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An Investigation of the Early Life-History of Brown Trout (*Salmo trutta*) and Potential Influences on Invasion Success in the Logan River, Utah

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AN INVESTIGATION OF THE EARLY LIFE-HISTORY OF BROWN TROUT (*SALMO TRUTTA*) AND POTENTIAL INFLUENCES ON INVASION SUCCESS IN THE LOGAN RIVER, UTAH

by

Jeremiah R. Wood

A thesis submitted in partial fulfillment
of the requirements for the degree

of

MASTER of SCIENCE

in

Fisheries Biology

Approved:

Phaedra Budy Major Professor	Brett Roper Committee Member
David Tarboton Committee Member	Byron Burnham Dean of Graduate Studies

UTAH STATE UNIVERSITY
Logan, Utah

2008

ABSTRACT

An Investigation of the Early Life-History of Brown Trout (*Salmo Trutta*) and Potential Influences on Invasion Success in the Logan River, Utah

by

Jeremiah R. Wood, Master of Science

Utah State University, 2008

Major Professor: Dr. Phaedra Budy
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Due to the significant threats posed by nonnative fish species worldwide, it is important to understand how life-history strategies of individual species interact with environmental conditions to explain the success or failure of nonnative fish invasions. Brown trout are prolific invaders, but often exhibit upstream distributional limits in Intermountain West streams, potentially due to a maladaptive reproductive life-history strategy influenced by hydrologic conditions in high-elevation areas. We used redd counts, egg survival experiments, and temperature modeling to investigate the reproductive life-history strategy of brown trout and its potential for success along an elevational stream gradient. We documented brown trout spawning in stream reaches at elevations higher than where we typically encounter brown trout during summer electrofishing surveys, indicating the potential for upstream invasion. We observed a decline in egg survival at higher elevation, cooler water sites, but did not document complete recruitment failure at these sites, again indicating the potential for successful invasion at this life-stage. Temperature data indicate that during most years, incubating brown trout eggs would likely fail to emerge from the gravel prior to peak spring flows in these high-elevation stream reaches, suggesting that damaging spring floods may cause significant egg and sac-fry mortality at high elevations, and may determine invasion success in these areas. Our results highlight the importance of identifying specific mechanisms of recruitment failure in order to better predict nonnative fish invasions in the future.

(57 pages)

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CONTENTS

LIST OF TABLES

LIST OF FIGURES

INTRODUCTION

As a result of widespread introduction, establishment, and dispersal, nonnative fish species pose one of the most significant threats to the persistence of native fishes worldwide (Ross 1991; Wilcove et al. 1998). The establishment of introduced fish species depends on reproductive success, which is governed by the relationship between life-history requirements and the conditions of the environment being invaded (Moyle and Light 1996; Fausch et al. 2001; Olden et al. 2006). However, the wide variety of environmental conditions encountered upon introduction, as well as the variability in life-history strategies among species, often make it difficult to make generalizations about invasion success (Williamson 1996; Leprieur et al. 2008). Further, shifting climatic conditions are expected to influence fish species distributions and invasions (Keleher and Rahel 1996; Rieman et al. 2007), confounding our ability to understand and predict invasion patterns. Therefore, it is important to understand how the specific life-history strategy of an individual species interacts with environmental conditions to explain the success or failure of nonnative fish invasions.

Brown trout are native to Eurasia and North Africa, and have been widely introduced to stream and lake environments throughout the world (MacCrimmon and Marshall 1968; Lever 1996). Notwithstanding their benefits as a popular sport fish, brown trout introductions have had negative impacts on native fish assemblages and community structure in many countries (see Courtenay and Stauffer 1984 for review), such that they are considered one of the “World’s 100 Worst Invasive Alien Species” (Lowe et al. 2000). The successful establishment of brown trout in streams often results in the displacement of native fish from low elevation stream areas (Behnke 2002; Weigel and Sorensen 2001; de la Hoz Franco and Budy 2005). Specific causes of displacement likely vary geographically, but include predation on galaxiid fishes in New Zealand (Townsend 1996), predation on brook trout in the Eastern and Midwestern United States (Metzelaar 1929; Evans 1952), and competition with native trout in western United States streams (Wang and White 1994; McHugh and Budy 2005; Shemai et al. 2007).

Despite widespread invasion success in many areas, brown trout often exhibit upstream limits to distribution in the Intermountain West (Vincent and Miller 1969; Gard and Flittner 1974; de la Hoz Franco and Budy 2005), indicating that some factor, or combination of factors, limits their expansion into many headwater areas where native trout still persist. However, because native and nonnative trout have similar physiological tolerances to many abiotic conditions in streams (e.g., Bjornn and Reiser 1991; Stolz and Schnell 1991) it can be difficult to explain distributional limits using abiotic factors alone (Bozek and Hubert 1992). The theory of condition-specific competition (the concept by which competitive advantage shifts between species along abiotic gradients) suggests that a combination of biotic and abiotic factors may influence species distribution (DeStaso and Rahel 1994; Taniguchi and Nakano 2000). Results of experiments testing this theory in the fisheries field have been inconsistent (see McHugh and Budy 2005 for review), and have failed to reveal a competitive disadvantage for brown trout in favor of native trout over a wide range of abiotic conditions. Instead, McHugh and Budy (2005) demonstrated that brown trout exhibit high survival and growth rates in areas above their observed upper elevational limits. They further explored the potential influence of biotic and environmental factors in limiting brown trout from expanding into these upstream areas. They found that while summer environmental conditions and interspecific competition were not likely to limit brown trout expansion, winter and spring conditions and their potential influence on early life-stages warranted further exploration. This inability to reveal the mechanism limiting adult brown trout from invading upstream areas highlights the need to investigate environmental influences on spawning and early life-stages. For instance, Fausch et al. (2001) characterized rainbow trout invasion success based on streamflow influences on fry survival, highlighting the importance of reproductive strategy in determining the outcome of invasion. Investigating the potential for abiotic conditions to influence brown trout reproductive success under changing environmental conditions is therefore important to understanding and predicting brown trout invasions.

A maladapted reproductive strategy and subsequent limitations to early life-stage survival offer a potential mechanism limiting the distribution of brown trout in Intermountain West streams (Moyle and Light 1996). In contrast to the spring spawning reproductive strategy employed by many native salmonids, brown trout spawn in the fall and their eggs incubate throughout the winter and hatch in the spring (Raleigh et al. 1986). This fall-spawning strategy may be counterproductive in high elevation stream reaches that experience cooler water, ice formation, and highly variable daily temperature fluctuations during the winter, because these conditions have the potential to negatively influence egg-to-fry survival. Extensive ice formation is prevalent in high elevation stream reaches, and despite a paucity of empirical evidence to date, anchor ice may cause egg mortality via freezing. Cooler, more variable water temperatures facilitate the formation and break-up of ice dams (Hirayama et al. 2002), often on a daily basis (personal observation), which can result in mechanical damage to eggs from streambed scour (Lapointe et al. 2000). Further, cooler water temperatures also prolong embryo development and fry emergence times (Pennell and Barton 1996), increasing their susceptibility to mortality while in the gravel (Stonecypher et al. 1994), particularly during high streamflow events. Mountain streams are characterized by large spikes in the hydrograph resulting from spring snowmelt, which have been shown to negatively influence brown trout recruitment (Latterell et al. 1998; Jensen and Johnsen 1999; Cattaneo et al. 2002). Specific mechanisms by which flows influence recruitment success include the scouring of eggs and fry prior to emergence (Seegrist and Gard 1972; Lapointe et al. 2000), and displacement of emerging fry seeking energetically suitable habitats (Elliott 1994). A prolonged incubation period in high elevation, cooler water stream reaches may influence the ability of fry to emerge from the gravel prior to high streamflow events, and therefore increase their susceptibility to such conditions.

We hypothesized that the fall spawning reproductive strategy employed by brown trout prevents successful invasion into high elevation stream reaches because: 1) overwinter ice conditions cause high egg mortality, and 2) longer incubation time prevents emergence prior to the onset of damaging peak spring flows. We tested these hypotheses by studying the spawning ecology and early life-history of brown trout in the Logan River, Utah, a mountain stream containing a population of brown trout apparently restricted to low and mid-elevation reaches. We documented the spatial and temporal extent of brown trout spawning activity throughout the Logan River and conducted field experiments to evaluate the potential for differential egg hatching success in areas above and below their upper distributional extent. In addition, we used empirical temperature measurements and derived literature values to predict the timing of brown trout emergence in low, mid, and high-elevation areas, and compared emergence times with the average timing of peak spring floods.

