

Section 5

Brown Trout as a Global Invader

Brown Trout as an Invader: A Synthesis of Problems and Perspectives in North America

Phaedra Budy^{1,2} and Jereme W. Gaeta²

¹ U.S. Geological Survey, Utah Cooperative and Wildlife Research Unit

² Utah State University, Department of Watershed Sciences and the Ecology Center, Logan, Utah, USA

Introduction

Brown trout are one of the most pervasive and successful invaders in North America, negatively impacting native fishes and ecosystems not only through predation and competition, but also by acting as vectors of exotic parasites. They do, however, represent a paradox as they are extremely popular sport fish (Figure 20.1), and they often thrive in novel, man-made ecosystems (e.g., dam tailwaters, reservoirs). Nonetheless, due to pervasive negative impacts, brown trout have recently been the focus of numerous removal programs, policy changes, and overall efforts to shift angler focus back to native trout. In this chapter, we synthesize the type and extent of invasive brown trout impacts on native ecosystems and their native fishes. We also discuss their paradoxical popularity as river and lake sport fish as well as their role in novel tailwater and reservoir ecosystems. Lastly, we discuss future management and the factors both limiting and facilitating their success, including the role of climate change. Our chapter is focused on the Intermountain West (IMW) of the USA, a geographic and geological region of the Western United States located between the Rocky Mountains on the east and the Cascade Range and Sierra Nevada Range on the west (Stewart *et al.* 2002). However, Utah is in many cases representative of surrounding states (from a brown trout perspective), and we have direct access to data and expert opinion in the state and a long history of detailed study. Thus, many of our examples are from within Utah but are generally applicable beyond (e.g., Logan River; Figure 20.2).

Many sources of information suggest that brown trout have been introduced and/or established in most areas of the world capable of supporting them (McIntosh *et al.* 2011). In the early 1900s, brown trout embryos from cultured European populations were stocked into the United States including in the IMW by the predecessor of the now United States Fish and Wildlife Service (Mather 1889; Courtney *et al.* 1984). These stocking efforts were very successful, in part because the IMW has ample high latitude areas, which are nearly ideal for brown trout, but also because of continued

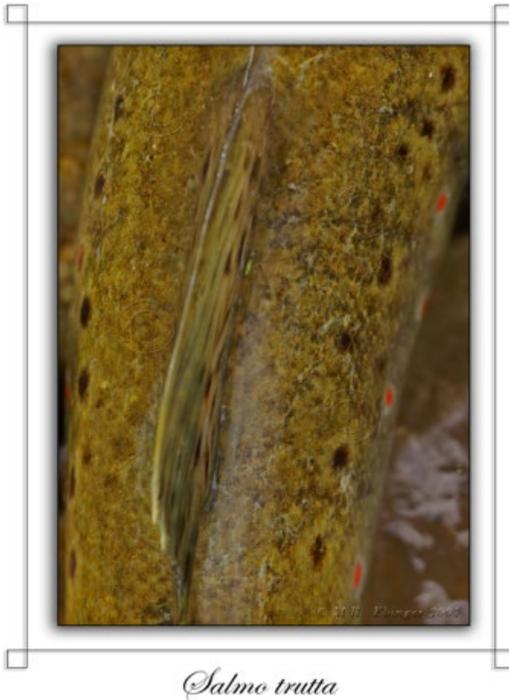


Figure 20.1 Brown trout photo taken in the Logan River, Utah, USA by Michael Ebinger showing spots.

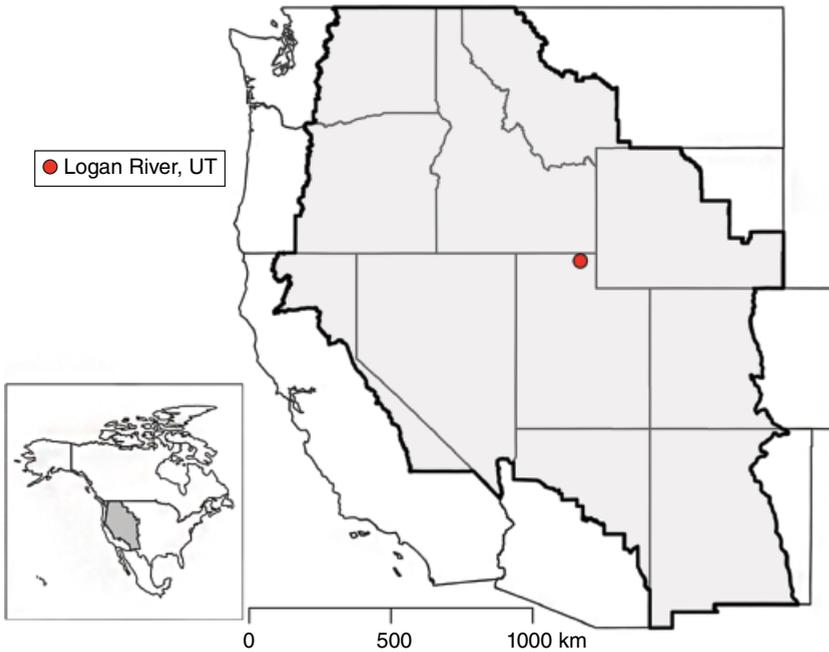


Figure 20.2 Map of the Intermountain West, USA, shown as an inset of North America. North America map reproduced with permission from Michigan State University Map Library, Data Source: ESRI. The red circle denotes the Logan River, Utah, an area of extensive and long-term studies on exotic brown trout referred to frequently in the text.

propagule pressure (i.e., repeated stockings; discussed further below). From the 1960s to the present, brown trout ranges have expanded as viable reproducing populations increased and stocking efforts continued. Now, brown trout are found in all eight of the IMW states (Montana, Idaho, Wyoming, Utah, Nevada, Colorado, New Mexico, and Arizona), and in many places, their densities greatly surpass those observed in their native range (McIntosh *et al.* 2011). In the Logan River, Utah, for example, densities of exotic brown trout reach almost two fish/m² (Budy *et al.* 2008), whereas in their native range, recorded densities average only 0.4 fish/m² (Budy *et al.* 2013). Exotic brown trout are widespread and abundant because they are vagile (capable of dispersal) and have a large fundamental niche (described in detail in McIntosh *et al.* 2011 and other chapters in this volume). However, in the IMW they thrive not only in nearly all types of natural aquatic ecosystems such as ponds, lakes, streams, and larger rivers (e.g., Budy *et al.* 2013), but also in novel and disturbed ecosystems in which natives may struggle to establish, such as reservoirs and tailwaters below dams (e.g., Dibble *et al.* 2015).

Brown Trout as Invaders: Negative Impacts on Aquatic Communities

Brown trout have been included in the top 30 worst invasive species on the globe due to their overwhelming success as invaders and the plethora of negative impacts they have had on invaded ecosystems (reviewed in McIntosh *et al.* 2011; International Union for the Conservation of Nature). Similar to places like New Zealand, aquatic ecosystems in the IMW may be highly sensitive to the negative impacts of brown trout due to naturally low native species diversity and lack of competitive ability of many natives developed over long geologic isolation (Griffith 1988; Dunham *et al.* 2002). Small stream size and isolation can also contribute to this sensitivity (Shemai *et al.* 2007). McIntosh *et al.* (2011) summarized the ‘mounting evidence’ of the negative impacts of exotic brown trout into three general categories: (1) distributional evidence suggesting historical displacement; (2) observational or experimental studies assessing mechanisms of impact; and (3) temporal data sets documenting decline following invasion.

