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Trout as Native and Nonnative Species: A Management Paradox

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Introduction

Native trout are threatened worldwide by introductions of nonnative trout that in many cases are themselves threatened within their native range and historical habitats. This chapter focuses on this paradox and addresses how information gained to protect and restore a species in its native range can be used to suppress the same species outside its native range, where it may be invasive. We describe examples of three trout species, Lake Trout *Salvelinus namaycush*, Brown Trout *Salmo trutta*, and Brook Trout *Salvelinus fontinalis*, that are managed for the opposing goals of restoration versus suppression, in relation to their opposing roles as both native and nonnative species in aquatic communities. We also attempt to develop insights into how this information might be used to accomplish both seemingly incompatible ends.

Lake Trout

The Lake Trout is native across much of northeastern North America, where the species was depleted in many habitats and has proven difficult to restore, but it has also been introduced across much of western North America, where the species has interacted negatively with other native trout species and has paradoxically proven difficult to control. In contrast to widespread introductions in North America, the Lake Trout has not been widely introduced beyond North America, and many introductions failed to persist (Crossman 1995). Consequently, examples of Lake Trout affecting native species are from western North America. Below, we review the paradox of restoring native Lake Trout in the Laurentian Great Lakes and suppressing nonnative Lake Trout in several lakes in the Intermountain West, USA (Table 1).

Restoration management in native range

The native distribution of Lake Trout is across much of North America north of latitude 41° (Crossman 1995), where it co-dominates coldwater lakes with the Lake

Table 1. Common causes of problems and potential solutions demonstrating the management paradox of these three trout species. These ideas are expanded upon in the text with literature cited accordingly. The species for which this is a primary issue is noted with the species boxes; N = native, NN = Nonnative.

Issue	Potential solution	Lake Trout	Brown Trout	Brook Trout	Comments and notes
		Invasion and introduction			
Purposeful introduction and migration from desired source populations, followed by exponential growth and negative impacts to popular fisheries and native fishes	Purposeful overharvest and cash incentives, education, and outreach	NN			• This strategy has been deemed desirable in selected lakes throughout western North America. However, suppression efforts must be balanced with conservation of native species and can be extremely costly. • Liberal regulations can also be used to promote reducation in abundance of nonnative species (e.g., high harvest limits for Lake Trout in Lake Pend Oreille and Yellowstone Lake).
Intense propagule pressure	Eliminate stocking		NN	NN	• Brown and Brook trouts were repeatedly stocked outside their native range and at extremely high stocking densities for several hundred years across the world and North America, respectively. While their abundance and distribution has declined dramatically in their native range, their densities in their nonnative range now far exceeds the densities of native fishes (trout invasion paradox). • Brook Trout invasion success is also partially attributed to high rates of immigration and emigration.

Table 1. Continued.

Issue	Potential solution	Lake Trout	Brown Trout	Brook Trout	Comments and notes
Genetic introgression and dilution.	Chemical and mechanical removal, selective barriers post natural (e.g., wildlfire) or managed removal, genetically sound reintroduction strategies		N	N	• Native Brown Trout hybridize with hatchery Brown Trout of lower fitness leading to negative impacts on native population viability and genetic diversity. • Brook Trout hybridize with Brown Trout; when done purposefully in the hatchery, this union produces sterile (mostly) tiger trout (Brown Trout × Brook Trout), a highly voracious predator and popular sport fish that cannot reproduce in the wild. • Brook Trout also hybridize with native Bull Trout *Salvelinus confluentus* in western North America. The resulting hybrids are sterile, leading to local extinction of Bull Trout. • Genetically sound reintroduction strategies require considerable resources, knowledge, and hatchery infrastructure that may not be possible everywhere.
			Habitat		
Local habitat degradation	Habitat restoration		N	N	• Habitat degradation often works synergistically to favor the success of nonnative trouts in native trout habitat (e.g., Brown Trout have a broader ecological niche than native Cutthroat Trout *Oncorhynchus clarkii*).

Table 1. Continued.

Issue	Potential solution	Lake Trout	Brown Trout	Brook Trout	Comments and notes
					• The Eastern Brook Trout Joint Venture program, for example, is implementing a multi-faceted and large-scale restoration program with explicit targets for success. Similar regional programs are needed to identify critical habitats for protection of remaining core native species habitats and to identify key habitats where restoration would be most effective. Many other restoration programs are too site-specific and do not embrace natural riverine function.
Increased fragmentation	Restored connectivity		N	N	• Restoration of connectivity is crucial for maintaining genetic diversity and population resiliency; however, restored connectivity may be detrimental to native fishes upstream if downstream nonnatives disperse. • To date, most population restoration has focused on construction of barriers in relatively small stream segments to prevent upstream movement of nonnatives. However, long-term effectiveness of isolation of small population isolates may be problematic; focus is now on more large-scale restoration efforts that encompass many more stream kilometers.

Table 1. Continued.

Issue	Potential solution	Lake Trout	Brown Trout	Brook Trout	Comments and notes
		Ecosystem and food web			
Competitive advantage over native fishes	Chemical and mechanical removal, selective barriers post natural disturbance (e.g., wildfire) or managed removal, potentially managing for biotic resistance		NN	NN	• Nonnatives displace native trouts outside of their native range, including Brown Trout displacing native Brook Trout or nonnative Brook Trout outcompeting native Cutthroat Trout and Bull Trout, for example. • Chemical removals have been more successful than mechanical removals, in general. Efforts to manually remove Brown Trout have, in some cases, caused increased recruitment. Chemical removals have become more effective and more accepted among the public in recent years.
Predatory impact	Chemical and mechanical removal, selective barriers post natural disturbance (e.g., wildfire)	NN	NN	NN	• All three species have the potential for significant predatory and food web impacts in their nonnative range. Lake Trout are natural and voracious predators in their native and nonnative range. Nonnative Brook Trout piscivory on juvenile native trout is an important cause of native trout decline. • Chemical removals have been more successful than mechanical removals in general. Efforts to manually remove Brown Trout have, in some cases, caused increased recruitment.

Table 1. Continued.

Issue	Potential solution	Lake Trout	Brown Trout	Brook Trout	Comments and notes
					• Chemical removal can be challenging if native species are also present and if there are legal restrictions (e.g., New Zealand)
Altered food web structure and function	Chemical and mechanical removal, selective barriers post natural disturbance (e.g., wildfire) or managed removal, potentially managing for biotic resistance	NN	NN	NN	• Lower trophic level impacts of trout in nonnative habitat have been repeatedly demonstrated in almost all locations where they are present and include changes to primary and secondary production, and community structure and function. • Naive prey are particularly sensitive to predatory impacts of nonnative predators with which they did not evolve (e.g., sculpin in the Intermountain West of the United States, galaxiids in New New Zealand).
		Harvest and fisheries			
Sensitive to commercial overfishing and population collapse	Unknown, regulation	N	N	N	• In the Great Lakes, Lake Trout have not recovered despite stocking, implementation of fishery regulations, and Sea Lamprey *Petromyzon marinus* control. • Brook Trout have been locally extirpated rangewide due to overharvest, but more restrictive harvest regulations have led to rebound in some areas in Lake Superior.

Table 1. Continued.

Issue	Potential solution	Lake Trout	Brown Trout	Brook Trout	Comments and notes
Species supports a popular sport fish when nonnative or from the hatchery, public misconception over wild, native, and nonnative identities of fishes, acclimatization societies	Strict regulation and fines for new translocations, education, and outreach, suitable native alternatives.	NN	NN	NN	• Lake Trout have been illegally introduced into many of the lakes where they now pose the greatest threats to native fishes; they often support a strong and politically powerful support group. • Nonnative Brown Trout are considered an extreme paradox because they remain a very popular sport fish, even in places where impacts are known and/or locally documented. • In Patagonia, for example, the nonnative trout fishery is one of the most important sources of income to a wide societal base. • Suppression efforts are most successful when an alternative, suitable (e.g., trout) native sportfish is present and available for angling. • In Europe, for example, the government is trying to find a more sustainable and publicly supported balance between harvest (e.g., increased minimum size, catch and release) and conservation of Brown Trout. • Promotion of angling for native trout can help enhance public appreciation and support for conservation programs.