METHODS

Study Area

Our study area encompassed a large stretch (approx. 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 Bear River in Cache Valley, Utah (1,343 m elevation; Figure 1). Primary tributaries to the Logan River include Beaver Creek (river km 10.5, 1,997 m elevation) Temple Fork (river km 22.5, 1,745 m elevation), Right Hand Fork (river km 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 above. We defined the mainstem 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 ($< 3\ m^3 \cdot s^{-1}$ to $> 30\ m^3 \cdot s^{-1}$) caused by spring snowmelt and dry summers. Key environmental attributes change notably along the elevation gradient in the Logan River; higher elevation sites are typically characterized by relatively low water temperature and moderate to steep gradient, larger substrate size, and higher 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 *(Oncorhynchus clarkii utah*) exhibit an allopatric distribution in the Logan river, with lower elevation areas occupied by brown trout, higher elevation areas occupied by cutthroat trout, and a transition zone where both species exist in sympatry (de la Hoz Franco and Budy 2005; Budy et al. 2007). Other species present in the river include native mountain whitefish (*Prosopium williamsoni)* and mottled sculpin (*Cottus bairdii*), as well as introduced rainbow trout (*Oncorhynchus mykiss*) and brook trout (*Salvelinus fontinalis*), the latter of which occur at low densities only in selected locations.

Brown Trout Spawning

Spawning Habitat Location - Prior to the brown trout spawning season in autumn of 2006, visual habitat surveys were conducted to identify potential spawning areas. Approximately 50 km of the Logan River and visually surveyed and potential patches of spawning gravel identified. Potential habitat was identified using specific literature-derived values (Raleigh et al. 1986) describing the range of substrate size (0.3-10 cm diameter), water depth (> 6.4 cm), and water velocity (15-90 $\text{cm} \cdot \text{s}^{-1}$) used by spawning brown trout. After determining that an area likely contained suitable spawning habitat, its location was marked using GPS coordinates with the intention of revisiting it during the spawning season.

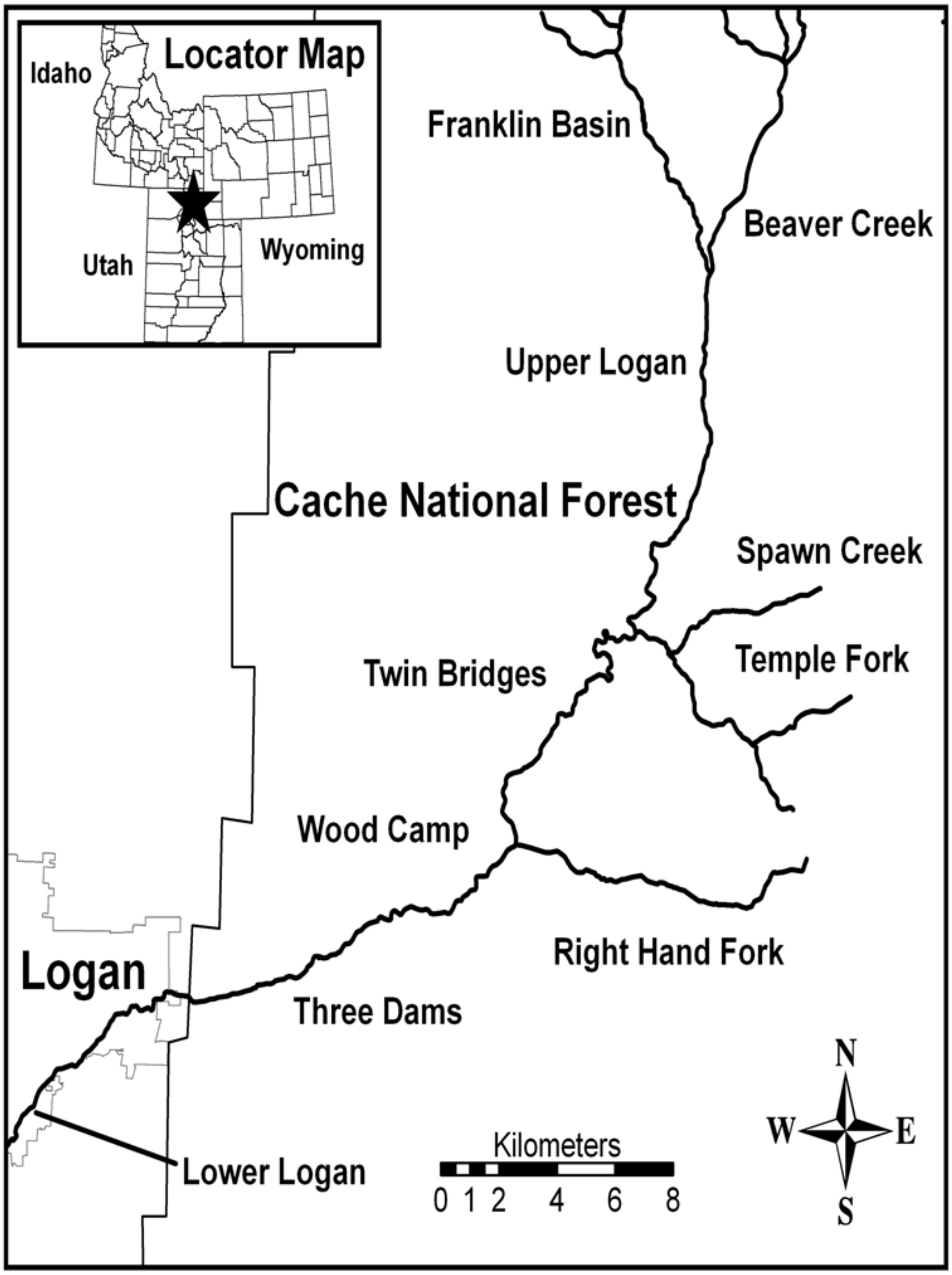

Figure 1 Map of the Logan River and its tributaries. Site names represent tributaries and mainstem reaches.

Redd Counts - Upon the first sign of brown trout spawning activity, we began conducting redd counts (weekly in 2006, biweekly in 2007) in the main stem of the Logan River and the tributaries (Right Hand Fork, Temple Fork, and Spawn Creek), and continued surveys 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 not identified as potential spawning habitat in the mainstem of the Logan River for validation of our preseason habitat evaluation. Redds were counted throughout complete sections of Right Hand Fork (2.3 km), Temple Fork (1.9 km), and Spawn Creek (750 m), as opposed to revisiting potential spawning areas within these reaches. We defined a redd as an area containing clean substrate in relation to surrounding conditions and characteristic structure containing a pit and tailspill (Ottoway et al. 1981; Witzel and MacCrimmon 1983). Each individual redd was marked with flagging tape and its location recorded using GPS coordinates. Based on previous research on fish distribution and abundance, abiotic factors, and natural breaks in topography and geomorphology, we divided the mainstem of the Logan River into five adjacent reaches for redd data analysis purposes. We then compared redd densities across sites and across years.

Egg Survival

We evaluated brown trout egg 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

PVC mesh material as recommended by Harris (1973), but at a slightly larger size (8.9 cm diameter, 8.9 cm height). We randomly located egg box sites within systematically-selected reaches in the Logan River (4 sites from low elevation to headwaters) and the tributaries (Right Hand Fork, Temple Fork, Spawn Creek, Franklin Basin). Upon random location of a site, we measured water depth, water velocity, and substrate size to ensure that the values fell within those described for spawning brown trout (Raleigh et al. 1986). If unsuitable, another site was randomly located and surveyed. Once we determined that a site was suitable, we drove a metal t-post into the gravel to anchor the egg boxes. We continued until we had selected four mainstem sites and four tributary sites. At each site, we buried three egg boxes in the gravel, each containing 100 eyed, hatchery eggs from the Utah Division of Wildlife Resources' Egan Fish Hatchery (Bicknell, Utah). 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 (approx. 5-10 cm; Crisp and Carling 1989). Boxes were wired to the base of the t-post at each site. Each location was accompanied by a temperature logger to predict development to hatch. We downloaded temperature loggers at varying times throughout the winter. Upon predicted hatching time, we revisited each site and verified that eggs had hatched. We then retrieved the egg boxes and counted the number of live sac-fry in each box and calculated mean survival at each site.