Distributional Patterns

We have all three types of evidence of negative impacts of brown trout in the IMW. First, native cutthroat trout (*Oncorhynchus clarkii*) did not persist in many places in the West after brown trout were stocked (reviewed in Fausch 1988; Benke 1992). Although this evidence is purely temporal (e.g., category 3 above) and distributional (e.g., category 1 above), the evidence strongly suggests that brown trout displace native fishes largely via the well-documented mechanisms of predatory and competitive interactions. Strong allopatric patterns of native cutthroat trout and exotic brown trout are common in the IMW and are often longitudinal along elevational gradients of montane rivers (Vincent and Miller 1969; de la Hoz Franco and Budy 2005; McHugh and Budy 2005). For instance, native trout are often found at high densities in upper elevation reaches while exotic brown trout (and often exotic rainbow trout, *Oncorhynchus mykiss*) dominate lower elevation reaches. The mid-elevation reaches often hold both species, but at very low densities. In most of these rivers,

cutthroat trout historically occupied the entire river, however, distributional evidence indicates exotic trout, often brown trout, have displaced these natives (Fausch 1988; Budy *et al.* 2007).

This type of allopatric pattern of species distribution can be the result of either contemporary competition, the ghost of competition past, and/or environmental constraints that co-vary with elevation (Fasuch *et al.* 1994; McHugh and Budy 2005). The former are discussed below under 'Competition.' As an example of the latter, brown trout in the Poudre River, Colorado, were found to be restricted to elevations of less than 2,680m, a boundary the authors assumed was based on thermal tolerance (i.e., above this elevation, stream temperatures were too cold; Vincent and Miller 1969; but see Saunders and Budy, in prep). Fausch (1989) similarly demonstrated that standing stocks of brown trout decreased with elevation in Colorado streams. In the Logan River, Utah, brown trout densities decrease with increasing diel temperature fluctuations, which are generally greater at higher elevations in this system (de la Hoz Franco and Budy 2005). Some observational and model-based evidence suggests that summer temperatures, stream scour and its influence on spawning gravel availability, and the presence of anchor ice all limit the upper distribution of brown trout in the Logan River, Utah (Meredith 2012; Meredith *et al.*, 2016). Bozek and Hubert (1992) were similarly able to predict the absence of brown trout with 94% accuracy based on elevation, gradient, and wetted width measurements in streams of Wyoming. Nonetheless, while some environmental factors may limit the expansion of brown trout into upper elevation reaches, brown trout are superior competitors to native trout, as has been firmly demonstrated experimentally (e.g., category 2 above). This competitive advantage explains why brown trout dominate the lower portion of many rivers and displace native trout.

Competition

Although strong anecdotal and observational evidence since the beginning of brown trout introductions have suggested that brown trout were superior competitors to native trout, the first experimental evidence did not emerge until the late 1990s (e.g., evidence category 2). In aquaria experiments in Montana with age-1 trout, Wang and White (1994) demonstrated that exotic brown trout were involved in more inter-specific agonistic events in sympatry with native greenback cutthroat trout (*O. clarkii stonias*). A more recent set of small scale enclosure experiments revealed that exotic brown trout reduced the growth and condition of native trout in several locations along elevational gradients (McHugh and Budy 2005). At the same time, likely because they are competing for space and dominating the preferred territories, brown trout were unaffected by the presence of native trout, and were more affected by intraspecific competition among brown trout (McHugh and Budy 2005). Somewhat surprisingly, competition in these enclosures was not mediated by temperature. In fact, when experimental brown trout were reared at cold, steep gradient, high elevation locations where they rarely occur, their growth rates were even higher than at low elevation sites, where they commonly establish. Notably however, all reaches of the Logan River, Utah, are within the suitable temperature range for brown trout and native trout; elsewhere, brown trout have a competitive advantage over native trout when habitat degradation has increased stream temperature to a range still suitable for exotic brown trout, yet too warm for native trout (Closs and Lake 1996; Keleher and Rahel 1996; McHuch and Budy 2005; Fausch *et al.* 2009).

In larger reach-scale experiments, brown trout similarly reduced the growth, altered the diet, and suppressed the movement of native trout (McHugh and Budy 2006). Based on a variety of other observations (e.g., Saunders and Budy, in prep), and because many brown trout streams flow over a limestone base and are extremely productive (e.g., Logan River; Almodóvar *et al.* 2006), we believe the likely mechanism is interference competition, i.e., competition for space, not food. Shemai *et al.* (2007) similarly observed that exotic brown trout were superior competitors to native Rio Grande cutthroat trout (*O. clarkii virginialis*) in stream enclosure experiments in New Mexico and concluded that elevated aggression by brown trout altered foraging behavior of native trout. Collectively these experimental studies, while not an exhaustive list, demonstrate that exotic brown trout out-compete native trout in the IMW and that the mechanism appears to be aggressive behavior and competition for space.

Predation

Negative impacts on native fishes due to novel predator-prey interactions with exotic brown trout are relatively straightforward and also well-documented based on observational and experimental studies. Based on observational studies in the Logan River, Utah, brown trout tend to have similar diet preferences as native trout, but ingest larger prey, including fishes (McHugh *et al.* 2006). Indeed, isotopic nitrogen signatures indicate brown trout occupy a higher trophic position than their native counterparts. In small-scale experimental studies aimed at understanding inter-specific interactions, predation of adult brown trout on adult native trout accounted for 20% of observed mortalities (Saunders and Budy, in prep). Further, in observational studies in the Logan River, Utah, up to 33% of brown trout diets were composed of native sculpin (*Cottus* sp.), while native trout consumed almost none (Meredith *et al.* 2014). Bioenergetics simulations based on these diet proportions indicates an adult brown trout consumes up to 34 native sculpins a year. Given brown trout densities of more than 1 per m², these rates of predation almost surely have negative effects that ramify through the fish community and likely have counterparts in similar systems (Budy *et al.* 2008). Furthermore, based on an international comparison spanning five countries, fluvial brown trout demonstrate a much greater degree of piscivory in their exotic habitat and reach substantially larger sizes and older ages, relative to their native habitat, further enhancing their predatory ability (Figure 20.3; Budy *et al.* 2013). Larger body size also typically infers superior competitive ability among fishes and can exacerbate other community-level impacts including interspecific competition discussed above (Fausch 1984; Rasmussen *et al.* 2011; Louhi *et al.* 2014).

The negative effects of predatory brown trout on native fish communities are not unique to the IMW and have been documented for eight families of native fish and numerous species across many countries and continents (reviewed in McIntosh *et al.* 2011). Further, although we do not have direct evidence of brown trout egg predation on native trout eggs in the IMW, brown trout have been observed eating native eggs elsewhere (Greeley 1932; Aymes *et al.* 2010). In addition, our observations of slightly higher nitrogen isotopic signatures (¹⁵N) in brown trout in the Logan River, Utah, could indicate egg or larval predation (McHugh *et al.* 2006), and we have directly observed brown trout eating eggs of other fishes (e.g., kokanee salmon, *Oncorhynchus nerka*) in Utah. Egg predation by exotic brown trout could exacerbate the other known negative impacts on native fishes.