Whitefish *Coregonus clupeaformis* (Johnson 1976). The Lake Trout is relatively slow-growing (length = 33–83 cm at age 10) and late-maturing (age at first maturity = 4–13 years), and therefore, it is more susceptible to overfishing than faster-growing and earlier-maturing species (Healey 1978; Martin and Olver 1980; Olver et al. 2004). For example, the largest Lake Trout populations in the world were overfished to extirpation in nearly all of the Laurentian Great Lakes (Hansen 1999; Krueger and Ebener 2004; Muir et al. 2012). Similarly, the Lake Trout population in the western arm of Great Slave Lake, Northwest Territories, Canada collapsed after only 10 years of commercial fishing (Keleher 1972; Healey 1978). Exploitation remains the most critical factor affecting Lake Trout populations in eastern Canada and the northeastern United States (Olver et al. 2004). In the Laurentian Great Lakes, restoration of self-sustaining Lake Trout populations has been elusive despite decades of intensive stocking, fishery regulation, and Sea Lamprey *Petromyzon marinus* control (Hansen 1999; Krueger and Ebener 2004; Muir et al. 2012).

The Lake Trout was important to native communities prior to European settlement of each of the Great Lakes, but the species underwent catastrophic collapses in each lake in the 19th and 20th centuries as Europeans settled the basin from east to west. Timing of Lake Trout stock collapses differed in each lake, as did causes of collapses, and these collapses have been the subject of much scientific inquiry and debate. Lake Trout yield from Lakes Huron and Michigan declined slowly from the late 1800s through the early 1900s and then collapsed in about one decade in Lake Huron and Lake Superior and one half-decade in Lake Michigan (Baldwin et al. 1979). Lake Trout yield declined from 2.7 million to 0.18 million kg during 1935–1947 in Lake Huron, from 3.1 million to 0.16 million kg during 1943–1949 in Lake Michigan, and from 2.1 million to 0.23 million kg during 1950–1960 in Lake Superior. Lake Trout stocks persisted in only two isolated locations in Lake Huron (Berst and Spangler 1972) and a few offshore locations in Lake Superior (Lawrie and Rahrer 1972; Lawrie 1978). Lake Trout were extirpated in the remaining Great Lakes before fishery management actions were implemented (Berst and Spangler 1972; Christie 1972; Hartman 1972; Wells and McLain 1972). Management of Lake Trout in the Great Lakes has therefore focused on the restoration of stocks, even in Lake Superior where some native stocks persisted despite the negative effects of overfishing and Sea Lamprey predation.

Fishery managers had little time to react to the collapse of Lake Trout stocks in the upper Great Lakes, and most were convinced that Sea Lamprey predation was the cause of those stock collapses rather than overharvest (Hile 1949; Hile et al. 1951a, 1951b). Moreover, Lake Trout stocks were mostly driven to extirpation before a selective Sea Lamprey toxicant was discovered in 1957 (Smith 1971; Smith et al. 1974; Smith and Tibbles 1980). State and federal fishery management agencies initiated stocking (1950), implemented Sea Lamprey control measures (1953), and closed Lake Trout fisheries (1962) in Lake Superior before stocks were extirpated (Pycha and King 1975). The Great Lakes Fishery Commission organized fishery management committees for each of the Great Lakes, with managers from each state, provincial, federal, and tribal management agency, to coordinate actions on each lake. By the mid-1980s, each lake committee developed Lake Trout restoration or rehabilitation plans that set targets for Lake Trout restoration or rehabilitation, prescribed management actions to enhance recruitment and survival, suggested pertinent topics for fishery research, and provided standards for coordinating stock assessment programs.

Although progress has been made toward controlling mortality sources, Lake Trout rehabilitation has only been achieved in Lake Superior, the most environmentally pristine of the Great Lakes. During the 2000s, several year-classes of natural Lake Trout recruits were detected in Lake Huron after parental stock size increased and mortality declined. Adult feral populations from hatcheries have been developed in the other lakes, but recruitment continues to depend on hatchery stocking. Adult Lake Trout abundance has been variable but increased across most areas of the Great Lakes since the early 1960s. Sea Lamprey mortality continues to be a major obstacle to reestablishment, particularly in northern Lake Michigan, Lake Huron, and Lake Erie. Spawning and production of juvenile Lake Trout has been observed in Lakes Ontario and Huron and to a limited extent in Lake Michigan. Increased survival of natural recruits coincided with declining Alewife *Alosa pseudoharengus* populations, stringent Sea Lamprey control, and reduced fishing mortality. Updated Lake Trout rehabilitation plans for each of the Great Lakes reflect a better understanding of the impediments to rehabilitation, a broader support community, an ecosystem approach to rehabilitation, and more specific and achievable rehabilitation objectives supported by fishery management, assessment, and research strategies.

Basinwide collapse of Lake Trout stocks in the Great Lakes, caused by overfishing, Sea Lamprey predation, interactions with nonnative species, and habitat degradation, led to one of the largest rehabilitation programs in the world. Primary impediments to Lake Trout reestablishment included population densities that were too low to recover, spawning aggregations that were not focused on appropriate spawning habitat, and survival of early life history stages that was too low to build adult abundance. To overcome these impediments, rehabilitation of Lake Trout into the Great Lakes focused on controlling Sea Lamprey populations, strictly regulating fisheries, preventing further introductions of nonnative species, genetically diversifying and innovating Lake Trout stocking programs, and coordinating among diverse stakeholders, politicians, and managers.

Suppression management outside native range

In contrast to the difficulty of restoring self-sustaining populations of Lake Trout in its native range, self-sustaining populations were established in many lakes outside of the Lake Trout native range by stocking and migration from source populations. The Lake Trout was widely stocked across North America in the late 1800s and early 1900s because of its popularity in its native range (Crossman 1995). Lake Trout were introduced into large lakes and reservoirs in eight states of the western United States (Martinez et al. 2009), where they negatively affected native salmonid populations (Donald and Alger 1993; Fredenberg 2002; Koel et al. 2005) and subsequently altered ecosystem structure and function (Tronstad et al. 2010; Ellis et al. 2011). In the United States, west of the continental divide, Lake Trout can reach high abundances and deplete native species through predation, competition, or both (Donald and Alger 1993; Ruzycki et al. 2003; Guy et al. 2011; Ferguson et al. 2012; Syslo et al. 2013). In some western lakes, the Lake Trout was of minor importance until *Mysis diluviana*, an opportunistic planktivore, was introduced to enhance growth of kokanee *Oncorhynchus nerka* (Martin and Northcote 1991). Lake Trout recruitment was limited in such lakes by a lack of native prey in deep waters for juvenile Lake Trout, so population density increased after *Mysis* were introduced (Stafford et al. 2002). For example, Lake Trout increased exponentially in numbers shortly after *Mysis* became established and suppressed kokanee and native Bull Trout *Salvelinus confluentus* and Westslope Cutthroat Trout *O. clarkii lewisi* in Lake Pend Oreille, Idaho (Hansen et al. 2008, 2010) and Flathead Lake and Swan Lake, Montana (Stafford et al. 2002; Syslo et al. 2013; Hansen et al. 2016). In other lakes with abundant prey for young Lake Trout, such as Yellowstone Lake, Wyoming, Lake Trout increased in abundance in the absence of *Mysis* and now limit abundance of Yellowstone Cutthroat Trout *O. c. bouvieri* (Ruzycki et al. 2003; Koel et al. 2005; Syslo et al. 2011).

Lake Pend Oreille.—Lake Trout were introduced into Lake Pend Oreille, Idaho in 1925, remained at low density through the 1990s, but then grew exponentially during 1999–2005, despite largely unregulated harvest since 2000 (Hansen et al. 2008, 2010). In 1999, Lake Trout exerted insignificant predation on kokanee (2% of kokanee production) compared to Rainbow Trout *O. mykiss* (53% of kokanee production) and Bull Trout (10% of kokanee production) predation on kokanee production (Vidergar 2000). However, after 1999, predation by the burgeoning population of Lake Trout, in combination with predation by the already robust population of Rainbow Trout, suppressed the kokanee population to levels that were too low to support a fishery or continued predation at such elevated levels (Maiolie et al. 2006). Lake Trout were also thought to present a threat to the Bull Trout population through competition for prey (Donald and Alger 1993; Fredenberg 2002; Guy et al. 2011). In response to the increase in the Lake Trout population, gill netting and trap-netting were used to remove Lake Trout, and cash incentives were used to encourage harvest of Lake Trout and Rainbow Trout by anglers on Lake Pend Oreille (Hansen et al. 2008, 2010). In 2006, these suppression programs removed 44% of the Lake Trout and 22% of the Rainbow Trout present in Lake Pend Oreille at the start of the year. For Lake Trout, total annual mortality (58%; Hansen et al. 2008, 2010) mostly exceeded the 50% threshold beyond which the species generally declined in abundance within its native range (Healey 1978).