In autumn 2007, we conducted the same experiment as in 2006 with 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 tubing (aperture size approx. 1 mm x 5 mm) and capping the ends with low density polyethylene end caps perforated with small (about 1.5 mm) holes and attached using plastic zip ties. In addition to the eight 2006 sites, we randomly selected four additional sites within predefined reaches to increase sample size and more effectively evaluate variability among sites, bringing our total to 12 sites (7 main stem, 5 tributary). We doubled our sample size to six boxes per site in 2007 to increase precision of our survival estimates within sites. We planted eggs and boxes using the same methods as in the 2006 experiment and retrieved them upon hatching time, counted live sac-fry, and calculated mean survival at each site. Because temperature can be considered an indicator of conditions affecting brown trout eggs (i.e., temperature influences ice conditions and egg development time), we evaluated the relationship between mean water temperature during the months of December and January (consistently the two coldest months of the year; independent variable) and percent egg survival to hatch (dependent variable) for both years using linear regression analysis (SAS Institute 2005; a priori α-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 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 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 model 1b for brown trout 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 eggs 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:

(1) $\log D = b \log (T-\alpha) + \log \mathrm{a}$

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 eggs and fry were incubated over a range of constant water temperatures. We evaluated time to 50% emergence, D_3, using the following equation:

(2) $D_3 = 1.66D_2 + 5.4$

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 likely achieved during each day ($1\bullet^{d-1}$ where d = number of days required for emergence for each specific daily average temperature), and 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 stream flow data from the USGS National Water Information System (Website: http://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 compared our predicted emergence dates to the streamflow data. We assumed that peak streamflow had the potential to affect brown trout egg-to-fry survival if it occurred prior to predicted emergence times.

RESULTS

Brown Trout Spawning

We observed the first brown trout redds on November 3 in 2006, and on October 22 in 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 mainstem, 269 in tributaries) in 2006, and 1,662 redds (1,285 in mainstem, 377 in tributaries) in 2007. We observed brown trout spawning at elevations as high as 1,983 meters. Redd densities varied widely across reaches (4-147 redds • ha $^{-1}$ in 2006; 4-242 redds • ha $^{-1}$ in 2007) and declined with increasing elevation in both the mainstem 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 mainstem of the Logan River (mean difference=0.61%) but increased by an average of 74% in the tributaries in 2007.

Egg Survival

Mean egg survival to the time of hatching generally declined with increasing elevation in the Logan River and tributary sites during 2006-07 and 2007-08, but the trend was not consistent across all sites (Figure 4). Survival was lower in 2007-08 than in 2006-07 (Figure 4). Variability in our estimates of egg survival was reduced in the tributaries in 2007-08, likely due to our increased sample size (Figure 4).

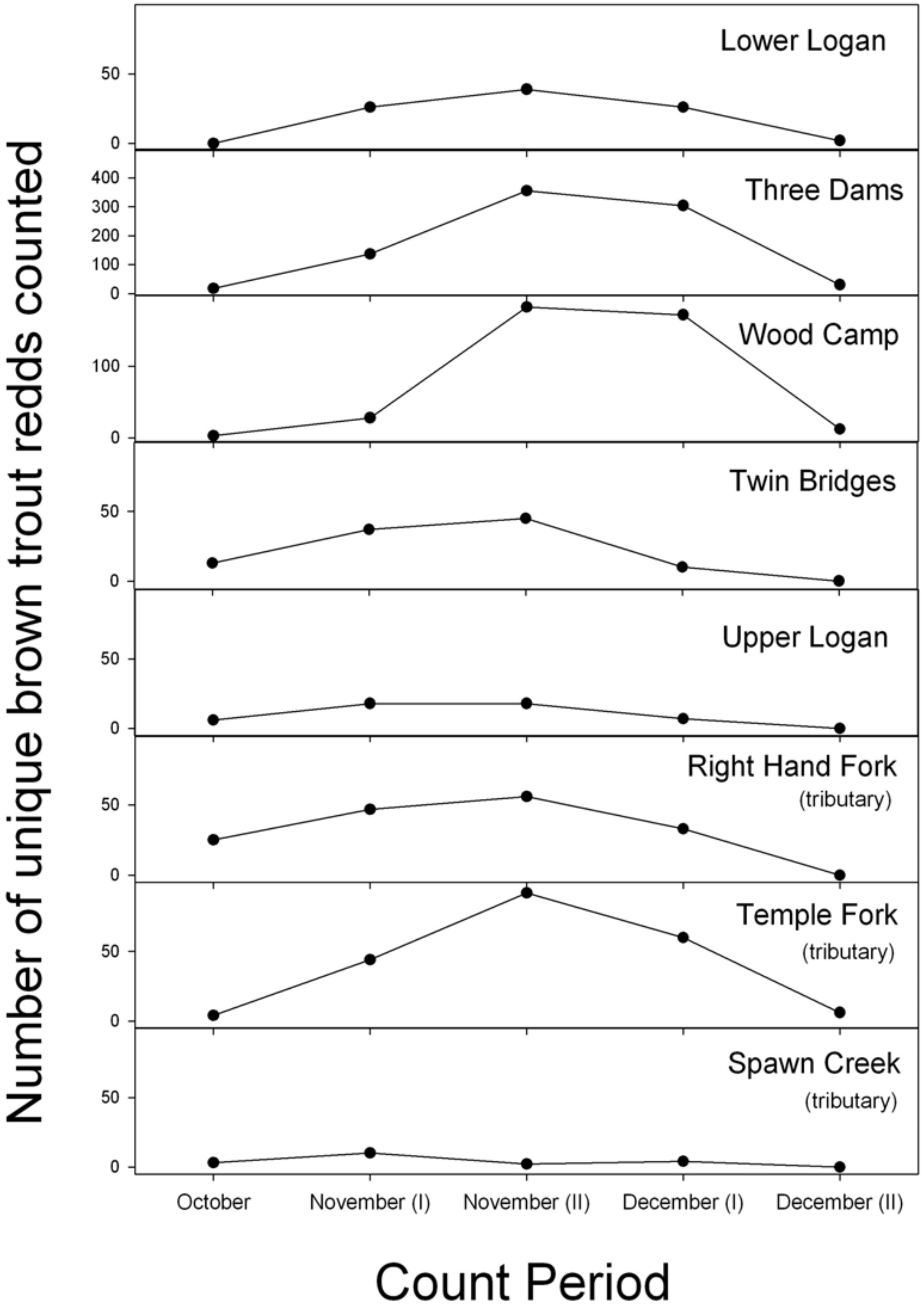

Figure 2 Number of brown trout redds counted by period at five mainstem and three tributary sites in 2007. Count periods began near the end of October and were separated by approximately two weeks at each site. Note scale changes on x-axis.

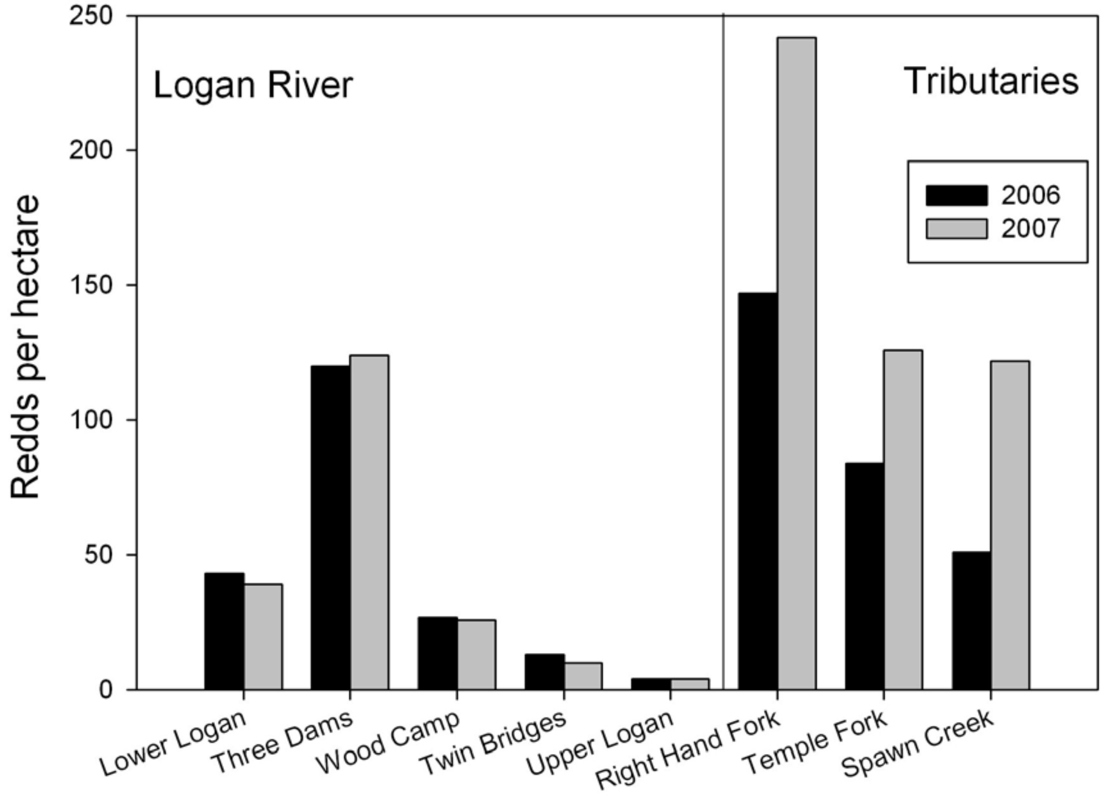

Figure 3 Brown trout redd densities calculated from redd counts in 2006 and 2007 at five adjacent reaches on the mainstem of the Logan River and three tributary reaches. Sites are arranged from low to high elevation on the x-axis within mainstem and tributary groupings.

