Ecology of Freshwater Fish 2014

ECOLOGY OF
FRESHWATER FISH

Demographic changes following mechanical removal of exotic brown trout in an Intermountain West (USA), high-elevation stream

W. Carl Saunders[1], Phaedra Budy[1,2,3], Gary P. Thiede[1]
[1]Department of Watershed Sciences, Utah State University, Logan, UT USA
[2]US Geological Survey, Utah Cooperative Fish and Wildlife Research Unit, Logan, UT USA
[3]Ecology Center, Utah State University, Logan, UT USA

Accepted for publication March 22, 2014

Abstract – Exotic species present a great threat to native fish conservation; however, eradicating exotics is expensive and often impractical. Mechanical removal can be ineffective for eradication, but nonetheless may increase management effectiveness by identifying portions of a watershed that are strong sources of exotics. We used mechanical removal to understand processes driving exotic brown trout (*Salmo trutta*) populations in the Logan River, Utah. Our goals were to: (i) evaluate the demographic response of brown trout to mechanical removal, (ii) identify sources of brown trout recruitment at a watershed scale and (iii) evaluate whether mechanical removal can reduce brown trout densities. We removed brown trout from 2 km of the Logan River (4174 fish), and 5.6 km of Right Hand Fork (RHF, 15,245 fish), a low-elevation tributary, using single-pass electrofishing. We compared fish abundance and size distributions prior to, and after 2 years of mechanical removal. In the Logan River, immigration to the removal reach and high natural variability in fish abundances limited the response to mechanical removal. In contrast, mechanical removal in RHF resulted in a strong recruitment pulse, shifting the size distribution towards smaller fish. These results suggest that, before removal, density-dependent mortality or emigration of juvenile fish stabilised adult populations and may have provided a source of juveniles to the main stem. Overall, in sites demonstrating strong density-dependent population regulation, or near sources of exotics, short-term mechanical removal has limited effects on brown trout populations but may help identify factors governing populations and inform large-scale management of exotic species.

Key words: mechanical removal; population response; density dependence; *Salmo trutta*; invasive species

Introduction

Anthropogenic activities have increased the rate of invasion by cosmopolitan species, leading to large-scale biotic homogenisation of fauna (Olden & Poff 2003; Olden et al. 2004). As a result, the introduction of exotic species constitutes one of the greatest threats to native species worldwide (Vitousek et al. 1997). This biotic homogenisation is particularly evident in freshwater ecosystems, where historic stocking of sport fish facilitated the spread of many exotic species across the globe. For example, rainbow trout *Oncorhynchus mykiss* and brown trout *Salmo trutta*, widely introduced as sport fish, have devastated native cold-water fisheries and altered ecosystem dynamics throughout the world. As a result, these two species have recently been identified as among the worst 100 invasive species by the International Union for Conservation of Nature and more recently have been placed among the top 30 (McIntosh et al. 2012). In the western United States, the introduction and subsequent naturalisation and spread of exotic brook trout *Salvelinus fontinalis*, rainbow trout and brown trout have had direct negative effects on native

Correspondence: W. C. Saunders, Department of Watershed Sciences, Utah State University, Logan, UT 84322-5210, USA. E-mail: carl.saunders@usu.edu

doi: 10.1111/eff.12143

Ecology of
FRESHWATER FISH

cutthroat trout *O. clarkii* through competition and hybridisation with native species or predation upon native species. As a result of these negative interactions with exotic species, and large-scale habitat alteration, many subspecies of native cutthroat trout now occupy only a portion of their historic range (Coffin & Cowan 1995; Young et al. 1996; Shepard et al. 2005; Williams et al. 2011).

In response to these detrimental effects on native fishes, there has been a recent focus on efforts to remove exotic salmonids for conservation and restoration purposes. Density-dependent responses and the potential for population dynamics to be strongly driven by movement (Riley & Fausch 1995), however, are two primary factors that determine the ultimate success of efforts to remove exotic salmonids. When only partial removal is achieved, higher juvenile survival or recruitment rates, driven by density-dependent processes, can compensate for population losses (Einum & Nislow 2005; Lobon-Cervia et al. 2011). However, density-dependent population regulation can be difficult to identify in observational field studies owing to high annual variability in abundance and the potential for multiple mechanisms for population regulation operating at a given time (Jenkins et al. 1999). Populations that demonstrate density-dependent survival or recruitment may also serve as sources of exotics to larger watersheds, if individuals emigrate from natal waters when population densities exceed carrying capacity (Dieterman & Hoxmeier 2011; Kvingedal & Einum 2011). Furthermore, high rates of individual movement, and long-distance dispersal or ranging behaviour, characteristic of many stream fishes (Dunham & Rieman 1999; Falke & Fausch 2010) may lead to rapid recolonisation following removal efforts (Peterson & Fausch 2003).

Two of the most common methods for removing exotic fishes are chemical toxicants (Meronek et al. 1996; McClay 2000) and mechanical removal via electrofishing (Thompson & Rahel 1996; Kulp & Moore 2000; Meyer et al. 2006). However, complete eradication is very costly (Koehn et al. 2000), and overall has met with varying rates of success (Meronek et al. 1996). Furthermore, using piscicides for eradication can impact nontarget fish species and invertebrate communities (Finlayson et al. 2010). While mechanical removal typically fails to completely eradicate the target species (Thompson & Rahel 1996; Meyer et al. 2006), in systems where capture probabilities are high (Saunders et al. 2011), mechanical removal can remove a substantial portion of an exotic population at a large spatial scale for a fraction of the effort of full-scale eradication programs. A benefit of this approach is that collection of data on population structure from sampled fish may provide a means to identify locations where high rates of dispersal resulting from strong density-dependent survival or recruitment serve as a source of individuals (e.g. propagule pressure) that facilitate expansion into other portions of a watershed. By focusing intensive management efforts on these ‘hot spots’, it may be possible to suppress the colonisation and establishment of exotic salmonids at greater spatial scales, allowing native trout to persist at a watershed scale without requiring complete eradication (Moyle & Light 1996; Levine et al. 2004).

Targeted management of exotic species may be particularly relevant for Bonneville cutthroat trout *O. c. utah*, which were historically distributed throughout the Bonneville basin. Currently, this important subspecies of cutthroat trout is often restricted to high-elevation reaches (Behnke 1992), in part, through competition with, and predation by, exotic species (McHugh & Budy 2005, 2006). The Logan River, a high-elevation stream located in northern Utah, USA, currently sustains one of the largest remaining populations of Bonneville cutthroat trout. Lower elevation sections of the watershed are dominated by brown trout, which occur in some of the highest subadult and adult densities reported in the world (Budy et al. 2007, 2008; McIntosh et al. 2012). At these high densities, strong intercohort interactions (i.e. competition and predation) may result in high rates of mortality and emigration of juvenile fish. These intercohort interactions may regulate fish density and population age structure, which may create a source of emigrating brown trout that drive the expansion into higher elevation sections of the watershed. As a result, there has been recent interest in understanding the effect of reducing brown trout densities in local areas (e.g. tributaries) in the Logan River drainage to eliminate a potential source of brown trout in the lower river, reduce the potential for brown trout to expand into high-elevation reaches of the main stem and re-establish Bonneville cutthroat trout populations in important spawning and rearing habitat in lower elevation reaches.