Flathead Lake.—Lake Trout threaten native fish assemblages throughout the Flathead River drainage in Montana, USA (Hansen et al. 2016). Lake Trout were introduced into Flathead Lake, Montana in 1905 and have subsequently colonized lakes throughout the Flathead River drainage (Spencer et al. 1991; Fredenberg 2002). In Flathead Lake (large, 497-km^2-surface-area natural freshwater lake), Lake Trout predation, combined with reductions in plankton density caused by *Mysis*, caused the kokanee population to collapse (Ellis et al. 2011), thereby culminating in a system dominated by Lake Trout and Lake Whitefish. Lake Trout were thought to threaten the Bull Trout population through competition or predation (Donald and Alger 1993; Fredenberg 2002; Guy et al. 2011), although Lake Trout may exert other controls over the food web (Ellis et al. 2011). To benefit native fishes such as the Bull Trout and Westslope Cutthroat Trout, the Confederated Salish and Kootenai Tribes are endeavoring to reduce Lake Trout abundance in Flathead Lake (Hansen et al. 2016). Specifically, the Confederated Salish and Kootenai Tribes are using incentivized angling and targeted netting to suppress nonnative Lake Trout abundance enough to reduce predation on native Bull Trout and Cutthroat Trout, thereby enabling both native species to recover to sustainable and possibly fishable levels (Hansen et al. 2016).

Quartz Lake.—Lake Trout are found in all the large lakes in Glacier National Park west of the Continental Divide, which drain into the north fork of the Flathead River, in the Flathead Lake drainage (Fredenberg et al. 2007). Consequently, an action plan was developed for Glacier National Park to prioritize lakes for Lake Trout suppression to conserve native species, with a primary focus on native Bull Trout (Fredenberg et al. 2007). Lakes were grouped into three threat categories: secure, vulnerable, and compromised. Quartz Lake was categorized as compromised and as a high priority for Lake Trout suppression (Fredenberg et al. 2007). Subsequently, natural resource agencies began a suppression feasibility study in Quartz Lake in 2009 because of the logistic challenges of suppressing a nonnative species in a remote backcountry lake (Fredenberg et al. 2017). Despite the logistic challenges, suppression was deemed feasible in Quartz Lake, and suppression began shortly after the initial invasion by Lake Trout (Fredenberg et al. 2017).

Yellowstone Lake.—The largest population of Yellowstone Cutthroat Trout in the world resides in Yellowstone Lake, Yellowstone National Park, the largest lake above 2,000 m in North America (Gresswell and Varley 1988). Unfortunately, Lake Trout were discovered in Yellowstone Lake in 1994 (Kaeding et al. 1996; Munro et al. 2005) and have subsequently decimated the Yellowstone Cutthroat Trout population. For example, 70,105 Yellowstone Cutthroat Trout ascended the Clear Creek spawning tributary in 1978, but only 1,438 were observed by 2004 (Koel et al. 2005). The dramatic change in abundance of Yellowstone Cutthroat Trout clearly illustrates how a nonnative apex piscivore can alter a freshwater ecosystem. This change was predicted early on by the National Park Service and an independent scientific panel (McIntyre 1995); thus, the National Park Service initiated a suppression program in 1995. Despite the removal of 830,000 Lake Trout from Yellowstone Lake between 1995 and

2011, the population continued to increase (Syslo et al. 2011). The population increase was less than if no harvest occurred, but netting effort was too little to suppress the population and perhaps limited because regulations restricted where netting could occur. For example, netting was not effective until the early 2000s and effort was insufficient until 2011. Similarly, nonmotorized areas of Yellowstone Lake were not fished until recently (when a special exception was granted), which provided a refuge from netting for Lake Trout. More recently, the suppression program may be positively affecting Yellowstone Cutthroat Trout because more are beginning to ascend Clear Creek, and grizzly bears *Ursus arctos* are again found feeding on Yellowstone Cutthroat Trout in spawning tributaries.

These examples illustrate the difficulty faced by resource management agencies when trying to suppress nonnative Lake Trout. Suppression of Lake Trout in lakes of western North America cannot realistically occur on a similar scale to that of Lake Trout collapses in the Laurentian Great Lakes during the 19th and 20th centuries. This level of effort is not feasible because natural resource agencies are also charged with conserving native species, some of which are negatively affected by Lake Trout, and are captured using the same methods used to suppress Lake Trout. Given this conundrum, Lake Trout suppression programs often have many caveats with regard to where and when netting can occur. The goal of Lake Trout suppression programs is to reduce Lake Trout for the benefit of native species by reducing competition, predation, or both (Koel et al. 2005; Hansen et al. 2010, 2016). However, targets for suppression programs must often be set for Lake Trout with little knowledge of the magnitude of Lake Trout population decline that would be required to reduce negative interactions with native species, while simultaneously restricting fishing methods (e.g., mesh size) and locations to minimize bycatch. This combination of conditions for suppression reduces efficacy of these programs, especially in terms of time necessary to achieve management targets. Finally, suppression programs are costly, and most are funded by a combination of taxpayer funds, private donations, and natural resource mitigation funds. These funding sources may not be reliable and sustainable, thereby making funding for fishing effort temporally variable. In balance, a realistic goal of Lake Trout control may best be stated as achieving the greatest possible reduction in abundance within a reasonable time and available budget while benefiting native species. Despite these difficulties, some programs are demonstrating success. For example, in Lake Pend Oreille, relative abundance of kokanee increased after Lake Trout suppression was initiated in 2006 (Wahl et al. 2015). Similarly, in Yellowstone Lake, the number of small Yellowstone Cutthroat Trout has increased, which suggests that predation by Lake Trout may be declining (Arnold et al. 2017b).

Brown Trout

The Brown Trout is celebrated as the "Princess of the Streams" in its native range yet is regarded as one of the world's worst invasive alien species by international conservation authorities for its effects on native species (Lowe et al. 2000; Lobon-Cervia and Sanz 2017). Brown Trout have also been included in the top 30 worst invasive species on the globe because of their overwhelming success as invaders and their negative effects on ecosystems (McIntosh et al. 2011; Budy and Gaeta 2017). Paradoxically, however, Brown Trout are loved by recreational anglers (Pascual et al. 2002; Budy and Gaeta 2017) and consequently have been introduced and have become established in many areas of the world (Budy et al. 2008; McIntosh et al. 2011, reviewed in detail in Lobon-Cervia and Sanz 2017). In addition, current estimates are that Brown Trout now occupy all potentially suitable habitat globally, and in some exotic habitats, their density and maximum size far exceed that in their native range (McIntosh et al. 2011; Lobon-Cervia and Sanz 2017). Ironically, however, many populations of Brown Trout in their native range in Europe have experienced dramatic reductions in range and abundance due to a suite of common anthropogenic factors (Table 1; FAO European Inland Fisheries Advisory Commission 2002).

Restoration management in native range

The native range of Brown Trout extends from Iceland, Scandinavia, and Russia in the north, the European coastline to the west, and the northern coastline of the Mediterranean and Atlas Mountains of North Africa to the south (Lobon-Cervia and Sanz 2017). In those countries, Brown Trout are important for both recreational and subsistence angling. However, in Europe, in particular, overharvest and genetic introgression with hatchery Brown Trout have caused the abundance and distribution of Brown Trout to decline severely (Almodóvar and Nicola 2004; Almodóvar et al. 2006). Until recently, on the Iberian Peninsula, wild stocks were reinforced with alien hatchery stocks of central European origin, thereby causing introgressive hybridization among many Mediterranean populations (García-Marín et al. 2017). This hybridization has reduced local genetic diversity, fitness, and effective population size of wild populations. Furthermore, in Spain, hatchery Brown Trout (used to sustain recreational fisheries) disperse into adjacent protected areas that subsequently act as a reservoir of nonnative genes. Consequently, trout managers in Spain are currently trying to reach a balance between harvest and conservation of wild genetic resources. In France, some rivers are considered genetic sanctuaries where both stocking and fishing are banned. Reaching a desired balance will require education of the importance of maintaining genetic diversity and a change in social attitudes to support reduced exploitation, a shift in values that appears challenging.