Mean egg survival never fell below 47% in the mainstem and 36% in the tributaries (Table 1). While water temperature declined with increasing elevation, this trend was not always consistent either (Table 1). Mean egg survival increased with mean winter water temperature during both 2006-07 ($y = 5.354x + 75.884$, $r^2 = 0.51$, $P = 0.289$) and 2007-08 ($y = 14.565x + 49.224$, $r^2 = 0.76$, $P = 0.010$; Figure 5), but this relationship was only statistically significant in 2007-08.

Table 1 Location and characteristics of 2007-08 egg survival experiment sites in the Logan River and tributaries.

	Site Name	UTM E	UTM N	Elevation (m)	Mean Winter Temp (°C)	Mean Egg Survival (%)
Mainstem						
	Lower Logan	429346	4617513	1364	2.18	87.17
	Zanavoo	438367	4621929	1510	1.73	71.17
	Third Dam	440940	4622944	1533	1.94	78.67
	Wood Camp	446461	4626377	1604	2.44	75.50
	Temple Mouth	450805	4631476	1756	1.50	72.50
	Weston's Run	451357	4633599	1821	0.16	47.33
	Red Banks	453286	4640167	1979	1.37	77.17
Tributaries						
	Right Hand Fork	447869	4623463	1646	8.20	56.83
	Temple Fork	452208	4630645	1814	1.69	36.67
	Spawn Creek	452538	4631290	1839	2.22	51.33
	Franklin Basin	452982	4642423	2032	1.22	26.50
	Beaver Creek	455066	4644879	2086	-0.05	50.00

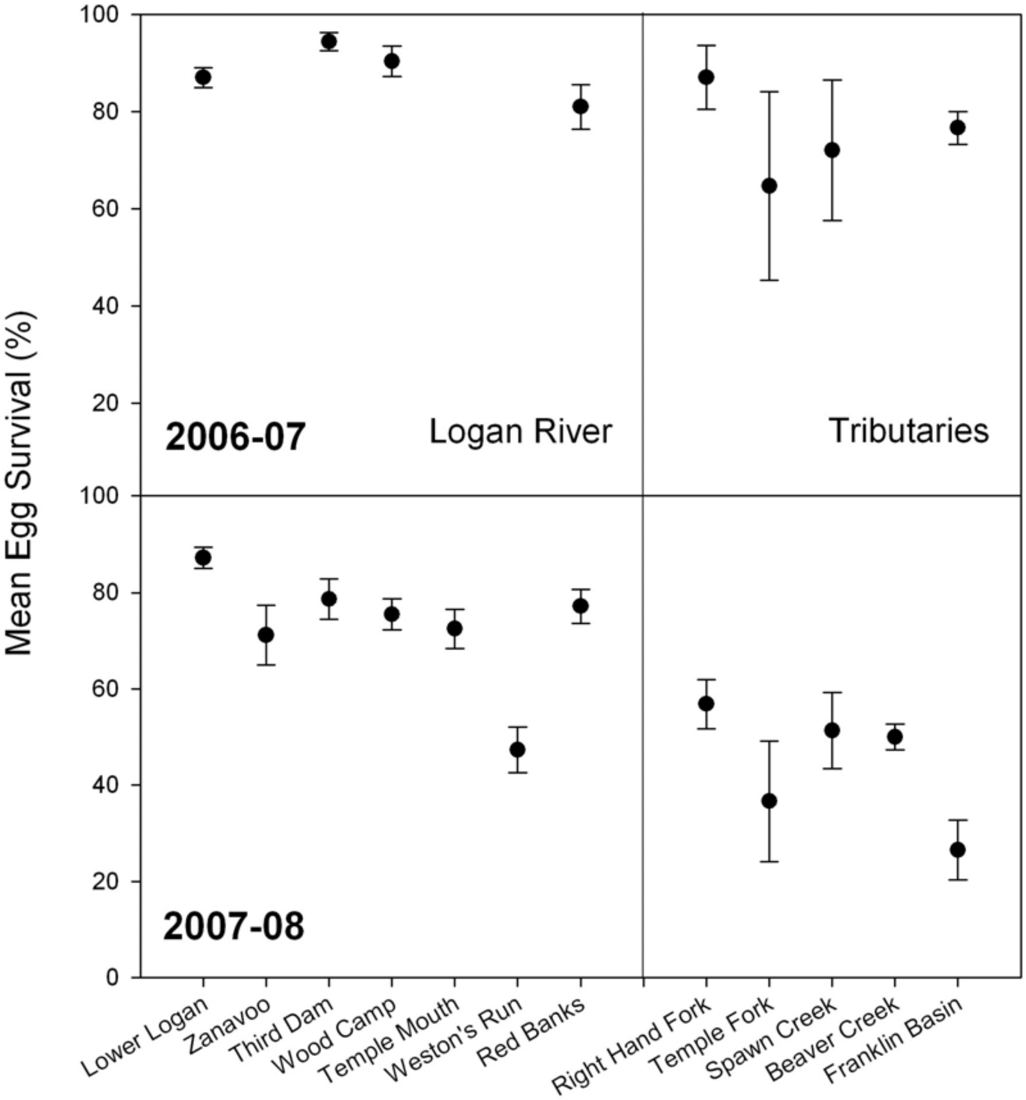

Figure 4 Mean brown trout egg survival to hatch at Logan River mainstem and tributary sites in 2006-07 and 2007-08. Error bars represent values one standard error from the mean. Sites are arranged from low to high elevation on the x-axis within mainstem and tributary groupings.

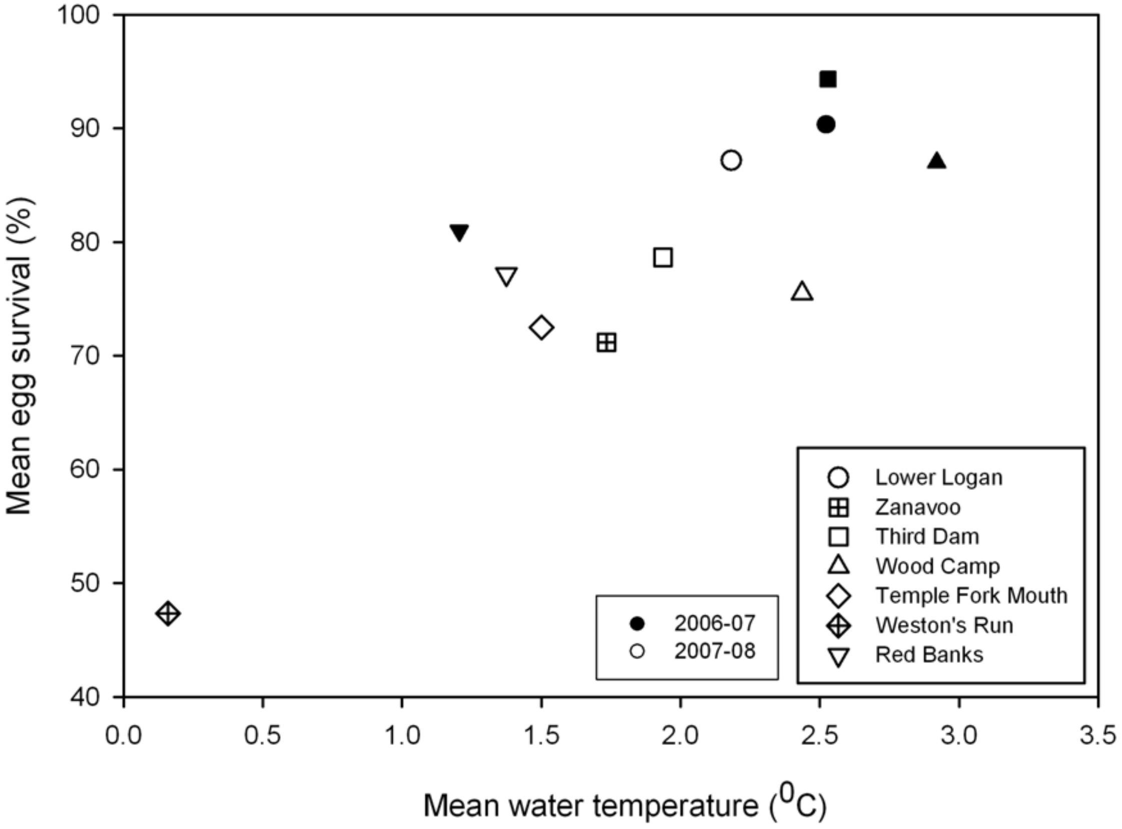

Figure 5 The relationship between mean winter water temperature and mean brown trout egg survival in the Logan River in 2006-07 (darkened symbols; $y = 5.354x + 75.884$, $r^2 = 0.51$, $P = 0.289$) and 2007-08 (open symbols; $y = 14.565x + 49.224$, $r^2 = 0.76$, $P = 0.010$).