We conducted a large-scale manipulation by mechanically removing exotic brown trout in two study sections of the Logan River during 2009 through 2011 to: (i) track rapid demographic responses to removal efforts; (ii) identify sections of the river that serve as sources of exotic brown trout; and (iii) evaluate the efficacy of single-pass removal to reduce densities of exotic brown trout. We compared fish abundance and size distributions prior to (7 years) and after 2 years of mechanical removal of brown trout from tributary and mainstem habitats. We present evidence for substantial changes in brown trout size distributions following mechanical removal and discuss these findings with implications for the management of exotic salmonids in lotic systems.

Methods

Study area

The Logan River originates in south-eastern Idaho in the Bear River Mountain Range and runs 64 km to its confluence with the Bear River in northern Utah. The climate throughout the Logan River watershed is characterised by cold, snowy winters and hot, dry summers. As a result, the hydrograph is dominated by spring snowmelt floods (ca. 16 $m^3 \cdot s^{-1}$) and base flow conditions that persist from August to April. Average summer temperatures range from approximately 9 °C (headwaters and tributaries) to 12 °C (mid-elevation main stem), and diel fluctuations can reach 9 °C (de la Hoz Franco & Budy 2004). In addition to endemic Bonneville cutthroat trout, resident fish in the Logan River include brown trout, stocked, sterile rainbow trout, brook trout, mountain whitefish *Prosopium williamson* and mottled sculpin *Cottus bairdii*. More detailed information describing the fish community of the Logan River is available in the study described by Budy et al. (2007, 2008).

During 2009 through 2011, we mechanically removed brown trout from 5.6 km of Right Hand Fork (hereafter RHF removal reach), a primary tributary to the Logan River (Fig. 1). RHF supports a robust population of naturalised brown trout, but no other fish species. A series of cascades located 500-m upstream of the confluence with the Logan River likely historically limited immigration from the Logan River at all but the greatest discharges. Further, Utah Division of Wildlife Resources and USDA Forest Service, during September 2010, fortified one of these cascades to construct a barrier impassible to all fish. As a result, most of the RHF removal reach was inaccessible to colonists for the duration of the study. The RHF removal reach is characterised by riffle-pool habitat and averages 4.3 m (SE = 0.2) wetted width at base flow (ca. 0.2 $m^3 \cdot s^{-1}$). Above the removal reach, RHF enters a steep canyon which experiences overland flows only during peak runoff in the spring and is naturally fishless (Fig. 1). Below the fishless portion, there are no perennial or fish bearing tributaries.

We also removed brown trout from 2.0 km of the mainstem Logan River downstream of RHF (hereafter Logan River removal reach). The Logan River removal reach is confined at the upstream and downstream extent by small hydroelectric impoundments that we hypothesised may serve as sources for brown trout colonisation in the watershed. The fish community found in the Logan River removal reach consists of all native and exotic fishes present in the watershed with the exception of brook trout. The Logan River removal reach is predominantly riffle and glide habitat with an average wetted width of 13.6 m (SE = 3.3) at base flow (ca. 3 $m^3 \cdot s^{-1}$).

These two removal reaches were chosen because of the following reasons: (i) both reaches contain a 100–200 m annual monitoring site sampled annually since 2003, providing detailed historical context for

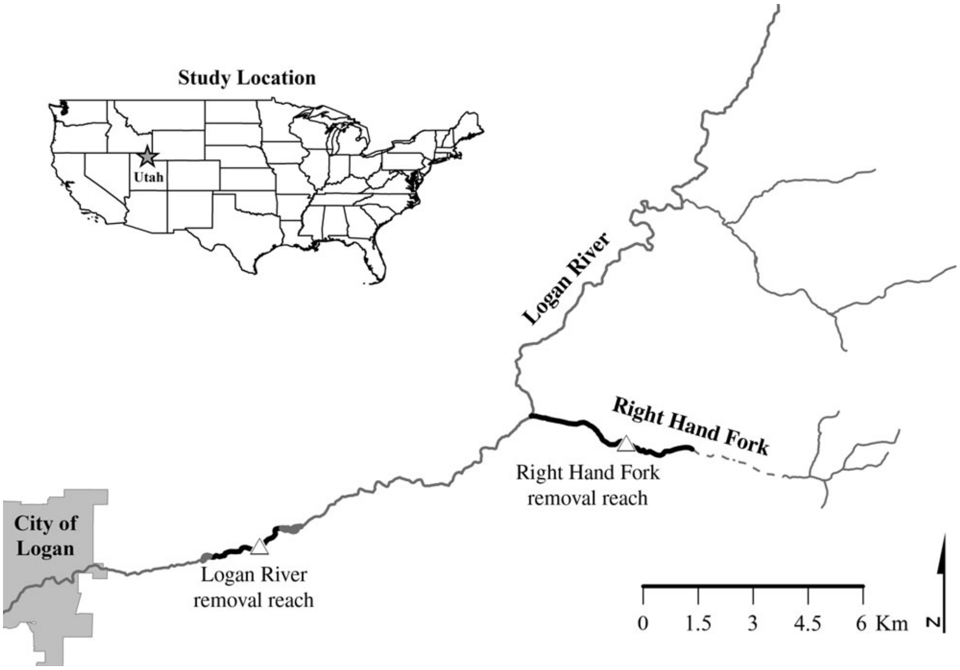

Fig. 1. Map of study area in northern Utah showing removal reaches (in black) on Right Hand Fork (RHF) and the Logan River and annual monitoring sites (open triangles within removal reaches, see Budy et al. 2007). Intermittent, fishless portion of RHF is represented by the dashed line.

evaluating the response to mechanical removal (hereafter RHF and Logan River annual monitoring sites); and (ii) both provide necessary contrast in fish densities and proximity to sources of brown trout recruitment from which to draw conclusions about the effectiveness of mechanical removal and managing exotic stream salmonids. The RHF annual monitoring site is a 100-m reach located 3.13 km above the confluence with the Logan River. The Logan River annual monitoring site is a 200-m reach located 1.48 km above the inlet to the Second Dam impoundment.

Potential responses to mechanical removal

Based on the proximity of the removal reaches to sections of the watershed that serve as sources of brown trout recruits, we hypothesised that single-pass electrofishing removal of brown trout could influence subsequent populations in four potential ways.

I Mechanical removal may have no detectable effect on the subsequent abundance if capture probabilities are too low or brown trout populations in the removal sections compensate for harvest mortality (i.e. mechanical removal) through reduced natural mortality (Meyer et al. 2006). Additionally, in the Logan River (no immigration possible to Right Hand Fork), brown trout may compensate for harvest mortality through immigration from nearby impoundments (Peterson & Fausch 2003).

II Mechanical removal may reduce brown trout abundance, such that the size distributions of brown trout in subsequent years reflect the size selectivity of electrofishing gear (Dolan & Miranda 2003).

III Density dependence is a well-established driver of brown trout populations (Lobon-Cervia et al. 2011), and mechanical removal may reduce density-dependent factors limiting recruitment, resulting in increased juvenile abundance in subsequent years.

IV If immigration rates to the Logan River removal reach are high, as has been documented for many stream fishes (Gowan & Fausch 1996; Lintermans 2000), and exceed removal rates, we would expect larger, more mobile individuals to represent a larger portion of the postremoval population as a result of recolonisation following removal.