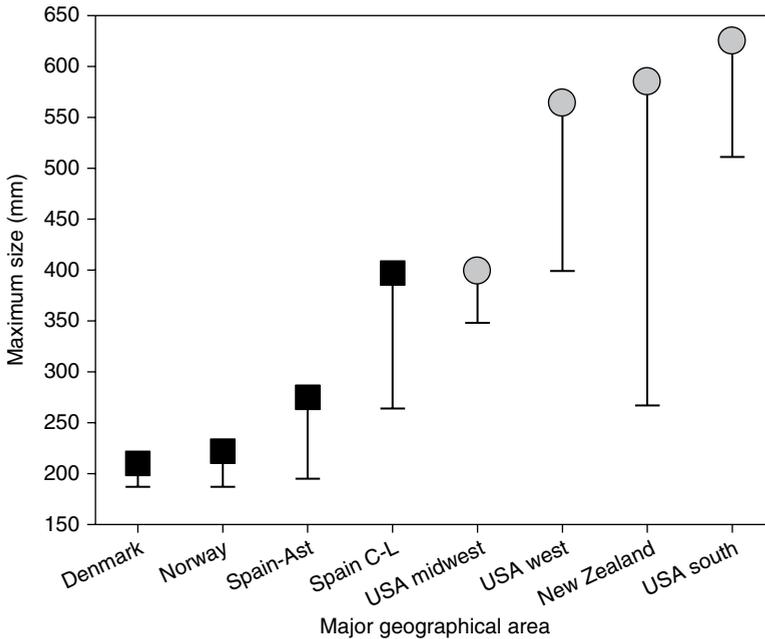


Figure 20.3 Reproduced with permission from the authors (Budy *et al.* 2013). Maximum body size (downward error bar represents range) attained by brown trout in different major geographical areas. Black squares are native habitat, and grey circles are exotic habitat.

Other, Indirect, and Synergistic Impacts

In addition to competitive and predatory impacts, there are other potential impacts of exotic brown trout on native fishes related to natural history and demography. For example, in contrast to most native fishes in the IMW, which spawn in the spring, brown trout are autumn spawners ('spring' here refers to when the weather becomes warmer and leaves and plants start to grow again). This reproductive timing may give exotic brown trout an advantage over native fishes or alternatively may leave brown trout maladapted to expand further under current climatic regimes. Because they spawn in the autumn and emerge during the early spring, age-0 brown trout will have a strong size advantage over native trout in the summer, a critical time period for growth ('summer' here refers to the warmest time of year and typically the period of greatest trout growth; Fausch 1998). This size advantage could intensify competitive interactions, particularly aggressive behavior and competition for space (e.g., Keeley 2001), thus giving brown trout a likely advantage.

Alternatively, brown trout may have a reproductive strategy maladapted to many mountain streams (Fausch 1988; Moyle and Light 1996; Fausch *et al.* 2001). Autumn spawning at high elevation in mountain streams can expose embryos and hatchlings to very cold water temperatures (which may delay in development), high spring snow melt floods (which scour and displace eggs), and anchor ice formation (which limits spawning success). For example, Reiser and Wesche (1979) experimentally demonstrated that intra-gravel ice limits brown trout egg survival in streams exposed to harsh winter conditions on the Laramie plains, even though the spawning habitat was

suitable and the eggs were buried at 15–18 cm. At a broader scale, in the Logan River, Utah, anchor ice was in the top performing models exploring the abiotic and propagule pressure covariates that best explained brown trout redd density along an elevational gradient (Meredith 2012; Meredith *et al.* 2016). In contrast, however, brown trout eggs reared in incubation boxes and placed along the elevational gradient of the Logan River, Utah, demonstrated that harsher over-winter conditions did not preclude hatching success; $\geq 36\%$ of eggs successfully hatched at high elevation sites, although survival was higher at low elevations (Wood and Budy 2009). In addition, most climate warming predictions for this region include warmer winters and wetter springs, conditions that could facilitate higher reproductive success of brown trout in high elevation areas. In contrast to elsewhere, however, in the IMW neither hybridization of native trout with exotic brown trout nor egg superimposition (e.g., Essington *et al.* 1998) represent native fish conservation issues associated with brown trout. They are autumn spawners and so temporally segregated, and they cannot hybridize with native trout (but see McIntosh *et al.* 2011).

In combination with the direct impacts that brown trout have on native fishes through inter-specific interactions, there are other potential impacts that are less direct. First, they serve as vectors of disease. Brown trout carry the exotic European parasite, *Myxobolus cerebralis* (*Mc*), which causes whirling disease; however, they are much less vulnerable to the impact of the disease than *Oncorhynchus* species (i.e., native trout; Baldwin *et al.* 2000). Furthermore, stressed fish are more susceptible to disease (Wedemyer *et al.* 1970; Fagerlund *et al.* 1995), as may be the case with native trout stressed by competitive interactions with exotic trout, a potentially important negative synergy (Rassmusen *et al.* 2010; Houde *et al.* 2015). In addition, brown trout are less sensitive to degraded habitat compared to most *Oncorhynchus* species (McIntosh *et al.*, 2011), and *Mc* secondary hosts prefer degraded habitat. Thus native fishes may have a further disadvantage in degraded habitat; exotic brown trout will have the competitive advantage, and the concentration of *Mc* parasites may be high. This is another complex synergy that could exacerbate the impacts of brown trout on native fishes (Wilson 2000; Hansen and Budy 2011). While we are aware of these potential synergies, it is likely that brown trout have other complex and unknown negative impacts on other aspects of aquatic ecosystems that may impact and trickle through multiple trophic levels (e.g., New Zealand; Townsend and Simmon 2006). For example, exotic brown trout have caused strong cascading effects on mayflies down to algae in New Zealand streams and also appear to alter primary and secondary production (Huryn 1988; McIntosh and Townsend 1996).

Paradoxical Popularity

Despite these well-documented and more recently accepted negative impacts of exotic brown trout, they remain extremely popular as sport fish and are still actively managed fisheries in many systems in the IMW. The history of brown trout stocking in Utah provides a good example of the extent and consistency of these stocking efforts as reported by the state fisheries management agency, Utah Division of Wildlife Resources (Figure 20.4). Stocking efforts were greatest and the most extensive from 1940 to 1950 and included most water bodies that were accessible (including by plane) and likely to