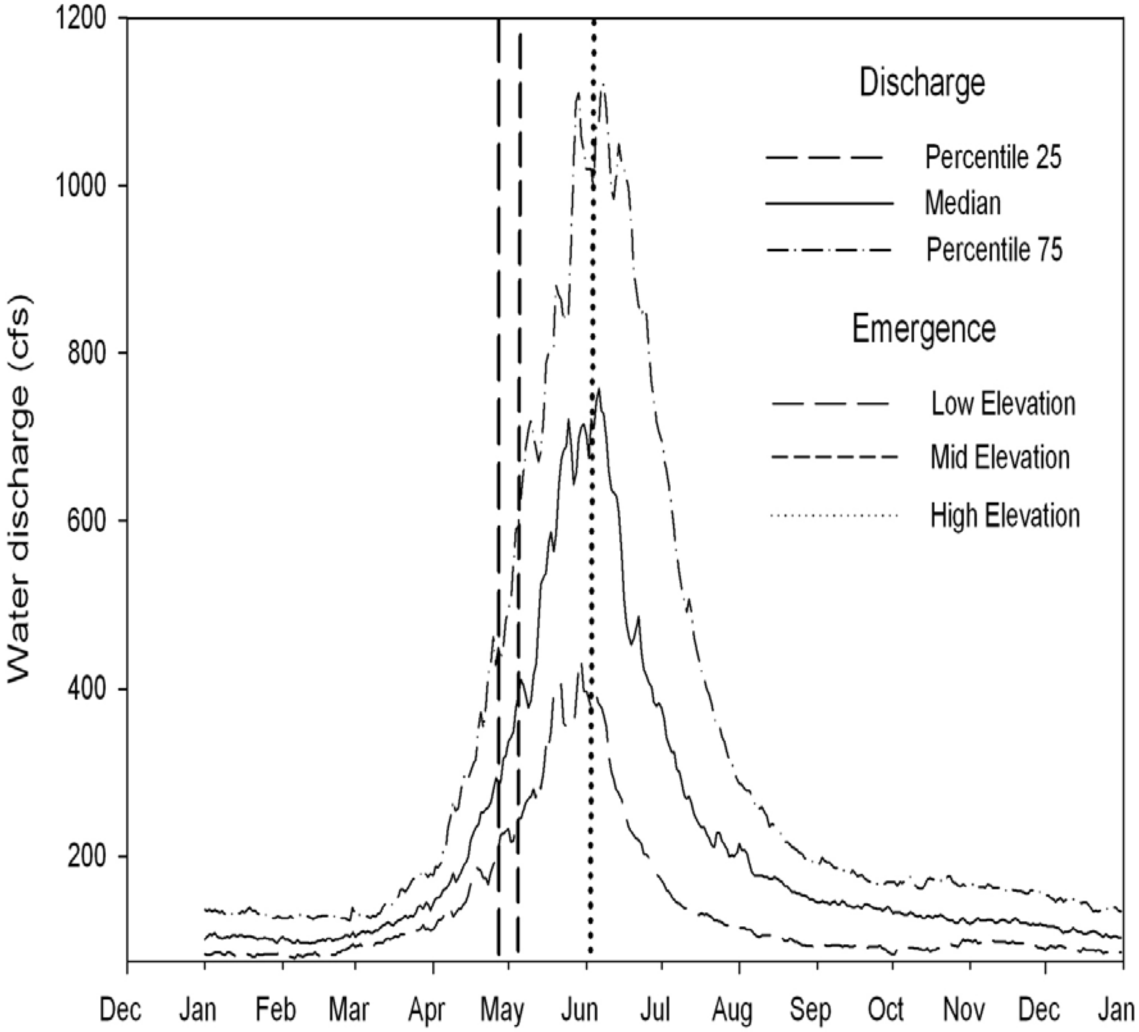

Figure 6 Predicted timing of peak brown trout fry emergence from the gravel at low, mid, and high elevation sites in the Logan River based on 2006-07 temperature data, in relation to the 25 percentile, median, and 75 percentile values of discharge (1971-2007).

Predicting Emergence

The timing of predicted peak emergence from the gravel varied significantly across elevations (Table 2; Figure 6). Peak brown trout emergence in low elevation areas was predicted to occur more than one 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 prior to peak flows. Finally, predicted peak brown trout emergence in high-elevation stream reaches did not occur prior to the median date of peak discharge, indicating that during most years, brown trout in these areas remain in the gravel during flood events.

Table 2 Predicted emergence times at three Logan River sites of varying elevation based 2006-07 water temperature data and a peak spawning date of 19 November, compared to the median and range of peak discharge (1971-2007).

		Incubation Period		Peak Discharge		
Site	Elevation (m)	Peak Spawning	Peak Emergence	Median	Range	
Low	1420	19-Nov	30-Apr	28-May	1 May -	16 June
Mid	1600	19-Nov	7-May	28-May	1 May -	16 June
High	2030	19-Nov	2-June	28-May	1 May	16 June

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 West stream may better explain the distributional limits of these ubiquitous invaders. We explored a wide range of potential limitations to the distribution of brown trout in our study stream and concluded that overwinter conditions and spring runoff likely 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), higher than where we typically encounter brown trout during summer electrofishing surveys, and indicating the potential for upstream invasion. We observed a decline in egg survival at higher elevation, cooler water sites, but did not document complete recruitment failure at these high sites, again indicating the potential for successful invasion at this life-stage. In light of our combined spawning and egg survival data, which indicate potential invasion to the egg hatching stage, our predictions of emergence timing emphasize that conditions between the egg hatching and emergence periods could possibly have the greatest influence on brown trout survival in high elevation stream reaches, and while direct evidence for the effect of streamflow on egg-to-fry survival is lacking, this may be an important determinant of invasion success.

Brown trout spawned from late October/early November through mid-December in the Logan River, which is considerably later than 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's elevation gradient, despite lower water temperatures (which delay incubation time; Stonecypher et al. 1994) at higher elevations. A spawning strategy adapted to survival in high elevation, cooler water areas may require that brown trout spawn considerably earlier in these areas such that fry emerge prior to peak streamflow in the spring (which will be discussed later). 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 likely originated from stocks adapted to relatively mild climates in Germany and Scotland (MacCrimmon and Marshall 1968; Lever 1996), and have only had a short period of time available to adapt a more favorable spawning strategy, their spawning timing appears to be maladapted to the cold temperatures and highly variable hydrologic conditions of high elevation mountain streams reaches (i.e., Fausch et al. 2001).

Because of the colder water and associated habitat conditions, we expected egg 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 is not expected to directly influence brown trout egg survival (Stonecypher et al. 1994), we considered it a surrogate for identifying the effect of other potential limiting factors such as anchor ice (Hirayama et al. 2002), which is difficult to quantify in the field (Doering et al. 2001) and is believed to significantly influence incubating eggs (cited by Kerr et al. 2002). Egg survival declined with increasing elevation, but this pattern may have been somewhat masked by the fact that 1) distances on the x-axis of the survival figures did not represent actual elevation differences, and 2) water temperature did not necessarily decline consistently with increasing elevation. In addition to elevation, sunlight and groundwater inputs likely influenced site-specific water temperature. However, while egg survival did decline with decreasing water temperatures, which generally patterned elevation, differences between low and high elevation areas were not as dramatic as we had expected. In fact, mean egg survival was far from zero at most sites during both years, indicating that conditions such as anchor ice are unlikely to influence overwinter egg survival at our sites. Similarly, Nuhfer et al. (1994) hypothesized minimal ice effects on recruitment when compared to influences of peak streamflow. The decline in hatching success we observed at low temperature, high elevation sites is likely due to longer incubation times, which result in longer exposure to other potentially lethal factors aside from temperature alone (Ojanguren and Brana 2003).