Field sampling

During 2009 through 2011, we conducted single-pass electrofishing during base flow conditions (August–September) to remove exotic brown trout. We sampled all available habitats in the RHF removal reach during all years and in the Logan River removal reach during 2010 and 2011. However, during 2009 in the Logan River removal reach, we sampled only 1.3 km owing to logistical constraints. Throughout the RHF removal reach, we used a single backpack electroshocker (150–300 V, 45–60 Hz, 0.5–1.0 A; model LR 12b or LR 24; Smith-Root, Inc., Vancouver, WA, USA) to collect fish, whereas in the larger Logan River removal reach, we used a canoe-mounted electrofishing unit (200–400 V, 45 HZ, 2–4 A; model GPP 2.5; Smith-Root, Inc.). During 2009–2011, we conducted sampling at annual monitoring sites immediately prior to single-pass mechanical removal to ensure consistency with previous sampling at these sites. We measured total length (nearest 1 mm) and weight (nearest 0.1 g) for all fish, after which all brown trout were euthanised and all other fish were returned to the approximate location they were collected.

Data analysis

Our analysis focused on detecting large-scale changes in abundance of brown trout, and short-term changes in population size structure of brown trout following single-pass mechanical removal. To quantify the short-term response of brown trout populations to mechanical removal, we estimated age-1 and older abundance of brown trout and quantified population size structure for the entire removal reach during 2009 through 2011. We also contrasted these data with the range of natural variability observed during 2003–2009 at annual monitoring sites. Removal estimates for age 1 and older fish, for which capture probability was relatively high ($P \geq 0.45$), can produce accurate estimates of fish abundance when heterogeneity in capture probability owing to fish size is accounted for and data are pooled (across years in the current study) to increase sample size (Saunders et al. 2011). As a result, estimates of age-1 and older brown trout provide a useful means to evaluate the response to removal efforts. In contrast, age-0 fish (<100 mm) are not sampled efficiently with single-pass electrofishing (ca. 25% capture probability), and thus removal estimates of capture probability and abundance are frequently biased (Peterson et al. 2004b; Rosenberger & Dunham 2005). Therefore, we did not estimate abundance of age-0 fish, but rather use total catches of this age class as a relative abundance index to compare across years. Capture probabilities for age-0 fish were expected to vary little among years, as sampling was consistently conducted during base flow conditions, instream habitat changed little during the course of the experiment (W. C. Saunders, unpublished data), and electrofishing crews were consistently lead by a supervisor with >3 years of experience sampling removal reaches.

To evaluate whether mechanical removal reduced brown trout abundance, we used age-specific capture probabilities estimated from annual monitoring data (Budy et al. 2007, 2008) to determine brown trout abundance for age-1 and older fish inhabiting the removal reach during 2009 through 2011. We pooled data from the yearly sampling at annual monitoring sites to estimate an average, single-pass, capture probability for age-1 through age-3 and older fish at either site using the Huggins closed capture estimator (Huggins 1989) in Program MARK (White & Burnham 1999). By pooling data across the 9 years of sampling, we averaged across 9 years of capture data ($N = 2174$ fish for RHF and 2072 for Logan River removal reaches) to integrate variability associated with different discharges and sampling crews. Fish ages were determined based on otolith verified length-at-age relationships for RHF and the Logan River (Budy et al. 2008). We then used AIC_C (Akaike information criterion corrected for finite sample sizes) to select the most parsimonious model from a set of four *a priori* models, where capture probability was: (i) constant among fish and passes, (ii) influenced by behavioural responses to subsequent electrofishing passes, (iii) dependent on individual fish length, and (iv) influenced by both behavioural effects and fish length (Saunders et al. 2011).

We then used capture probability estimates for the median length fish in each of the four age classes (Table 1), and the single-pass removal data, to estimate the abundance of brown trout present in the Logan River and RHF removal reaches during 2009 through 2011. We used the delta method (DeGroot & Schervish 2002) to derive 95% log-normal confidence intervals for the number of fish inhabiting removal reaches from the standard error of the 9-year average capture probability. We judged significance of removal efforts to alter fish abundance based on non-overlapping 95% confidence intervals for age-1 through age-3 and older separately.

Table 1. Summary of single-pass electrofishing removal efforts conducted on Right Hand Fork and the Logan River during 2009 and through 2011. Capture probability (SE) represents the probability of capturing the median length fish for a given age class with a single pass of electrofishing. Capture probability range (range) represents the range in annual capture probabilities for each age class during annual monitoring 2003–2009.

	Fish removed					
Age class	2009	2010	2011	Capture probability	SE	Range
Right Hand Fork						
Age-0	406	1844	474	–	–	–
Age-1	1488	1614	2684	0.45	0.024	0.29, 0.7
Age-2	2549	1603	1495	0.63	0.024	0.47, 0.84
Age-3 and older	383	392	313	0.74	0.028	0.61, 0.90
Logan River						
Age-0	39	173	107	–	–	–
Age-1	522	700	454	0.50	0.023	0.31, 0.67
Age-2	154	714	172	0.76	0.012	0.58, 0.86
Age-3 and older	410	596	133	0.90	0.01	0.79, 0.95

We compared abundance estimates for the entire RHF and Logan River removal reaches for 2009 through 2011 to evaluate changes at the reach scale. We also used data from the RHF and Logan River annual monitoring sites to evaluate the response to manual removal within the range of natural variability observed during 2003–2009. For each removal reach, we compared length-frequency data among years to evaluate changes in population size structure and used a two sample Kolmogorov–Smirnov test, to examine statistical differences in the size distribution of populations (Sokal & Rohlf 1995). We pooled across all fish capture data and constructed annual length-frequency distributions for 2009 through 2011 using 10-mm size bins separately for the RHF and Logan River removal reaches. To compare postremoval (i.e. 2010 and 2011) size distributions to preremoval data (i.e. 2003–2009) at annual monitoring sites within each removal reach, we compared annual size distributions with a two sample Kolmogorov–Smirnov test and applied a Bonferroni correction for multiple comparisons. We conducted all statistical analyses using SAS 9.2 (SAS 2008) and evaluated all significant differences at the $\alpha = 0.05$ level.

Results

Following mechanical removal during 2009–2011, the age structure of brown trout populations in both tributary (RHF) and main stem (Logan River) habitats shifted temporarily towards a greater proportion of smaller, juvenile fish. In the RHF removal reach, we observed a large brown trout recruitment pulse following the initial removal effort, which exceeded the range of variability observed at annual monitoring sites during 2003–2009. However, a similar recruitment event was not observed in the Logan River removal reach. Overall, we observed strongly contrasting population age structures between the RHF and Logan River removal reaches. In the RHF removal reach, 95% of the brown trout, both before and after mechanical removal, were <3 years of age, whereas the Logan River removal reach supported large proportions of age-3 and older brown trout during 2009 (26%) and 2010 (21%), but not during 2011 (10%).