Suppression management outside native range

Outside of their native range, Brown Trout also support popular recreational fisheries where they have been stocked extensively and where many populations now reproduce successfully. Of these, New Zealand and Patagonia are two of the most famous internationally, but the distribution of the species now includes populations on all continents except Antarctica (MacCrimmon and Marshall 1968). Extreme examples include the attempt to introduce Brown Trout to Malawi, Africa, which involved sea voyage around Africa to the mouth of the Zambezi River, followed by transport up the Zambezi River where fish were relayed by porters 200 km to the Zomba Plateau. Porters carried extra coolers of ice to replenish melted ice during the trip (Weyl et al. 2017).

Brown Trout were first introduced into New Zealand in 1864 after multiple failures to transport fish and eggs from the Northern Hemisphere (Jones and Closs 2017). However, once introduced, Brown Trout prospered in New Zealand and now have self-sustaining populations in all large rivers of the South Island and most large rivers of the North Island. This success is attributed to an abundance of suitable habitat, limited competitors and predators, and an energetically rich and abundant food source including naive and small-bodied native fishes. One old report even advertises a 5-kg (11 lb) Brown Trout with 85 native fishes in its stomach. However, based on a targeted research program clearly demonstrating negative impacts of Brown Trout on New Zealand native fishes and ecosystems, a paradigm shift now promotes native galaxiid conservation. Despite this emerging conservation ethic, trout fishing values still reign and trout are still actively stocked in some areas of the country.

Brown Trout were first introduced into Patagonia (Chili–Argentina) in 1906, but successful establishment was not documented until 1931 (Casalinuovo et al. 2017). As in New Zealand, the primary objective of these introductions was to increase diversity of fishes and develop a recreational fishery of high economic value. The Brown Trout adapted well to Patagonia. It is now established in most of this region's lakes and rivers and is one of the most widely distributed fishes across Patagonia. Unfortunately, however, little is known about the aquatic ecosystems and native fish communities of Patagonia before Brown Trout were introduced. Nonetheless, negative effects on these ecosystems from Brown Trout establishment appear to include competition for food with native fishes and a native duck, predation on native fishes, distributional shifts of native fishes, and altered benthic and trophic structure and function. These negative ecological effects, however, are balanced by the fact that Patagonian recreational fisheries are extremely lucrative, with profits distributed among many subgroups that support the fishery (e.g., guides and hotels). Furthermore, the Argentinian fishery in the Grande River, Tierra del Fuego is considered the best Brown Trout fishery in the world based on both catch rates and size. Consequently, research and education of overall riverine ecosystem function are currently considered the only options on the table that might influence management of nonnative Brown Trout in Patagonia.

Brown Trout eggs were first shipped to the United States (New York) by Herr Von Behr in 1883, and despite limited early success, by 1897, eggs of this strain of Brown Trout had been shipped to hatcheries in Michigan, Washington, Virginia, Pennsylvania, New Hampshire, and California (MacCrimmon and Marshall 1968). In 1885, eggs of the Loch Leven strain of Brown Trout were shipped to hatcheries in Maine, New Hampshire, Iowa, and Minnesota, and by 1887, this strain became established in hatcheries located in Maine, Maryland, Illinois, Colorado, and California (MacCrimmon and Marshall 1968). Despite early concerns about the negative effects of Brown Trout on native Brook Trout, MacCrimmon and Marshall (1968) reported that Brown Trout had been stocked in 45 of 50 states in the United States, and wild populations persisted in 34 states (all introduced before 1936).

Indeed, in spite of established wild populations and documented consequences to native salmonids, stocking of Brown Trout persisted. For example, stocking rates in Utah, USA were highest and spatially most extensive from 1940 to 1950 but continued into the 2000s (Budy and Gaeta 2017). Most accessible water bodies and those accessible only by plane were stocked to support Brown Trout fisheries across Utah, with numbers exceeding 10 million Brown Trout over a 10-year period (Budy and Gaeta 2017).

In Utah, most areas with introduced Brown Trout were historically occupied by native Bonneville Cutthroat Trout *Oncorhynchus clarki utah*, a trout (the state fish of Utah) that grows to large size and occupies pristine habitat at high density (Budy et al. 2007). Bonneville Cutthroat Trout, like most subspecies of Cutthroat Trout, were reduced to a fraction of their historical range by many factors, including negative effects of nonnative species like the Brown Trout (Budy et al. 2007). In addition to propagule pressure from repetitive Brown Trout stocking and their competitive advantage over native fishes, Brown Trout have been remarkably successful invaders because of their broad ecological niche (McIntosh et al. 2011). Subsequently, Bonneville Cutthroat Trout have become the subject of comprehensive and expensive recovery programs, a common outcome that has been repeated with native and nonnative trout species across North America (Chapter 18).

The maximum body size recorded for Brown Trout (600 mm) has been documented outside the native range, and maximum size was consistently below 400 mm in the native range. Large size is attributed to rapid growth, piscivory, and naive prey (Figure 1; Budy et al. 2013). In the United States, state records of large Brown Trout are notable, with trophy Brown Trout commonly exceeding 1 m in length (Budy and Gaeta 2017). Such state records, while impressive, pale in comparison with the world record, also a nonnative Brown Trout caught in a New Zealand canal that was estimated to be at least 19 kg. Angler motivations for targeting Brown Trout include (1) a belief that the Brown Trout is the most challenging trout species to catch, (2) that Brown Trout are often the largest fish in a stream, and (3) that Brown Trout are often found in streams that are of marginal quality for native trout. With regard to the latter, Brown Trout are often a predominant and successful species in novel, managed, and artificial riverine ecosystems, such as reservoirs and tailwaters.

The popularity of Brown Trout is illustrated by their favorable status within Trout Unlimited, one of the most prominent and the largest coldwater fishery conservation association in the United States (with more than 150,000 members, including lawyers, policy experts, and scientists). Trout Unlimited frequently features the Brown Trout in its *Trout* magazine, publishes videos of anglers catching "monster browns,"