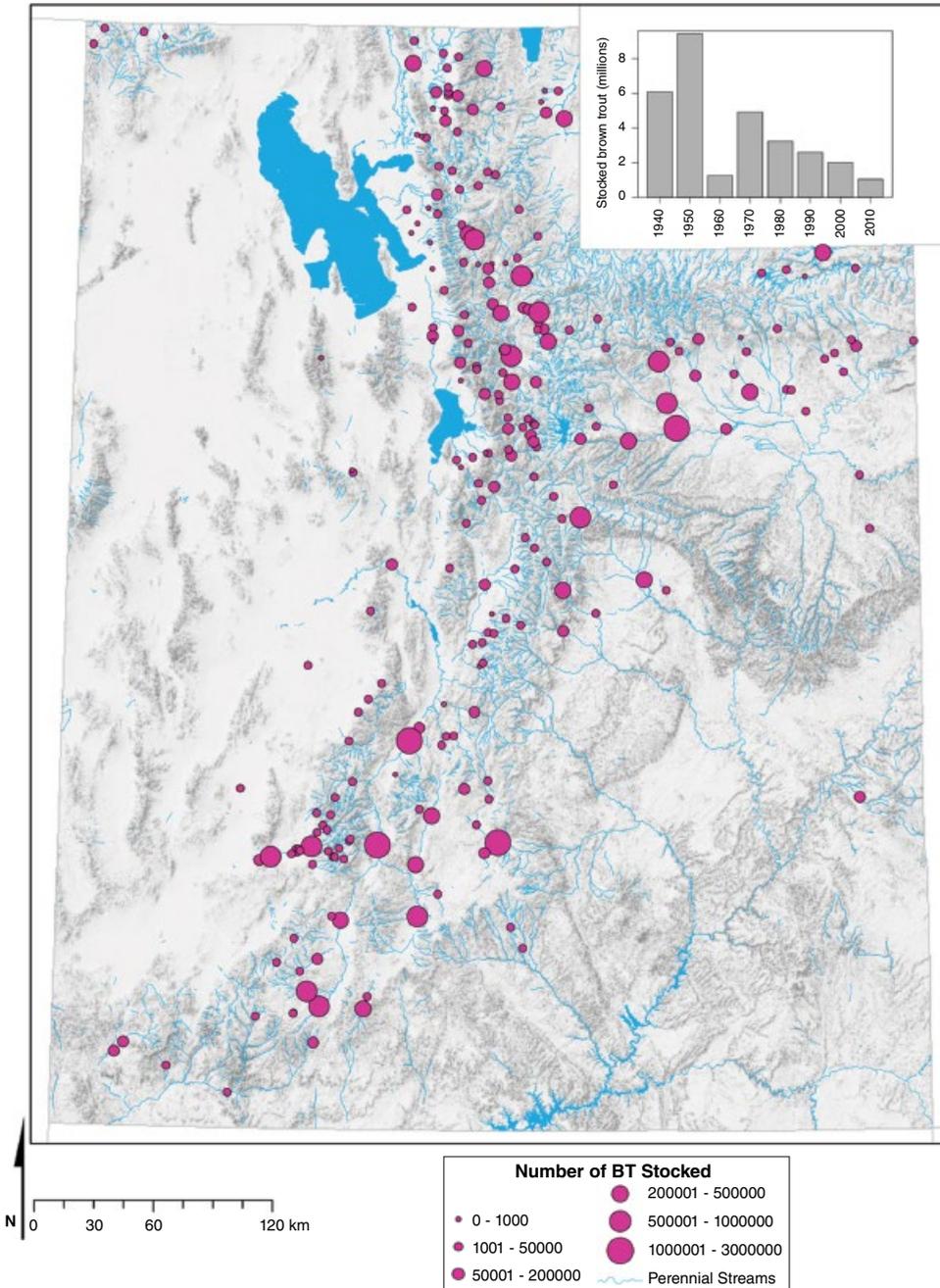


Figure 20.4 Map showing the intensity and spatial distribution of records of individual brown trout stocking efforts throughout the state of Utah for time periods 1940–2010. The upper right insert bar graph represents the millions of brown trout stocked (y axis) by decade (x axis) over this time period.

support brown trout statewide. After an odd drop in the 1960s these stocking efforts continued at relatively high levels from 1970 to 1990, but then began to substantially decline after 2000. In fact, over the last ten years, there have been only approximately 50 brown trout stocking events in Utah, and similar trends are noted anecdotally in other western states. A noteworthy point, however, is that many stocking events were unrecorded and/or unofficial (i.e., private parties stocking), suggesting our records represent a likely significant underestimate of stocking effort both temporally and spatially. Nonetheless, this intensive and extensive stocking effort clearly contributed to the expansion and establishment of exotic brown trout in the IMW via continued propagule pressure (MacCrimmon and Marshall 1968).

Brown trout prosper in many natural and managed ecosystems, with the state trophy brown trout recorded in reservoirs in Idaho, Wyoming, and Utah, in lakes in Arizona, Montana, and Nevada, and even in ponds in Colorado (Table 20.1). These state trophy records, and other non-recorded, big brown trout catches represent impressive fish, but anglers also enjoy catching more modest-sized brown trout as well (Figure 20.5). The state records, while impressive, cannot however compete with the world trophy record, ironically also an exotic brown trout captured in a canal in New Zealand that was 140% bigger than any USA – IMW state trophy records.

Brown trout anglers in the IMW have varied opinions but do point out several motivations for targeting this exotic species including: (1) the belief that they are the most challenging of the trout species to catch; (2) they are often found in streams that are of marginal quality for other native trout; and (3) they are often the biggest fish in a stream, and anglers like big fish. A comparison of brown trout populations in catch-and-release and harvest (i.e., take) sections of a river demonstrated that the catch-and-release section held brown trout and rainbow trout, with rainbow trout comprising approximately 60% of the population relative to only 20% in the more heavily fished

Table 20.1 Official state trophy catches of exotic brown trout shown by U.S. state, location, year caught, and size (weight [kg] and length [m]). The worldwide recorded record is also shown for an exotic brown trout caught in New Zealand. Data are taken from: <https://www.landbigfish.com/staterecords/> and <https://www.igfa.org/>.

State in USA	Location	Year	Weight (kg)	Length (m)
Arizona	Reservation Lake	1999	10.4	0.91
Colorado	Roaring Judy Ponds	1988	13.8	0.92
Idaho	Ashton Reservoir	2007	12.4	0.93
Montana	Wade Lake	1966	13.2	NA
Nevada	Cave Lake	1984	12.4	0.84
New Mexico	Chama River	1946	9.2	0.88
Utah	Flaming Gorge Reservoir	1977	15.3	1.02
Wyoming	Anvil Draw, Flaming Gorge Reservoir	1982	11.7	0.87
WORLD				
New Zealand	Oahu Canal	2013	19.1	NA



Figure 20.5 Happy anglers showing off their brown trout catches. In the top panel, Paul Thompson, avid angler and fish biologist holds a 0.71 m brown trout caught in the Weber River, northern Utah. In the bottom, Kiera Saltern holds a more modest and commonly-caught size brown trout captured in Porcupine Reservoir, also in northern Utah.

downstream reach (Anderson and Nehring 1984). In other words, many more brown trout survived in the heavily fished section potentially providing support to the argument they are more challenging to catch. With regard to their presence in streams of marginal habitat, across streams, brown trout account for more of the caught fish (as compared to rainbow trout) as temperature increases (see also ‘novel habits’ below; McMichael and Kaya 1991). And because they are difficult to catch, from a state management perspective, in some cases it is easier to maintain a brown trout fishery since it is difficult to overfish. Alternatively, in other cases, the difficulty of anglers catching (and keeping) brown trout may lead to higher densities of smaller-sized brown trout than desired (e.g., Blacksmith Fork River, Utah; Jenkins *et al.* 1999). Nonetheless, the difficulty of catching brown trout and the declining desire to keep

them once caught may mean managers do not have to rely as heavily on expensive stocking efforts that are not always successful, a perspective driving the trout management in the state of Wyoming, for example (Wiley *et al.* 1993).