A number of studies have investigated the egg-to-fry survival of stream salmonids, but most have focused on the effects of deposited sediment (Hausle and Coble 1976; Olsson and Persson 1988; Levasseur et al. 2006a) and/or water chemistry (Lacroix 1985; Rubin and Glimsater 1996; Geist et al. 2006). To our knowledge, ours is the only study investigating differential egg survival along an elevational stream gradient. Despite our attempt to isolate other potential sources of egg mortality (by selecting physically similar sites among reaches), sediment deposition did influence survival at some of our sites, particularly in the tributaries. At these sites, sediment would sometimes accumulate in one or two boxes and cause low survival, while not affecting the others, only inches apart. We overcame this problem somewhat by doubling our sample size in 2007-08, which resulted in more precise estimates within sites. We did not attempt to quantify sedimentation within egg boxes because of the difficulty of accurately measuring sediment via simple, cost effective techniques (see Carling and Reader 1981; Levasseur et al. 2006b). Thus our results may have underestimated survival due to the potentially confounding effects of artificially trapping sediment within the boxes (i.e., Reiser et al. 1998). Note, however, that Harris (1973) documented that these boxes allowed silt and fine gravel to pass through, and overall, the patterns of sedimentation we observed among egg boxes and among sites appeared to be rather random (i.e., silt levels did not appear to be higher at high elevation sites). As such, we believe that they did not significantly influence our relative comparison across sites. While we postulated that our egg survival estimates were fairly representative of the study system, it is important to note that here we evaluated egg survival to the hatching stage. A significant proportion of development occurs between hatching and emergence (Crisp 1988), and the potential for further mortality of sac-fry and emerging fry is significant (e.g., MacKenzie and Moring 1988).

Another potential source of mortality between the sac-fry and emergence stage 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 washout of brown trout redds during high flow periods has been firmly established (Elliott 1976; Crisp 1989). In fact, Crisp (1989) documented a near complete washout of salmonid eggs buried at 5-10 cm depth during a 10-20 year flood event. Such displacement can cause significant mortality, particularly during stages at which eggs and fry are most susceptible to damage (Hayes 1949; Roberts and White 1992). Therefore, it is reasonable to expect that peak stream flows, which often exceed more than 10 times base flow levels in a mountain stream like the Logan River (e.g., $< 3\ m^3 \cdot s^{-1}$ base flow to $> 30\ m^3 \cdot s^{-1}$ peak) can cause substantial mortality to alevins incubating in the gravel during such events. In fact, Kondolf et al. (1991) suggested that brown trout were more successful than rainbow trout in eastern Sierra Nevada streams because they emerged from the gravel prior to peak spring flows. While we predicted emergence patterns similar to Kondolf et al. (1991) in low elevation reaches, in high elevation reaches (where we have documented brown trout spawning, but have not observed successful recruitment; this study), brown trout likely remain in the gravel during peak annual streamflow during most years. Our observations were limited by the short period (only one year) over which we had available water temperature data, as well as the single low-elevation gage 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 the literature and general patterns we observed, streambed movement and scour have the potential to substantially influence brown trout survival in high-elevation stream reaches.

Based on our observations (this study), the lack of successful brown trout recruitment in high elevation reaches limits their invasion success; while not ultimately determined by spawning site selection and intragravel conditions during the egg incubation period, invasion success may be dependent on the interaction between peak streamflow and emergence timing. Our results demonstrate that brown trout establish spawning areas in high elevation stream reaches; while egg survival is lower in these areas, overwinter conditions do not preclude hatching success. Therefore, we conclude that invasion to the egg hatching stage is possible in these high elevation stream reaches, highlighting the importance of the period between hatching and emergence where streamflow may significantly influence recruitment success. However, we did not specifically evaluate the effects of streamflow conditions on egg-to-fry survival. While an abundance of research has documented the relationship between peak streamflow and brown trout recruitment, we suggest that future work seek to identify more specific mechanisms of recruitment failure. A better understanding of the differential success of a fall-spawning life-history strategy along stream gradients will aide in identifying drivers of invasion success and better predict nonnative fish invasions in the future.

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APPENDIX

PREDATORY POTENTIAL OF INVASIVE BROWN TROUT (*SALMO TRUTTA*) IMPACT ON NATIVE BONNEVILLE CUTTHROAT TROUT (*ONCORHYNCHUS CLARKII UTAH*)

Introduction

Exotic fishes have the potential to influence the distribution and abundance of native fish in many systems via predation (Jackson et al. 2001; Ruzyki et al. 2003). One such predator, the brown trout (*Salmo trutta*), is considered one of the world's worst invaders due to significant ecological consequences resulting from its introduction and spread (Lowe et al. 2000). Introduced brown trout have repeatedly been reported to impact the diversity and abundance of fish species via predation, including, for example, native galaxiid fish communities in New Zealand streams (Townsend 1996), nongame fishes in Virginia (Garman and Nielsen 1982), and native suckers in California (Moyle and Marciochi 1975).

Brown trout have been naturalized throughout the United States (MacCrimmon and Marshall 1968; Lever 1996) and have displaced native trout in many Intermountain West stream reaches (Behnke 2002; de la Hoz Franco and Budy 2005). Presumed mechanisms driving displacement of cutthroat trout include competition (Wang and White 1994; McHugh and Budy 2005; Shemai et al. 2007), and predation (Behnke 2002). However, predation on other salmonids by brown trout has been little studied (Krueger and May 1991), and empirical evidence to date appears limited to a few observations in Eastern brook trout streams (e.g., Alexander 1977). In an Intermountain West stream where they co-occur with cutthroat trout, brown trout occupied a higher relative trophic position; however, cutthroat trout were not identified in the stomachs of brown trout and sample sizes and spatial extent of samples were somewhat limited (McHugh et al. 2008).

The accepted status of the brown trout as a predatory piscivore, combined with the paucity of evidence for predatory effects of exotic brown trout on native trout, highlight the need for further diet analysis to examine the predatory potential of stream-dwelling brown trout. The goal of this study was to quantify the potential consumption of imperiled native Bonneville cutthroat trout (*Oncorhynchus clarkii Utah)* by exotic brown trout in an Intermountain West stream where the two species co-occur. To do this, we conducted an investigation of brown trout diet composition across a large spatial and temporal scale in the Logan River, a native cutthroat trout stream in northern Utah.

Methods

The headwaters of the Logan River originate near the Utah-Idaho border in the Bear River Mountains, and the river flows southwest through northern Utah (Figure A.1) until it joins the Bear River, which ultimately drains into the terminal Great Salt Lake. The major tributaries to the Logan River include Temple Fork (1,745 m elevation) and Right Hand Fork (1,590 m elevation); both enter the river in locations where brown trout and cutthroat trout co-occur. The Logan River is a typical mountain stream, characterized by cooler water, steep gradient reaches in high elevations, transitioning to warmer water and lower gradient reaches at low elevations.

Native Bonneville cutthroat trout and introduced brown trout exhibit an allopatric distribution in the Logan River; high elevation areas are occupied by cutthroat trout, low elevation areas are occupied by brown trout, and a mid-elevation transition zone exists where the two species occur in sympatry (de la Hoz Franco and Budy 2005; McHugh and Budy 2005). Our study area included reaches dominated by brown trout, as well as areas containing brown trout and cutthroat trout at relatively similar densities. In addition to native Bonneville cutthroat trout and exotic brown trout, native mountain whitefish (*Prosopium williamsoni)*, native mottled sculpin *(Cottus bairdii)* and the occasional introduced rainbow trout (*Oncorhynchus mykiss*) were also present in our study area.

To determine whether brown trout were piscivorous throughout the Logan River, we collected fish via backpack electrofishing at haphazardly selected sites spanning the range of brown trout distribution in the Logan River and the tributary Right Hand Fork from September through November 2006. We counted and released nontarget species at the site of capture, and kept and returned brown trout to the lab for processing. Because piscivory is strongly influenced by predator size (Garman and Nielsen 1982), we only kept fish ≥200 mm, the minimum size attained by age-2 fish during the summer sampling period. We examined the stomach contents of captured brown trout in the laboratory and identified them as invertebrates, fish, or organic matter. We identified all fish and fish remains in stomachs to species using standard fish identification methods and our knowledge of fish species composition in the Logan River. We excluded fish with empty stomachs from our sample for data analysis purposes.

To further quantify the degree of brown trout consumption of Bonneville cutthroat trout, we sampled via backpack electrofishing in reaches of the Logan River and the tributary Temple Fork where brown trout and cutthroat trout are known to exist in relatively equal densities (1,600-1,800 m elevation; de la Hoz Franco and Budy 2005).

We sampled in late July and early August, during the timing of juvenile cutthroat trout emergence from the gravel at spawning locations. We only sampled when the presence of juvenile cutthroat trout was visually confirmed in the general location of each sample site. We counted all nontarget species captured and returned them to the site of capture. We euthanized and retained a subsample of brown trout from each location for laboratory diet analysis (26 % overall), extracted stomach contents via gastric lavage techniques (Hartleb and Moring 1995) and preserved stomach contents in 90% ethanol for later processing. In the laboratory, we identified stomach contents as invertebrates, fish, or organic matter. We identified all fish to species and recorded the weight (blot-dried) of items within each stomach content category. Fish with empty stomachs were not included in data analysis.