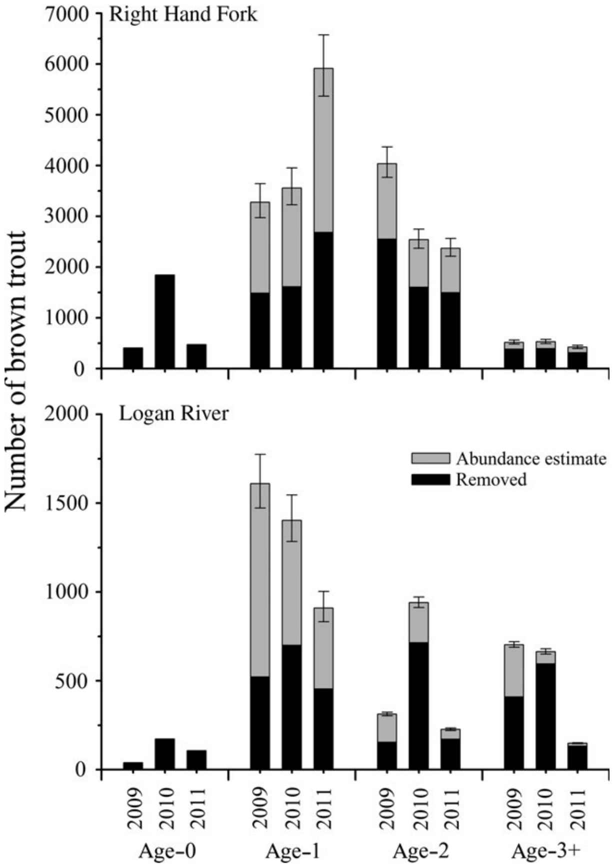

Fig. 2. Number of brown trout estimated to be present (grey bars) and removed during annual single-pass electrofishing removal (black bars) during 2009 through 2011 in the Right Hand Fork (top panel) and Logan River (bottom panel) removal reaches. Abundance estimates and the number of brown trout removed are presented separately for age-0 through age-3 and older (age-3 +) individuals. Error bars are 95% log-normal confidence intervals for the abundance of brown trout in each age class. Abundance estimate for the Logan River removal reach in 2009 corresponds to the estimated brown trout abundance for the entire removal reach, whereas the number of brown trout removed corresponds only to the 1.3 km sampled that year (see text).

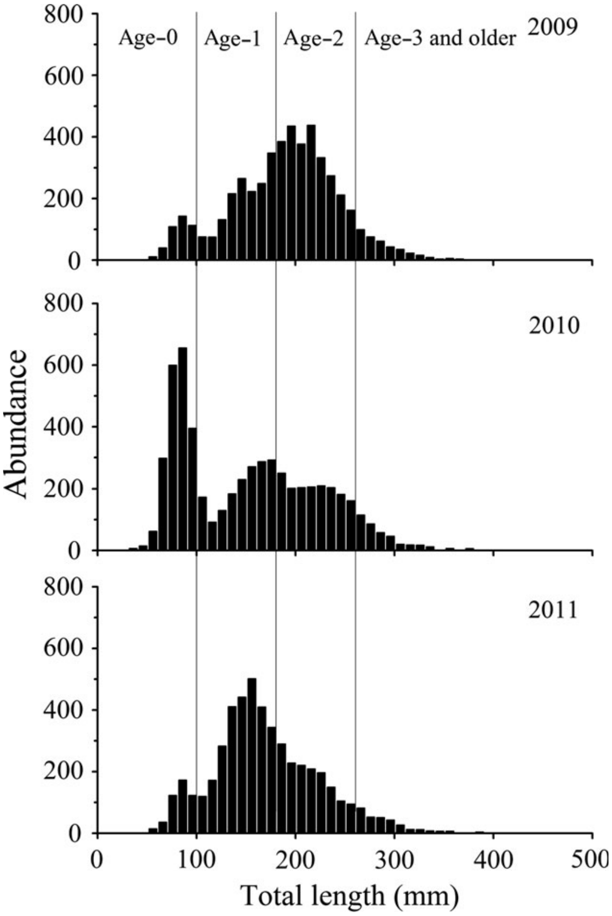

Fig. 3. Length-frequency distribution for brown trout removed from Right Hand Fork removal reach during 2009 through 2011. Vertical bars designate the size range for age classes (see Methods).

Right Hand Fork removal reach

We removed 4826 brown trout from the 5.6-km RHF removal reach during 2009 [0.2 fish m^{-2}, 581 technician hours (Th) of effort], 5453 (0.22 fish m^{-2}, 757 Th) during 2010, and 4966 (0.20 fish m^{-2}, 720 Th) during 2011 (Fig. 2). Although the total number of brown trout removed was similar during 2009–2011, the age distribution of brown trout in the RHF removal reach shifted significantly towards juvenile fish (age-0 and age-1) during 2010 and 2011 ($D_{2009\text{–}2010} = 0.27$, $P < 0.001$; $D_{2009\text{–}2011} = 0.24$, $P < 0.001$; Fig. 3). During 2009, age-2 brown trout (180–260 mm) was the most common age class (ca. 44% of the brown trout population), based on estimated fish abundances (Fig. 2). However, during 2010 and 2011, age-0 and age-1 fish cumulatively comprised, on average, 74% of the population and age-2 brown trout comprised, on average, only 22% of the population. Further, the abundance of age-2 brown trout in the RHF removal reach (Table 1) was reduced by 37% in 2010 and 41% in 2011, relative to pre-removal (2009) abundances (Fig. 2). In contrast, abundance of the cohort born immediately following the initial mechanical removal (i.e. 2010) was greater than previously observed in RHF and remained high for the duration of the study. Age-0 (<100 mm) brown trout were 4.5 times more abundant during 2010, and age-1 brown trout (100–179 mm) were 1.8 times more abundant during 2011 than during 2009.

The RHF annual monitoring site demonstrated a greater proportion of juvenile brown trout than the removal reach, but overall, there was a similar shift towards more age-0 and age-1 brown trout following mechanical removal. In general, natural, annual variation in brown trout abundance and age structure was low at the RHF annual monitoring site prior to conducting mechanical removal (Fig. 4). During 2010,

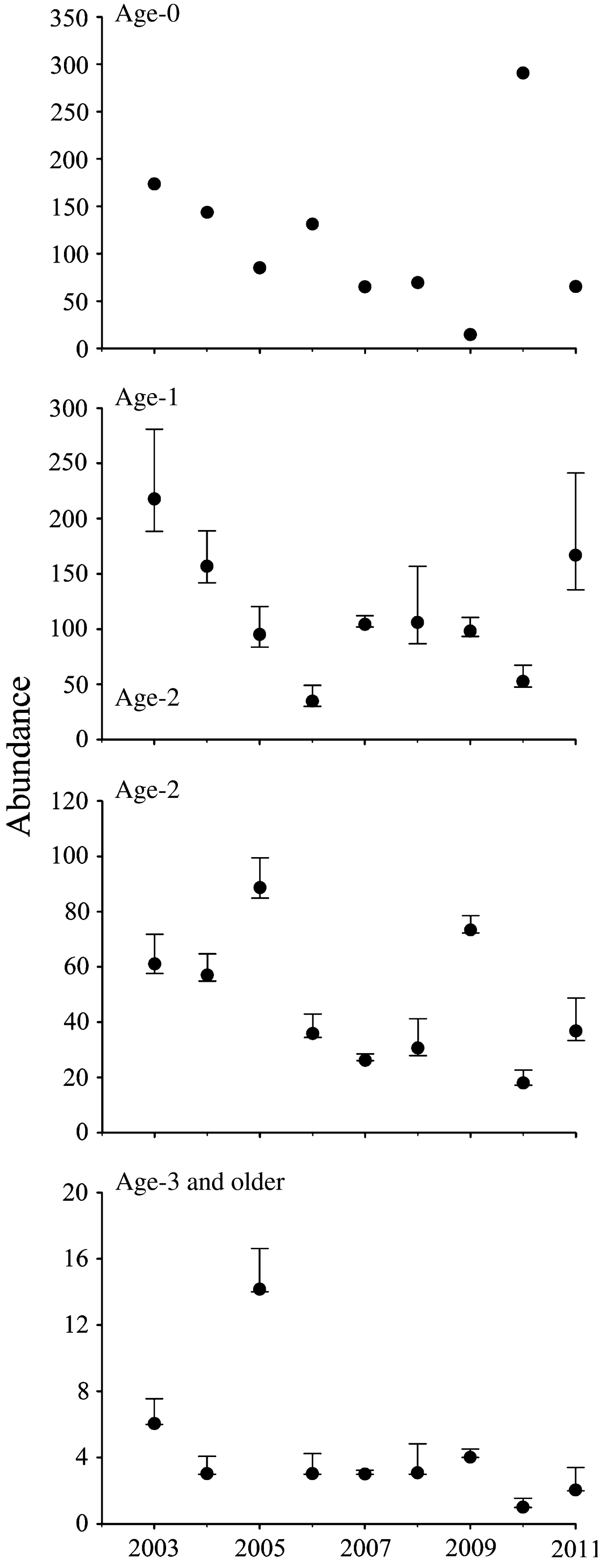

Fig. 4. Abundance estimates of age-0 through age-3 and older brown trout in the Right Hand Fork annual monitoring site during 2003 through 2011. Confidence intervals are 95% log-normal confidence intervals for the abundance of brown trout in each age class. Note changes in *y*-axis scales.

