. Further, the overall patterns of sedimentation we observed among egg boxes and among sites appeared to be random (i.e., silt levels did not appear to be higher at high-elevation sites, where survival was lower), and thus we do not believe sedimentation had a substantial effect on our relative comparison across sites. Nevertheless, our overall estimates of survival may not precisely reflect absolute embryo survival due to the potential for egg boxes to hamper survival by collecting fine sediment (Reiser et al. 1998) or to enhance survival by protecting embryos from physical damage. Further, while we postulated that our comparative embryo survival estimates were fairly representative of the study system, it is important to note that here we evaluated embryo survival to the hatching stage. A large proportion of development occurs between hatching and emergence (Crisp 1988), and the potential for further mortality of yolk sac fry and emerging fry is significant (e.g., MacKenzie and Moring 1988).

In addition to those environmental factors described, another potential source of mortality between the yolk sac fry stage and fry emergence is the mechanical displacement and damage to alevins via streambed mobility resulting from high flows (Seegrist and Gard 1972; Montgomery et al. 1996; Lapointe et al. 2000). While such effects are difficult to predict and depend on stream mechanics and egg burial depths (Crisp 2000), the potential for brown trout redds to be washed out during high-flow periods has been firmly established (Elliott 1976; Crisp 1989). Because embryos and fry are sensitive to physical disturbance (Roberts and White 1992), it is reasonable to expect that peak streamflows, which often exceed more than 10 times base flow levels in a mountain stream like the Logan River (e.g., $<3\text{-m}^3/\text{s}$ base flow to $>30\text{-m}^3/\text{s}$ peak flow), can cause substantial mortality to alevins incubating in the gravel during such events. While we predicted early emergence patterns in low-elevation reaches (e.g., Kondolf et al. 1991), in high-elevation reaches (where we have documented brown trout spawning but have not observed successful recruitment) brown trout probably remain in the gravel at the onset of peak annual streamflow during most years. Our observations were limited by the short period (only 1 year) over which we had continuous annual water temperature data, as well as the single low-elevation gauge station where streamflow data were collected. Nevertheless, the Logan River is characterized by a snowmelt-pulse-dominated hydrograph, and peaks in spring discharge are closely synchronized across elevation. As indicated by published studies and general patterns we observed, streambed movement and scour may limit brown trout yolk sac fry survival in high-elevation stream reaches.

Based on our observations (Budy et al. 2008; this study), the lack of successful brown trout recruitment in high-elevation reaches limits their invasion success. Recruitment can be limited by environmental conditions throughout a variety of life stages, including spawning, embryonic development, hatching, emergence, and postemergence. Since brown trout in our study area spawned in high-elevation areas and survival to the hatching stage has been documented, invasion success is probably limited by environmental conditions affecting fish between hatching and postemergence. Our predictions of emergence timing imply that successful recruitment may depend on the interaction between peak streamflow and emergence timing; however, we did not specifically evaluate the effects of streamflow conditions on brown trout survival. While streambed scour and resultant mechanical displacement of embryos, yolk sac fry, or both may be the mechanism influencing recruitment failure, the effect of high flows on postemergent fry seeking refugia may be important as well (Ottaway and Clarke 1981; Ottaway and Forrest 1983; Heggenes and Traaen 1988). For instance, even if streambed scour does not influence survival, high streamflow during emergence may prevent weak-swimming fry from accessing sheltered backwater areas of the stream (Elliott 1994), resulting in relatively high rates of mortality. Considerable research has documented the general relationship between peak streamflow and brown trout recruitment (e.g., Lobon-Cervia 2007). We suggest that future work seek to identify more specific mechanisms of brown trout recruitment failure between hatching and postemergence via thorough experiments and detailed observations. A better understanding of the differential success of a fall-spawning life history strategy along stream gradients will aid in identifying drivers of invasion success in the future.

Acknowledgments

This research was funded by the Utah Division of Wildlife Resources, Project XII, Sport Fisheries Research, Grant Number F-47-R, Segment 20, and the USGS. Thanks go to the U.S. Forest Service for providing equipment and assistance in the field. Brett Roper, David Tarboton, and Jack Schmidt provided crucial insight, ideas, and advice on earlier drafts of this manuscript. Special thanks go to Gary Thiede for technical advice and logistical oversight and to our field crews, laboratory technicians, and graduate students in the Fish Ecology Laboratory at Utah State University.

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