Based on clear differences between brown trout diet composition in samples collected in the mainstem of the Logan River relative to those collected in the tributaries, we separated diet data into two categories for further analyses: 1) mainstem, and 2) tributary samples. We conducted a two-sample t-test (Zar 2007) to compare mean total length between the mainstem and tributary fish and determine whether differences in diet composition could be attributed to fish size.

Results

We collected 200 adult brown trout (200-463 mm total length; ≥ age 2) between August and October of 2006. Invertebrates were the most common diet item, occurring in 67% of stomachs, followed by fish (16.5% occurrence), rocks (7.5% occurrence), and organic matter (5% occurrence; Figure A.2). Fish occurred much more frequently in the diets of brown trout from the mainstem of the Logan River (21.3%) than in the tributary site (7.1%; Figure A.2). All fish were readily identified in the diet as sculpin.

We collected a total of 169 adult brown trout (215-390mm total length; ≥ age 2) in the Logan River and the tributary Temple Fork during July and August 2007 in areas where brown trout and cutthroat trout co-occurred. Of these, we found no cutthroat trout and only one juvenile brown trout in diets. All other fish consumed were identified as sculpin.

Of the 169 brown trout we collected, 118 (69.8%; ≥ 200mm, ≥ age 2) were from the mainstem of the Logan River. Sculpin abundance varies considerably among the Logan River and its tributaries; the mainstem of the river contains much higher sculpin abundances than the tributaries. Of these mainstem fish, invertebrates were the most commonly occurring diet item, while fish (primarily sculpins) were the most important diet item by weight (Figure A.3). Similar to summer 2006 data, fish occurred much more frequently in the diets of brown trout in the mainstem of the Logan River than in the tributary site (Figure A.3). Brown trout sampled in the tributary site consumed mostly invertebrates and few fish (Figure A.3). Mean total length of brown trout sampled in the mainstem did not differ from that of fish sampled in the tributaries ($p=0.376$; $df=167$), affirming that the contrasting piscivory rates were unlikely due to size differences. Instead, this pattern of piscivory is consistent with sculpin density estimates at these sites, indicating that brown trout consume more sculpins where they are more readily available.

Brown trout with fish observed in their stomachs ranged in size between 235-390 mm total length (Figure A.4), indicating that a shift to piscivory occurred at a size of around 235 mm or greater. The proportion of fish in the diet increased steadily with predator size between the 230 mm and 300 mm size classes, above which it remained high in most size classes.

Discussion

In this study, we analyzed the diets of 369 adult brown trout in areas throughout the Logan River, including 169 fish captured in the confirmed presence of juvenile cutthroat trout. We found no evidence of predation on cutthroat trout by brown trout, and found only one case of cannibalism by brown trout. However, we did observe evidence of substantial brown trout predation on another native fish species, the mottled sculpin.

Our results answer some key questions posed by McHugh et al. (2008) concerning the potential for brown trout to impact Bonneville cutthroat trout via predatory effects. Their data indicated that despite the considerable diet overlap between the two species, brown trout consume more fish and occupy a higher trophic level than cutthroat trout, suggesting the possibility that brown trout prey on cutthroat trout. However, similar to our study, they did not observe any direct evidence of predation. In addition to collecting a much larger sample of fish (369 vs. 35), we targeted brown trout of a larger size (mean TL=285 mm) than those collected by McHugh et al. (2008; mean TL=192 mm) and purposefully collected brown trout diet samples from sites where they were sympatric with cutthroat trout, based both on direct observations and previous knowledge of the system (Budy et al. 2007). Prior research has shown that brown trout become highly piscivorous at larger sizes (≥ 280mm; Garman and Nielsen 1982); the fact that we targeted larger fish almost certainly explains the higher level of piscivory observed in our study compared to McHugh et al. (2008).

Given the high level of piscivory observed in brown trout in the literature (cited in the introduction) and in our data, we were surprised by the lack of evidence for predation on cutthroat trout, particularly when sampling in areas with confirmed observations of juvenile cutthroat trout. However, the lack of piscivory is not uncommon in stream dwelling brown trout populations within their native range (Steingrimsson and Gislason 2002; Fochetti et al. 2003; Kara and Alp 2005) and may be influenced by the abundance of other food sources in streams. The Logan River is a very productive system that supports high densities of aquatic insects (de la Hoz Franco and Budy 2005). In addition, sculpin are abundant in many areas of the river, and their sedentary bottom-dwelling behavior may make them more susceptible to predation by brown trout than juvenile trout and mountain whitefish, which occupy shallow water stream habitats during potentially vulnerable, early life-stages (Pettit and Wallace 1975; Heggenes 1988). Furthermore, because sculpin density is believed to be relatively similar to the density of mountain whitefish and lower than the density of cutthroat trout in the Logan River (Budy et al. 2007), the lack of the latter two species in the diet of brown trout indicates that brown trout may be selectively foraging on sculpin.

While we did not document direct evidence of predatory effects of brown trout on cutthroat trout, predation could potentially be a mechanism, combined with interspecific competition, that caused the displacement of cutthroat trout by invading brown trout in the past. Because of the established allopatric distribution of brown trout and cutthroat trout in the Logan River, predation on cutthroat trout may only take place on a small scale where both species co-occur, making it difficult to identify using our sampling efforts. Also, field experiments have indicated strong competitive effects of brown trout on cutthroat trout in the Logan River and other similar systems (McHugh and Budy 2005; Shemai et al. 2007). Therefore, we suggest a strong precautionary approach when considering potential effects of brown trout on native trout, particularly during the initial stages of brown trout invasions. In addition, the abundance of sculpin observed in brown trout diets indicates the potential for predatory impacts on another native fish as well as ecosystem-level effects of predation similar to those observed in other systems (e.g., Power 1990). The importance of forage species such as sculpin to the growth of brown trout and subsequent influences on invasion success should be considered.

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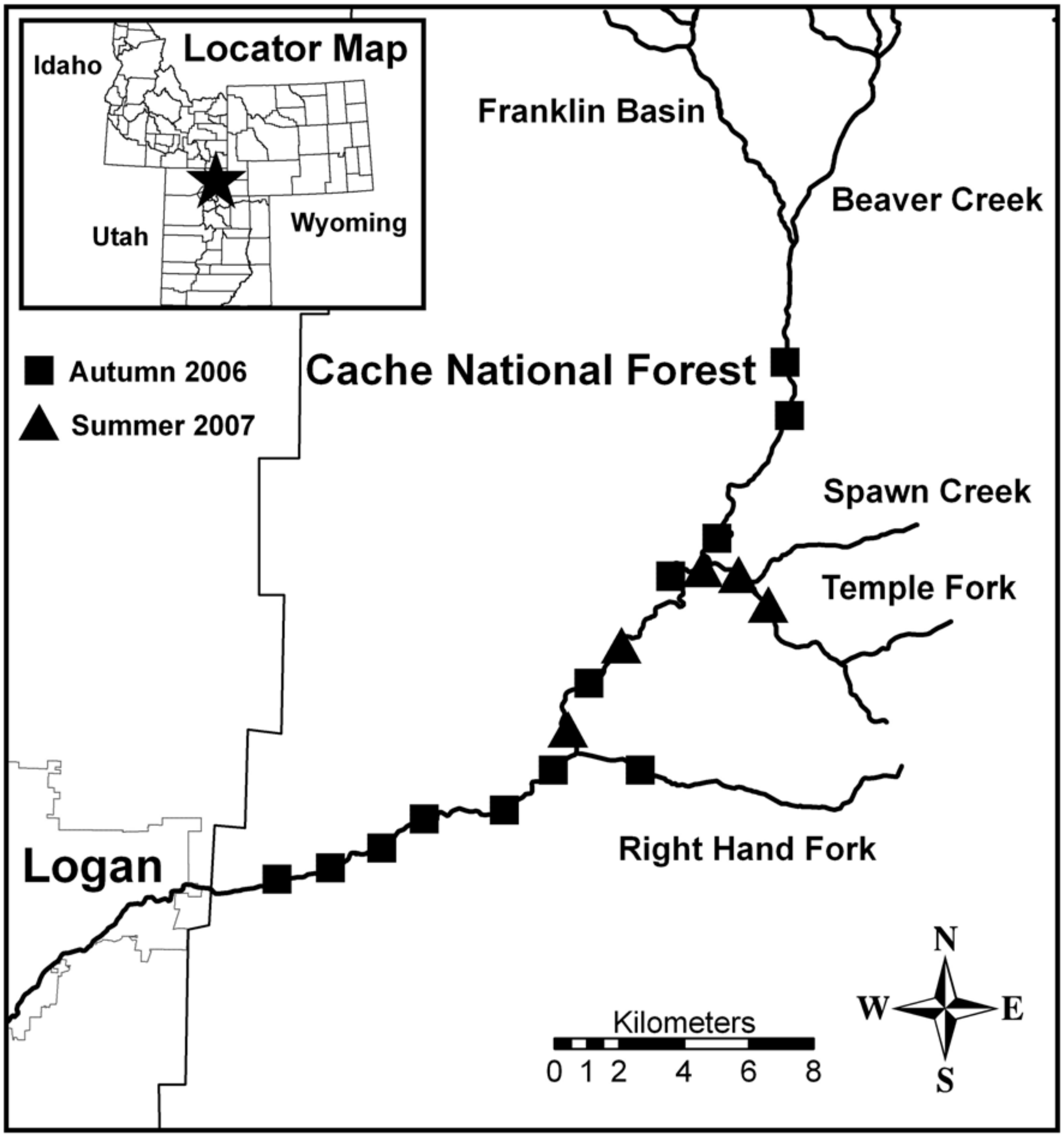

Figure A.1 Map of the Logan River and its tributaries in northern Utah. Symbols represent site locations for the each of the diet sampling periods.