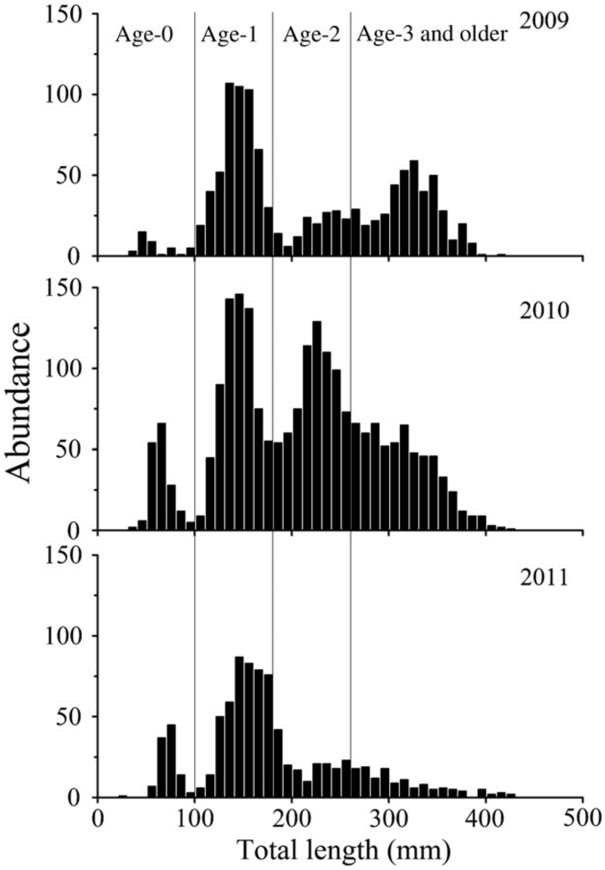

Fig. 5. Length-frequency distribution for brown trout removed from Logan River removal reach during 2009 through 2011. Vertical bars designate the size range for age classes (see Methods).

we collected 1.7 times more age-0 brown trout than previously observed (Fig. 4). Furthermore, during 2010 age-0 fish comprised 75% of all brown trout collected at the annual monitoring site, relative to, on average, only 28% during 2003 through 2009 ($D = 0.21$–0.69, $P < 0.001$, after Bonferroni correction for multiple pairwise preremoval vs. postremoval comparisons). Similarly, the abundance of age-1 brown trout during 2011 was among the greatest observed during the 9-year monitoring period. However, the 2011 age distribution differed significantly from only 2005 and 2009 when the greatest number of mature fish were collected and 2006 when few age-1 fish were collected ($D = 0.26$–0.39, $P < 0.001$, after Bonferroni correction for multiple pairwise preremoval vs. postremoval comparisons).

Logan River removal reach

We removed 1125 brown trout from 1.3 km during 2009 (0.05 fish m^{-2}, 121 Th, Fig. 2). During 2010 and 2011, we sampled the entire removal reach (2.0 km) and removed 2184 (0.06 fish m^{-2}, 200 Th) and 866 (0.02 fish m^{-2}, 72 Th) brown trout, respectively. During 2010, there were 3.0 times more age-2 and 2.9 times more age-0 brown trout present than during 2009 (Fig. 2), resulting in a temporary increase in the proportion of the annual brown trout population composed of these age classes ($D_{2009–2010} = 0.14$, $P < 0.001$; Fig. 5). The significantly greater numbers of brown trout present during 2010 were likely not an artefact of sampling efforts as: (i) during 2010, the age structure of brown trout was similar among habitats sampled during both 2009 and 2010 and those sampled only during 2010, and (ii) the greater number of brown trout removed during 2010 could not be explained by the total additional area sampled during 2010, after accounting for habitat type and average brown trout density. During 2011, there were significantly fewer age-1 and age-3 and older brown trout relative to the two prior years (ca. 36–41% reduction in age-1 and 78% reduction in age-3 and older brown trout). Furthermore, the age structure of the brown trout population in the Logan River removal reach during 2011, as in the RHF removal reach, shifted significantly towards a greater percentage of juvenile fish ($D_{2009–2011} = 0.26$, $P < 0.001$; $D_{2010–2011} = 0.32$, $P < 0.001$).

In comparison with the RHF annual monitoring site, both abundance and age structure of the brown trout population in the Logan River removal reach were highly variable during 2003–2011 (Fig. 6). As a result, the effects of mechanical removal on this population of brown trout did not fall outside the range of variability of fish collections for age-0 or abundance estimates for age-1 and age-2 fish. Counts of age-0 brown trout and estimates of age-1 brown trout abundance for the Logan River annual monitoring site were similar during all 3 years mechanical removal was conducted and similar to abundance estimates from the previous time period 2003–2008. Although significantly more age-2 individuals were observed during 2010, the 2010 abundance was less than that observed during the preremoval period from 2003 to 2006. In contrast, the abundance of age-3 and older brown trout during both 2010 and 2011 at the Logan River annual monitoring site was significantly lower than during 2003–2009.

Discussion

The results of our large-scale, mechanical removal suggest that the high densities of subadult and adult brown trout supported by the RHF removal reach prior to conducting the removal (1.03 fish m^{-2}, Budy et al. 2008) resulted in either low survival rates (potentially owing to competition or predation) or high emigration rates during early life stages (hypothesis III above). Prior to removal, there was extremely low natural, interannual variation in brown trout abundance and age structure in the Right Hand Fork