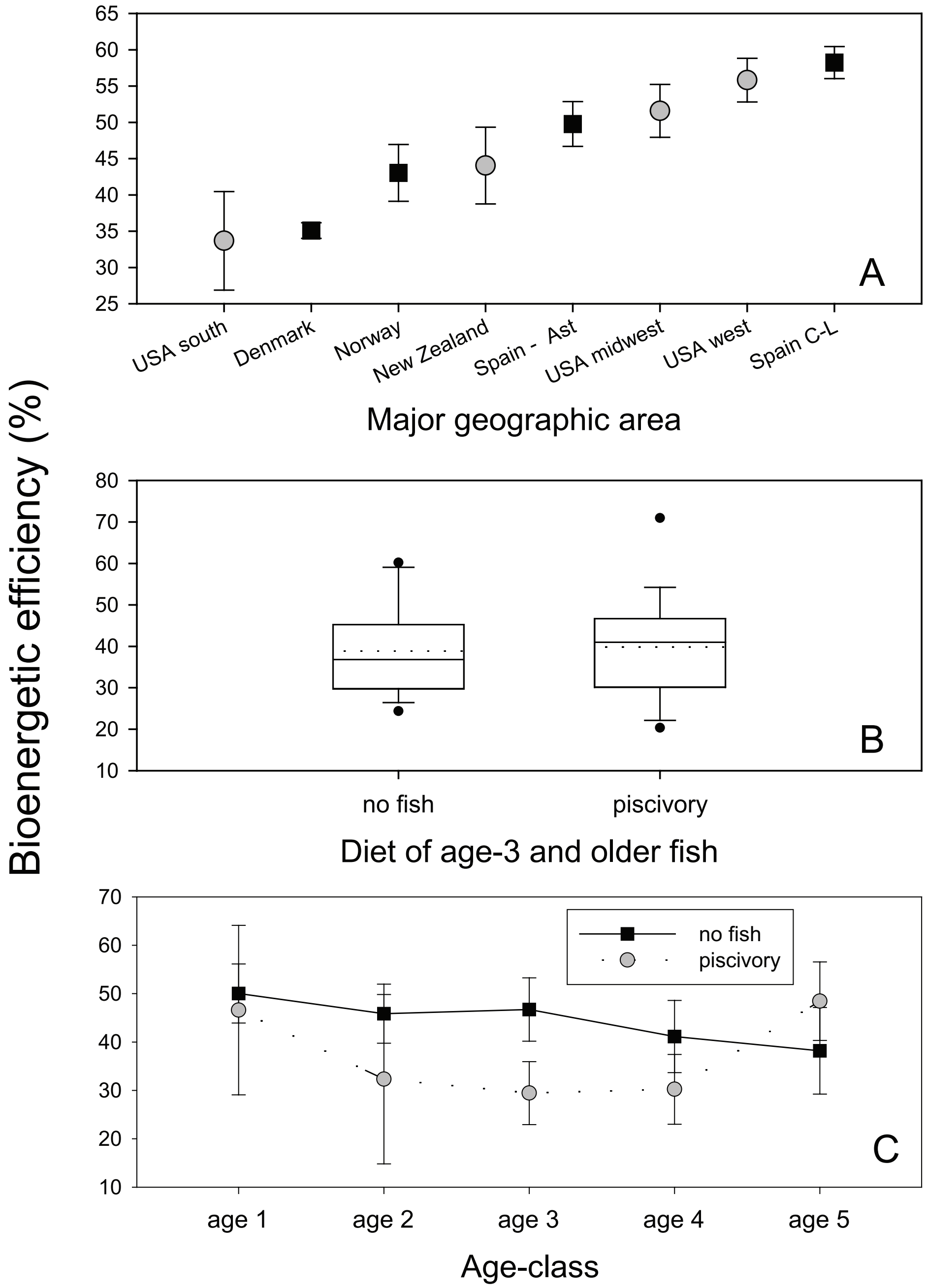

Figure 1. Bioenergetic efficiency of Brown Trout **(A)** averaged among major geographic areas (error bars = 2 SE; black squares = native areas; gray circles = nonnative areas), **(B)** as a function of inclusion of fish (no fish or piscivory) in the diet of age-3 and older Brown Trout (box = 25–75 percentiles; solid line = median; dashed line = mean; error bars = 10–90 percentiles; dots = 5–95 percentiles), and **(C)** for five age-classes of Brown Trout (least-squares means ± 95% confidence intervals) that were piscivorous (gray circles) and did not consume fish (black squares) combined among all geographic areas (reproduced from Budy et al. 2013).

provides helpful tips for catching Brown Trout, and supports restoration efforts to enhance Brown Trout angling opportunities. Attitudes are changing, however, and Trout Unlimited has recently acknowledged the paradox of simultaneously promoting and enhancing Brown Trout fisheries in some places while acknowledging negative effects of Brown Trout on native trout in other places (Trout Unlimited 2015). For example, a 2-year experimental mechanical removal of Brown Trout was completed in a tributary of the Logan River, Utah in 2014, where such a program had no support 10 years earlier (Saunders et al. 2014).

Collectively, these histories demonstrate the paradox of Brown Trout management in their native and nonnative ranges. The species is a popular recreational species actively managed in many systems despite well-documented negative effects (Budy and Gaeta 2017). Opinions are quite diverse across the extensive landscape of policy and science. For example, Javier Lobón-Cerviá, considered by some to be the father of Brown Trout research, recently characterized Brown Trout in a book devoted entirely to the species: "its image wanders into a maze of contradictory feelings including the opposite extremes of enthusiasm, love and passion versus hate and confusion" (Lobón-Cerviá and Sanz 2017). Although strategies for managing Brown Trout in their native habitat are relatively obvious and obtainable, strategies for managing the Brown Trout as a nuisance invader and as a popular recreational fish in their nonnative habitat are less obvious and not always feasible.

In many places where Brown Trout are nonnative, their negative effects are certain, significant, and ubiquitous and may be best documented in the United States and New Zealand. The negative effects of nonnative Brown Trout fall into three categories: (1) distributional evidence suggesting historical displacement, (2) observational or experimental studies assessing mechanisms of effect, and (3) temporal data sets documenting decline following invasion (McIntosh et al. 2011; Budy and Gaeta 2017). For example, native Cutthroat Trout did not persist in many places in the western United States after Brown Trout were stocked (Behnke 1992; Fausch 1998). Furthermore, strong allopatric patterns of native Cutthroat Trout and nonnative Brown Trout are common in the western United States and often follow longitudinal, elevational gradients of montane rivers, where native trout are now limited to headwaters (Vincent and Miller 1969; de la Hoz Franco and Budy 2005; McHugh and Budy 2005). In controlled experiments at large and small scales, Brown Trout out-compete native trout, likely through aggressive behavior and competition for space (reviewed in McIntosh et al. 2011; Budy and Gaeta 2017).

Negative effects on native fishes through predator–prey interactions with nonnative Brown Trout have also been documented. For example, in the Logan River, Utah, USA, an average adult Brown Trout consumed up to 34 native Mottled Sculpin *Cottus bairdii* each year, an even more staggering number when expanded up to Brown Trout densities of more than 1/m^2 over a large spatial area (Budy et al. 2008). Furthermore, in some of the most ecologically notorious examples in New Zealand (McIntosh et al. 2011), negative effects of nonnative Brown Trout cascaded down food webs from mayflies to algae and even altered ecosystem function (McIntosh and Townsend 1996; Huryn 1998). Additional ecological effects of Brown Trout include transmission of nonnative disease, synergistic responses to habitat degradation and climate change providing advantage over native species (Budy and Gaeta 2017), and damaging introgressive genetic effects within their historic range (McIntosh et al. 2011).

Managing nonnative Brown Trout can provide opportunities to learn and support native fish and aquatic ecosystem restoration. In the Logan River (Utah), mechanical removal of more than 15,000 Brown Trout resulted in strong recruitment, which suggests that adult Brown Trout previously suppressed their own recruitment through density-dependent reduced survival or increased emigration (Saunders et al. 2014). These results suggested that mechanical removal to reduce Brown Trout abundance may stimulate recruitment that increases, rather than decreases, overall density, and therefore that eradication would likely require extensive and repeated chemical treatment (Finlayson et al. 2005; Meyer et al. 2006).

In contrast, piscicides have been used to eliminate nonnative trout in both Australia and the United States (Meronek et al. 1996; Lintermans 2000). For example, in the Logan River, after 2 years of Brown Trout removal with piscicides followed by 2 years of stocking juvenile native Bonneville Cutthroat Trout, densities of native Bonneville Cutthroat Trout in the river are now high. Five age-classes are now present, and large adults are available for angling. Furthermore, the Logan River has abundant spawning and rearing habitat, a characteristic that promotes persistence of the metapopulation (Budy et al. 2012).

Education and policy offer a variety of tools for reducing both nonnative trout effects within invaded systems and the probability of illegal stocking. Policy options include laws, regulations, and voluntary agreements. For example, the New Zealand Biosecurity Act of 1993, a model for aggressive invasive species legislation (Simberloff et al. 2005), imposes fines of up to NZ$100,000 (plus imprisonment) for releasing unwanted species (McIntosh et al. 2011). In addition, where Brown Trout are nonnative and invasive, management agencies can require nonnative Brown Trout to be harvested, in conjunction with high creel limits. However, when density is high and anglers are predominantly fly fishers who prefer to catch and release, such policies may have little ecological effect.

Education and outreach, in contrast, can offer powerful tools for helping the public to develop informed opinions (Bonar and Fraidenburg 2010). Success of these efforts is often greatest if users (i.e., anglers) are actively engaged in decision making (e.g., Cowx et al. 2010). As described above, local constituents did not originally support experimental removal of Brown Trout from the Logan River. However, after 3–4 years of working directly with local anglers to collect eggs and release native juvenile Bonneville Cutthroat Trout, and educating both local anglers and managers about effects, the state management agency readily agreed to the removal. Simultaneously, researchers educated the public about native fish and aquatic ecosystem management. Overall, these management and policy opportunities are most likely to be successful where a native species is available for anglers and least likely to be successful where Brown Trout are the only species of choice (McIntosh et al. 2011).