The popularity of brown trout is also exemplified by their status with Trout Unlimited, the largest and certainly most prominent cold-water fishery conservation association in the USA with more than 150,000 members including lawyers, policy experts, and scientists (<http://www.tu.org>). Accordingly, brown trout are featured frequently in their magazine 'Trout Magazine', they publish videos of anglers catching 'monster browns', tips for catching brown trout, and support restoration efforts that enhance brown trout angling opportunities. In fact, as in New Zealand (Chapter 22, this volume), in Utah, some anglers refer to brown trout as 'native browns' and are clearly unaware they are exotic or invasive (Budy and others, personal observation). Trout Unlimited, however, has more recently acknowledged the paradox of which they are part, as they simultaneously promote and enhance brown trout fisheries in some places while acknowledging they have a negative effect on native trout in other places (Williams *et al.* 2015).

In addition to general sport fish popularity, brown trout may play a special role as one of the more dominant and successful sport fish in novel, managed, and artificial riverine ecosystems including reservoirs and tailwaters behind dams. Reservoirs differ from the natural riverine environment in that they are low or no velocity, often warmer and stratified, and behave in general more like a lentic environment. Food sources and energetic pathways differ accordingly. Conversely, tailwaters in the IMW are often hypolimnetic release and thus very cold relative to the natural riverine system and can also be extremely variable in terms of flow due to hydro-peaking management at the dam (e.g., Dibble *et al.* 2015). Consequently, these novel riverine systems differ significantly from the natural and historical river ecosystem and thus may not be hospitable to native western fishes and trout, which have, in general relatively narrow fundamental niches (e.g., Benke 1992). Exotic brown trout have been stocked and maintained in these novel and highly-managed ecosystems, and in many cases they thrive and reproduce naturally due to their plasticity (e.g., Dibble *et al.* 2015).

In order to qualitatively document the quality of brown trout fisheries in reservoirs and tailwaters, we solicited experts throughout the IMW to participate in a survey where they were asked to rank the quality of brown trout fisheries. Specifically, we included reservoirs, tailwaters, and adjacent reaches immediately upstream of the reservoir (0–5 miles upstream) and downstream of the tailwater, below the physical effects of the dam. Respondents were asked to consider the given system or systems they are most familiar with relative to the average quality of all brown trout fisheries they manage, study, or work on within the IMW. Quality was qualitatively defined as 'a metric based on size-structure, body condition, density, and angler satisfaction.' Experts included avid anglers, guides, state and tribal government resource managers and biologists (hereafter, resource managers), and members of Trout Unlimited (TU; TU 'members' identified themselves as 'Public Lands Coordinator', 'Chairman of State TU Council', 'Backcountry Coordinator', 'Project Manager', or 'Western Agriculture and Water Policy Counsel').

A total of 79 unique respondent-system observations were collected. Of those, 25 were repeat system observations for a given system. We only report the opinion of one respondent per system. The process of choosing which respondent was based on the following criteria: resource managers were selected over any other group; finally, if

multiple resource managers responded, we selected the manager with the most years of experience. Finally, if a respondent answered 'I do not know' for any reach, the entire response was excluded; this final step eliminated three systems from our final results. Our selection criteria reduced the dataset to opinions from one angler, one member of Trout Unlimited, two fishing guides, one member of a tribal government, and 19 resource managers, resulting in a total of 51 systems from eight states.

Brown trout fisheries in tailwaters were ranked as 'Excellent' or 'Above average' for 55% of systems and ranked 'Poor' in only 8% of ranked systems (Figure 20.6). The downstream reach, upstream reach, and the reservoir were ranked as 'Excellent' or 'Above average' for 24%, 22%, and 18% of systems, respectively, and received the rank of 'Poor' in 8%, 6%, and 12%, respectively. Brown trout fisheries were absent from the upstream reach, the reservoir, or the downstream reach in 31%, 33%, and 10% of systems, respectively. The waters adjacent to the tailwater were also ranked relative to the tailwater in each system. The survey indicated that the brown trout fisheries in tailwaters were ranked as the best reach in 69% of systems and were the best or second best in 96% of systems (Figure 20.7). The tailwater fishery was *never* ranked as the worst reach in a given system. Collectively, our expert opinion survey indicated that tailwaters are unique habitats that often support superior brown trout fisheries relative to adjacent lotic reaches and reservoirs. Indeed, our findings indicate that brown trout tailwater fisheries are very often among the best brown trout fisheries in the IMW.

Management in the Future

Despite their popularity as sport fish and given the widespread impacts brown trout have had on native fish communities, management and angler perspectives towards exotic brown appear to be shifting in the IMW. With support from the state government and most anglers, Saunders *et al.* (2014) completed a two-year experimental mechanical removal of brown trout in a tributary of the Logan River, Utah. Ten years prior to this, such an effort would have had no support. The mechanical removal of more than 15,000 brown trout resulted in a strong recruitment pulse of small fish, demonstrating that prior to the removal, adult fish suppressed recruitment through some sort of density-dependent effect (i.e., reduced survival or increased emigration). These results suggest that mechanical removal is not a viable management strategy for reducing brown trout abundance, and rather, eradication requires extensive and repeated chemical treatment (Finlayson *et al.* 2005; Meyer *et al.* 2006). In related work, we hypothesized that biotic resistance (Elton 1958), in this case expressed as high densities of native cutthroat trout, is the mechanism limiting the expansion and establishment of brown trout into the upper headwaters of IMW streams (Saunders and Budy, in prep). We demonstrated experimentally that while brown trout are unaffected by increasing densities of native cutthroat trout, cutthroat trout performance increases with increasing densities of conspecifics. We theorize, once cutthroat trout densities are high enough, it may be difficult for brown trout to expand and become established. These results are promising for native fish management, as they indicate that it may be sufficient to shift the balance of dominance back to native fish, rather than try to eliminate every unwanted brown trout. In addition, the use of beavers (*Castor canadensis*) for passive stream restoration is increasing