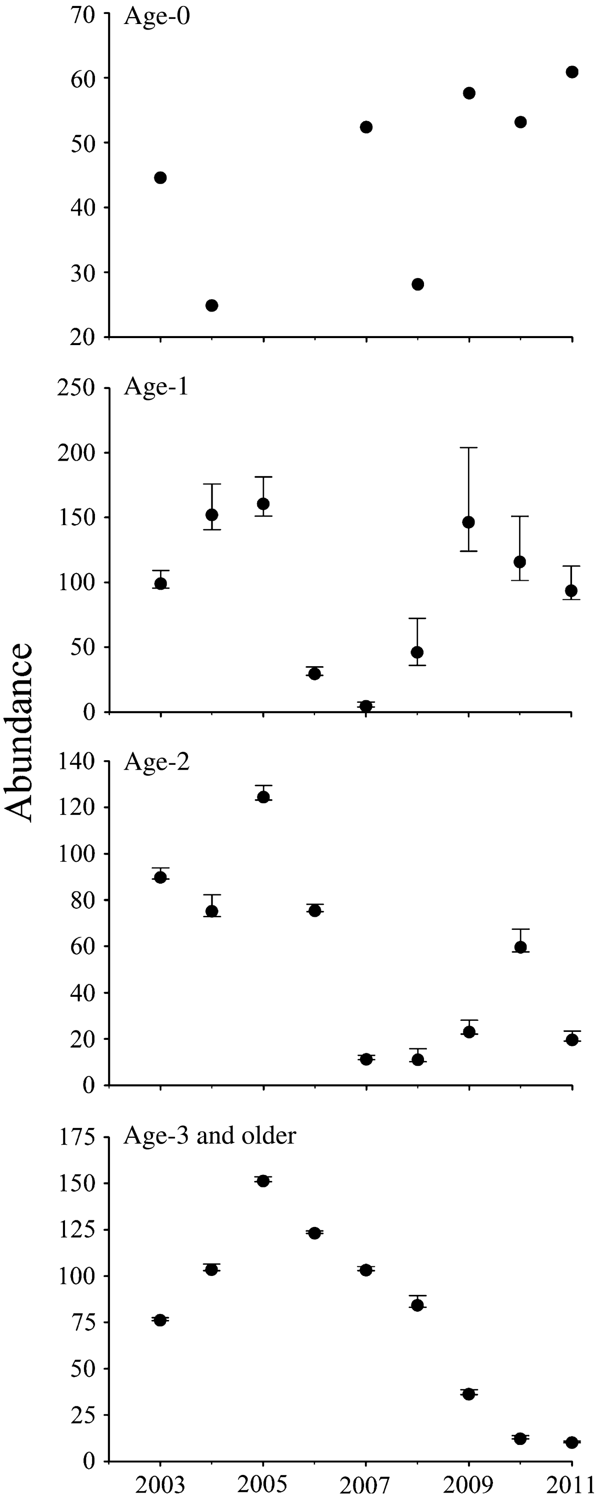

Fig. 6. Abundance estimates of age-0 through age-3 and older brown trout in the Logan River annual monitoring site during 2003 through 2011. Confidence intervals are 95% log-normal confidence intervals for the abundance of brown trout in each age class. Note changes in *y*-axis scales.

removal reach (Budy et al. 2008) relative to other brown trout populations (Lobon-Cervia et al. 2011). In contrast, during 2010, there were 4.5 times more age-0 brown trout present in the RHF removal reach than during 2009, and, on average, 5.4 times more present in the monitoring reach than during 2003–2009. Despite having removed 63–74% of adult brown trout prior to spawning during 2009, the significantly greater numbers of age-0 brown trout present during 2010 and the high survival of this postremoval cohort during 2011, suggest that strong intercohort interactions may drive density-dependent mechanisms regulating the brown trout sub-population in Right Hand Fork. These results contrast those of Budy et al. (2008), who analysed 8 years of age-1 and older brown trout density and growth data for the Logan River and observed only weak evidence of density dependence among adult brown trout, but none at early life stages. The contrasting inferences about the structure of density-dependent regulation of brown trout in the Logan River between our manipulation of brown trout subpopulations and annual monitoring efforts, provide further evidence that density-dependent processes are difficult to detect based on observational data alone (Jenkins et al. 1999; Daufresne & Renault 2006), even when the temporal and spatial extent of sampling is relatively large, as is the case in the Logan River (Budy et al. 2008).

Annual monitoring and large-scale population manipulation on Right Hand Fork have demonstrated that this low-elevation tributary to the Logan River supports extremely high densities of juvenile and adult brown trout (in excess of 1 fish m^{-2}, Budy et al. 2008). A combination of low elevation, resulting in moderate snow accumulations, and large groundwater inputs in the Right Hand Fork removal reach result in high base flow, moderate peak spring discharge, and water temperatures that vary little throughout the year (e.g. 2010 annual average = 9.7 °C, SE = 0.92). These conditions allow for nearly year round growth and little risk of physical damage to overwintering eggs (Fausch et al. 2001; Wood & Budy 2009). Under these near ideal conditions, it is not surprising that brown trout reach high densities where population abundance is regulated by density-dependent mechanisms.

Density-dependent effects on brown trout populations during early life stages may occur through a variety of mechanisms (Milner et al. 2003), and when present, may increase the probability that local populations serve as sources of recruitment for connected habitats. Brown trout populations can demonstrate high rates of juvenile dispersal (e.g. 30%, Crisp 1993) and strong intercohort interactions (Nordwall et al. 2001; Kvingedal & Einum 2011). These demographic processes could account for the substantial emigration of age-0 brown trout from the RHF removal reach prior to mechanical removal, and help explain the relatively low levels of recruitment observed at the RHF annual monitoring site. As a result, the RHF removal reach may serve as an important source of brown trout for the lower Logan River and should be a priority for management of exotic brown trout in this system.

Although we observed evidence for a density-dependent increase in brown trout recruitment following mechanical removal, it is likely that brown trout remaining after annual removals in the RHF removal reach also had lower, natural mortality rates. During 2011, there were significantly more age-1 brown trout present in the RHF removal reach and annual monitoring site than during other years, resulting from high survival of the 2010 cohort (no immigration was possible). Additionally, there was likely lower natural mortality of age-2 and older brown trout following mechanical removal as well, as we observed no subsequent reduction in adult abundance after 2010. Therefore, brown trout that were not removed from the RHF removal reach may have partially compensated for removal efforts via lower natural mortality and high reproductive success. For example, Meyer et al. (2006) observed a 700% increase in brook trout recruitment 2 years after removal stopped, which they attribute to low mortality rates for fish that were not removed, and eventually were recruited to the spawning population after removal efforts ceased. Nonetheless, the large recruitment event that occurred immediately following the initial removal, suggest that density-dependent population regulation had a primary role in determining the response of the brown trout population to mechanical removal in the RHF removal reach. These results have important implications for management of brown trout, and thus the conservation of native trout.

Habitats capable of supporting high densities of exotic brown trout may also provide suitable and preferred habitat for native cutthroat trout, given the ecological similarities between these two species. As such, management targeting these locations may yield high returns for conservation of native trout through both brown trout suppression and expansion of cutthroat trout populations. For example, the high densities of salmonids supported in Right Hand Fork suggest that this tributary could likely eventually become a viable sub-population of native cutthroat trout. Further, for systems like the Logan River where nearly all spawning habitat available to cutthroat trout is used annually (Budy et al. 2012), locations that contain high quality spawning and rearing habitat, in relatively high abundance, but were previously unavailable to native fish, could provide a significant increase to cutthroat trout production at the watershed scale. Therefore, restoration of Right Hand Fork to Bonneville cutthroat trout could provide abundant new spawning gravels and rearing habitat, as brown and cutthroat trout have similar spawning criteria (Hickman & Raleigh 1982; Raleigh et al. 1986), and the habitat in Right Hand Fork is highly preferred.

In contrast to Right Hand Fork where there was limited potential for recolonisation, brown trout response to mechanical removal in the Logan River removal reach may be driven by high rates of movement between the removal reach and adjacent impoundments (hypothesis IV above). Rapid recolonisation by stream dwelling fishes has been repeatedly documented following mechanical or chemical removals (Lintermans 2000; Peterson et al. 2004a) and large-scale physical disturbances (Roghair et al. 2002), when there is a nearby source for immigrants. Instream impoundments adjacent to the Logan River reach may serve as important sources for brown trout immigrants, and likely contributed, in part, to the significantly greater numbers of age-2 brown trout present during 2010. Preliminary results from ongoing mark-recapture sampling in the Logan River removal reach suggest that emigration of large adults from the downstream impoundment (ca. 55 immigrating adults per year, data not reported) likely serves as a substantial source of brown trout for the removal reach.