Less traditional options for management of Brown Trout are promising and worthy of further study (Budy and Gaeta 2017). First, biotic resistance (Elton 1958), expressed as high density of native Cutthroat Trout, is the mechanism limiting expansion and establishment of Brown Trout into upper headwaters of western U.S. streams. Although Brown Trout are unaffected by high density of native Cutthroat Trout, Cutthroat Trout performance increases with increasing density of conspecific species. Therefore, if Cutthroat Trout density is high enough, Brown Trout may not be able to expand, which is promising for native fish management, The potential for biotic resistance suggests that shifting the balance of predominance back to native fish may be sufficient, rather than trying to eradicate Brown Trout. Second, nonnative Brown Trout have difficulty passing American beaver *Castor canadensis* dams that do not impede native Cutthroat Trout (Lokteff et al. 2013). This presents a potentially promising management option for passive stream restoration across the western United States (e.g., Pollock et al. 2015), as beaver dam densities increase in the future. Third, natural large-scale wildfire can be used to reset native trout stream ecosystems (Chapter 18). After a fire that may kill many of the Brown Trout present, any surviving Brown Trout can be removed and streams restocked with native trout. In such cases, fire can help with public support because public agencies are not directly responsible for removing Brown Trout, but they provide the means to reestablish fishing opportunities with native trout in a postfire environment. In the western United States, more than 80% of anglers do not prefer Brown Trout to other trout as long as they can fish in a mountain stream to catch trout (Budy and Gaeta 2017). This general angler attitude enables Brown Trout removal in conjunction with native trout conservation (Saunders et al. 2014).

McIntosh et al. (2011) described four key issues for managers and scientists to address for future control of Brown Trout as invaders and for minimizing their negative effects. First, the mechanisms and geographic scope of effect of Brown Trout on invaded habitats must be characterized (most studies are from a few countries). Second, the extent to which Brown Trout are actively invading new habitats must be monitored because contemporary distributional boundaries are not likely static. A third key issue is the need to obtain sustained financial support to manage Brown Trout as a pest species. Last, McIntosh et al. (2011) called for reconciliation of recreational angling and conservation values.

Brook Trout

The native range of Brook Trout covers a large expanse of northeastern North America, from Hudson Bay to the southern Appalachian Mountains and the Great Lakes region (MacCrimmon and Campbell 1969; Behnke 2002). Several distinct genetic lineages of this species have formed, likely because of isolation and recolonization from several different glacial refugia (Danzmann et al. 1998). Brook Trout occur in a variety of habitats, from small, cool streams and ponds to large, cold rivers and lakes. Growth and maturity differs greatly. Brook Trout in warmer, more productive, lower latitudes and elevations are characterized by fast growth, early sexual maturity (age 1 or 2), and small size (maximum near 300 mm). In contrast, Brook Trout in cold, large rivers and lakes are older (9–10 years) and larger (4–4.5 kg; Behnke 2002; Kennedy et al. 2003). The largest angler-caught Brook Trout was a 6.57-kg, 86.4-cm-long fish caught in 1915 from the Nipigon River, a tributary to Lake Superior (Scott and Crossman 1973). Two unique migratory forms, the large-bodied lacustrine–adfluvial coaster Brook Trout from the Great Lakes region (Huckins et al. 2008) and the anadromous salter Brook Trout from the eastern U.S. and Canada seaboard (Dauwalter et al. 2014) are now rare, and several unnamed subspecies from isolated lakes have been extirpated (Behnke 2002).

Brook Trout were among the first species cultured in North America, and by the late 1800s, Brook Trout were widely stocked as a solution to their rapid decline in abundance throughout New England related to unregulated harvest, dams that blocked migratory corridors, and siltation and warming temperatures from land clearing (Table 1; Bowen 1970; Halverson 2010). Popular among anglers and appreciated for their beauty, Brook Trout were soon widely introduced across North America and other continents. Wide distribution of Brook Trout was facilitated when early culturists discovered that fertilized eggs in damp moss survived transport over great distances by railroad or ship, and later, young fry in tanks within specialized railroad cars (Green 1870; Bowen 1970). Widespread stocking by acclimatization societies was also popular at the time in both the United States and other countries (Halverson 2010). The Brook Trout, in particular, were considered by early fishery management agencies in the western United States as superior to native trout species, and hatcheries were developed to support their propagation and stocking (Van Kirk and Griffin 1997). Nearly 2.5 million Brook Trout were stocked in Idaho in 1909–1910 (Stephens 1910), and more than 200 million were stocked in Colorado in 1885–1953 (Metcalf et al. 2012).

Within a few decades, self-sustaining populations of Brook Trout were established outside their native range in 19 countries worldwide and in 14 U.S. states and 4 Canadian provinces in North America (MacCrimmon and Campbell 1969). Outside of North America, Brook Trout are locally common in mountainous areas of Europe, South America, New Zealand, and Japan. The largest concentrations of naturalized Brook Trout occur in western North America where the areal extent of their distribution is comparable to that of their entire native range. Within about 100 years, Brook Trout colonized waters from Alberta to New Mexico, and their distribution was concentrated in the Sierra Nevada and Cascade mountains to the west and the Rocky

Mountains to the east. In a study of 689 random stream sites that represented 650,000 km of streams across 12 western states, Brook Trout were the most common nonnative species and occurred in 17.2% or ~110,000 km of total stream length (Schade and Bonar 2005). Range expansion of Brook Trout is implicated in the concurrent contraction of the range of a highly diverse group of native Cutthroat Trout subspecies that now occupy only a fraction of their historical habitat (Thurow et al. 1997; Behnke 2002; Young 2008). Brook Trout are also implicated in the decline of Bull Trout, a char native to North America (Kanda et al. 2002; McMahon et al. 2007; Warnock and Rasmussen 2013). Substantial efforts are underway to suppress Brook Trout from selected locations to protect native trout from further decline.

Restoration management in native range

Owing to their occurrence in nearly all coldwater streams, ponds, and lakes throughout most of northeastern North America, Brook Trout provided an important subsistence fishery for native people and European settlers during colonial times. Subsequently, Brook Trout became the favorite quarry of recreational anglers and numerous fishing clubs, and resorts for Brook Trout soon sprang up in Maine, New York, and the Great Lakes that targeted areas legendary for large trophy Brook Trout weighing 2–5 kg (Karas 2015). Recreational harvest was largely unregulated, and by the mid-1800s, trophy Brook Trout fisheries declined significantly from overharvest (Karas 2015).

Cumulative effects of rapid urbanization and industrialization of much of the eastern and north-central United States at the same time precipitated widespread decline in Brook Trout populations over much of its native range. Broad-scale stocking of nonnative Rainbow Trout and Brown Trout began in the early 1900s over much of the native range of Brook Trout in the United States, further accelerating range contraction, especially in the southern edge of their range in the Appalachian Mountains (Larson and Moore 1985; Habera and Strange 1993). Of 5,355 subwatersheds along the Appalachian Mountains from Maine to Georgia, Brook Trout were extirpated or persisting at low numbers in 63% of all watersheds and were self-sustaining with intact habitat (>50% of estimated historic distribution) in only 31% of the estimated historic range (Hudy et al. 2008). Moreover, Brook Trout inhabiting large rivers are largely extirpated, and lake populations, historically abundant in the northern part of this region, are now substantially reduced except for a few in Maine (Hudy et al. 2005).

Current threats and extent of decline vary among regions. In the southern United States, Brook Trout are extirpated or rare in 98% of 362 watersheds, a consequence of Rainbow Trout and Brown Trout displacement, urbanization, and poor land management (Hudy et al. 2008). In the central United States, only ~5% of Brook Trout populations remain because of siltation, increased water temperature, poor land-use practices, and acidification from abandoned mine drainage. In Pennsylvania and New York, Brook Trout persist in 15% (221) of 1,435 historically occupied watersheds, primarily because of high water temperature, siltation, and Brown Trout invasion. In New

York, only 2 of 136 watersheds that historically supported renowned lake fisheries for Brook Trout remain, primarily because of invasions by nonnative Smallmouth Bass *Micropterus dolomieu* and Yellow Perch *Perca flavescens* (Hudy et al. 2005). In contrast, Brook Trout are common in 70% of streams and 18% of lakes historically occupied in Maine. In Canada, a rangewide status review is not presently available, and although Brook Trout populations appear to be largely intact in 70% of the native range, local extirpations because of migration barriers are likely widespread (Gibson et al. 2005). In the Great Lakes region, coaster Brook Trout historically occupied more than 100 tributaries in Lake Superior, but most persist as remnant populations in few tributaries (Newman et al. 2003). Along the New England coast, few populations of salter Brook Trout remain, although status is uncertain in many watersheds (Dauwalter et al. 2014).