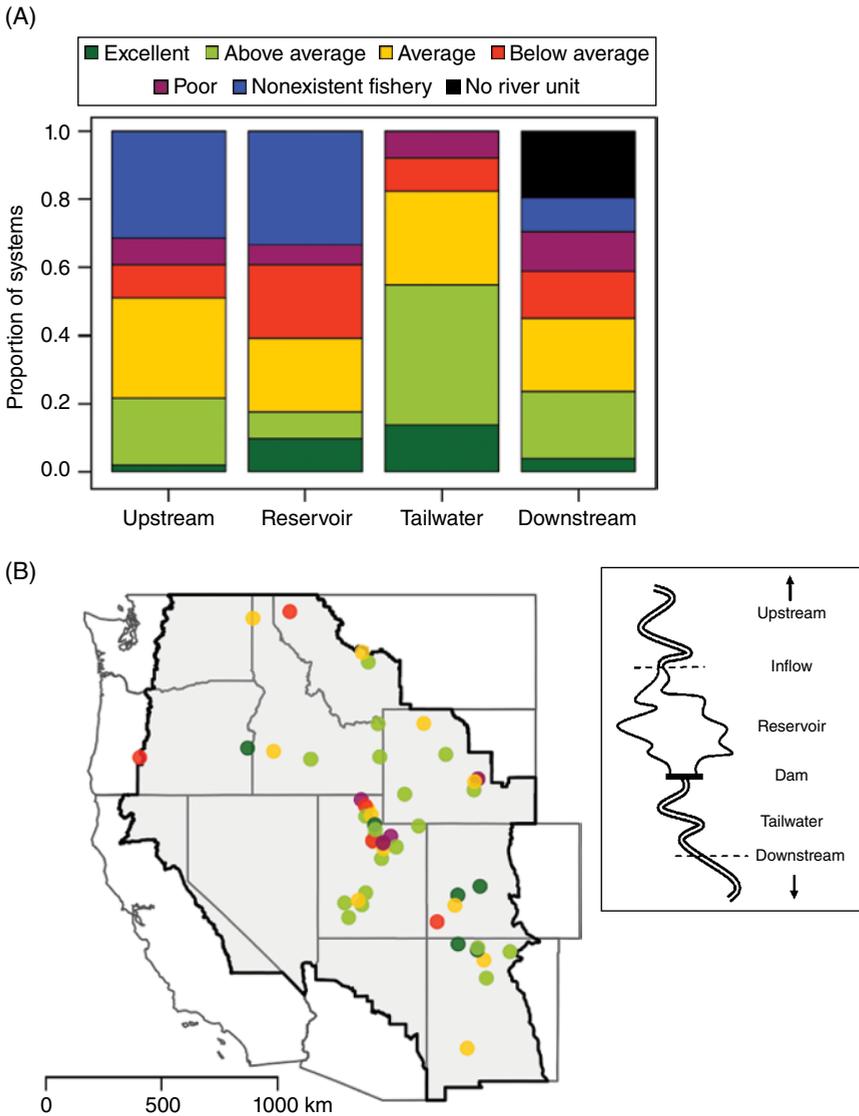


Figure 20.6 (A) The quality of brown trout fisheries in various river reaches (upstream of the reservoir, the reservoir, the tailwater, and downstream of the effects of the tailwater) relative to other brown trout fisheries as classified by expert opinion survey respondents, and (B) the spatial location and quality of tailwater fisheries (n=50) shown with the Intermountain West boundary. The color in (B) corresponds to the tailwater bar in (A).

dramatically in popularity and application across the IMW (Pollock *et al.* 2015). While movement of native cutthroat trout is not impeded by beaver dams, exotic brown trout have difficulties passing through dams (Lokteff *et al.* 2013). This difference in passage ability past beaver dams could favor native trout as beaver dam densities increase in the future.

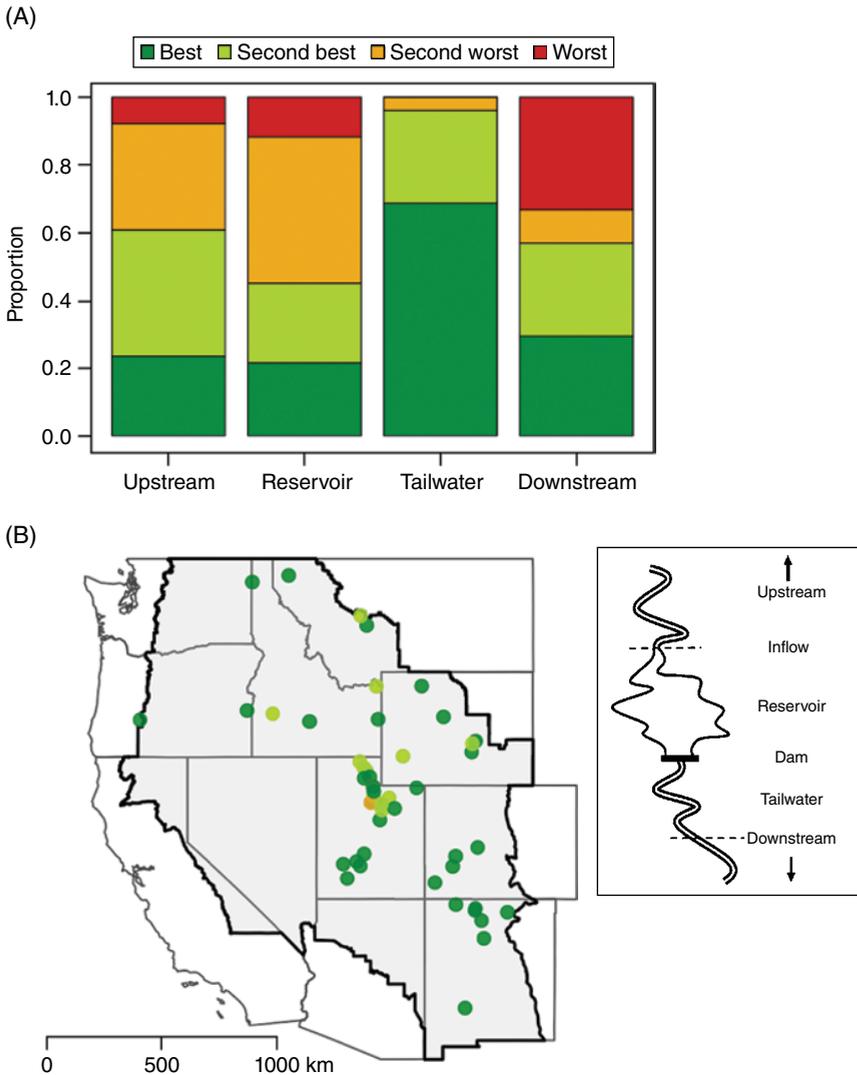


Figure 20.7 The system-specific ($n = 50$) rank of each river unit evaluated by survey respondents. (A) the proportion of systems in which the river unit-specific brown trout fishery was ranked or tied as the best, second best, second worst, or worst. (B) the spatial location and ranking of each tailwater fishery ($n = 50$); shown with the Intermountain West boundary. The color in (B) corresponds to the tailwater bar in (A).

The Utah Division of Wildlife Resources has also been monopolizing on natural large-scale wildfire as a reset for native trout streams (Hepworth and Whalen, personal communication). After the fire, they remove the few remaining exotic brown trout and restock the streams with native trout. In this case, the fire helps with public support, as they are not killing very many brown trout themselves. After native trout are re-established, anglers will likely be largely satisfied. In the IMW, more than 80% of anglers do not have a preference for brown trout over other trout, as long as they can fish in a

beautiful mountain stream and catch trout (Budy *et al.* 2003; Nadolski and Penne 2013). Similarly, in a recent statewide 'Attitudinal Survey' about angling in Utah, survey respondents ranked exotic brown trout and native cutthroat trout about equally in terms of their preference of species they are interested in catching (Krannich 2011). This general angler attitude opens doors for brown trout removal and native trout conservation in the future (Saunders *et al.* 2014; Saunders *et al.* in prep). However, the great majority of stream anglers in the IMW are also catch-and-release fishermen, which suggests increasing or lifting bag limit regulations would have little utility in reducing brown trout numbers unless this change was also accompanied by an extensive outreach effort to educate anglers.