Overall, the brown trout population in the Logan River removal reach demonstrates high annual variation in abundance and age structure, likely resulting from brown trout immigration and altered hydrology owing to management of the impoundments. As such, effects of mechanical removal on the brown trout population in the Logan River removal reach were likely tempered by fish immigration and recruitment dynamics that resulted in substantial natural temporal population variability. For example, although we observed greater brown trout recruitment and age-2 abundance following the initial removal, abundance of these age classes were within the range of variability observed at the Logan River annual monitoring site during 2003–2008. Ultimately, mechanical removal may be of limited use to control exotic brown trout if potential sources of colonists (e.g. impoundments) are not first identified and controlled, as has been suggested for other exotic salmonids (Peterson & Fausch 2003).

Although single-pass mechanical removal alone is unlikely to eradicate exotic species, suppression of brown trout may be sufficient to tip the ecological balance in favour of native species. For example, brown trout suppression may be sufficient to alter competitive interactions between native and exotic salmonids and allow native salmonids to withstand further invasion by exotic fishes through biotic resistance (Moyle & Light 1996; Levine et al. 2004). The level of biotic resistance exhibited will be a function of the diversity, density and/or distribution of the community of native species (Carey & Wahl 2010), and their potential for strong interactions with exotic species. Therefore, by reducing exotic brown trout densities via mechanical removal, native salmonids may be able to reduce the per capita rate of interaction with exotic species and retain a competitive advantage through superior numbers; however, caution must be taken owing to the potential for substantial brown trout recruitment following a short-term removal event.

Our results suggest that populations of exotic brown trout rapidly compensate for moderate reductions in population density via mechanisms commonly reported for exotic salmonids in western watersheds. Immediately following mechanical removal, high rates of immigration from nearby sources (Peterson & Fausch 2003), compensatory mortality (Meyer et al. 2006) and density-dependent recruitment drove population dynamics of brown trout in main stem and tributary habitats of the Logan River watershed. Given the rapid increase in biological invasions in freshwater ecosystems, and the cost of eradication programs, there is a strong need to develop tools to prioritise management efforts. Our results demonstrate how single-pass mechanical removal programs can help identify regional hotspots that serve as sources for exotic species, and allow managers to prioritise management efforts in these areas. Intensive management or eradication efforts in such habitats may have a disproportionately large effect on the population dynamics of exotic species at the watershed scale and improve management efforts to control exotic species at larger spatial scales.

Acknowledgements

We thank many folks for assistance and guidance in the field and laboratory: J. Baker, W. Gordon, K. Hafen, P. Holden, S. Klobucar, P. Mason, N. Salant, P. Tuttle, T. Walsworth, S. Wing, and T. Wright. We would like to thank Paul Burnett, Craig Schaugaard, Paul Thompson, the Fisheries Experiment Station in Logan (Utah Division of Wildlife Resources [UDWR]), and Paul Chase (US Forest Service) for providing assistance and support. Primary funding was provided by the US. Geological Survey Western Region State Partnership Program, Cooperative Agreement No. G10AC00507, and the UDWR, Endangered Species Mitigation Fund: Project # 1111. Other funding and support was provided by the US Forest Service, the U.S. Geological Survey, Utah Cooperative Fish and Wildlife Research Unit at Utah State University (in-kind; USU), the Ecology Center (USU), the Intermountain Center for River Rehabilitation and Restoration at USU, and Cache Anglers Chapter of Trout Unlimited. Tracy Bowerman, Christopher Keleher, Kevin Meyer, and two anonymous reviewers provided valuable comments on a previous version of this manuscript. Research was conducted under state COR permit 2COLL5415 and IACUC Protocol 1038. Any use of trade, firm, or product names is for descriptive purposes only and does not imply endorsement by the U.S. Government.

References

Behnke, R.J. 1992. Native trout of western North America, Monograph 6. Bethesda: American Fisheries Society.

Budy, P., Thiede, G. & McHugh, P. 2007. Quantification of the vital rates, abundance, and status of a critical, endemic population of Bonneville cutthroat trout. North American Journal of Fisheries Management 27: 593–604.

Budy, P., Thiede, G.P., McHugh, P., Hansen, E.S. & Wood, J. 2008. Exploring the relative influence of biotic interactions and environmental conditions on the abundance and distribution of exotic brown trout (*Salmo trutta*) in a high mountain stream. Ecology of Freshwater Fish 17: 554–566.

Budy, P., Wood, S. & Roper, B. 2012. A study of the spawning ecology and early life history survival of Bonneville cutthroat trout. North American Journal of Fisheries Management 32: 436–449.

Carey, M.P. & Wahl, D.H. 2010. Native fish diversity alters the effects of an invasive species on food webs. Ecology 91: 2965–2974.

Coffin, P.D. & Cowan, W.F. 1995. Lahontan cutthroat trout (*Oncorhynchus clarki henshawi*) recovery plan. Portland: U.S. Fish and Wildlife Service. 147 pp.

Crisp, D.T. 1993. Population-densities of juvenile trout (*Salmo trutta*) in 5 upland streams and their effects upon growth, survival, and dispersal. Journal of Applied Ecology 30: 759–771.

Daufresne, M. & Renault, O. 2006. Population fluctuations, regulation and limitation in stream-living brown trout. Oikos 113: 459–468.

DeGroot, M.H. & Schervish, M.J. 2002. Probability and statistics. Boston: Addison Wesley. 893 pp.

Dieterman, D.J. & Hoxmeier, R.J.H. 2011. Demography of juvenile and adult brown trout in streams of southeastern Minnesota. Transactions of the American Fisheries Society 140: 1642–1656.

Dolan, C.R. & Miranda, L.E. 2003. Immobilization thresholds of electrofishing relative to fish size. Transactions of the American Fisheries Society 132: 969–976.

Dunham, J.B. & Rieman, B.E. 1999. Metapopulation structure of bull trout: influences of physical, biotic, and geometrical landscape characteristics. Ecological Applications 9: 642–655.

Einum, S. & Nislow, K.H. 2005. Local-scale density-dependent survival of mobile organisms in continuous habitats: an experimental test using Atlantic salmon. Oecologia 143: 203–210.

Falke, J.A. & Fausch, K.D. 2010. From metapopulations to metacommunities: linking theory with empirical observations of the spatial population dynamics of stream fishes. In: Gido, K.B. & Jackson, D.A., eds. Community ecology of stream fishes: concepts, approaches, and techniques. Bethesda: American Fisheries Society (Symposium 73), pp. 207–233.

Fausch, K.D., Taniguchi, Y., Nakano, S., Grossman, G.D. & Townsend, C.R. 2001. Flood disturbance regimes influence rainbow trout invasion success among five holarctic regions. Ecological Applications 11: 1438–1455.

Finlayson, B., Somer, W.L. & Vinson, M.R. 2010. Rotenone toxicity to rainbow trout and several mountain stream insects. North American Journal of Fisheries Management 30: 102–111.

Gowan, C. & Fausch, K.D. 1996. Long-term demographic responses of trout populations to habitat manipulation in six Colorado streams. Ecological Applications 6: 931–946.

Hickman, T. & Raleigh, R.F. 1982. Habitat suitability index models: Cutthroat trout. No. FWS/OBS-82/10.5. USDI Fish and Wildlife Service, 38 pp.

de la Hoz Franco, E.A. & Budy, P. 2004. Effects of biotic and abiotic factors on the distribution of trout and salmon along a longitudinal stream gradient. Environmental Biology of Fishes 72: 379–391.