Successful Brook Trout restoration is taking place in a variety of ways. For example, removal of nonnative Rainbow Trout led to recovery of Brook Trout in 44.2 km of southern Appalachian streams (Kanno et al. 2016). Following application of limestone sand in an acidified Virginia stream, Brook Trout reproduced for the first time in 20 years (Hudy et al. 2000). In Lake Superior, restrictive harvest regulations in the Lake Nipigon area led to a doubling of spawning Brook Trout within 5 years (Bobrowski et al. 2011). Habitat restoration and harvest restrictions have increasingly been emphasized because stocking programs, formerly the primary mitigation tool for declining Brook Trout fisheries, have been discontinued or scrutinized in many areas because of poor success and concern over effects on wild stocks (Schreiner et al. 2008; Leonard et al. 2013; McKenna et al. 2013). Assessment of fine-scale genetic diversity (e.g., Buonaccorsi et al. 2017) should improve identification and protection of unique stocks for judicious use in reintroduction programs (Leonard et al. 2013). Development of environmental DNA sampling for detecting Brook Trout occurrence (Baldigo et al. 2017) should also improve distribution assessments, an important knowledge gap when Brook Trout abundance is low (Hudy et al. 2008; Dauwalter et al. 2014). For example, many undetected Brook Trout populations have been located in Pennsylvania through the Unassessed Waters Initiative, which relies on qualified universities, research entities, and conservation organization partners, in addition to state agency staff, to survey waters that were not previously surveyed (Weltman-Fahs and Taylor 2013).

Restoration successes must be tempered by the magnitude of the decline and looming threats. For example, restoring Brook Trout to 44.2 km of stream in the southern Appalachians (Kanno et al. 2016) represents a small fraction of the 7,220 km of formerly occupied habitat (Habera and Strange 1993). Looming threats to Brook Trout recovery include possible effects of planned natural gas drilling in extensive shale formations of the central Appalachians (Weltman-Fahs and Taylor 2013), and climate change that is predicted to cause further range contractions of temperature-sensitive Brook Trout in its southern range (Meisner 1990; Flebbe et al. 2006). However, heightened recognition of threats and development of detailed restoration plans from different regions are encouraging (Newman et al. 2003; Dauwalter et al. 2014).

The unique Eastern Brook Trout Joint Venture program (EBTJV 2011), developed in recognition of a need for large-scale, multijurisdictional restoration to address Brook Trout declines, has set specific restoration goals directed towards protecting remnant populations, reconnecting fragmented populations by removing migration barriers, reducing nonnative species interactions, and improving degraded habitat (EBTJV 2011). Management actions are funded according to regional priorities (Lynch and Taylor 2010; EBJTV 2011), and each state is developing restoration plans to address specific threats (e.g., DeGraaf 2014; Pennsylvania DCNR 2016). Promising aspects of this effort include explicit targets for success with specific timeframes, recognition of a need for monitoring and information on population status, data sharing among partners, and involvement of the public in restoration efforts (EBTJV 2011).

Suppression management outside native range

Stocking of Brook Trout throughout western North America in the late 1800s and early 1900s altered diversity of native trout in the region (Behnke 1992, 2002). Bull Trout and 12 extant Cutthroat Trout subspecies are now mostly confined to <10-km sections of small, high-gradient, high-elevation headwaters where they are hemmed in by Brook Trout and other nonnative salmonids downstream (Paul and Post 2001; Rieman et al. 2003, 2006; Wenger et al. 2011), the same conditions Brook Trout face in their native range. This unexpected nonnative dominance over native species throughout extensive areas of their naturalized range has been referred to as the "trout invasion paradox" (Fausch 2008). Invasion success of Brook Trout over native trout species is partly attributable to Brook Trout demographic (younger age at maturity, larger size at hatching, and higher density and biomass; McMahon et al. 2007; Benjamin and Baxter 2012) and behavioral (greater immigration, aggression, and piscivory) attributes (Dunham et al. 2002; Peterson and Fausch 2003; Peterson et al. 2004). In addition, a habitat disturbance paradox has likely favored Brook Trout over native trout. Paradoxically, Brook Trout extirpations in the native range are associated with warming temperatures and habitat simplification from land use (Hudy et al. 2008), whereas Brook Trout in the naturalized range are surprisingly more resilient than native trout to habitat disturbances (Griffith 1988; Rich et al. 2003; Shepard 2004).

Brook Trout have generally not been stocked during the past several decades in western North America, and most states and provinces now have liberal creel limits to discourage further spread (e.g., daily creel limit of 20 in Montana). Brook Trout range expansion seems to have stabilized in some areas (Adams et al. 2002; Meyer et al. 2014) but is still occurring in other areas (Roberts et al. 2017). The precarious status of native trout species (Gresswell 1988; Behnke 1992) in light of climate change (Haak et al. 2010; Al-Chokhachy et al. 2013; Roberts et al. 2017) and rapid Brook Trout invasions (Leary et al. 1993; Peterson et al. 2004; Roberts et al. 2017) has led to a large, concerted effort to suppress Brook Trout.

Multiple suppression methods have been tested over the past 25 years with varying success. One of the first Brook Trout suppression experiments was the use of the piscicide antimycin in Yellowstone National Park in 1985–1986 to eradicate a newly discovered Brook Trout invasion into a tributary of Yellowstone Lake, a major stronghold of Yellowstone Cutthroat Trout (Gresswell 1991). After removal of 4,525 Brook Trout from a 16-km section of stream over 2 years, Yellowstone Cutthroat Trout recovered rapidly, and Brook Trout have not been detected for 31 years (1986–2017). Multiple suppression methods were used over 19 years to remove Brook Trout from a headwater stream in Oregon to protect a rapidly declining population of Bull Trout (Buktenica et al. 2013). Eradication was finally achieved by a combination of repeated antimycin treatments in combination with construction of an artificial barrier to prevent reinvasion. Brook Trout have been absent from the stream since 2005 while Bull Trout distribution increased from 1.9 to 11.2 km and abundance increased 10-fold.

Mechanical suppression of Brook Trout has been widely tested because of the difficulty in obtaining approval for piscicide applications (Finlayson et al. 2005). Brook Trout were successfully eradicated from 10.8 km of Montana headwater streams by intensive, repeated electrofishing removals over 4–8 years, followed by a several-fold increase in native Cutthroat Trout (Shepard et al. 2014). Brook Trout were also eradicated from a small alpine lake–stream complex in Banff National Park by intensive gill netting and electrofishing (Hoffman et al. 2004; Pacas and Taylor 2015). In contrast, intensive electrofishing removals of Brook Trout from larger streams, or with fewer years of removals, successfully removed large numbers but failed to eradicate Brook Trout (Thompson and Rahel 1996; Meyer et al. 2006; Carmona-Catot et al. 2010). Collectively, these examples suggest that mechanical eradication is possible in small, simple streams and lakes but requires substantial sustained effort (e.g., 64–171 person-days/km; Shepard et al. 2014) and cost (US$3,500–$10,000/km; Meyer et al. 2006; Carmona-Catot et al. 2010; Shepard et al. 2014). In general, piscicide treatment is more effective and requires less effort than mechanical suppression (Buktenica et al. 2013) but may not be publicly acceptable or feasible in sensitive areas (Pacas and Taylor 2015). Models have been developed to assess effectiveness of electrofishing suppression of Brook Trout when piscicide eradication is not feasible (Peterson et al. 2008a).

Eradication of Brook Trout and isolation of native trout above artificial or natural barriers are crucial for restoration. Of 37 translocations of Greenback Cutthroat Trout *O. c. stomias* in Colorado above putative migration barriers, 23 (62%) were unsuccessful, primarily because of reinvasion by, or incomplete removal of, Brook Trout during chemical treatment (Harig et al. 2000). Artificial barriers can often be breached by

Brook Trout (Thompson and Rahel 1998), and further research is needed on swimming and leaping ability of Brook Trout to improve barrier design (Kondratieff and Myrick 2006). Illegal reintroductions of Brook Trout above barriers by anglers can also lead to failure (Roberts et al. 2017).

Many restored populations of native trout occupy less than 3.6 km of stream length that are isolated from downstream habitats and populations and therefore are at high risk of extirpation (Fausch et al. 2009; Roberts et al. 2017). A decision support tool was developed to help managers assess risks and benefits of isolation versus invasion by Brook Trout (Peterson et al. 2008b). To enhance population persistence, the scale of restoration projects has been greatly increased in both streams and lakes. In streams, large-scale piscicide applications eradicated Brook Trout and other nonnative species from Cherry Creek, Montana, USA (90 km; Wilkinson 2012) and Soda Butte (47 km) and Grayling (95 km) creeks in Yellowstone National Park, USA (Arnold et al. 2017a; Ertel et al. 2017). The largest stream eradication project to date was the 193-km-long Rio Costilla restoration in New Mexico, USA (Kruse et al. 2007). In lakes, large-scale chemical applications eradicated nonnative trout, including various mixes of Brook Trout, Rainbow Trout, and Yellowstone Cutthroat Trout from 15 Montana high-mountain lakes (4–60 ha) within the native range of Westslope Cutthroat Trout (MDFWP 2005; Boyer 2012).