In contrast to promising changes in perspective about exotic brown trout, predictions of future climate change favor the expansion of brown trout. Although variable and a difficult region within which to make climate predictions, most predictions of the future climate on the IMW are for warmer winters, less snow, and more precipitation as rainfall (Kunkel *et al.* 2013; Cook *et al.* 2015). Less snow pack equates to smaller spring floods and less scour, and there is some evidence that scour may limit reproductive success and early survival of exotic brown trout in the upper portions of mountain streams (Jensen and Johnson 1999; Wood and Budy 2009). In addition, in the Logan River, Utah, we are observing less anchor ice, a factor that may also partially limit brown trout spawning success in the upper portion of mountain rivers (Meredith 2012; Meredith *et al.* 2016).

Finally, the IMW has increased in average annual temperatures by almost 3°C (Kunkel *et al.* 2013). Although we have not observed evidence of temperature-mediated competition in previous experiments, those experiments were not completed at temperatures near the thermal limits of native trout (McHugh and Budy 2005). Brown trout have a broader thermal niche than most native trout in the IMW (McIntosh *et al.* 2011), they have strong potential to adapt to changing temperature regimes (Jensen *et al.* 2008), and they exhibit flexibility in spawn time and migratory behavior (Valiente *et al.* 2010). Collectively these characteristics could mean that warmer streams could give exotic brown trout an even greater competitive advantage over native trout in the future. The future of exotic brown trout in the IMW will depend on the nexus of public sentiment and policy, the effectiveness of eradication efforts, and the effect of climate change on both the native fishes and exotic brown trout. Regardless, brown trout are pervasive and have a broad distribution through the IMW – these factors will likely ensure that local populations of this species will persist into the future in spite of public sentiment/policy, eradication efforts, and changing climate change.

Acknowledgements

Primary project funding was provided by the U.S. Geological Survey – Utah Cooperative Fish and Wildlife Research Unit, Utah State University (in-kind) and the Department of Watershed Sciences and Ecology Center at Utah State University. Brett Roper (U.S. Forest Service), James DeRito and Paul Burnett, and Paul Thompson, (Utah Division of Wildlife Resources; UDWR), and Gary P. Thiede (USU; Fish Ecology Lab) contributed significantly to the text and provided data and/or supportive information. Craig Schaugard (UDWR) provided the stocking records for the state of Utah, and Joshua

Gilbert and Wally MacFarlane (USU, Fluvial Habitats Center) completed the GIS analysis and mapping of stocking locations over time and space. Mike Ebinger gave permission to print the photo in Figure 20.1. Kimberly Dibble provided helpful suggestions in the early development of the chapter. We thank Deanna Strohm for extensive editorial support. We thank the numerous anglers, members of Trout Unlimited, guides, members of tribal governments, and resource managers for participating in our expert opinion survey. Previous drafts of this manuscript were greatly improved by the comments from two anonymous reviewers. The use of trade names or products does not constitute endorsement by the United States Government.

References

- Almodóvar, A., Nicola, G.G. & Elvira, B. (2006). Spatial variation in brown trout production: the role of environmental factors. *Transactions of the American Fisheries Society*, **135**, 1348–1360.
- Anderson, R. & Nehring, R.B. (1984). Effects of catch and release regulation on a wild trout population in Colorado and its acceptance by anglers. *North American Journal of Fisheries Management*, **4**, 257–265.
- Baldwin, T.J., Vincent, E.R., Silflow, R.M. & Stanek, D. (2000). Myxobolus cerebralis infection in rainbow trout (*Oncorhynchus mykiss*) and brown trout (*Salmo trutta*) exposed under natural stream conditions. *Journal Veterinary Diagnostic Investigation*, **12**, 312–321.
- Bozek, M.A. & Hubert, W.A. (1992). Segregation of resident trout in streams as predicted by three habitat dimensions. *Canadian Journal of Zoology*, **70**, 886–890.
- Budy, P., Thiede G.P., Lobon-Cervia, J., Gonzales, G., *et al.* (2013). Limitation and facilitation of one of the world's most invasive fish: an intercontinental comparison. *Ecology*, **94**, 356–367.
- 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.
- Closs, G.P. & Lake, P.S. (1996). Drought, differential mortality and the coexistence of a native and an introduced fish species in a south east Australian intermittent stream. *Environmental Biology of Fishes*, **47**, 17–26.
- Cook, B.I., Ault, T.R. & Smerdon, J.E. (2015). Unprecedented 21st century drought risk in the American Southwest and Central Plains. *Science Advances*, **1**, e1400082.
- Courtenay, W.R., Jr., Hensley, D.A., Taylor, J.N. & McCann, J.A. (1984). Distribution of exotic fishes in the continental United States. In: Courtenay, W.R. Jr. & Stauffer, J.R. Jr. (Eds). *Distribution, Biology and Management of Exotic Fishes*. Johns Hopkins University Press, Baltimore, Maryland, pp. 41–77.
- de la Hoz Franco, E.A. & Budy, P. (2005). 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.
- Dunham, J.B., Adams, S.B., Schroeter, R.E. & Novinger, D.C. (2002). Alien invasions in aquatic ecosystems: toward an understanding of brook trout invasions and potential impacts on inland cutthroat trout in western North America. *Reviews in Fish Biology and Fisheries*, **12**, 373–391.