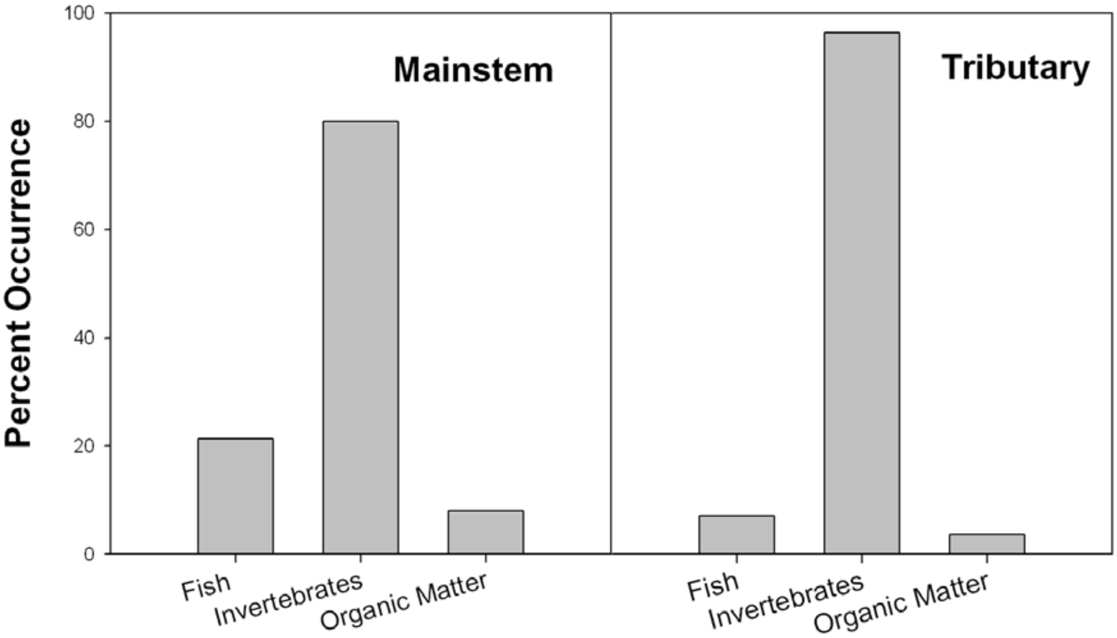

Figure A.2 Percent occurrence of different food types identified in the stomachs of brown trout from the Logan River and the tributary Right Hand Fork during the fall 2006 sampling period.

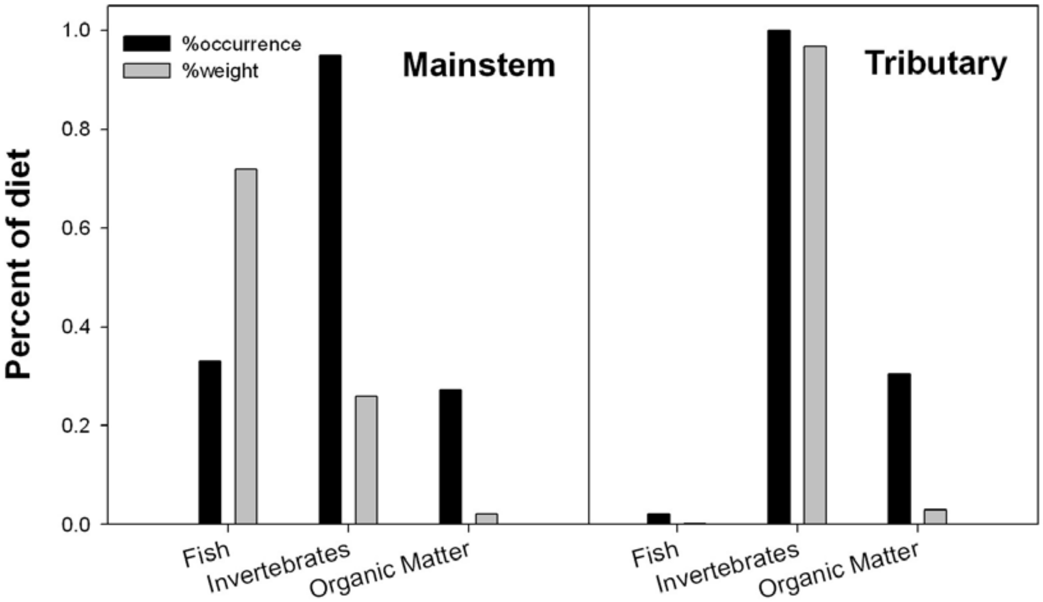

Figure A.3 Percent of total brown trout diet by occurrence and by weight for each of three different food types identified in stomachs in the Logan River and the tributary Temple Fork during the summer 2007 sampling period.

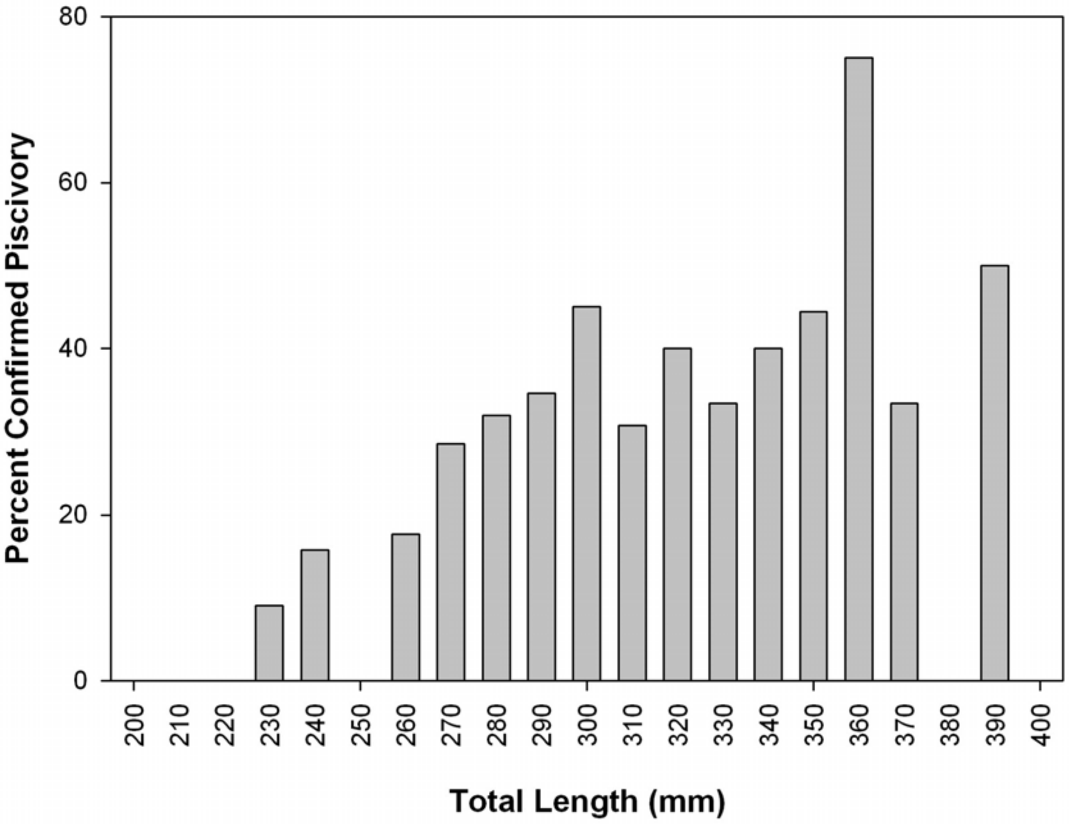

Figure A.4 The percent of brown trout confirmed as being piscivorous (fish found in stomachs) for each 10 mm TL size class of brown trout captured in the mainstem of the Logan River during fall 2006 and summer 2007 sampling.