Success of these large-scale projects has been bolstered by improving methods of piscicide applications over time and heightened public acceptance of their use to benefit native species (cf. Quist and Hubert 2004; Skaar et al. 2017). The enhanced public value of native trout is exemplified by the popular Cutt-Slam program in Wyoming wherein anglers specifically catch the four subspecies of native Cutthroat Trout in the state. Other innovative biocontrol methods developed to control Brook Trout may be applicable elsewhere, including (1) release of YY-male Brook Trout (Schill et al. 2016), (2) stocking sterile tiger muskellunge (Northern Pike *Esox lucius* × Muskellunge *E. masquinongy*) (Koenig et al. 2015), and (3) pheromones to attract Brook Trout for selective removal (Lamansky et al. 2009).

Suppression has not been attempted at large spatial scales in other parts of the naturalized range of Brook Trout. In Japan, Brook Trout are not widely distributed, but concern over effects on native species, particularly hybridization with native trout, has led to a ban on stocking but not suppression (Kitano 2004). In Europe, Brook Trout are considered one of the top invasive aquatic species (Savini et al. 2010). Of particular concern is their effect on native Brown Trout. For example, Brook Trout have replaced native Brown Trout in boreal lakes in northern Sweden (Spens et al. 2007) and headwater streams in Finland (Korsu et al. 2007), and introgressive hybridization between the two species in French streams produces sterile hybrids (Cucherousset et al. 2008). Brook Trout were eradicated by intensive gill netting and electrofishing four historically fishless alpine lakes in Italy (Tiberti et al. 2017), but other active suppression efforts have been limited thus far.

In conclusion, Brook Trout and other nonnative trout have been successfully eradicated in hundreds of kilometers of stream and hundreds of hectares of lakes in the western United States, arguably the largest successful restoration of native fish species in the world. Costs of suppression, barrier installation, and monitoring can be significant (Quist and Hubert 2004; Shepard et al. 2014), but Brook Trout invasions combined with climate change present an ever-increasing threat to persistence of isolated populations of native trout. Continued efforts to limit invasion by Brook Trout will be vital to maintaining viable populations of native trout populations in the future (Roberts et al. 2017).

Lessons Learned

Restoration and suppression are equally challenging for a species that is the focus of population recovery within its native range and population control outside its native range (see Chapter 18). Paradoxically, all three trout species reviewed herein are seemingly vulnerable to decline in their native range (e.g., Lake Trout and Brook Trout in the eastern United States and Brown Trout worldwide) but are adept at colonizing ecosystems outside their native range (e.g., Lake Trout and Brook Trout in the western United States and Brown Trout in Europe and Asia). Similarly, these three trout species are vulnerable to invasions by other trout species in their native range (e.g., nonnative Brown Trout versus native Brook Trout) but are adept at replacing other species outside their native range (e.g., nonnative Brook Trout versus native Cutthroat Trout). Importantly, knowledge gained from restoring a species in its native range (e.g., Lake Trout are vulnerable to overfishing) may be useful for guiding suppression of the same species outside its native range (e.g., commercial fishing methods used to suppress Lake Trout).

Restoration of native trout species in their native ranges and suppression of the same species outside their native ranges require similar keys to success. First, public support is equally as important for suppression programs as it is for restoration programs because nonnative species are often equally or more popular with stakeholders than native species. Second, balancing the value of nonnative and native species is challenging because values and opinions of stakeholders may change through time (e.g., when management agencies engage in competing programs aimed at removing one species to benefit another). Third, experience with the planning process for native species that require recovery plans is equally relevant to the need to plan for suppression of nonnative species because both efforts are temporally protracted, geographically broad, and jurisdictionally complex. This may be especially challenging for agencies that necessarily operate with short-term interest, local geographical focus, and single-agency authority. Taken together, success of both restoration and suppression programs requires public involvement and commitment, balancing costs against benefits of effort exerted, and commitment to extensive effort that is exerted over a long time period.

Future Research

Research and development related to species invasions have increased understanding of mechanisms promoting nonnative species colonization and native species displacement along with enhanced tools for suppressing nonnative species to benefit native species. For example, early research primarily focused on interactions among adults, whereas recent research has highlighted the previously unrecognized importance of interactions among age-0 individuals for driving recruitment dynamics. Similarly, invasion studies have driven studies of dispersal in fishes and of the effectiveness of barriers for limiting further expansion of nonnative species. Last, the need for suppression has prompted research and development of more diverse and improved suppression tools. Such developments have enhanced success of suppression programs (e.g., small stream eradications) and expanded the scope of suppression programs to greater spatial scales appropriate for larger populations of native species.

Continued development of some tools could simultaneously enhance restoration programs for trout in their native ranges and suppression programs for the same species outside their native ranges. For example, development of environmental DNA methods are enhancing monitoring systems for accurately documenting rangewide distributions of native species (e.g., Brook Trout in the eastern United States), but also for detecting new invasions and for evaluating eradication program effectiveness (e.g., Brook Trout in the western United States). Similarly, development of pheromones to enable stocked trout to locate suitable spawning reefs in their native range (e.g., Lake Trout in the Great Lakes; Buchinger et al. 2015) would be equally useful for attracting nonnative trout into traps for selective removal (e.g., Brook Trout in western U.S. lakes; Lamansky et al. 2009). The use of sterile triploid trout can reduce both the spread of hatchery genes into wild populations but also the expansion of nonnative trout via reproduction; however, the potential ecological impacts of such fishes should be thoroughly evaluated prior to use (e.g., tiger trout hybrids [Brown Trout × Brook Trout) are extremely voracious predators; Winters et al. 2017). Although not yet clearly proven effective for trout, the concept of biotic resistance through increased density of native trout is promising and makes ecological sense.

Some tools may be useful for only one purpose. For example, methods have been developed for using YY-male Brook Trout to eradicate nonnative populations in the western United States, including culturing (Schill et al. 2016), simulating numbers needed for eradication (Schill et al. 2017), and experimental releases into wild populations (Kennedy et al. 2017, 2018). Such methods may be expanded to other species suppression programs (e.g., Lake Trout) but may not be useful for restoration programs for either of these species. Similarly, stocking sterile tiger muskellunge has been used to eradicate Brook Trout from high-mountain lakes (Koenig et al. 2015) and may be useful for other trout species: however, this strategy would not likely be useful for restoration programs of trout species in their native ranges. Finally, in some places (e.g., Argentina, Africa) basic research and monitoring is still required to understand ecosystem function and native fish communities in order to inform nonnative trout management (Lobón-Cerviá and Sanz 2017).

Future Challenges

The cost and motivation to sustain recovery or suppression efforts are likely the greatest challenges facing resource management agencies, especially as agency budgets tighten in the future. To provide accountability and justification for use of public funds in long-term recovery or suppression programs, agencies need to invest in monitoring systems with clearly defined targets to evaluate success or failure of long-term recovery and suppression programs that are often unpopular with some stakeholder groups. Furthermore, continual monitoring for new invasions, as part of native species restoration programs, will be needed in the future, given the likely continued expansion of nonnative species through human-mediated (and often illegal) introductions and climate-mediated expansion of species outside their native ranges.

In addition, education and outreach are critical. In many places where nonnative trout have been introduced, support popular sport fishers, and wreak ecological havoc, many people actually believe they are native (USA, Patagonia, and Africa; Lobón-Cerviá and Sanz 2017). Likewise, in the face of differing values, effective management may depend upon open and difficult dialogue among the complex sociocultural and economic entities involved in trout management. Without some degree of public support, suppression efforts may fail for a whole suite of ecological (e.g., illegal reintroduction), management (e.g., angler outcry, legal reintroduction), and social (e.g., expense, spiritual values regarding euthanasia) reasons. Similarly, trout management could beneficially shift away from an angler-centric focus, with the link between ecosystem management and trout management explicitly accepted and celebrated (Young et al. 2017). These future challenges are substantial but with the necessary support and momentum can be overcome both to protect native trout species within their native range and to suppress nonnative trout species outside their native range.

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