Huggins, R.M. 1989. On the statistical analysis of capture-recapture experiments. Biometrika 76: 133–140.

Jenkins, T.M., Diehl, S., Kratz, K.W. & Cooper, S.D. 1999. Effects of population density on individual growth of brown trout in streams. Ecology 80: 941–956.

Koehn, J., Brumley, A. & Gehrke, P. 2000. Managing the impacts of carp. Canberra: Bureau of Rural Sciences (Department of Agriculture, Fisheries, and Forestry – Australia), pp. 249.

Kulp, M.A. & Moore, S.E. 2000. Multiple electrofishing removals for eliminating rainbow trout in a small southern Appalachian stream. North American Journal of Fisheries Management 20: 026–266.

Kvingedal, E. & Einum, S. 2011. Intracohort and intercohort spatial density dependence in juvenile brown trout (*Salmo trutta*). Canadian Journal of Fisheries and Aquatic Sciences 68: 115–121.

Levine, J.M., Adler, P.B. & Yelenik, S.G. 2004. A meta-analysis of biotic resistance to exotic plant invasions. Ecology Letters 7: 975–989.

Lintermans, M. 2000. Recolonization by the mountain galaxias Galaxias olidus of a montane stream after the eradication of rainbow trout *Oncorhynchus mykiss*. Marine and Freshwater Research 51: 799–804.

Lobon-Cervia, J., Gonzalez, G. & Budy, P. 2011. Factors driving spatial and temporal variation in production and production/biomass ratio of stream-resident brown trout (*Salmo trutta*) in Cantabrian streams. Freshwater Biology 56: 2272–2287.

McClay, W. 2000. Rotenone use in North America (1988-1997). Fisheries 25: 15–21.

McHugh, P. & Budy, P. 2005. An experimental evaluation of competitive and thermal effects on brown trout (*Salmo trutta*) and Bonneville cutthroat trout (*Oncorhynchus clarkii utah*) performance along an altitudinal gradient. Canadian Journal of Fisheries and Aquatic Sciences 62: 2784–2795.

McHugh, P. & Budy, P. 2006. Experimental effects of nonnative brown trout on the individual- and population-level performance of native Bonneville cutthroat trout. Transactions of the American Fisheries Society 135: 1441–1455.

McIntosh, A.R., McHugh, P. & Budy, P. 2012. Brown trout (*Salmo trutta*). In: Francis, R.A., ed. A handbook of global freshwater invasive species. London: Taylor and Francis. 460 pp.

Meronek, T.G., Bouchard, P.M., Buckner, E.R., Burri, T.M., Demmerly, K.K., Hatleli, D.C., Klumb, R.A., Schmidt, S.H. & Coble, D.W. 1996. A review of fish control projects. North American Journal of Fisheries Management 16: 63–74.

Meyer, K.A., Lamansky, J.A. & Schill, D.J. 2006. Evaluation of an unsuccessful brook trout electrofishing removal project in a small rocky mountain stream. North American Journal of Fisheries Management 26: 849–860.

Milner, N.J., Elliott, J.M., Armstrong, J.D., Gardiner, R., Welton, J.S. & Ladle, M. 2003. The natural control of salmon and trout populations in streams. Fisheries Research 62: 111–125.

Moyle, P.B. & Light, T. 1996. Biological invasions of fresh water: empirical rules and assembly theory. Biological Conservation 78: 149–161.

Nordwall, F., Naslund, I. & Degerman, E. 2001. Intercohort competition effects on survival, movement, and growth of brown trout (*Salmo trutta*) in Swedish streams. Canadian Journal of Fisheries and Aquatic Sciences 58: 2298–2308.

Olden, J.D. & Poff, N.L. 2003. Toward a mechanistic understanding and prediction of biotic homogenization. American Naturalist 162: 442–460.

Olden, J.D., Poff, N.L., Douglas, M.R., Douglas, M.E. & Fausch, K.D. 2004. Ecological and evolutionary consequences of biotic homogenization. Trends in Ecology and Evolution 19: 18–24.

Peterson, D.P. & Fausch, K.D. 2003. Upstream movement by nonnative brook trout (*Salvelinus fontinalis*) promotes invasion of native cutthroat trout (*Oncorhynchus clarki*) habitat. Canadian Journal of Fisheries and Aquatic Sciences 60: 1502–1516.

Peterson, D.P., Fausch, K.D. & White, G.C. 2004a. Population ecology of an invasion: effects of brook trout on native cutthroat trout. Ecological Applications 14: 754–772.

Peterson, J.T., Thurow, R.F. & Guzevich, J.W. 2004b. An evaluation of multipass electrofishing for estimating the abundance of stream-dwelling salmonids. Transactions of the American Fisheries Society 133: 462–475.

Raleigh, R.F., Zuckerman, L.D. & Nelson, P.C. 1986. Habitat suitability index models and instream flow suitability curves: Brown trout, revised. No. Biological Report 82(10.124). USDI Fish and Wildlife Service, 65 pp.

Riley, S.C. & Fausch, K.D. 1995. Trout population response to habitat enhancement in six northern Colorado streams. Canadian Journal of Fisheries and Aquatic Sciences 52: 34–53.

Roghair, C.N., Dolloff, C.A. & Underwood, M.K. 2002. Response of a brook trout population and instream habitat to a catastrophic flood and debris flow. Transactions of the American Fisheries Society 131: 718–730.

Rosenberger, A.E. & Dunham, J.B. 2005. Validation of abundance estimates from mark-recapture and removal techniques for rainbow trout captured by electrofishing in small streams. North American Journal of Fisheries Management 25: 1395–1410.

SAS. 2008. Statistical analysis system, version 9.2. Cary, NC, USA: SAS Institute, Inc.

Saunders, W.C., Fausch, K.D. & White, G.C. 2011. Accurate estimation of salmonid abundance in small streams using nighttime removal electrofishing: an evaluation using marked fish. North American Journal of Fisheries Management 31: 403–415.

Shepard, B.B., May, B.E. & Urie, W. 2005. Status and conservation of westslope cutthroat trout within the western United States. North American Journal of Fisheries Management 25: 1426–1440.

Sokal, R.R. & Rohlf, F.J. 1995. Biometry: the principles and practice of statistics in biological research. New York: W.H. Freeman and Co.

Thompson, P.D. & Rahel, F.J. 1996. Evaluation of depletion-removal electrofishing of brook trout in small Rocky Mountain streams. North American Journal of Fisheries Management 16: 332–339.

Vitousek, P.M., Mooney, H.A., Lubchenco, J. & Melillo, J.M. 1997. Human domination of earth's ecosystems. Science 227: 494–499.

White, G.C. & Burnham, K.P. 1999. Program MARK: survival estimation from populations of marked animals. Bird Study 46: S120–S139.

Williams, J.E., Haak, A.L., Neville, H.M. & Colyer, W.T. 2011. Potential consequences of climate change to persistence of cutthroat trout populations. North American Journal of Fisheries Management 29: 533–548.

Wood, J. & Budy, P. 2009. The role of environmental factors in determining early survival and invasion success of exotic brown trout. Transactions of the American Fisheries Society 138: 756–767.

Young, M.K., Schmal, R.N., Kohley, T.W. & Leonard, V.G. 1996. Conservation status of Colorado River cutthroat trout. General Technical Report RM-GTR-282. Fort Collins, Colorado: U.S. Forest Service, Rocky Mountain Forest and Range Experiment Station, Department of Agriculture. 32 pp.