- Elton, C.S. (1958). *The Ecology of Invasions by Animals and Plants*. John Wiley & Sons, New York.
- Essington, T.E., Sorensen, P.W. & Paron, D.G. (1998). High rate of redd superimposition by brook trout (*Salvelinus fontinalis*) and brown trout (*Salmo trutta*) in a Minnesota stream cannot be explained by habitat availability alone. *Canadian Journal of Fisheries and Aquatic Sciences*, **55**, 2310–2316.
- Fagerlund, U.H.M., McBride, J.R. & Williams, I.V. (1995). Stress and tolerance. In: Groot, C., Margolis, L. & Clarke, W.C. (Eds.) *Physiological Ecology of Pacific Salmon*. UBC Press, Vancouver, Canada, pp. 461–503.
- Fausch, K.D. (1984). Profitable stream positions for salmonids: relating specific growth rate to net energy gain. *Canadian Journal of Zoology*, **62**, 441–451.
- Fausch, K.D. (1989). Do gradient and temperature affect distributions of, and interactions between, brook charr (*Salvelinus fontinalis*) and other resident salmonids in streams? *Physiology and Ecology Japan*, **1**, 303–322.
- Fausch, K.D., Nakano, S. & Ishigaki, K. (1994). Distribution of two congeneric charrs in streams of Hokkaido Island, Japan: considering multiple factors across scales. *Oecologia*, **100**, 1–12.
- Fausch, K.D. (1998). Interspecific competition and juvenile Atlantic salmon (*Salmo salar*): on testing effects and evaluating evidence across scales. *Canadian Journal of Fisheries & Aquatic Sciences*, **55**, 218–231.
- Fausch, K.D., Rieman, B.E., Dunham, J.B., Young, M.K. & Peterson, D.P. (2009). Invasion versus Isolation: trade-offs in managing native salmonids with barriers to upstream movement. *Conservation Biology*, **23**, 859–870.
- Finlayson, B., Somer, W., Duffield, D., Propst, D., *et al.* (2005). Native inland trout restoration on national forests in the western United States: time for improvement? *Fisheries*, **30**, 10–19.
- Greeley, J.R. (1932). The spawning habits of brook, brown and rainbow trout, and the problem of egg predators. *Transactions of the American Fisheries Society*, **62**, 239–248.
- Griffith, J.S. (1988). Review of competition between cutthroat trout and other salmonids. In: Gresswell, R.E. (Ed.) *Status and Management of Cutthroat Trout* American Fisheries Society Symposium 4, Bethesda, MD, pp. 134–140.
- Hansen, E.S. & Budy, P. (2011). The potential of passive stream restoration to improve ecosystem health and minimize the impact of fish disease: a short-term assessment. *Journal of the North American Benthological Society*, **30**, 573–588.
- Houde, A.L.S., Wilson, C.C. & Neff, B.D. (2015). Competitive interactions among multiple non-native salmonids and two populations of Atlantic salmon. *Ecology of Freshwater Fish*, **24**, 44–55.
- Jenkins, Jr., 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.
- Keeley, E.R. (2001). Demographic responses to food and space competition by juvenile steelhead trout. *Ecology* **82**, 1247–1259.
- Keleher, C.J. & Rahel, F.J. (1996). Thermal limits to salmonid distributions in the rocky mountain region and potential habitat loss due to global warming: a Geographic Information System (GIS) approach. *Transactions of the American Fisheries Society*, **125**, 1–13.
- Kunkel, K.E., Stevens, L.E., Stevens, S.E., Sun, L., *et al.* (2013). Regional Climate Trends and Scenarios for the U.S. National Climate Assessment Part 5. NESDIS 142-5, NOAA Technical Report.

- Louhi, P., Mäki-Petäys, A., Huusko, A. & Muotka, T. (2014). Resource use by juvenile brown trout and Alpine bullhead: influence of interspecific versus intraspecific competition. *Ecology of Freshwater Fish*, **23**, 234–243.
- MacCrimmon, H.R. & Marshall, T.L. (1968). World distribution of brown trout, *Salmo trutta*. *Journal of the Fisheries Board of Canada*, **25**, 2527–2548.
- Mather, F. (1889). Brown trout in America. *U.S. Fish Commission Bulletin*, **7**, 21–22.
- McHugh, P. & Budy, P. (2006). Experimental effects of non-native brown trout on the individual- and population-level performance of native cutthroat trout. *Transactions of the American Fisheries Society*, **135**, 1441–1455.
- McMichael, G.A. & Kaya, C.M. (1991). Relations among stream temperature, angling success for rainbow trout and brown trout, and fisherman satisfaction. *North American Journal of Fisheries Management*, **11**, 190–199.
- McHugh, P. & Budy, P. (2005). An experimental evaluation of competitive and thermal effects on brown trout (*Salmo trutta*) and cutthroat trout (*Oncorhynchus clarki utah*) performance along an altitudinal gradient. *Canadian Journal of Fisheries and Aquatic Sciences*, **62**, 2784–2795.
- McHugh, P. & Budy, P. (2006). Experimental effects of non-native 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.A. & Budy, P. (2011). Brown trout (*Salmo trutta*). In: Francis, R.A. (Ed.) *A Handbook of Global Freshwater Invasive Species*. Earthscan, London, pp. 285–296.
- Meredith, C., Budy, P. & Thiede, G.P. (2014). Predation on native sculpin by exotic brown trout exceeds that by native cutthroat trout within a mountain watershed (Logan, UT, USA). *Ecology of Freshwater Fish*, **24**, 133–147.
- Meredith, C.S., Budy, P., Hooten, M. & Prates, M.O. (2016). Assessing abiotic conditions influencing the longitudinal distribution of exotic brown trout in a mountain stream: a spatially-explicit modeling approach. *Biological Invasions*. DOI 10.1007/s10530-016-1322-z. USGS IP-069503.
- Meyer, K.A., Lamansky Jr, 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.
- Nadolski, B. & Penne, C. (2013). Weber River Creel Study. Utah Division of Wildlife Resources, Final Report, pp. 1–25.
- Pollock, M.M., Lewallen, G., Woodruff, K., Jordan, C.E. & Castro, J.M. (2015). The beaver restoration guidebook: working with beaver to restore streams, wetlands, and floodplains. *United States Fish and Wildlife Service*, Portland, Oregon.
- Rasmussen, J.E., Belk, M.C., Habit, E., Shiozawa, D.K., Hepworth, R.D. & Anthony, A. (2011). Variation in size-at-age between native cutthroat and introduced brown trout in allopatry and sympatry: implications for competitive interaction. *Aquatic Biology*, **13**, 285–292.
- Resier, D.W. and Wesche, T.A. (1979). In situ freezing as a cause of mortality in brown trout eggs. *The Progressive Fish Culturist*, **41**, 58–60.
- Saunders, W.C. & Budy, P. (In Prep.). Can high densities of Bonneville cutthroat trout prevent brown trout establishment through biotic resistance. *USGS IP-049187*.
- Saunders, W.C., Budy, P. & Thiede, G.P. (2014). Demographic changes following mechanical removal of exotic brown trout in an Intermountain West (USA), high-elevation stream. *Ecology of Freshwater Fish*, **24**, 252–263.

- Stewart, J.Q., Whiteman, C.D., Steenburgh, W.J. & Bian, X. (2002). A climatological study of thermally driven wind systems of the US Intermountain West. *Bulletin of the American Meteorological Society*, **83**, 699–708.
- Williams, J.E., Hook, A.L., Fessenmyer, K., Dauwalter, D.C., *et al.* (2015). State of the trout. A report dedicated to the memory of 'Dr. Trout' (Robert J. Behnke (1929–2013) who was the recognized expert on Native Trout Diversity in North America and among their greatest champions. *Trout Unlimited*, 1–75.
- Vincent, R.E. & Miller, W.H. (1969). Altitudinal distribution of brown trout and other fishes in a headwater tributary of the South Platte River, Colorado. *Ecology*, **50**, 464–466.
- Wang, L. & White, R.J. (1994). Competition between wild brown trout and hatchery greenback cutthroat trout of largely wild parentage. *North American Journal of Fisheries Management*, **14**, 475–487.
- Wiley, R.W., Whaley, R.A., Satake, J.B. & Fowden, M. (1993). Assessment of stocking hatchery trout: a Wyoming perspective. *North American Journal of Fisheries Management*, **13**, 160–170.
- Wedemeyer, G. (1970). Stress of anesthesia with MS-222 and benzocaine in rainbow trout (*Salmo gairdneri*). *Journal of the Fisheries Research Board of Canada*, **27**, 909–914.
- Wilson, M.E. (2000). Environmental change and infectious disease. *Ecosystem Health*, **6**, 7–12.
- Wood, J. & Budy, P. (2009). An investigation of the early life-history and potential influences on invasion success of exotic of brown trout (*Salmo trutta*). *Transactions of the American Fisheries Society*, **138**, 756–767.